Chironomids (Diptera, Nematocera)

of

Temporary Pools

- an Ecological Case Study

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I dedicate this thesis to my parents

Mechthild Elisabeth Dettinger-Klemm, née Walz

and

Dr. jur. Martin Dettinger-Klemm

as an expression of my love and gratefulness

Contents

1. Preface and acknowledgements

When I started working on temporary pools of the Lahnberge (Marburg, Hesse, Germany) in 1992 with a student research project on mosquitoes (samplings from April 25 to July 30), I never imagined that I would keep my mind on the topic for about one decade. In 1993, I collected the data for my Master's thesis (May 11, 1993-January 26, 1994), which was finished in July 1994 and published in 1995 as a microfiche version (DETTINGER-KLEMM 1995a). In this thesis, the benthos (with special emphasis on Chironomidae and Culicidae) of pools 1, 2 and 3 - which are also the focus in the present investigation - was investigated using emergence traps, net-samplings and flooding of desiccated soils. Because data collection for my Master's thesis started relatively late, the spring aspect of the pools' fauna was only known fragmentarily. To fill this gap, I continued with emergence samplings until the end of May 1994 and determined the Chironomidae down to species level (including the chironomids collected in 1992) in 1995. The data collected from 1992-1994 were then published in 1996 (DETTINGER-KLEMM & BOHLE 1996). I successfully wrote applications for a scholarship (Hessian scholarship: granted on October 11 from 1.3. 1996-28.2.1998 (reference: 5.55.01.05)) and financial support to cover the material equipment (DEUTSCHE FORSCHUNGSGEMEINSCHAFT (DFG): granted on October 10, 1996 (31,555 DM, reference: Bo 412/7-1+2); and STIFTERVERBAND FÜR DIE DEUTSCHE WISSENSCHAFT: granted on April 4, 1996 (2,345 DM, reference: 40095/705.6.256)) used in the present research. The financial assistance of the DFG was not directly granted for my PhD thesis but to a larger project on temporary pools within the frames of which five student research projects and four Master's theses dealing with temporary pools or temporary habitats were undertaken. All these thesis were supervised jointly by my supervisor Prof. Dr. HANS WILHELM BOHLE and myself (except for [1] that was guided by WOLFRAM SONDERMANN):

a) Term theses

MARGOT KURELLA & KATHRIN SCHUSTER (1995): Dolichopodiden temporärer Tümpel auf den Lahnbergen. (Dolichopodidae of temporary pools of the Lahnberge);

MARCUS HOOF (1997): Scirtidae temporärer Tümpel auf den Lahnbergen (Scirtidae of temporary pools of the Lahnberge);

DAVID THIELTGES & FRIEDERIKE VOIGT (1998): Besiedlung künstlicher Kleinstgewässer: Faunistik, Phänologie und Strategien von Culiciden, Chironomiden und Wasserkäfern. (Colonization of experimental pools by chironomids, mosquitoes and water beetles: faunistics, phenology and strategies);

SILKE SCHNEGELBERGER (1999): Die Köcherfliegen eines Tümpels zwischen Roth und Bellnhausen nahe Marburg (Caddis flies of a temporary pool in the vicinity of Roth and Bellnhausen near Marburg);

ANDREA SUNDERMANN (2000): Autökologische Untersuchungen an köcherbauenden Chironomiden - *Stempellina* cf. *bausei* (Kieffer, 1911) und *Stempellinella flavidula* (Edwards, 1929) – in einem Quellbach bei Mardorf (Hessen). (Autecology of the case-bearing chironomids *Stempellina* cf. *bausei* (Kieffer, 1911) and *Stempellinella flavidula* (Edwards, 1929), dwelling in a temporary spring brook near Mardorf (Hesse)).

b) Master's theses

TEICHMANN, S. (1998a): Faunistisch-ökologische Untersuchungen an Dolichopodiden (Diptera: Brachycera) temporärer Tümpel. (Dolichopodidae (Diptera: Brachycera) of temporary pools - faunistical and ecological investigations).- *unpubl. Master's thesis, Philipps-University of Marburg (Germany): 115 pp.*

SCHNABEL, SI. (1999): Faunistisch-ökologische Untersuchung der Chironomidae (Diptera: Nematocera) temporärer Tümpel in der Lahnaue bei Marburg (Temporary pools in the floodplain of River Lahn near Marburg (Hesse, Ger-

many) - faunistical and ecological investigations of the Chironomidae (Diptera: Nematocera)).- *unpubl. Master's thesis, Philipps-University of Marburg (Germany): 221 pp.*

HOOF, M. (2001): Autökologische Untersuchungen an Scirtiden temporärer Tümpel unter besonderer Berücksichtigung der Art *Microcara testacea* LINNAEUS, 1767 (The autecology of scirtids (Coleoptera: Scirtidae) dwelling in temporary pools, with special emphasis on *Microcara testacea* LINNAEUS, 1767).- *unpubl. Master's thesis, Philipps-University of Marburg (Germany): 80 pp.*

[1]SCHNEIDER, S. (2000) Faunistisch-ökologische Untersuchungen an Wasserkäfern temporärer Tümpel unter besonderer Berücksichtigung der Helophoridae (Faunistical and ecological investigations of water beetles (Insecta: Coleoptera) dwelling in temporary pools, with special emphasis on Heloporidae.- *unpubl. master's thesis, Philipps-University of Marburg (Germany): 103 pp.*

SUNDERMANN, A. (2001): Untersuchungen zur Autökologie von *Stempellina montivaga*/*Stempellina* spec. nov. (Diptera, Chironomidae), einer köcherbauenden Zuckmücke helokrener Quellen (Autecological studies on *Stempellina montivaga/Stempellina* spec. nov. (Diptera, Chironomidae), a case bearing chironomid dwelling in helocrene springs.- *unpubl. Master's thesis, Philipps-University of Marburg (Germany): 90 pp*.

Only parts of these investigations have been published to date (see references) but I hope that we will be able to publish the rest relatively soon. Insects other than chironomids, which were caught during my studies on temporary pools, were determined down to species or family (Diptera other than Culicidae, Chaoboridae and Dixidae) level but are not considered in this thesis. I however plan to publish these results in the future.

The collection of field data for the present thesis started in spring of 1996 and ended in July 1999. The faunistical study of the Lahnberge's three temporary pools includes all data collected from 1992 to 1995, so that information's of five- (pool 3), six- (pool 2) and seven (pool 1) years are presented in the present study - a comparatively long time span.

There are many people who contributed in various manners to this thesis and to whom I am indebted:

My supervisor Prof. Dr. HANS-WILHELM BOHLE (Philipps-University of Marburg, Germany), was always willing to get into discussions that always proved fruitful and his human, kind, and non-authoritarian manner of guidance gave me all the freedom possible.

Prof. Dr. PETER ZWICK ('Limnologische Fluss-Station' of the Max-Plank-Institute of Limnology, Schlitz, Germany) generously agreed to be the second referee of my present thesis.

I am greatly indebted to many chironomid researchers for their help with species determinations, (see Appendix 3), discussions and providing information. Chironomid researchers are endangered species amongst biologists and such are needed more than ever:

Dr. FRIEDRICH REISS, who sadly left us too early on the 17th of August 1999, helped me with many critical determinations, especially with Chironomini and Tanytarsini. He always welcomed me in a friendly manner on each of my several visits at the Zoologische Staatssammlung München (Germany).

Prof. Dr. OLE A. SÆTHER (Museum of Zoology, Bergen, Norway) was very influential in helping me deal with all the problems concerning determinations and taxonomy of Orthocladiinae. He was invariably friendly, patiently answered my numerous questions and checked a huge amount of determinations. It is thanks to him that I concerned myself more intensively with taxonomy and he helped me through my first taxonomic paper (DETTINGER-KLEMM 2001a) from its begin-

ning and until its publication.

I corresponded at length with HENK K. M. MOLLER PILLOT (The Netherlands), predominantly on ecological subjects. This exchange was an immense and valuable source of information for me (see e.g. section 4.3.1.). Henk also helped me with some critical determinations and kindly checked some of the material.

I had a very valuable exchange of letters, material and data with Dr. MARTINA STEINHART (Freie Universität Berlin, Germany), particularly concerning *Limnophyes asquamatus*.

Dr. RUTH CONTRERAS-LICHTENBERG (Naturhistorisches Museum Wien, Austria), Dr. PETER H. LANGTON (Northern Ireland), Dr. DECLAN MURRAY (University College Dublin, Belfield, Ireland), Prof. Dr. BRUNO ROSSARO (University of Milano, Italy), and HENK J. VALLENDUUK (The Netherlands) kindly inspected some of the critical determinations.

MARTIN SPIES (Zoologische Staatssammlung München, Germany) enormously broadened my horizon in taxonomy through a lively correspondence.

Prof. Dr. LOTHAR BECK (Philipps-University of Marburg, Germany) kindly helped me produce the SE-micrographs and LUCY LENNARTZ (Philipps-University of Marburg, Germany) developed them.

DAVID THIELTGES and FRIEDERIKE VOIGT (Philipps-University of Marburg, Germany) conducted the colonizing experiment (except for the determinations of chironomids and mosquitoes).

SOPHIE ROUYS (New Caledonia) checked the manuscript for linguistic correctness.

I express my deep gratitude to all these people.

My greatest thanks are directed to my parents MECHTHILD and Dr. jur. MARTIN DETTINGER-KLEMM. Germany is currently a harsh environment for aquatic entomologists and survival rates are low. Unable to fall into dormancy, I survived periods of shortage thanks to my parents' help, which is why I dedicate this thesis to them.

2. Introduction

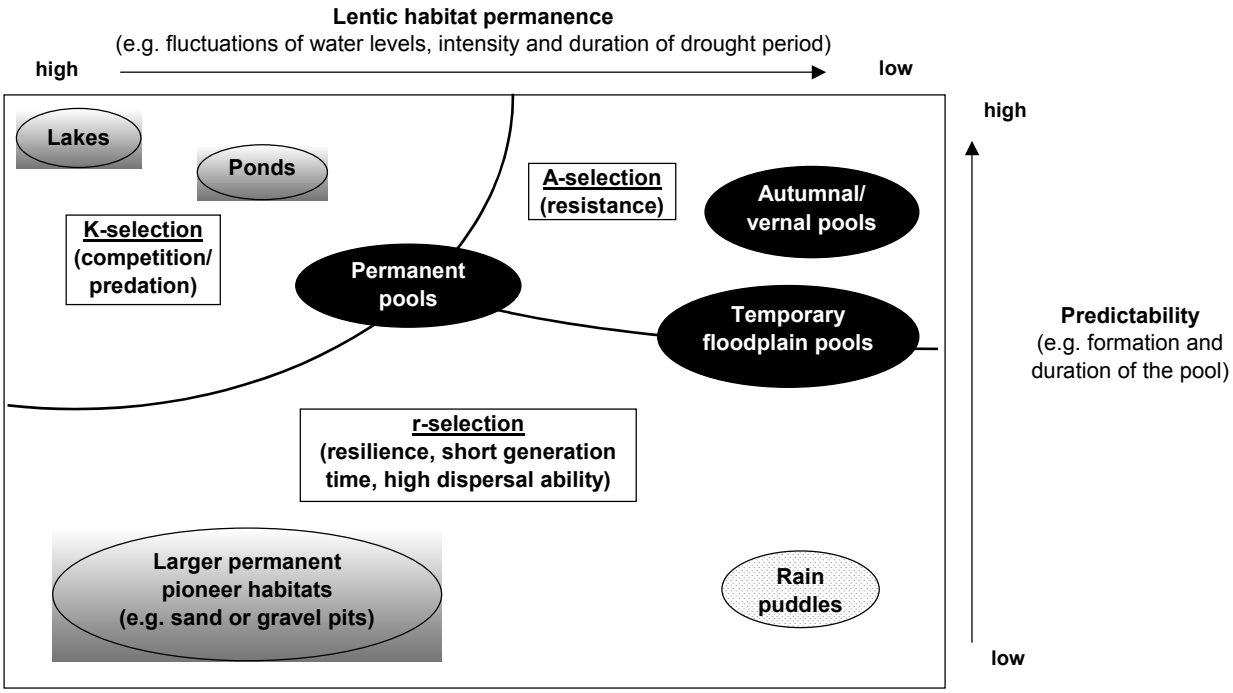

Figure 1: A habitat templet of the predicted occurrence of three characteristic life history strategies in lentic waters (after WILLIAMS 1985, WILLIAMS 1996 and DETTINGER-KLEMM 2000b).

In respect to its inhabitants and abiotic characteristics, temporary pools represent a distinct type of lentic waters (WILLIAMS 1997) of ubiquitous distribution. Although they are particularly widespread in arid and semi-arid regions (WILLAMS 1985), temporary pools are also frequent in temperate regions. WILLIAMS (1997) mentioned that, in 1880, more than one million ponds and pools occurred in England and Wales, which averages 5.4 ponds per km². The density of Canadian prairie ponds was estimated to be 50 per km², approximately 94 % of which were temporary (DRIVER 1977). To date large-scale land drainage has often strongly reduced the past high number of small water bodies. This applies to Germany accordingly where ponds and pools also occurred frequently and then strongly declined since World War II (RINGLER 1987). Unfortunately very few freshwater ecologists have paid attention to temporary pools, despite the ubiquity of this type of water body. MCLACHLAN & LADLE (2001) wrote in a refreshingly provocative manner: 'Indeed, at least in terms of number of separate water bodies, highly ephemeral waters are probably typical of most of the earth's surface, especially in the tropics and subtropics. This point has, we suggest, been obscured by the Eurocentric permanent lake model perpetrated by a generation of limnologists.' To continue with WILLIAMS (1996), temporary pools '..may be loosely defined as bodies of fresh water that experience a recurrent dry phase of varying length...'. There are two major categories of temporary pools: temporary wetland pools and temporary non-wetland pools. Temporary pools of wetlands (marshes adjacent to lakes and flood plain pools) are temporarily connected to permanent water bodies, which allows for an exchange of organisms. The present study is concerned with temporary non-wetland pools, which have no connection to permanent water bodies and can therefore be con-

sidered islands in a terrestrial desert. Life in these pools therefore depends on colonization (be it through crawling on land, aerial dispersal or phoresy) or survival of individuals in the mud. The organisms must therefore exhibit exclusively adaptive- or pre-adaptive traits in order to cope with this harsh environment (for reviews on that matter see WIGGINS et al. 1980, WILLIAMS 1987, 1996, 1997, HEITKAMP 1989, BATZER & WISSINGER 1996, DETTINGER-KLEMM 2000b). Two factors are considered to be important determinants of animal communities and serve as a coarse habitat templet to predict major biological traits in lentic waters (Figure 1): (a) predictability of favourable periods for species development (in time and space, e.g. formation and duration of a pool); and (b) the intensity of disturbance (e.g. intensity and duration of the drought). In permanent lentic waters, biotic interactions are supposed to be very important for controlling community composition (K-selection), pioneer habitats, which are often unpredictable in time and/or space, are expected to filter out r-selected species, and habitats with strong but highly predictable harshness of environmental factors are supposed to be controlled by the abiotic environment and select species that evolved resistance mechanisms (A-selection).

Chironomids or non-biting midges constitute a large proportion of the annual production of aquatic insects not only in streams (POEPPERL 2000), rivers (MEYER 1991), lakes (LINDEGAARD 1994) and permanent ponds (OERTLI 1995), but also in many types of temporary pools (DETTINGER-KLEMM 1995a, BAZZANTI 1996, ANTUNES 1997, LEEPER & TAYLOR 1998, BROOKS 2000). Faunistical studies of temporary pool chironomids - which are summarized in the Appendix 11 - are still relatively scarce, which can be mostly attributed to the difficulties of species determination and chironomid taxonomy. It is still unclear whether temporary pools are home to specific chironomid communities or whether they predominantly shelter euryoecious and opportunistic species, which represent stranded faunas from other habitats. There is however great evidence that African rock-pools shelter endemic (obligatory) chironomids (for rewiew see MCLACHLAN & LADLE 2001). Should there be no obligatory chironomids in the temporary pools of temperate regions, the papers listed in the Appendix 11 show that this habitat is however often home to some typical species. Such typical species are *Limnophyes asquamatus*, *Paralimnophyes hydrophilus*, *Polypedilum tritum* and *Chironomus dorsalis* (DETTINGER-KLEMM & BOHLE 1996). The first three species are known to be desiccation tolerant, the latter probably a colonizing species exhibiting exceptionally high powers of dispersal (DETTINGER-KLEMM & BOHLE op. cit.). Following several authors (e.g. WIGGINS et al. 1980), we interpreted many features observed in these species as adaptations, representing survival strategies to cope with the temporary habitat. Justifiably BUTLER (1984) argued that 'over-reliance on adaptationism' may be problematic, as some species traits might 'have arisen through natural selection (adaptations)' whereas others '-may exist for historical reasons (exaptations (= pre-adaptations, note by the present author))'. Indeed, to date available empirical data on the autecology of most species are few and statements on adaptations must await testing before becoming anything else than speculation. There lies the great paradox for those working with chironomids: our knowledge on chironomids' ecology is still scarce in contrast to the species richness of Chironomidae and the family's quantitative importance in many fresh waters. Any limnologist working with chironomids

would have a tale or two to that effect. Delighted to have determined a chironomid down to species level (a feat which still remains impossible in many cases), our ecologist wants to know whether that species is common or not or whether it prefers a distinct habitat or not. But there is a great dearth of information, and compilations as those existing for Chironomidae of The Netherlands (MOLLER PILLOT & BUSKENS 1990) are still an exception. In many cases the species remains a 'black box' or the information available obscures rather than reflects the species' true ecology. There are four main aspects to the present study, each of these aspects aims at improving the current knowledge on chironomids in the following manner:

1. In a faunistical study of four different types of temporary pools I test the hypothesis that the predictability of the aquatic phase and of the duration and intensity of drought cause systematic changes in the composition of the chironomid community and the major traits of individuals (resistance and resilience). I expected differences (a) between pools located in different parts of the habitat templet (Figure 1); and (b) for each individual pool, between years of differing hydrological regimes.

2. An experimental investigation of the basic aspects of the autecology of *Limnophyes asquamatus*, *Paralimnophyes hydrophilus*, *Chironomus dorsalis* and *Polypedilum tritum/uncinatum*, contributing to the following issues:

- dispersal in *Chironomus dorsalis* to determine whether the species' dispersal power is higher than that of most other species;
- growth and development to clarify whether species of temporary pools develop faster than species of permanent lentic waters and whether they are psychrophilic, thermophilic or eurythermous;
- timing of the life cycle to find any indications that the species are specifically linked via kinds of diapause (parapause or eudiapause sensu MÜLLER 1992) to the temporary habitat as is the case for many mosquitoes;
- determinants affecting the adult body size (used as indicator of reproductive success);
- whether overcrowding induces a prolongation or reduction of development time;
- interspecific competition and predation (only pilot studies) to find out (a) if species of temporary pools are less competitive and more vulnerable to predation than species of permanent waters; and (b) if there is an advantage in being the first species to be present after pool formation because the larger larvae are the better competitors;
- reactions to drought:(a) drought tolerance (which developmental stage is able to survive, and which degree of tolerance is realized? is drought tolerance higher as in permanent water species?); (b) is development into an adult accelerated by desiccation? and (c) is an adult eclosion possible under quasi terrestrial conditions?

- parthenogenesis in *Limnophyes asquamatus* to clarify whether parthenogenesis is facultative and if it is of advantage to effectively exploit short-term events of favourable environments.

3. Accoring to FITTKAU (1961, quoted in SPIES 2002): 'if one wants to practice ecology successfully, the mastery of systematics remains prerequisite.....', a chapter of this thesis deals with the morphology and taxonomy of the four species investigated, with particular attention to *Limnophyes asquamatus*.

4. Finally, the biology of the four species is investigated in their natural habitat and interpreted in conjunction with the laboratory data.

The main aim of the present study is to answer the simple question of whether the four species investigated should be considered as specifically adapted to temporary pools or as being opportunistic.

3. Materials and methods

3.1. Study of the natural habitat

Three natural pools were investigated in the present study. In the text, these pools are referred to as pools 1, 2 and 3, they are characterized and described in section 4.1..

3.1.1. Abiotic studies

3.1.1.1. Meteorological data

Data on precipitation had been measured since 1977 by the meteorological station 'Lahnberge', these were kindly provided by the HESSISCHE LANDESAMT FÜR UMWELT UND GEOLOGIE (HLUG). Whenever necessary, further meteorological data recorded by the meteorological station 'Am Stempel' were consulted, these data were kindly provided by M. KÄMPF (unpublished data).

3.1.1.2. Continuous recordings of water temperature and sampling sites

Water temperatures were measured by Tynytalk®II IP68 G (GEMINI Dataloggers (UK) LDT) data loggers (sampling interval: 2 hours) on site 2 (pool 1), site 5 (pool 2) and site 7 (pool 3) from November 25, 1997 to August 1, 1999 (pool 1), March 18, 1997-January 31, 1999 (pool 2) and November 25, 1996 to August 10, 1998 (pool 3) (see Figures 9 p 42 (pool 1), Figure 11 p 45 (pool 2) and Figure 13 p 45 (pool 3)). Temperature recording in pool 2 originally began at the same time as in the other pools but the logger became faulty during the first logging period from November 25, 1997 until March 18, 1997 and the data were therefore lost for this period of time. The loggers were placed at the bottom of the pools (for maximum depths see Table 16 p 55 (pool 1), Table 17 p 56 (pool 2) and p 59 (pool 3) as well as the Appendix 1) and pressed into the mud after desiccation (which provided the temperature of the uppermost substrate layer).

3.1.1.3. Water depth and substrate humidity

Table 1: Definition of three eco-phases in relation to five grades of soil moisture.

Eco-phase	Grade of humidity	Explanation
aquatic phase	5	Mud beneath an emergence trap totally covered with water.
semiaquatic phase	4	As grade 3, but very small puddles still present beneath the emergence trap.
	3	Substrate like a wet sponge.
terrestrial phase	2	Substrate compact, not much different from the terrestrial surroundings, but still humid.
	1	As grade 2, but more or less dry.

Water depths at sites 2, 5 and 7 were measured to the nearest centimetre when clearing the trap jars of the emergence funnels (section 3.1.2.). Water depths were measured more irregularly at the other sampling sites (Appendix 1). The different moisture contents of the mud were classified on a scale ranging from 1 to 5 and then attributed to the three eco-phases characteristic for the temporary pools (Table 1). From the 10th of July 1997, until refilling at the end of 1997, the moisture content (% of

saturation) at sampling sites 2, 5 and 8 was measured at soil depths of 5 and 20 cm, by soil moisture blocks (14.22.05, EIJKELKAMP, The Netherlands) and a soil moisture meter (14.22, EIJKELKAMP, The Netherlands).

3.1.1.4. Single measurements of physicochemical factors

The following gauging methods were used to measure the contents of PO_4-P, NH_4^+-N, NO_3^--N, Ca^{2+}, PH and conductivity:

PO4-P: (a) photometrical by RQflex (MERCK, Germany) and Reflectoquant^R Phosphate-test (5-120 mg/l), (b) Aquamerck Phosphate-test (PMB) (MERCK, Germany) (0.25-3mg/l);

$NH4^+$-N: photometrical by RQflex (MERCK, Germany) and Reflectoquant^R Ammonium-test (0.2-7 mg/l);

NO_3^--N: photometrical by RQflex (MERCK, Germany) and Reflectoquant^R Nitrate-test (3-90 mg/l);

Ca^{2+}: photometrical by RQflex (MERCK, Germany) and Reflectoquant^R calcium-test (5-50 mg/l);

pH: microprocessor pocket-pH/mV-meter pH 323 (WTW, Germany) with standard pH combined electrode with integrated temperature probe (SenTix 97T);

Conductivity: microprocessor LF 90 (WTW, Germany);

All parameters were measured at sampling sites 2 (pool 1), 5 (pool 2) and 8 (pool 3), except in 1995, when pH and conductivity were also measured at sampling sites 9 and 10 (pool 3). The RQflex meter also provides values below the measuring range and above the absolute limit of detection (LO): although provided in mg/l, these values are on an ordinal scale. Ortho-phosphate, ammonium, nitrate and calcium were only measured irregularly during the emergence study spanning from 1996 to 1998 (pool 2 and 3) and 1996 to 1999 (pool 1) (see section 3.1.2.) at the following dates:

26.6.1996, 16.7.1996, 1.11.1996, 20.12.1996, 18.3.1997, 11.4.1997, 14.5.1997, 3.6.1997, 5.7.1997, 5.1.1998, 23.3.1998, 22.4.1998, 25.6.1998, 25.6.1998, 17.7.1998, 18.8.1998, 21.9.1998, 19.10.1998, 12.2.1999, 6.4.1999, 19.5.1999.

PH and conductivity were measured from 1993 to 1999, the dates of measurements can be taken from Appendix 1.

3.1.1.5. Day-runs

Diurnal fluctuations of some physicochemical factors along with vertical and horizontal temperature gradients were measured during five day-runs that lasted one to three days (Table 2).

The data were recorded by a Squirrel 1000 Series data logger (ELTEK, Great Britain) to which were connected up to four temperature probes (DS-P4-V3 (DIESEN & KERN, Germany), an oxygen-meter (Oxi 597-S, WTW, Germany) with CellOx 325 dissolved oxygen probe and battery stirrer BR 325 (0.00-19.99 mg/l, nearest to 0.01 mg/l), a conductivity-meter and a pH-meter (the two latter see

section 3.1.1.4.)

During the day-run that spanned from March 27 to 28 in 1999, water samples were additionally taken on a four-hourly basis. These samples were then immediately frozen and later measured for ortho-phosphate (≥ 20 µg/l), ammonium (≥ 10 µg/l) and nitrate (≥ 50 µg/l) by an autoanalyser (TECHNICON, Ireland).

Oxygen was measured in mg/l and additionally converted into percentage of saturation using the temperatures measured at the probe and table 3 in SCHWOERBEL (1986).

Table 2: Day-runs for physicochemical parameters in pool 1 and 3.

Sampling period	Sampling interval	Site/pool	Water depth	Parameters
4.6. 19:00- 5.6. 19:00, 1997	30 min	2/1 + *Glyceria**	20 cm + 5cm*	Temp. (s, m, g, *Glyceria*); O_2; pH; cond..
27.5. 16:00 - 28.5. 16:00, 1999	10 min[1] 4 h[2]	2/1 + *Glyceria**	20 cm + 5cm*	[1]Temp. (air, s, g, *Glyceria*); O_2; pH;cond.; [2] PO_4^{3-}-P; NH_4^+-N; NO_3^--N.
21.2. 18:00 - 22.2. 18:00, 2000	30 min	7/3	45 cm	O_2; pH; Temp. (oxi).
28.2. 19:00 - 2.3. 14:00, 2000	30 min	7/3 + shallow**	45 cm + 5cm**	Temp. (g, shallow, oxi); O_2, pH, cond..
13.5. 18:00 - 15.5. 18:00, 2000	30 min	7/3	16 → 9 cm	Temp. (air, s, g, oxi); O_2, pH, cond..

Abbreviations and explanations:

Site/pool = No. of sampling site/No. of pool, see Figures 9-14 pp 42-46, section 4.1.1.2.; * shallow site 5 m east of site 2; ** shallow site 5 m south-east of site 7.

Water depth = maximum water depth at sampling site; **16 → 9 cm** = water column shrank from 16 to 9 cm during the period of measurement (only a puddle remained just before the drought);

Parameters = physicochemical parameters measured: **Temp.** = temperature (measured on: s = subsurface (2 cm above the water's surface), m = middle of the water column, g = 2 cm above the ground, Glyceria site*, air = air temperature just above the water's surface, oxi = oxigen probe, shallow site**); **cond.** = conductivity; **NH_4^+-N** = ammonium; **NO_3^--N**; **O_2** = oxygen; **pH** = pH-value **PO_4^{3-}-P** = phosphate .

3.1.2. Emergence study

The chironomid communities of pools 1 to 3 were investigated using emergence funnels, which consisted of pyramid-shaped aluminium frames, covered by 300 µm nylon mesh. The funnels were mounted on polystyrene frame-forming floats which inside measures were 40 x 40 cm (see Figures 3, 10, 12 and 14 on pp 21, 43, 45 and 46, respectively). The traps were loosely tethered to permit vertical movement with water-level fluctuations. If the sampling sites became dry, the gaps between the polystyrene float and the substrate were carefully obstructed. A removable trap jar with a no-return entrance tube topped the pyramid. The jar was filled with a mixture consisting of 50 % ethyl-eneglycol and 50 % water. A drop of detergent was also added to reduce surface tension. When clearing the trap jar, its contents were poured through a 300 µm sieve and transferred into a storing vial filled with 70 % ethanol. For exceptions to the above protocol, the number of traps exposed and the sequence and duration of annual samplings see Table 3.

Table 3: Data on the emergence samplings taken from 1992 to 1999 in pools 1, 2 and 3.

Year	Pool	Sites investigated	Clearing of trap jars (Samplings)
1992	1, 2	2[(1)], 5[(2)]	24.4.↑[pool 1], 25.4.↑[pool 2], 27.4., 30.4., 4.5., 5.5., 10.5., 13.5., 16.5., 21.5., 27.5., 3.6., 10.6., 14.6., 22.6., 27.6., 1.7., 8.7., 16.7., 20.7., 24.7., 30.7.↓
1993	1, 2	1, 2, 3, 4, 5, 6	11.5.↑, 14.5., 19.5., 22.5., 26.5., 29.5., 2.6., 6.6., 9.9., 14.6., 18.6., 21.6., 25.6., 29.6., 3.7., 7.7., 12.7., 17.7., 19.7., 21.7., 26.7., 30.7., 4.8., 9.8., 13.8., 18.8., 23.8., 28.8., 1.9., 6.9., 11.9., 16.9., 24.9., 30.9., 7.10., 14.10., 25.10., 10.11., 14.12.
1994	1, 2, 3	1, 2, 4, 6, 7[(3)], 9[(3)]	26.1., 11.3.↑[pool 3], 11.4., 22.4., 28.4., 6.5., 19.5., 28.5.↓[pool 1 + 2], 23.8.↓[pool 3]
1995	(1), 3	2[(4)], 3[(4)], 7, 9, 10	5.5.↑[pool 3], 9.5., 12.5., 15.5., 18.5., 22.5., 26.5., 29.5., 31.5., 2.6., 6.6., 8.6., 12.6., 15.6., 22.6., 26.6., 28.6., 29.6., 30.6., 2.7., 3.7., 4.7., 5.7., 6.7., 7.7., 8.7., 9.7., 10.7., 11.7., 12.7., 17.7., 20.7.↑[pool 1], 26.7.↓[pool 3], 2.8., 21.9. ↓[pool 1]
1996	1, 2, 3	2, 3, 5, 6, 7, 8	7.4.↑, 16.4., 19.4., 23.4., 25.4., 28.4., 1.5., 4.5., 7.5., 11.5., 15.5., 22.5., 28.5., 1.6., 5.6., 10.6., 14.6., 18.6., 26.6., 2.7., 10.7., 16.7.[pools 1,2], 23.7., 31.7.[pools 1,2], 6.8.↓[pool 1], 14.8., 21.8.[pool 2], 28.8.[pool 2], 10.9., 30.9., 18.10., 1.11.↓[pool 2,3]
1997	1, 2, 3	2, 3, 5, 6, 7[(4)], 8[(4)], 9[(4)]	28.3.↑[site 2,3,5,6,7,8], 5.4., 11.4.↑[site 9], 19.4., 26.4., 3.5., 10.5., 15.5., 22.5., 30.5., 5.6., 12.6., 19.6.↓[site 9], 28.6., 5.7.↓[site 7,8], 11.7.↓[site 3,6], 19.7.↓[site5], 26.7., 5.8.↓[site 2]
1998	1, 2, 3	2, 3, 5, 6, 7, 9,	23.3.↑, 30.3., 7.4., 15.4., 22.4., 30.4., 6.5., 13.5., 20.5., 27.5., 3.6., 10.6., 17.6., 25.6., 2.7., 9.7., 17.7., 24.7., 3.8., 10.8., 18.8., 26.8., 2.9., 11.9., 21.9., 30.9., 9.10., 19.10., 2.11.↓
1999	1	1b, 1c[(5)], 2, 3	6.4.↑[site 1b,2,3], 16.4.↑[site 1c], 24.4., 30.4., 7.5., 19.5., 27.5., 2.6., 9.6., 18.6., 25.6., 1.7., 8.7., 18.7., 27.7., 1.8.↓

Explanations and comments:

↑ = exposure of trap;
↓ = removal of trap;
(1) pool 1, 1992: inside measures of float 80 x 80 cm, funnel without trap jar. Individuals (for chironomids only individuals of medium and large size (collected in the context of a term thesis on mosquitoes)) were removed from the funnel by an aspirator similar to that illustrated by figure 63b in MÜHLENBERG (1989), these individuals were killed with ethyl acetate and then preserved in 70 % alcohol;
(2) pool 2, 1992: nylon mesh with mesh size of 1 mm;
(3) pool 3, 1994: floats with inside measures of 50 x 50 cm;
(4) after the water had disappeared, the floating funnels were replaced by traps of the same size and shape, the base of which could easily be pressed into the soil;
(5) pool 1, 1999 on site 1c: no polystyrene float, the funnel's metal base was pressed deeply into the soil.

3.2. Colonizing experiment

See DETTINGER-KLEMM 1995a and DETTINGER-KLEMM & BOHLE 1996 for details about the colonizing experiment undertaken in 1993 (C1). In 1998, a second colonizing experiment was conducted with help of DAVID THIELTGES and FRIEDERIKE VOIGT. The aim of that second experiment was to answer the following questions:

1. which midge species is/are the best colonizer/s?
2. do the nearest aquatic habitats influence the colonization in time and space?

Ten colonizing pools (125 x 85 x 25 cm) were exposed in the evening of May 19, 1998 as illustrated by Figure 2. The pools were designed so as to simulate natural puddles, e.g. car tracks etc. Each colonizing pool was filled with 10 l (1 bucket) of dry soil (all taken from the same place) and then filled with tap water until obtaining a water column of 10-15 cm. A small puncture in the middle of the pool's wall prevented water levels to become deeper than 10-15 cm. Each experimental pool was finally equipped with one tuft of *Juncus effusus* (taken from a humid but never inundated meadow) and one floating emergence funnel (see section 3.1.2.) (Figure 3). The experiment was

finished on July 21, only experimental box 4 was exposed until August 11. The trap jars of the emergence funnels were cleaned weekly as described in section 3.1.2.. The distances of the single colonizing pools to the closest potential colonization sources are listed in Table 4.

Table 4: Distances (meters) of the colonizing pools from the closest aquatic habitats.

Colonizing source	Number of colonizing pool									
	1	2	3	4	5	6	7	8	9	10
Pond (1)	825	800	850	838	1075	963	1138	1238	1413	1438
Permanent pool (2)	463	288	200	575	738	1038	1225	1125	1063	1325
Sewage plant (3)	1150	950	750	450	225	600	700	475	325	625

Water temperatures in box 2 (shaded) and 4 (not shaded) were recorded by Tynytalk®II IP68 G data loggers from June 8 to July 16 (sampling interval: 30 minutes). Water depths (nearest to 1 cm), pH (microprocessor pocket-pH/mV-meter pH 323, WTW, Germany) and conductivity (microprocessor LF 90, WTW, Germany) were measured during weekly inspections. A day-run was performed in experimental box 4 from 10 a.m. on the 11th of August to 10 a.m. on the 12th of August 1998. During the day-run, the following variables were sampled at intervals of 10 min: temperature ((a) air temperature on the ground beside the experimental pool; (b) 2 cm below the water's surface, (c) in the middle of the water column and (d) on the pool's ground (water depth 14 cm)) and oxygen

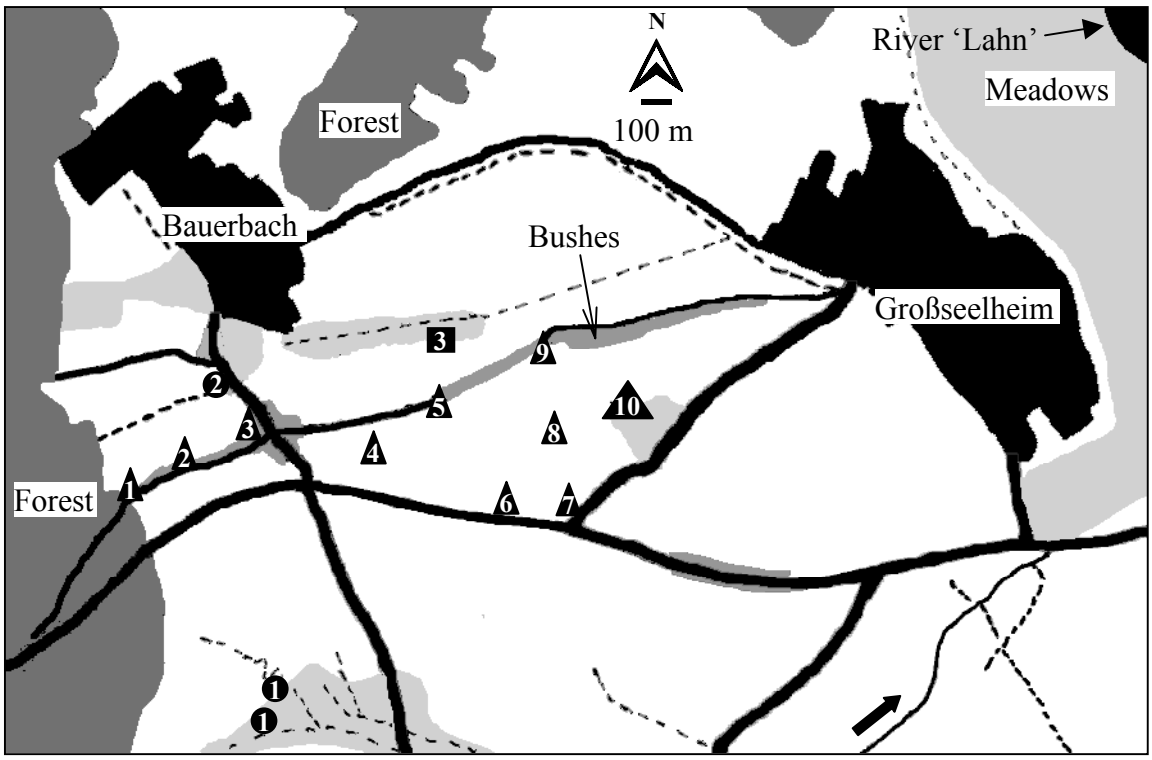

Figure 2: The arrangement of the colonisazion pools (black triangulars 1-10) in 1998 near Marburg, Germany.

Signs and signatures:

Black circles: 1 = ponds; 2 = permanent pool; **black rectangular** (3) = sewage plant;

bold black lines = main roads and asphalt roads; **finer black line with arrow beside** = brook; **interrupted lines** = ditches;

white areas = fields; **dark grey** = forest and bushes; **lighter grey** = grasslands; **black areas** = villages (and river 'Lahn').

(middle of water column) (see section 3.1.1.5.).

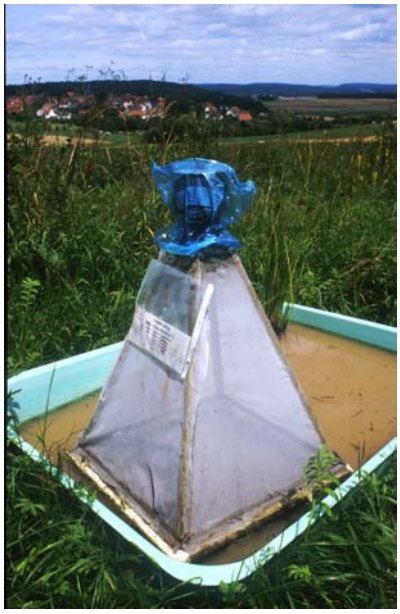

Figure 3: Colonization pool 10.

3.3. Laboratory studies

3.3.1. Rearing methods

3.3.1.1. Limnophyes asquamatus

In 1996 and 1997 huge efforts were made to establish laboratory cultures with individuals from the temporary woodland pool (pool 3). The adults were captured

(a) by sweeping the vegetation within and beside pool 3 (1996 and 1997);

(b) by emergence funnels without trap jars, these funnels had been exposed in the drainage ditches near trap sites 7 and 8 (the adults were removed from the funnels by an aspirator) (only 1996);

(c) from culture vessels 23 and 25 (see Table 5 and comments on Tables 5 and 6) (only 1996);

Captured adults were transferred into 27 culture vessels as summarized in Table 5. Diverse environmental conditions were applied: small tubes up to large flight cages, different substrates, light conditions and temperatures and a sequence of environmental conditions in order to mimic the annual cycle of the abiotic environment in a natural habitat. Mating was never observed.

In 1996, some females produced an egg mass, which never showed signs of development. Whenever a female was unequivocally associated with an egg mass, it was slide-mounted either singly or in a group with other individuals (see section 3.4. and Table 5).

There were also no matings in 1997 (culture vessel 26 and 27, see Table 5). But contrasting with the situation of 1996, parthenogenetic populations developed in both culture vessels. These parthenogenetic females were used as the initial stock for culture vessels 28-32 and 143 + 143. The rearing

Table 5: Rearing conditions in the attempts to rear *L. asquamatus* in 1996 and 1997. (For comments and abbreviations see pp 24-26)

Nr.	a/"m"	Date	Vessel	Substrate	Water	Light	Sugar	Temp (°C)	Humidity	Adults/mounted/Ind.Nr.	Mass
1	a	23.4.1996	T1	transsternat + plant	tap	LD	+	20	3/5→3→3/5	20,10/0,1/1382	1
	"m"	28.4.1996	P	transgravel2	tap	LD		20	3/5		
2	a	25.4.1996	T2	transclay	tap	LD	+	20	3/5→5	6,6/4,0/-	
	"m"	28.4.1996	P	transgravel2	tap	LD		20	3/5		
3	a	24.4.1996	T2	transblott	tap	LD	+	20	3/5→5	18,3/9,1/1383	1
	"m"	28.4.1996	P	transgravel2	tap	LD		20	3/5		
4	a	25.4.1996	tube	diffsub	tap	LD	+	20	3	5,5/	
	"m"	1.5.1996	tube	diffsub	tap	LD		10	3		
5	a	23.4.1996	cryst	transclay	tap	LD	-	20	3/5	7,2/7,2/1341 + 1344	
6	a	28.4.1996	tube	transgravel	tap	LD	+	20	3/5	8,4/8,4/1364 - 1367	3
	"m"	5.5.1996	tube	sternat	tap	LD		20	3		
7	a	28.4.1996	tube	transgravel	tap	LD	+	20	3/5	4,1/3,1/1360	1
	"m"	6.5.1996	P	sternat	tap	LD		15	3		
8	a	28.4.1996	tube	transgravel	tap	LD	-	20	3/5	3,3/3,3/1379 -1381	2
	"m"	1.5.1996	P	transgravel2	tap	LD		20	3/5		
9	a	28.4.1996	tube	transgravel	tap	LD	-	20	3/5	3,2/3,0	1
	"m"	1.5.1996	P	transgravel2	tap	LD		15	3/5→1→3		
10	a	1.5.1996	tube	transgravel	tap	LD	-	20	3/5	3,5/2,2/1356 + 1357	5
	"m"	4.5.1996	tube	sternat	tap	LD		20	2		3
		4.5.1996	tube	sternat	tap	LD		20	3		2
11	a	1.5.1996	tube	transgravel	tap	LD	-	20	3/5→3	1,2/1,0/-	2
12	a	1.5.1996	cryst	transclay	tap	LD	?	20	3/5	3,3/0,2/1350 + 1351	2
	"m"		P	sternat	tap	LD		20	3		
13	a	4.5.1996	T2	comp	tap	LD	?	20	2/3/5→5	first run: 7,3/-/- second run: many	
14	a	6.5.1996	tube	sternat	tap	LD	-	20	2→5→3→5	9,4/-/-	2
15	a	6.5.1996	tube	sternat + blott	tap	LD	-	20	2	0,4/-/-	1
16	a	6.5.1996	tube	transgravel	tap	LD	-	20	3/5→5	0,2/-/-	
	"m"	12.5.1996	P	sternat	tap	LD		20	3		
17	a	11.5.1996	tube	sternat	tap	LD	-	20	2	1,2/-/-	
18	a	22.5.1996	T6	transsternat + plant	tap	LD	+	20	3/5	many/-/-	
19	a	1.6.1996	T1	transsternat + plant	nat P1	LD	+	20	3/5	>50/-/-	
20	a	5.6.1996	T3	transnatcent	nat P3	LD→room	+	20→room	3/5	>20/-/-	
21	a	7.6.1996	tube	transgravel	tap	LD	-	20	3/5	<10/-/-	
22	a	10.6.1996	tube	transgravel	tap	LD	?	20	3/5	<10/-/-	
23	a	23.4.1996	In	natural	tap	natural	-	natural	5	many/-/-	
24	a	23.4.1996	T4	transnatural	tap	LD	-	20	3/5	many/-/-	
25	a	14.6.1996	T5	transnatural	tap	LD→room	+	20→room	3/5	many/-/-	
26	a	8.4. + 9.4.1997	T7	transsternatl + plants	tap	LD	+	20	3/5	± 50 (♂♂ + ♀♀)/-/-	
27	a	7.7.1997	T8	transnatural	tap	LD	+	25	3/5	many ♂♂ + ♀♀	

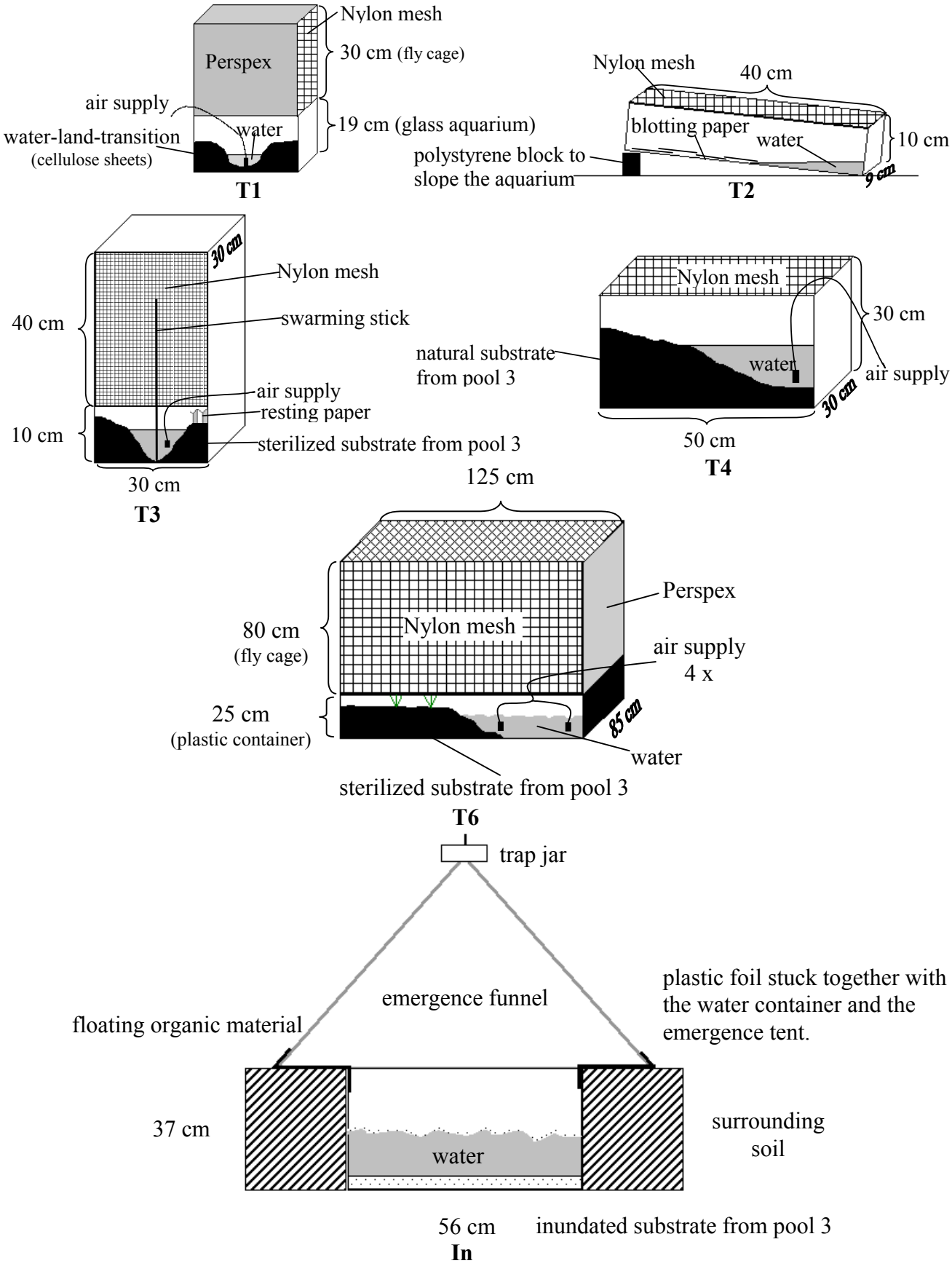

Figure 4: Different culture vessels used to rear *Limnophyes asquamatus* (see text and Table 5).

conditions of these parthenogenetic cultures are summarized in Table 6. Again, some of the females were slide-mounted either singly or in a group. The larvae of the parthenogenetic lab rearings were fed with powdered stinging nettles and with a water suspension of sludge the latter of which was made from the powder of the stinging nettles (see FISCHER 1969).

Table 6: The environmental conditions in the different parthenogenetic lab rearings of *L. asquamatus*. (For explanations see comments on Tables 5 and 6 pp 24-26)

Nr	Vessel	Substrate	Sequence	Date	Humidity	Ind. Nr.	Comment
28	T1	transcell (arranged as in the sketch for T1)	20 °C LD →0.1 °C SD →10 °C LD	8.4.1997 - 7.1.1998 7.1. - 29.1.1998 29.1.1998 -	3/5	1512 - 1516*; L146 - 150*; 1537 - 1541**; 1625 - 1661**	*specimens preserved during the 20 °C period (6.10.1997, low larval densities). **specimens preserved during the 10 °C period (15.2.1998, high larval densities).
29	T1	transnatural + plant	20 °C LD 20 °C LD 20 °C LD 20 °C LD 0.1 °C SD 10 °C LD	May 1997 June 1997 July - November 1, 1997 November 1 - 15, 1997 16.11.1997 - 1.1.1998 1.1.1998 -	3/5 →5 →4→3→1/2 →5	1551 - 1558*; L155 - 167*	*specimens preserved during the 10 °C period, low larval densities.
30	cryst	transcell	15 °C LD	24.6. - 15.8.2000	3/5	1542 - 1545; 1559; L141	Low larval densities.
31	cryst	transcell	15 °C LD	24.6. 15.7.2000 15.7. - 25.7.2000*	3/5	1560 - 1562*; L99 - 110; L135 - 139	*2 larvae and 1 pupa were isolated and reared into the adult separately in Petri dishes.
32	T1	transcell	20 °C LD	8.4.1997 - 15.8.2000	3/5	1523 + 1527 - 1536 + 1546 - 1550 + 1563 - 1624*; L14 - 94, L111 - 125, 127 - 134	*All specimens preserved in 1998, high larval densities.
143 + 144	C	transcell	21.5 °C	28.2. - 17.4.1998 13.3. - 17.4.1998	3/5		see Appendix 8

Abbreviations and comments for Tables 5 and 6:

Nr. = number of the culture vessel.

a/"m" = if the rearing conditions of the adults (a) and the egg masses (sometimes inclusive dead females which had not laid an egg mass ("m")) were different, they are listed separately.

Date = date of stocking in Table 5, length of rearing and time of change of the rearing conditions given in Table 6.

Vessel = type of vessel used in the experiment:

P = Petri plastic dish: diameter 9 cm, height 1.5 cm (no air supply);

Tube = plastic tube (diameter 5 cm, height 10 cm) which could be closed by a foam stopper (no air supply);

C = crystallizing dish: diameter 9 cm, height 5 cm (+ air supply);

cryst = crystallizing dish: diameter 14.5 cm, height 7.5 cm (no air supply);

T1 = Terrarium 1 (Figure 4): glass aquarium (29 x 19 x 19 cm) with connected and removable fly cage with a height of 30 cm. The broadsides and the top of the fly cage were built of Perspex. The two small sides were covered with fine nylon mesh, which was then loosely covered by plastic foil. The latter guarantied a high humidity content in the air of the fly cage but covered only a part of the nylon mesh to prevent condensation inside the box (+ air supply);

T2 = Terrarium 2 (Figure 4): glass aquarium (40 x 9 x 10 cm) with its topside covered by fine nylon mesh (no air supply);

T3 = Terrarium 3 (Figure 4): glass aquarium (30 x 30 x 50 cm). The lower 10 cm of the front side were also covered by glass, the upper 40 cm were covered by a removable nylon mesh (+ air supply);
T4 = Terrarium 4 (Figure 4): glass aquarium (50 x 30 x 30 cm, + air supply);
T5 = Terrarium 5: glass aquarium (40 x 14 x 25). Equipment as illustrated for T4. This vessel was constructed to enable using an operation microscope so as to observe the adults in any place within the aquarium;
T6 = Terrarium 6 (Figure 4);
T7 = Terrarium 7: as T6 but other measures: plastic container 60 x 40 x 12 cm; fly cage 60 x 40 x 70 cm. All sides of the fly cage were covered with nylon mesh, which was additionally loosely covered by a plastic foil (+ air supply);
T8 = Terrarium 8: as T6 but height of fly cage 225 cm (+ air supply);
In = inundation experiment 1993 (Figure 4) and inundated substrate in 1996 (1996 = vessel 23: without trap jar!): round plastic container: diameter 56 cm, height 37 cm (no air supply).
Substrate = type of substrate:
comp = the bottom of T2 was subdivided into 5 equal compartments by plastic stripes with a height of 1 cm, which were stuck to terrarium using aquarium silicone . The compartments were filled with the following substrates: a) humid and b) wet sterilized substrate from pool 3, c) water, d) humid- and e) wet cellulose sheets covered by a sheet of blotting paper;
diffsub = different substrates were layered in the following sequence (from bottom to top): cellulose sheets, sand, cellulose sheets, sterilized substrate from pool 3, two sheets of blotting paper;
natural/transnatural = natural unsterilized substrate from pool 3 that was totally (natural) or partly (transnatural) inundated (see Figure 4 (T4 and In)). Large numbers of adults emerged from these soils;
sternat/transsternat = natural but sterilized (oven-dried at 100 °C), substrate from pool 3 which was humid or wet (sternat) or partly inundated (transsternat);
transblott = The bottom of the vessel was lined with blotting paper, the water-land transition was created as illustrated in Figure 4 (T2);
transcell = water-land transition was formed by cellulose sheets as illustrated in Figure 4 (T1);
transclay = water-land transition was formed by clay and then the whole bottom of the culture vessel was lined with blotting paper;
transgravel = water-land transition was achieved forming a slope by help of fine-grained gravel (≤ 2mm), then a layer of cellulose and then two sheets of plotting paper were put on the gravel. Water was added until it reached the lowest point of the substrates surface. One sheet of paper without contact to the soil was clamped into the vessel so the adults could rest on it;
transgravel2 = water-land transition was formed by a slope of aquarium gravel, followed successively by a layer of blotting paper and cellulose sheets topped by finely crushed sterilized substrate from pool 3;
transnatcent = as transnatural but the water formed a puddle within the natural substrate from pool 3. Fur further information see Figure 4 (T3);
+ plants = small plants (e.g. *Juncus bufonius*, *Care*x spec.) were added to the land part of the terrarium;
+ paper = a sheet of paper was folded and attributed to the land part of the terrarium to provide dry resting places.
Sequence = temperature- and light-regime. If the temperature and/or light regime was changed, the sequence of change is provided (each change is separated by an arrow (→)). For further explanations see below.
Water = type of water.
Light = light cycle:
LD = long days (16 h/8 h); SD = short days (8 h/16 h); room = quasi-natural light regime within a room; natural = natural light regime in the open.

Sugar:
- = no food for the adults was added; **+** = one Eppendorf cup was added to the vessel. It was filled with a sucrose solution, which was in contact with a wick of cotton wool partly drilled through the top of the cup.
Temp = temperature (°C):
room = temperature within a room without air-conditioning; natural = natural temperature regime in the open.
Humidity: The numbers show the grade of humidity of the substrate (see section 3.1.1.3.). Changes in humidity levels during rearing are marked by an arrow (→).
Adults/mounted/Ind.Nr. = stock of males, females at the beginning/mounted males, females after death/Individual number of adults and larvae (L) mounted (see section 3.4.).
Mass = number of egg masses laid/observed.

3.3.1.2. Chironomus dorsalis, Polypedilum tritum and *Paralimnophyes hydrophilus*

In 1996, *Polypedilum tritum* and *Paralimnophyes hydrophilus* adults were caught alive by two emergence traps without trap jars, which had been exposed in pool 1. The adults were removed from the emergence funnels by an aspirator and then transferred - each species separately - into different culture vessels (T1, T6, T8, see Figure 4 and 'abbreviations and comments for Tables 5 and 6' pp 24-26).

Swarming *Paralimnophyes hydrophilus* males always hit the top part of the fly cage, regardless of its height (see section 4.4.1.1.), but fertilisation rates were always high (>75-100 %, mainly dependant on the numbers of males present in a culture vessel). Therefore T1 (20 °C LD) was finally used to maintain the *Paralimnophyes hydrophilus* laboratory cultures (Figure 4). The 'tanssternat' substrate was used at the beginning, but 'transcell' also showed good results and was finally used as the standard substrate (see 'abbreviations and comments for Tables 5 and 6' p 25 and Figure 4 (T1)). The larvae were fed in the same manner as those of *L. asquamatus* (section 3.3.1.1.).

Polypedilum uncinatum was reared at first in two T1 (see 'abbreviations and comments for Tables 5 and 6' p 24). The aquarium was filled with 1 cm of sterilized mud from the original habitat (boiled for 0.5 h, then covered with tap water, which was changed every day during one week before it was added to the culture vessel) and with water up to a level of about 10 cm. Though these cultures were maintained for 2 years before being stopped, they reached only a small fertilization rate of the eggs. Larger rearing units were therefore used (T6 and T8, see 'abbreviations and comments for Tables 5 and 6' p 25 and Figure 4 (T6)). In both T8 and T6 swarming by males was undisturbed (see section 4.4.1.1.) and 100 % of the egg masses were fertilized. T6 (20 °C LD) was accordingly used as the standard breeding unit to maintain laboratory populations of *Polypedilum tritum*. The bottom of the plastic container was filled with 1-2 cm of sterilized mud from pool 1 (see above) and filled up to 10 cm with tap water. The water body was always aerated by four air-stones, which had been connected to a membrane pump. The larvae were fed with a water suspension of sludge the latter of which was made from the powder of the stinging nettles (see FISCHER 1969).

Despite using T8 (20 °C LD, see 'abbreviations and comments for Tables 5 and 6' p 25), it was not

possible to establish laboratory cultures of *Chironomus dorsalis*. The plastic container was filled with substrate and water following the same protocol as for *Polypedilum tritum*. An initial stock of larvae was obtained from two plastic containers, that had been exposed outdoors (see section 3.3.2.1.). These larvae were fed with a water suspension of sludge the latter of which was made from the powder of the stinging nettles (FISCHER op. cit.) or a suspension of yeast. Hundreds of adults emerged from the initial stock and repeated attempts to establish laboratory cultures of *Chironomus dorsalis* were made. But the egg masses usually remained unfertilised - as described by STRENZKE (1959) - though several types of illumination (with and without simulations of dawn and dusk, direct and indirect illumination etc.), swarm markers (e.g. twigs) or sugared water were offered to the adults. I also tried to obtain fertilized egg masses by forcing copulation (with and without decapitation of the adult male) as described by FISCHER (op. cit.), but the males never grasped the female genitals.

3.3.2. Experiments on the impact of temperature and photoperiod on larval growth and the adult emergence

3.3.2.1. Collection of the egg masses

Because *Paralimnophyes hydrophilus* is a small species, adult males and females were transferred, with use of an aspirator, from the culture vessels into an oviposition vessel identical to the former (section 3.3.1.2.) but with a different lining at the bottom. A water-land transition was formed by a slope of aquarium gravel and the whole bottom was then lined with black paper, to facilitate detection of the light-coloured egg masses. In the morning and evening the vessel was checked for newly deposited egg masses and new adults were transferred from the culture vessels into the oviposition vessel once a day. This was done as long as egg masses were needed for the temperature experiments.

Polypedilum tritum females laid their egg masses at dusk, which was artificially simulated in the laboratory. During this time, gauze was laid on the water's surface. Two hours later the egg masses could be collected from the margins of the gauze and water puddles that had formed on the surface of the gauze.

The egg masses of *Chironomus dorsalis* were collected from two plastic containers (125 x 85 x 25 cm), which had been exposed beside pool 1 (see 'D' in Figure 9 p 42) in 1996 and 1997 (see section 4.4.2.3.3.). The plastic containers were filled with water and daily inspected for newly laid egg masses whenever egg masses were needed for the experiments.

See Table 6 (vessels 143 and 144) and Appendix 8 for information on *Limnophyes asquamatus* and Table 7 for data on the other species reared in the present study.

3.3.2.2. Incubation temperature and light regime, culture vessels, inspections and samplings

Appendix 8 provides an overview of the rearing conditions applied in each replicate.

Table 7: Collection of the egg masses, sampling site and rearing conditions of 11 additional species raised during the present investigation from the egg mass up to imagoes.

Species	Method	Date	Site	Vessel
Acricotopus lucens	D	2.7.1996	1	1; C_{mud}→$T1_{mud}$; 20 °C
Limnophyes minimus	A	21.6.2000	2	1; C_{trans}, A_{trans}; 15 °C
Parametriocnemus stylatus	E	2.10.1998	3	1; A_{mud}; 10.1 °C*
Chironomus annularius	A	10.8. + 14.8. 1997	4	1; A_{mud}; diverse
Chironomus luridus	D	5.7.1996	1	1; Appendix 8 and text; diverse
Chironomus cf. *nuditarsis*	A	10.8.1997	5	1/3; A_{mud}; 19.6, 24.2, 30.2 °C
Chironomus plumosus agg.	A	14.8.1997	4	1; A_{mud}; 11.0 °C SD and LD
Dicrotendipes notatus	A	7.8. 1997	6	1/2; A_{mud}; 19.6 °C
Glyptotendipes foliicola	A	9.8. 1997	6	1/2; A_{mud}; 24.2 °C and 30.2 °C
Glyptotendipes pallens	A	10.8.1997	4	1/2; A_{mud}; 19.6 °C
Paratanytarsus grimmii	L	24.10.1996	7	10; $T1_{mud}$; 24.2 °C

Abbreviations and explanations:

Species: Literature used for species identification see Appendix 3, except *Parametriocnemus stylatus* (Kieffer, 1924) (PINDER 1978, SÆTHER et al. 2000), *Chironomus annularius* sensu Strenzke (STRENZKE 1959, LINDEBERG & WIEDERHOLM 1979, VALLENDUUK & MOLLER PILLOT 1999), *Chironomus nuditarsis* (Keyl, 1961) (LINDEBERG & WIEDERHOLM 1979, VALLENDUUK & MOLLER PILLOT 1999), *Chironomus plumosus* aggregate sensu MOLLER PILLOT & VALLENDUUK (LINDEBERG & WIEDERHOLM 1979, MOLLER PILLOT & VALLENDUUK 1999), *Glyptotendipes foliicola* (Kieffer, 1981) (VALLENDUUK 1999, CONTRERAS-LICHTENBERG 2001) and *Glyptotendipes pallens* (Meigen, 1808) (CONTRERAS-LICHTENBERG 1999, VALLENDUUK 1999);

Method = method used to collect the egg mass: **A** = an adult female was caught alive in the evening flying above the water's surface at the sampling site. The female was then transferred into T1 (Figure 4) to which only water was added. The egg mass was usually deposited within the corresponding night; **D** = egg mass was collected from a plastic container (see text, *Chironomus dorsalis*); **E** = egg mass was collected from the natural habitat; **L** = a parthenogenetic laboratory culture was raised from larvae collected in the field. At the start of the experiment females from these rearings were transferred into the culture vessel where the egg masses had been laid;

Date = date of sampling;

Site = sampling site: **1** = artificial plastic container (see text (*Chironomus dorsalis*) and 'D'in Figure 9); **2** = helocrene spring near Mardorf (Hesse, Germany) (see Table 32 p 101); **3** = in the moss of a hygropetrical site in a temporary woodland spring brook near the 'Bittersbach' (Neckarsteinach, Baden-Württemberg, Germany); **4** = reservoir for motorway sewage at exit 'Kassel Nord' (A7, Hesse, Gemany); **5** = water-filled pit (permanent, deep) near 'Amöneburg' (Hesse, Germany); **6** = permanant pond near pool 1 (see Figure 8) (Marburg, Hesse, Germany); **7** = water-filled car tyre on a farm in Großseelheim (Hesse, Germany).

Vessel = rearing conditions. Three positions separated by an semicolon: **1st position** = **1/3-**, **1/2-**, **1-** and **10** egg mass(es) per culture vessel; **2nd position** = culture vessel and kind of substrate: **A** = plastic aquarium, **C** = crystallizing dish (see section 3.3.2.2.); **T1** = terrarium 1 (see Figure 4 and 'abbreviations and comments for Tables 5 and 6 p 24), **mud** = sterilized mud from pool 1, **trans** = water-land-transition as explained in section 3.3.2.2.; **3rd position** = rearing temperature(s) and light cycle (if not otherwise stated long-days (= LD: 16/8 hours).

The water temperatures within the incubators were continuously controlled by Tynytalk®II IP68 G (GEMINI Dataloggers (UK) LDT) data loggers (sampling interval: 0.5 hours). Usually cooled incubators were used in the experiments (2 x WTB BINDER, Germany; 1 x LMS, Great Britain; 2 x EHRET (KLT 2), Germany; 2 x HERAEUS, Germany) except for rearing temperatures of 27.3 °C, 30.4 °C, 31.1 °C, 33.5 °C, 35.0 °C and 41.0 °C (non-cooled incubators (HERAEUS, Germany)). At 21.5 °C and 24.2 °C the rearings were conducted in air-conditioned breeding rooms.

Plastic aquaria (18.2 x 12 x 15 cm (A)), normal Petri plastic dishes (diameter 8.8 cm, height 2.0 cm (P)) and crystallizing dishes (diameter 9 cm, height 5 cm (C)) were used for the rearings. The Petri dishes were partly used during embryonic development and for the first days after hatching (usually

two replicates per experiment, see Appendix 8). When the larvae were large enough to be seen in the bigger vessels, they were all transferred into crystallizing dishes or plastic aquaria (see Appendix 8). During embryonic development, the Petri dishes were filled only with water. When the larvae started to hatch, sterilized mud from pool 1 was added with a pipette (aquatic species) or a water-land transition was formed by cellulose sheets (aquatic-semiaquatic species). The crystallizing dishes (Figure 5) and plastic aquaria were filled with 0.5 to 1 cm of sterilized mud from pool 1 (aquatic species) and then with 3 centimetres of water. Until the end of the larval development polyethylene lids reduced water loss by evaporation. For the aquatic-semiaquatic *Paralimnophyes hydrophilus*, a water-land transition was formed by cellulose sheets surrounding a central puddle of water (as explained for T1 and T3 in Figure 4) with a maximum water depth of 3 cm. The culture vessels (except the Petri dishes) were always aerated by an air stone connected to a membrane pump and the larvae were fed as described in section 3.3.1..

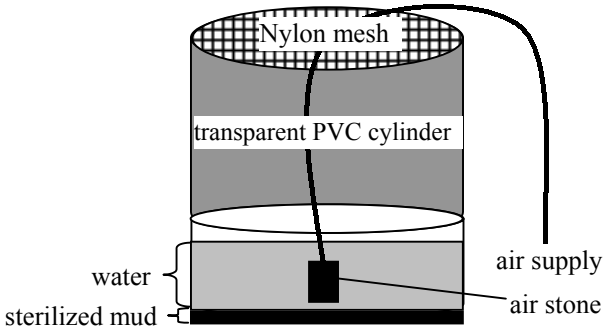

Figure 5: Crystalizing dish for aquatic species with PVC emergence cylinder.

The vessels were checked every day unless temperatures were low (4.5°C, 9.5°C and 13.8 °C SD/LD). During inspections, food was supplied, the water quality and the air supply controlled and if necessary water was added. Additionally, to document larval growth and development, five larvae per vessel were usually preserved in 70 % ethanol for two replicates per treatment. The sequence of inspections and the number of larvae preserved are presented in Appendix 9. Before adult emergence started, the plastic aquaria were covered by fine nylon meshing and the crystallizing dishes by an emergence cylinder as illustrated in Figure 5. When the adult emergence started, the number of males and females at the beginning of each artificial night was noted. After counting, all adults were removed and partly preserved. The experiment came to an end when no or only very few adults emerged in several days. If the emergence period was very long with only a few adults per day, longer control periods were chosen. In this case the mean of the two checks was taken (e.g. 1st control: 20 days, 2nd control: 23 days $\Rightarrow$ 21.5 days).

3.3.3. Experiment on interspecific interactions

The impact of an antagonistic species on length of development and survival of a target species was investigated in this pilot experiment. The species on which this experiment focussed were the typical pond species *Chironomus annularius* and *Chironomus plumosus*-aggregate, the colonizing species *Chironomus dorsalis* and the aestivator species *Polypedilum tritum*. The original intention was

for the *Chironomus plumosus*-aggregate to be the only representative of a permanent pond species. But it turned out that one of the two egg masses used as experimental stock actually was *Chironomus annularius*. The egg mass of *Chironomus annularius* was collected on site 4 on August 14, 1997 (Table 7), and that of the *Chironomus plumosus*-aggregate on site 5 on August 9 (Table 7). The collection of the *Chironomus dorsalis* and *Polypedilum tritum* egg masses was done as described in section 3.3.2.1.. The first instar larvae introduced to the treatments were always newly hatched and held in Petri dishes during embryonic development. The larger larvae (a mixture of instars II to small instars IV) were directly taken from (a) the standard breeding units (*Polypedilum tritum*, section 3.3.1.2.); (b) from glass aquaria (29 x 19 x 19 cm, filled with 2 cm of sterilized mud taken from pool 1, water to a level of 5 cm and aerated by two air-stones) to which the offspring of one egg mass was added after hatching and held until the start of the experiment (*Chironomus annularius* and *Chironomus plumosus*-aggregate); and (c) from plastic aquaria (*Chironomus dorsalis*, see section 3.3.2.2.), to which the offspring of one egg mass was added after hatching as well. Crystallizing dishes as illustrated in Figure 5 and described in section 3.3.2.2. were used as experimental units. The following combinations were tested and replicated twice:

(a) Standard (0): only one species per experimental unit: *Chironomus plumosus*-aggregate (80 instars I), *Chironomus dorsalis* (80 instars I), *Polypedilum tritum* (80 instars I);

(b) plumosus 1 ↔ dorsalis 2: 80 instars I of *Chironomus plumosus*-aggregate together with 80 larger larvae of *Chironomus dorsalis*;

(c) plumosus 1 ↔ tritum 2: 80 instars I of *Chironomus plumosus*-aggregate together with 160 larger larvae of *Polypedilum tritum*;

(d) tritum 1 ↔ dorsalis 1: 160 instars I of *Polypedilum tritum* together with 80 instars I of *Chironomus dorsalis*;

(e) tritum 1 ↔ dorsalis 2: 80 instars I of *Polypedilum tritum* together with 80 larger larvae of *Chironomus dorsalis*;

(f) tritum 1 ↔ annularius 1: 160 instars I of *Polypedilum tritum* together with 80 instars I of *Chironomus annularius*;

(g) tritum 1 ↔ annularius 2: 80 instars I of *Polypedilum tritum* together with 80 larger larvae of *Chironomus annularius*;

(h) dorsalis 1 ↔ annularius 1: 80 instars I of *Chironomus dorsalis* together with 80 instars I of *Chironomus annularius*;

(i) dorsalis 1 ↔ annularius 2: 80 instars I of *Chironomus dorsalis* together with 80 larger larvae of *Chironomus annularius*;

(j) dorsalis 1 ↔ tritum 2: 80 instars I of *Chironomus dorsalis* together with 160 larger larvae of *Polypedilum tritum*;

The experiment was conducted in an air-conditioned breeding room (20.5 °C LD (16:8h)). Food was supplied in excess. A suspension of stinging nettle sludge (FISCHER 1969) or a suspension of yeast was added daily with a pipette along with ½ tablet of TABIMIN (TETRA, Germany), that was added at the start of the experiment and a second time after the first adults had emerged. The water quality was checked daily and part of the water was replaced by new tap water whenever necessary (foam). The number of emerging males and females was noted every day and the specimens were then preserved in 70 % ethanol. When the emergence had ceased, the sediment of each treatment was searched for remaining larvae that had not developed into adults.

3.3.4. Experiment on larval density

In this pilot experiment, the impact of larval density on survival, adult body size and development time of *Chironomus dorsalis* and *Polypedilum tritum* was investigated. Crystallizing dishes (Figure 5 p 29) were used as rearing unit. Each dish was stocked with 5, 10, 20, 40, 80, 160, 320, 640, 1280 and 2560 newly hatched larvae. The treatments were checked daily for water quality and the larvae were fed with a suspension of stinging nettle sludge and a suspension of yeast. The amount of food added to a treatment was doubled for each level of density. As in the other experiments, the number of emerging males and females was noted every day and the adults were preserved in 70 % ethanol. The experiment was conducted in an air-conditioned breeding room (20.5 °C LD).

3.3.5. Experiment on predation

This pilot experiment tested whether small geophilous dragonfly larvae effectively feed on sediment-living and tube-building larvae of *Chironomus dorsalis*, *Chironomus plumosus*-aggregate and *Polypedilum tritum*. The egg mass of the *Chironomus plumosus*-aggregate was collected from site 4 on August 14, 1997 (Table 7) and the egg masses of the two other species as previously described. Six small geophilous larvae belonging to *Libellula depressa* (determined at the end of the experiment using the key developed by HEIDEMANN & SEIDENBUSCH (1993)) were collected from site 5 (Table 7) on August 29, 1997 and weighed nearest to 1 µg at the beginning and end of the experiment (Table 51 p 159).

Plastic aquaria (18.2 x 12 x 15 cm) were used for the treatments and filled with 500 ml of sterilized mud from pool 1 and 1500 ml of tap water. One piece of tile (5 x 10 x 1 cm) was added to each vessel as solid substrate. At the beginning of the experiment, one tablet of TABIMIN (TETRA, Germany) was added to each culture vessel, which were aerated by an air-stone. Three vessels, each stocked with 300 newly hatched larvae, were used for each species considered in the experiment (except the control for *Chironomus dorsalis* which was only stocked with 155 larvae) and the larvae had 5 (*Chironomus dorsalis* and *Polypedilum tritum*) or 8 (*Chironomus plumosus*-aggregate) days to settle before one dragonfly larva was introduced into two of the three vessels containing a given species. The treatment without dragonfly larva served as a control. During the experiment, the larvae were fed with a suspension of stinging nettle sludge and a suspension of yeast. The adult emergence was documented by daily inspections. At the end of emergence the vessels were searched for re-

maining larvae before finishing the experiment. The experiment was conducted in an air-conditioned breeding room (20.5 °C LD).

3.3.6. Experiments on drought tolerance

Table 8: Basic conditions and information on the experiments on larval drought tolerance.

Species	Instar	Unit	Substrate	Medium	Stock	Days	Humidity
L. asquamatus	III	b	20, pool 3	silicate, 50	20 (360)	180, 180	direct
	IV	b	20, pool 3	silicate, 50	20 (360)	180, 180	direct
P. hydrophilus	I	a	20, pool 3	silicate, 50	20 (340)	180, 90,	indirect
	II	a	20, pool 3	silicate, 50	20 (360)	180, 180	indirect
	III	a	20, pool 3	silicate, 50, 5	20 (540)	180, 180, 180	indirect
	IV	a	20, pool 3	silicate, 50, 5	20 (540)	180, 180, 180	indirect
C. dorsalis	Ia	a	10, pool 1	50	30 (180)	30	indirect
	Ib	a	10, pool 1	50	30 (150)	24	indirect
	III/IV	b	25, pool 1	50	20 (140)	60	indirect
	IV	b	25, pool 1	50	20 (140)	60	indirect
C. plum.-agg.	I	a	10, pool 1	50	30 (180)	30	indirect
	II	a	10, pool 1	50	20 (120)	30	indirect
	III/IV	b	50, pool 1	50	20 (140)	60	indirect
	IV	b	50, pool 1	50	15 (105)	60	indirect
P. tritum	Ia	a	10, pool 1	silicate, 50, 5	30 (480)	30, 24, 24	indirect
	Ib	a	10, pool 1	silicate, 50, 5	30 (810)	180, 180, 180	indirect
	III	b	20, pool 1	silicate, 50, 5	30 (810)	180, 180, 180	indirect
	IV	b	20, pool 1	silicate, 50, 5	30 (810)	180, 180, 180	indirect

Abbreviations and explanations:

Instar = larval instar I - IV (I and Ia = newly hatched instars I, Ib = late instars I, III/IV = a mixture of instars III and very early instars IV);

Unit = experimental unit (a = small plastic tray (5.2 x 5.2 x 2.4 cm, b = large plastic tray (10.8 x 5.2 x 2.4 cm);

Substrate = amount (approximate wet weight in g) and kind of substrate used (pool 1/pool 3 = sterilized (boiled) mud originating from pool 1/pool 3;

Medium = hygroscopic medium (silicate = silicate granulate; 50 = 50 % KOH; 5 = 5 % KOH). If more than one hygroscopic medium is listed, different runs were carried out (see text.);

Stock = initial stock of larvae per experimental unit (total number of larvae used in the experiment);

Days = maximum duration of the experiment (one tray per species, hygroscopic medium and instar was inundated after 3, 6, 12, 18, 24, 30, 60, 90 and 180 days (see text)). If more than one number is given, the different numbers show the maximum duration of the different runs with different hygroscopic media (see above);

Humidity = method by which the water content at the end of the experiment was determined (see text).

The experiments were carried out in an air-conditioned breeding room (20.5 °C LD).

Preliminary experiments had shown that the egg masses were not drought tolerant. The very short-lived pupal stage (see Table 43 p 147) was also excluded from further analysis. Experiments were therefore only carried out on larvae. Table 8 provides an overview of the species and instars tested for drought tolerance and of the experimental conditions applied. *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* were already known to be drought tolerant aestivators (DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996) and the experiment was focused on these three species. As representative of non-drought tolerant species, *Chironomus dorsalis*- and *Chironomus plumosus*-aggregate were included in the analysis. The two latter species had been investigated less intensively in a pilot experiment.

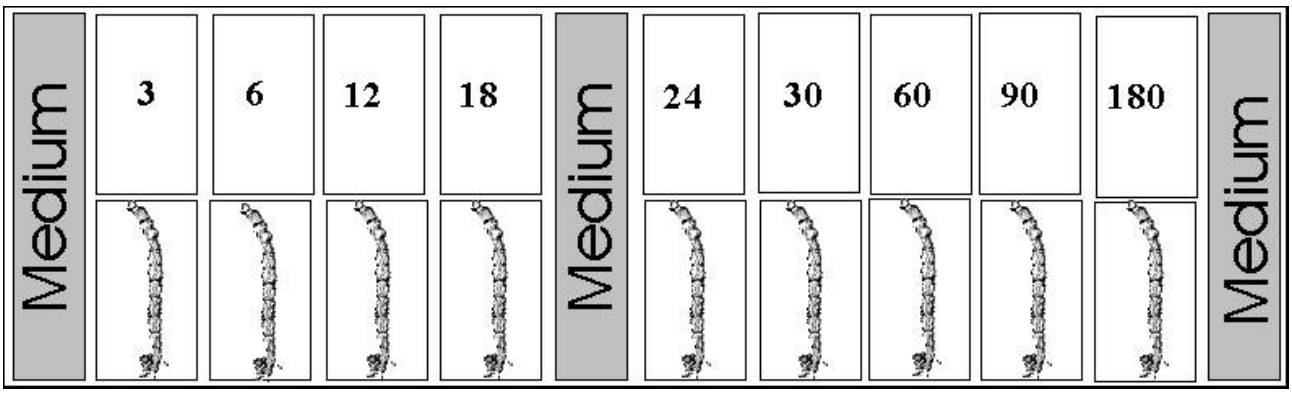

Figure 6: Arrangement of larval (bottom) and mud trays (top) in an experimental box. Hygroscopic medium = (a) silicate granulate; (b) 50 % KOH; (c) 5 % KOH. Each medium was used in a different experimental box (= run) resulting in drying processes of different lengths and intensities. The numbers show the duration of the drought periods (days).

Except in *Limnophyes asquamatus* (see end of this section), it was generally intended to investigate the degree of drought tolerance for each instar separately. Instars I were usually newly hatched when introduced into the experimental units (the female of *Chironomus plumosus*-aggregate was collected on site 4 (see Table 7) on August 10, 1997, for collection and origin of the egg masses of the other species see section 3.3.2.1.). 'Instars II' were reared from instars I which had been transferred into crystallizing dishes (section 3.3.2.2.) with only a little amount of sterilized mud in order to facilitate the detection of the larvae. *Chironomus dorsalis* and *Polypedilum tritum* 'instars II' actually turned out to be late instars I (spot checks of 30 larvae per instar and species were preserved in 70 % ethanol and later determined to the instar using the width of head capsules, see sections 3.4., 4.3.1.2.2. and 4.3.2.3.). 'Instars III' and instars IV were directly taken from (a) the standard breeding units (*Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* (see sections 3.3.1.1. and 3.3.1.2.); (b) from a glass aquarium (29 x 19 x 19 cm, filled with 2 cm of sterilized mud from pool 1, water to a level of 5 cm and aerated by two air-stones) to which the 'instars II' of one egg mass were added and raised up to instars III and IV (*Chironomus plumosus*-aggregate); and (c) from plastic aquaria (*Chironomus dorsalis*, see section 3.3.2.2.), to which the 'instars II' of one egg mass were added and raised up to instars III and IV. 'Instars III' of *Chironomus dorsalis* and of the *Chironomus plumosus*-aggregate turned out to be a mixture of instars III and very early instars IV.

Two different plastic trays filled with sterilized mud from pool 1 or 3 (Table 8) and tap water were used as experimental units. During the following five days, the water was replaced every day and on the sixth day the trays (larval trays) were stocked with larvae (number of larvae per larval tray see Table 8). The larvae had one day to settle before the water was removed with a pipette. The same number of trays was treated in the same manner but remained without larvae to control humidity (mud trays). After removal of the water, the trays were left uncovered one more day in the air-conditioned breeding room (20.5 °C LD) so that the remaining water film could evaporate. Then, for each instar, groups of at most 9 (if the latest larval tray was flooded after 180 days) larval and mud trays were transferred into closed experimental boxes (Figure 6) with different hygroscopic

media (Table 8) (beginning of the experiment). The different hygroscopic media resulted in drying processes of different lengths and intensities. Each hygroscopic media therefore represents a different run. After 3, 6, 12, 18, 24, 30, 60, 90 and 180 days (maximum length of the experiments for each species and instar stand in Table 8), for each species, instar and hygroscopic medium one larval- and one corresponding mud tray was taken from an experimental box. The larval tray was flooded and the survival of larvae determined. Larval survival was assessed in three different ways:

1. Because of their small size and the difficulty to find them the instars I and II were reared at least up to the instar IV (the number of larvae, pupae and adults was counted, when the first adult(s) had emerged). For these rearings, the complete content of a larval tray was transferred into a crystallizing dish and then reared as explained in section 3.3.2.2..
2. The instars III and IV were directly counted one day after flooding by subsequently transferring parts of the substrate into water-filled Petri dishes, which were then inspected with a dissecting microscope (3.6-98 fold amplification) and tweezers.
3. The larvae of *Limnophyes asquamatus* were all raised up to imagoes. For these rearings, the complete content of a larval tray was transferred into a crystallizing dish and then reared as explained in section 3.3.2.2. for *Paralimnophyes hydrophilus*. The vessels were inspected once a day and the adults immediately preserved in 70 % ethanol.

The soil water content of the mud trays was given as the percentage water of the mud weight ([(mud weight at the end of drought period – dry weight of mud)/mud weight at the end of drought period] x 100) and determined by weighing to the nearest 1 µg. The larval- and corresponding mud trays did not dry up identically. The water content of the mud in the larval trays at the end of the drought period was therefore only subdivided into five classes of humidity (class 1: 0 – 19.9%, class 2: 20 – 39.9%, class 3: 40 – 59.9%, class 4: 60 – 79.9%, class 5: 80 – 90%). In *Paralimnophyes hydrophilus*, *Chironomus dorsalis*, *Chironomus plumosus* and *Polypedilum tritum*, the larval tray's water content was not directly determined, as the sterilized soft wet mud of pool 1 greatly changed its consistency once it was oven-dried. If re-wetted the mud remained hard as corn flakes. However, the intention was to replicate natural conditions as closely as possible, and as tubes are known to be essential to the larvae's ability to withstand drought periods (e.g. JONES 1975), I chose to determine indirectly the mud's water content at the end of the drought period.

The experiment on drought tolerance in *Limnophyes asquamatus* began one year later. The previous experiments had shown that the larvae did not survive extreme desiccation and that there were no great differences between the instars. It was additionally observed that the substrate of pool 3 did not greatly change its consistency when oven-dried and subsequently re-wetted. Contrasting with what was done for the other species, the larval tray's water content at the end of the drought period was therefore determined directly in *Limnophyes asquamatus.* About 20 g sterilized wet substrate taken from pool 3 was added to each plastic tray and then oven-dried at 50 °C until its weight did not vary anymore. After the substrate had been re-wetted, the procedure was more or less the same

as explained above and the water content (% of mud weight) was determined as previously described for the mud trays. The manner in which *Lymnophyes asquamatus* larvae were handled differed in a further three points from that of the other species: (a) only instars III and IV were used in the experiments (instars III and IV of the other species exhibited the strongest tolerance to drought); (b) only silicate granulate and 50 % KOH were used as hygroscopic media (with 5 % KOH as hygroscopic medium, the drying process was very slow); and (c) the individual trays were partly covered with lids after irregularly periods of time so as to prevent a too strong desiccation of the substrate and to obtain a greater variety of the substrate's water contents at the end of the drought period.

3.4. Species determination, mounting and measurements of morphological parameters

For determination of chironomids, the larvae, pupae and adults were partly mounted on slides as described in PINDER (1983a, 1996 & 1989), and LANGTON 1991 (voucher collection). EUPARAL was always used as the final mountant. The slides were examined with a ZEISS microscope (Photomikroskop III), equipped with phase- and interference contrast. Microscopic measurements were all taken with a LEITZ micrometer with a vernier scale and microscopic drawings were done with a LEITZ drawing mirror. The literature used for determinations, colleagues who had also inspected the material and the deposition of vouchers is listed in the Appendix 3 and in Table 7. Once several slide-mounted specimens of a species had been identified, it was often possible to recognize the species with a dissecting microscope (3.6-98 fold amplification). However, individuals which identification was uncertain, were always slide-mounted in order to determine the species. In many species it was always necessary to examine some of the morphological parameters with the ZEISS microscope. In such cases a more simple dissecting procedure was chosen which depended on the part of body, which was to be studied. Wings, legs or antennae were removed from the body, temporarily transferred to a drop of glycerine or EUPARAL on a slide and finally covered by a cover slip. If necessary, the abdomen or thorax was cleared in hot 10 % KOH (1-2 min), transferred into glacial acetic acid (~5 min) and finally in 100 % ethanol (~10 min), before being mounted on slides using glycerine or EUPARAL as mountant. If glycerine was used, the specimen or part of its body was finally put back into the alcohol vial (70 % ethanol). In many cases the whole specimen was macerated as previously described and mounted laterally, singly or in groups, on slides (e.g. all females of *Limnophyes asquamatus* if not mounted as described in PINDER 1989).

In the colonizing experiment the mosquitoes were determined using the keys compiled by MOHRIG (1969) and CRANSTON et al. (1987).

Body size parameters were measured to the nearest 0.2-0.001 mm, depending on the magnification used and the object's size. Larval body length was measured from postoccipital margin of head to procerci. Larval head length was measured from the anterior margin of the frontoclypeus to its postoccipital margin. Head width was taken at the head's maximum breadth. For measurements, the

larvae were first dehydrated in 98 % ethanol. Then, to prevent shrivelling, the larvae were first transferred into a solution of EUPARAL and 98 % ethanol in equal proportions (~10 min), before being embedded in pure EUPARAL. The larvae were always straightened as much as possible when mounted on slides (preferably dorsal view, in most cases the head was separated from remainder of body and covered by a separate cover slip). For body size measurements, the adults were either mounted whole on slides or not mounted at all. Individuals that were mounted were first dehydrated in 98 % ethanol before being straightened and embedded in EUPARAL. The adult total length was measured from anterior margin of thorax to posterior margin of gonocoxites (males) or cerci (females). The adult thorax length was measured from anterior margin of thorax to posterior margin of postnotom. Wing length was measured from arculus to apex and wing width at the wing's maximum breadth. As the adults, pupae were either mounted on slides or left unmounted for size measurements. The pupae's total length was measured from the anterior margin of the cephalothorax to the apex of anal lobe. All further measurements of morphological parameters were done according to SÆTHER (1980).

3.5. Mathematical and statistical analysis

The statistical analysis was done with STATISTICA for Windows 5.1 ('97 edition) and MS EXCEL 2000.

3.5.1. Location and scatter parameters

The *arithmetic mean* ($\bar{x}$), the *median value* ($\tilde{x}$) (see LORENZ 1996) and the *geometric mean* ($\bar{x}_g$) were used as parameters that provide data averages. The geometric mean was only used to provide mean values of larval growth (section 4.4.1.2.2.). In contrast to the arithmetic-, the geometric mean is less strongly influenced by extreme values and therefore better suited to describe relative differences, as is the case in processes of growth. In some cases the average deviation from the arithmetic mean is provided by the *standard diversity* (sd).

The range of data is provided in a *minimum-maximum; mean ($\bar{x}$) standard*, when listed in a table or mentioned in the text. *Box-and-whisker-plots* are always provided as illustrated in Figure 7.

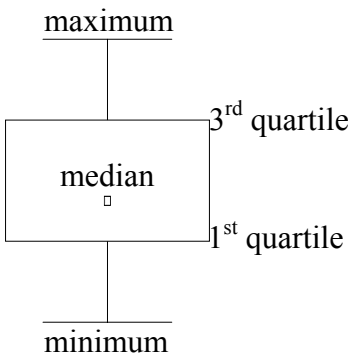

Figure 7: Box-and-whisker-plot.

3.5.2. Pearson's χ^2-test and α-levels

The distributions of nominal and ordinal data in crosstabulation tables were tested with a PEARSON's χ^2.test (section 4.3.1.1.5.). The null hypothesis (H_0) assumes that the variables are independent from one another. If $p < \alpha = 0.05$, H_0 has to be rejected in favour to the alternative hypotheses (H_1: there is a contingency between the variables). The *α-levels* used in the present study can be taken from Table 9.

Table 9: Levels of significance

α-level	Probability (p)
$\alpha > 0.05$	not significant
$\alpha = 0.05$	significant
$\alpha = 0.01$	highly significant
$\alpha = 0.001$	extremely significant

3.5.3. Test for normality

Many statistical tests are based on the assumption that the data are normally distributed. In the present study, the data's distribution was tested for normality with a SHAPIRO-WILK'S W-test. Due to it's high selectivity, this test has to be preferred to many others (SHAPIRO et al. 1968). If n is high (e.g. > 50), it is sufficient to refer to normal probability plots. Due to the central limit theorem (LORENZ 1996), the data can be considered to fulfil normality, if deviations from the expected line of a normal probability plot are not grave.

3.5.4. 95 % confidence limits

In the present study 95 % limits for normal distributions were sometimes calculated, if the SHAPIRO-WILK W-test showed no significant result (low n) or normal probability plots showed no strong deviations from normality and n was quite high (n > 20).

3.5.5. Analysis for differences

Table 10 refers to the tests applied for detecting differences in the location of values of a dependent variable on an ordinal- or interval scale (e.g. body size) between two or more groups of an independent variable (grouping variable) on a nominal scale (e.g. sex, species etc.).

3.5.6. Correlations and regressions

Six different regression models were used in the present study:

(a) Linear regressions: $y = a + bx$ (a = intercept; b = slope). E.g. linear regression in section 4.4.1.2.2.: $BL = K' * t + a$ (BL = body length of larva, K´ = growth coefficient, a = hatching size, t = days after hatching);

(b) Quasi-linear regressions: $\log D = -p * \log T + \log a$ (= log-linearized alternative of the potential regression in point d);

(c) Double linear regressions: $S = a * t + b * h + c$ (S = survival, a, b and c = parameters, h = hu-

Table 10: Statistical tests applied for group differences.

Test	Preconditions
(a) Independent variable (grouping variable) subdivided into two groups	
MANN-WHITNEY U-test for independent samples	- dependent variable values (grouping variable) measured on an ordinal or interval scale. The shape of distribution of both data groups should be equal. If the data were on interval scales, this test was used when normality was rejected; - a significant result refers to two different populations.
t-test for independent samples	- dependent variable values (grouping variable) measured on an interval scale and do not reject normality; interpretations as the MANN-WHITNEY U-test.
(b) Independent variable (grouping variable) subdivided into more than two groups	
KRUSKAL-WALLIS ANOVA and subsequent MANN-WHITNEY U-tests	- preconditions apply to the MANN-WHITNEY U-test. - a significant result of the KRUSKAL-WALLIS ANOVA refers to at least one different population within the groups compared. - subsequent comparisons with MANN-WHITNEY U-tests show which groups are significantly different. For multiple comparisons, the p-values of the MANN-WHITNEY U-test must be adjusted according to the standard BONFERRONI-technique: $p_{new} = \alpha * k$; k = a (a-1)/2 (a = number of samples) (HORN & VOLLANDT 1995).
One-way analysis of variance (one-way ANOVA)	- preconditions are an interval scale, homoscedasticity and normality. Homoscedasticity was tested with a LEVENE'S test (if $p < 0.05 \rightarrow$ homoscedasticity has to be rejected), normality as described in section 3.5.3.. Deviations from normality are not grave and according to the central limit theorem they can be neglected if n is high; - a significant result refers to at least one different population within the groups compared. - differences between the groups were tested with a TUKEY'S honest significant difference test for unequal n, or if n of groups were equal by the NEWMAN-KEYLS-test (HORN & VOLLANDT 1995, STATSOFT 1997).

midity of soil (%)) (see section 4.4.1.6.2.). In this kind of regression one variable is dependent on two independent variables;

(d) Potential regressions: $D = a * T^{-p}$ (D = duration of development (days), a and p are parameters, T = mean ambient temperature) (see section 4.4.1.2.4.). This model was preferred according the results obtained by ELLIOT et al. (1987) (power-law equation);

(e) Exponential regressions sensu RIEDE (1993): $BL = e^{(p*t + bo)} + c$; (BL = body length of larvae, p = specific growth rate, $b_0 + c$ = parameters, t = days after hatching, see section 4.4.1.2.2.);

(f) Logistic regressions sensu RIEDE (1993): $BL = \frac{K}{\left(D * e^{(-p*t)} + 1\right)}$ (BL = body length of larvae, K = capacity, D = parameter, p = specific growth rate, t = time after hatching, see section 4.4.1.2.2.).

Linear regressions and quasi-linear regressions were fitted by the least-squares method, the other regressions by non-linear least-squares, using an iterative method to minimize the residual sum of squares. The QUASI-NEWTON method was used as algorithm. The goodness of fit of a regression

(percentage of explained variance) was always estimated by the variance ratio

$$R^2 = F = \frac{\text{regression sum of squares}}{\text{total sum of squares}} * 100,$$

which is equivalent to r^2, the *coefficient of determination* (see below). The significance of regression coefficient (slope) (linear-, quasi-linear- and double-linear models) against zero was tested using analysis of variance (null hypothesis rejected if $F_{obs} \geq F_{1-\alpha}$; $\alpha = 0.05$), F-value, degrees of freedom (df) and p-value are provided.

The following three correlation coefficients tested whether or not there was a correlation between two sets of data:

(a) PEARSON'S product-moment correlation (r) was applied if both variables did not reject normality. The r-value was assessed by STUDENT'S distribution (t-value and p-value);

(b) SPEARMAN'S rank order correlations (ρ or r_s) was used for correlations if one or both of the variables tested did reject normality or if they were on an ordinal scale. The ρ-value was assessed by a t-statistics as in the PEARSON'S r;

(c) The GOODMAN-KRUSKAL'S-γ was preferred to the SPEARMAN'S- ρ if the data contained several ties. As in PEARSON'S-r or SPEARMAN'S-ρ it is: $-1 \leq \gamma \leq +1$. GOODMAN-KRUSKAL'S-γ was assessed by a z-statistics with corresponding p-value.

3.5.7. Cluster analysis

The faunistical data (section 4.2.) were also investigated with joining cluster analyses. The Euclidean distances were used as the distance measure and the method sensu WARD (1963) as the amalgamation rule. WARD'S method differs from the other amalgamation rules available, in that it uses an analysis of variance for the calculation of clusters. For the construction of two hypothetical clusters, the method minimizes the sum of squares. This method is considered to be very efficient but tends to construct clusters of small size.

3.5.8. Equations for growth rates, rates of development, thermal constant and Q_{10}-value

Larval growth of some Chironomidae can be described by a linear or exponential model function (section 4.4.1.2.2.). In the latter case, the *growth rate* can be computed from the following equation (sensu OSTROVSKY 1995, modified):

$$Gr = \frac{\left(\ln\left(BL_{t2}\right) - \ln\left(BL_{t1}\right)\right)}{D}$$

(Gr = growth rate, BL = geometric mean of body length, t = days after hatching, D = days between samplings).

The growth rates calculated for a treatment were summarized as *mean growth rate* (mGr) for the whole period of larval growth:

$$mGr = \frac{Gr}{N}$$ (N = number of single growth rates determined).

Rates of development (Rd) were calculated by following the equation given by CLEMENTS (1992):

$$Rd = \frac{1}{\text{Duration of total development (days)}}$$

For poikilothermous animals like insects, the heat gain necessary to complete development is more or less the same over the central span in temperature that lays between the upper lethal limits and the lower developmental threshold (CLEMENTS 1992). The product of developmental period and temperature above the lower threshold is called *thermal constant* with units called *degree-days*. The formula is the following:

$$\mathbf{k = t * (T - c)}$$

(k = thermal constant, t = duration of total development (days), T = mean ambient temperature, c = temperature of zero growth).

The thermal constants distinctly differ from the normal values at temperatures towards the upper lethal limit, the lower threshold of temperature and/or cue temperatures for dormancy.

The Q_{10}-value is a standardized measure, which allows a comparison of VAN'T HOFF's rule (reaction-rate/temperature rule) for any gradients of temperature and has the following equation:

$$Q_{10} = \left(\frac{D_{t_1}}{D_{t_2}} \right)^{\frac{10}{(t_2 - t_1)}}$$

(D = duration of development; t_1/t_2 = lower/upper rearing temperature). VAN'T HOFF's rule states that within the central span in temperature, the time of development doubles to quadruples if temperature is lowered by 10 °C (LAMPERT & SOMMER 1999). Strong deviations from Q_{10}-values between 1.5-4 indicate that there must be dormancies, sublethal temperatures or other deviations from normal development. Q_{10}-values < 1 indicate that the time of development is longer at the upper temperature, Q_{10}-values = 1 indicate that the time of development at both temperatures are identical and Q_{10}-values > 1 finally show that the time of development is shorter at the upper temperature.

4. Results

4.1. The Habitat

4.1.1. Three natural pools of the Lahnberge mountain range

4.1.1.1. Location

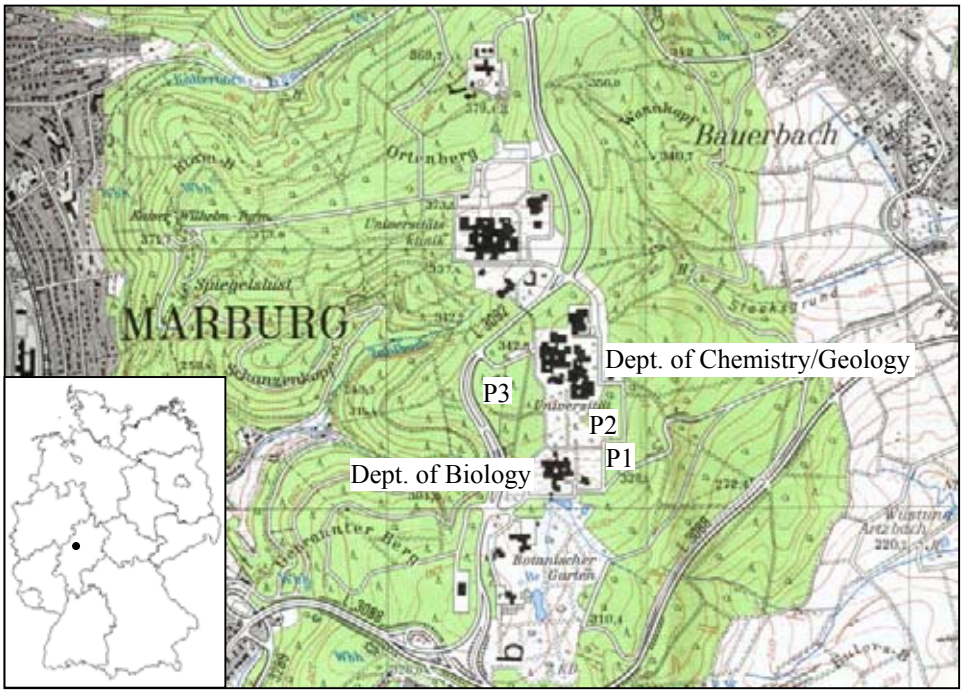

Figure 8: Location of Marburg (inset map of Germany with state borders) and the temporary pools investigated (P1-P3 = pool 1-pool 3) (Topographic map 1:25 000, 5118 Marburg).

In the following text, the three temporary pools investigated will be referred as pools 1, 2 and 3 (P1, P2, P3). These pools lie at an altitude of 350 m above sea-level in the Lahnberge mountain range, east of Marburg (administrative district Marburg-Biedenkopf, Hesse, Germany) (Figure 8). The pools' geographical coordinates are as follows: 50° 48′ 30′′ N, 8° 48′ 54′′ E (pool 1), 50° 48′ 36′′ N, 8° 48′ 54′′ E (pool 2) and 50° 48′ 36′′ N, 8° 48′ 30′′ E (pool 3). The 'Lahnberge' belongs to the area of Bunter Sandstone (Upper Hesse). This region's predominant geological subsoils are Middle Bunter Sandstone, sandy loam and clay (BLUME 1949). Damp soils are therefore a characteristic feature of the study area. The annual temperature and precipitation in Marburg averages 8.1 °C and 637 mm, respectively (WAGNER 1961).

4.1.1.2. Surroundings and vegetation

4.1.1.2.1. Pool 1

Pool 1 (Figure 9) lay for one part within a meadow dominated by *Calamagrostis epigeios* and *Lupinus polyphyllus* ('helophyte zone', see below (a)) and for the other part within a thicket area that mainly consisted of *Salix caprea* ('grass zone', see below (b)).

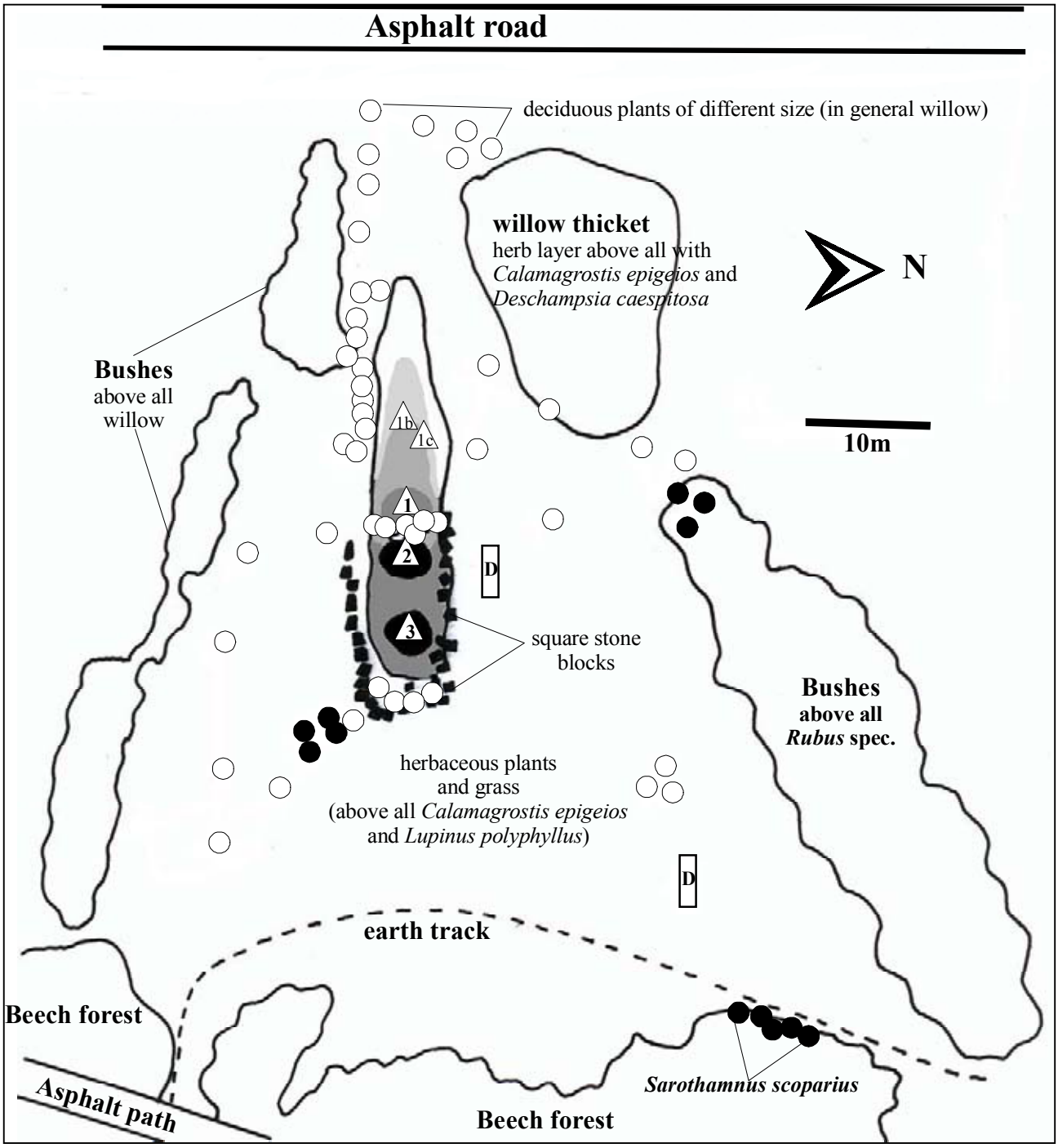

Figure 9: Sketch of pool 1 with surroundings. The numbered triangles symbolize the emergence traps within the pool and the rectangles the plastic containers for the collection of the egg masses of *Chironomus dorsalis* (D). The different shadings within the pool characterize different situations of water filling: the white area was only infrequently and temporarily flooded, whereas water remained the longest at the black sites; colourations in-between reflect intermediate hydrological situations.

The pool itself could be accordingly subdivided into two different parts:

(a) The 'helophyte zone' was the part of the pool to the east of the willow bushes growing within the pool area in which emergence traps 2 and 3 had been placed (Figures 9, 10b, 10d). This area dried up later than the 'grass zone' (see b) and was only little shaded by the surrounding vegetation. Helophytes were dominant, above all *Carex* sp., *Eleocharis* sp., *Glyceria fluitans*, *Juncus*

Figure 10: Photographs of pool 1: (a) the 'grass zone' and (b) the 'helophyte zone' in spring (both photographs taken from the willow bushes growing within the pool); (c) grass zone in winter and (d) the helophyte zone around emergence trap 2 in spring.

effusus, *Sparganium errectum* and *Typha latifolia*. The only abundant hydrophyte was *Lemna minor*. Non-helophytes were not frequent and only present at the edges of the pool area (*Calamagrostis epigeios*, *Cirsium palustre*, *Deschampsia caespitosa*, *Epilobium adenocaulon*, *Galium aparine*, *Galium palustre*, *Holcus lanatus*, *Lotus corniculatus*, *Lupinus polyphyllus*, *Lycopus europaeus*, *Poa annua*, *Poa nemoralis*, *Ranunculus flammula*, *Ranunculus repens*, *Stellaria uliginosa*, *Taraxacum officinale* and *Urtica dioica*.).

(b) Grasses were dominant in the area referred to as the 'grass zone'. Emergence traps 1, 1b, 1c were placed in this area that was usually only shortly inundated. The 'grass zone' lies to the west of willow bushes that grow within the pool area (Figures 9, 10a and 10c). Sourrounding shaded the pool in this area and *Alopecurus geniculatus* was one of the dominant plants of the herb layer. *Calamagrostis epigeios*, *Carex*. sp. *Cirsium palustre*, *Deschampsia caespitosa*, *Epilobium adenocaulon*, *Epilobium angustifolium, Glyceria fluitans*, *Holcus lanatus*, *Juncus effusus*, *Lycopus europaeus* and *Poa nemoralis* were other frequent plants in the herb layer. On the other hand *Cerastium* sp., *Dryopteris filix-mas*, *Festuca* spec., *Galium uliginosa*, *Lotus corniculatus*, *Myosotis arvensis*, *Poa annua*, *Ranunculus repens*, *Taraxacum officinale*, *Tussilago farfara*, *Urtica dioica*, *Vicia* cf. *sepium* and *Vicia tetrasperma* were present but not frequent.

4.1.1.2.2. Pool 2

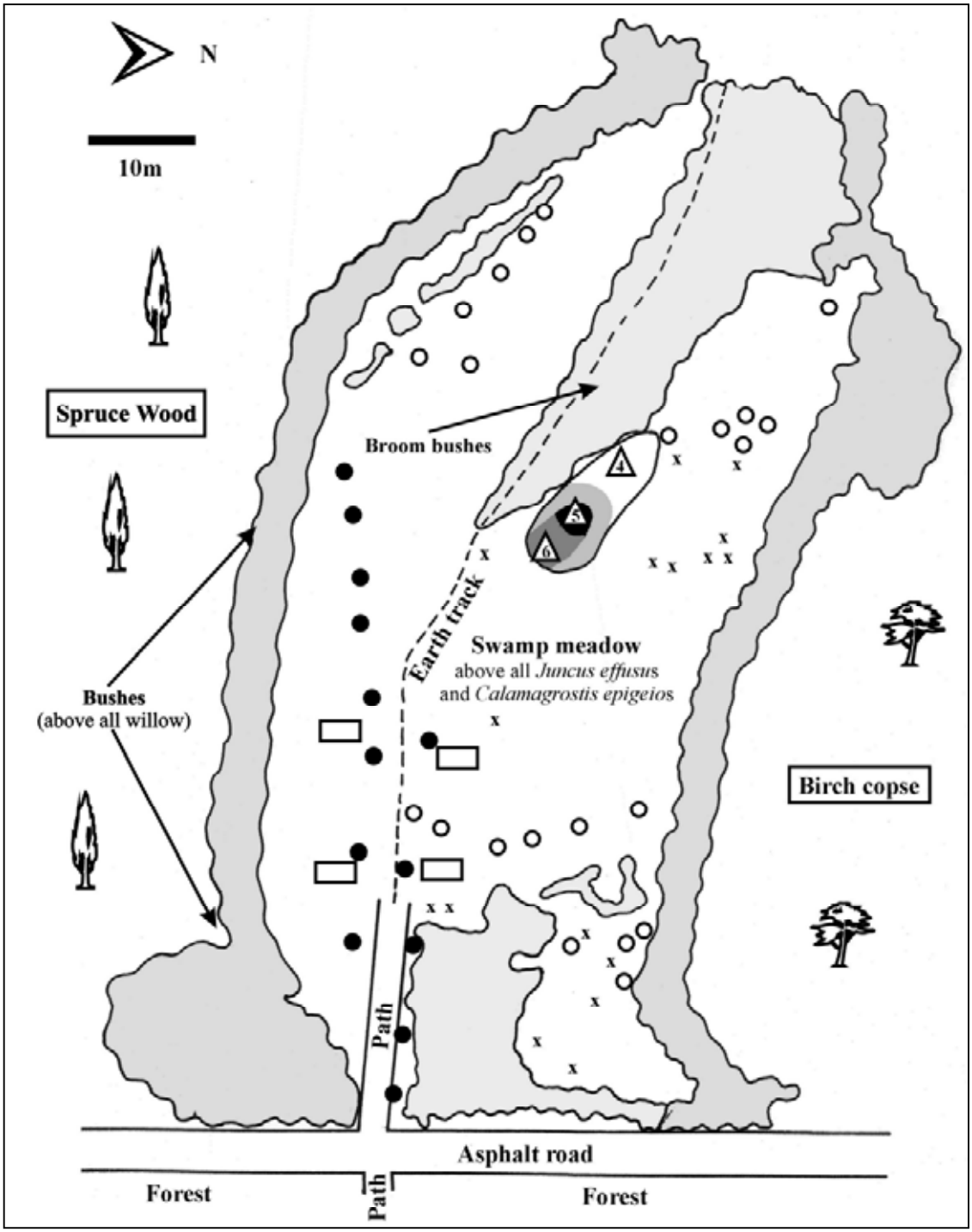

Figure 11: Sketch of pool 2 and surroundings. Signs: △ = emergence taps within the pool, ▯ = wooden bee hives, ● = planted young oak trees, ○ = single young willows, x = single brooms. The different shadings within the pool characterize different situations of water filling: white areas only temporary flooded and black symbolizing the areas drying up last (semipermanent).

Pool 2 (Figure 11) was located in a swamp meadow dominated by *Calamagrostis epigeios* and *Juncus effusus*. The pool itself was densely covered by the helophytes *Juncus effusus* and *Typha latifolia*, which in combination with a locally dense cover of *Lemna minor* resulted in a relatively strong

shading of the water surface (Figure 12). Restricted stocks of *Callitriche* sp. and *Potamogeton berchtholdii* and single specimens of *Potamogeton natans* were also present.

Figure 12: Photographs of pool 2 during spring: (a) overview and (b) around emergence traps 5 and 6.

4.1.1.2.3. Pool 3

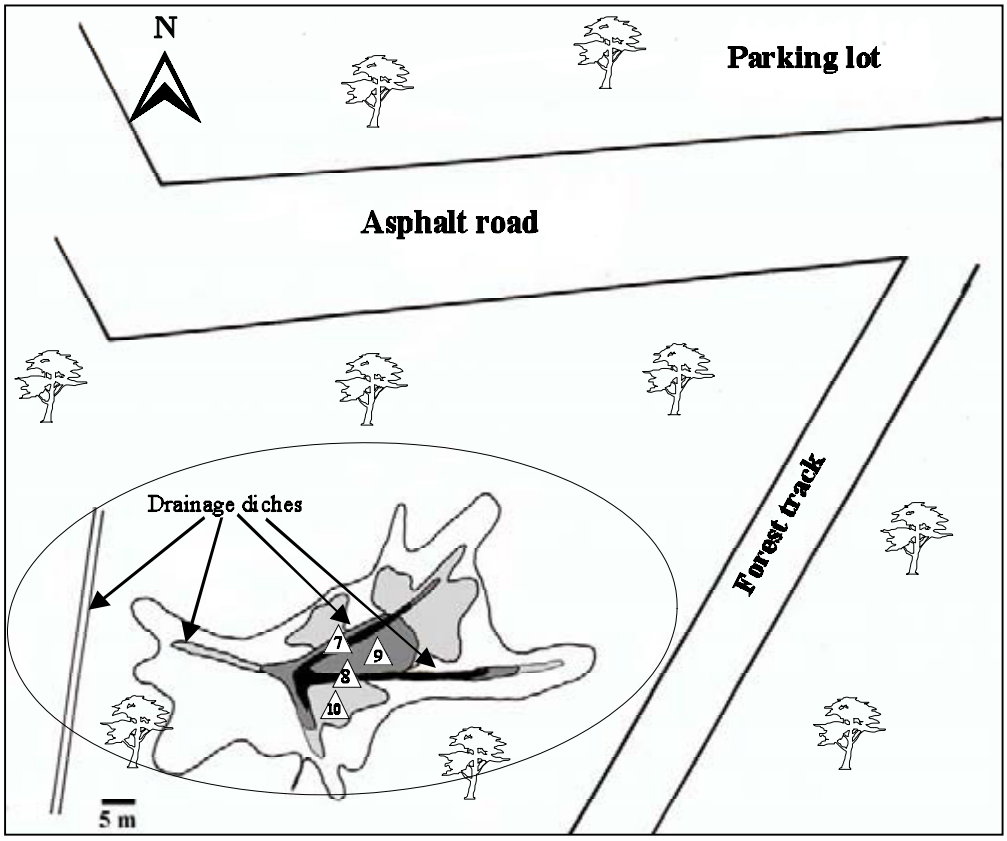

Figure 13: Sketch of pool 3 and surroundings. The ellipse indicates the area of the swamp forest which is potentially flooded. The pool is outlined at different water levels: black = water restricted to the central drainage ditches; dark grey = limited flooding; light grey and white reflect two different situations of extended flooding. The emergence traps are symbolized by the numbered triangles.

Pool 3 was located in a swamp forest which was dominated by *Betula pendula* (Figures 13, 14). Other representatives of the bush-tree canopy were *Frangula alnus*, *Larix dicidua*, *Picea abies*, *Pinus sylvestris*, *Quercus petrea*, *Rubus idaeus*, *Sambucus nigra* and *Sorbus aucuparia*. The swamp forest had been drained by several ditches, two of which join in the central part of pool 3 (dark grey

Figure 14: Photographs of pool 3: (a) and (b) show two different aspects of the flooded swamp forest in February 2000 ('extensive flooding' see section 4.1.1.4.3.); (c) - (f) show the central part of the pool: (c) during 'extensive flooding' in January 2000; (d) in spring 1994; (e) emergence traps 7 (left) and 8 (right) during 'restricted flooding' (see section 4.1.1.4.3) in spring 1998; and (f) terrestrial phase in October 1998.

zone in Figure 13 with emergence traps 7, 8 and 9). This central part (to the exception of the drainage ditches) was more or less free from wooden plants and mainly covered by large *Carex* sp. and *Juncus effusus* (also present: *Agrostis canina*, *Spagnum* sp. and *Stellaria uliginosa*). Different aspects of the central part of pool 3 are shown in Figure 14 (c-f). Large parts of the swamp forest were flooded depending on rainfall intensity in winter and spring (Figure 14a, b). The ground of the swamp forest was mainly covered by leaf litter and a mostly sparse vegetation consisting of *Carex* sp., *Dicranum* sp., *Dryopterix filix-mas*, *Festuca* sp., *Polytrichum formosum*, *Sphagnum* sp. and *Vaccinium myrtillus*.

4.1.1.3. Physicochemical factors

4.1.1.3.1. PO_4^{3-}-P, NH_4^+-N, NO_3^--N, Ca^{2+}, pH, conductivity and O_2

Table 11: Physicochemical characterization of the pools.

Parameter	Pool 1		Pool 2	Pool 3	
	Single (A) + (R)	Day runs (T)	Single (A) + (R)	Single (A) + (R)	Day runs + Single (T)
PO_4^{3-}-P (mg/l)	LO (n = 4) 0.25-1 (n = 13) 2-10 (n = 3)	May 27-28, 1999: 2-6; 4.2 (n = 5)	LO (n = 15) 0.25-1 (n = 1)	LO (n = 7)	0.001-0.112; 0.041 (n = 8)^H
NH_4^+-N (mg/l)	LO (n = 10) 0.1-1.0 (n = 6) 1.4-3.8 (n = 4)	May 27-28, 1999: 0.128-0.406; 0.204 (n = 6)	LO (n = 14) 0.1-1 (n = 2)	LO (n = 3) 0.1-1 (n = 4)	0.041-1.209; 0.384 (n = 8)^H
NO_3^--N (mg/l)	LO (n = 17) 1 (n = 3)	May 27-28, 1999: 0.043-0.078; 0.057 (n = 6)	LO (n = 15) 1 (n = 1)	LO (n = 7)	0.020-0.454; 0.151 (n = 8)^H
Ca^{2+} (mg/l)	7.9-23.8; 14.0 (n = 20)		15.7-58.6; 33.3 (n = 16)	6.2-19.2;15.3 (n = 8)	
pH	5.3-7.7;6.7 mg/l (n = 47)	June 4-6, 1997: 6.2-8.1; 7.7 (n = 50) May 27-28, 1999: 6.2.-6.6; 6.3 (n = 143)	4.5-7.9;6.9 (n = 37)	5.0-6.7;6.0 (n = 25)	Feb. 21-22, 2000: 4.1-5.0; 4.6 (n = 50) Feb. 28-Mar 2, 2000: 5.0-5.6;5.2 (n = 150) May 13-15, 2000: 5.1-5.7; 5.6 (n = 72) 4.7-6.5; 5.7 (n = 9)^H
Conductivity (µS/cm)	76-271; 145	June 4-5, 1997: 202-288; 232 (n = 50) May 27-28, 1999: 152-204; 167 (n = 143)	302-1620; 628 (n = 37)	80-417; 237 (n = 24)	Feb. 28-Mar 2, 2000: 254-320; 289 (n = 150) May 13-15, 2000: 244-290; 268 (n = 72) 231-515; 306 (n = 9)^H
O_2 (mg/l)		June 4-5, 1997: 0.1-1.7; 1.0 (n = 50) May 27-28, 1999: 0.0-0.9; 0.15 (n = 143)			Feb. 21-22, 2000: 1.0-4.6; 3.0 (n = 50) Feb. 28-Mar 2, 2000: not detectable (n = 150) May 13-15, 2000: 0.2-0.8; 0.5 (n = 82)
O_2 (%)		June 4-5, 1997: 1-19; 11 (n = 50) May 27-28, 1999: 0-9; 2 (n = 143)			Feb. 21-22, 2000: 8-35; 23 (n = 50) Feb. 28-Mar 2, 2000: not detectable (n = 150) May 13-15, 2000: 2-9; 4 (n = 82)

Abbreviations and explanations:

- The parameters were measured in single measurements (= **single**) throughout the study (section 3.1.1.4.) or during **day runs** (section 3.1.1.5.);

(A) + (R) = PO_4^--P, NH_4^+-N, NO_3^--N, and Ca^{2+} were measured with REFLECTOQUANT^R and AQUAMERCK tests (section 3.1.1.4.);

(T) = PO_4^--P, NH_4^+-N and NO_3^--N were measured with an TECHNICON autoanalyser (section 3.1.1.5.);

LO = values below the absolute limit of detection (section 3.1.1.4.);

^{H} = single measurements collected by HOOF (2001) in 2000.

The contents of **phosphate** (PO_4^{3-}-P), **ammonium** (NH_4^+-N) and **nitrate** (NO_3^--N) were higher in pool 1 than in pool 2 and 3 (Table 11). Phosphate, ammonium and nitrate could not be detected in most measurements of pools 2 and 3 using REFLECTOQUANT^R and/or AQUAMERCK. During a day run on May 27-28 (pool 1) and throughout a Master's thesis in 2000 (HOOF 2001) (pool 3) phosphate, ammonium and nitrate were measured with the TECHNICON-Autoanalyzer (section 3.1.1.5.). These values are also provided in Table 11. Especially high values were measured in pool 1 in 1996, a year when wild boars often rooted within the pool area. The mean value of **calcium** (Ca^{2+})

present in pool 2 (33.3 mg/l) was about twice as high as in pool 1 (14.0 mg/l) and pool 3 (15.3 mg/l), respectively. The **pH-values** show that the water of pool 3 was clearly acidic and almost neutral in pools 1 and 2. The mean values of **conductivity -** an unspecific measure for the total content of ions – show the ratios between pool 1 and pool 2 and pool 1 and pool 3 to be 1:4.3 and 1:2.1, respectively. The total contents of ions were therefore the lowest in pool 1 and the highest in pool 2. Correlations of conductivity with water depth (for raw data see the Appendix 1) were significant for pools 1 and 2 (pool 1: $r = -0.41$, $F = 6.6$, $df = 1.5$, $p = 0.015$, $n = 35$; pool 2: $r = -0.59$, $F = 18.5$, $df = 1.4$, $p < 0.001$, $n = 37$) and not significant for pool 3 ($r = +0.31$, $F = 1.4$, $df = 1.1$, $p = 0.259$, $n = 15$). This indicates that water loss in pools 1 and 2 was strongly influenced by evaporation and probably dominated by seepage in pool 3 (SCHNEIDER & FROST 1996).

Because the **oxygen** (O_2) level is highly variable even within a day-night cycle, single measurements are of low significance. As an indication, this factor was therefore measured in five day runs

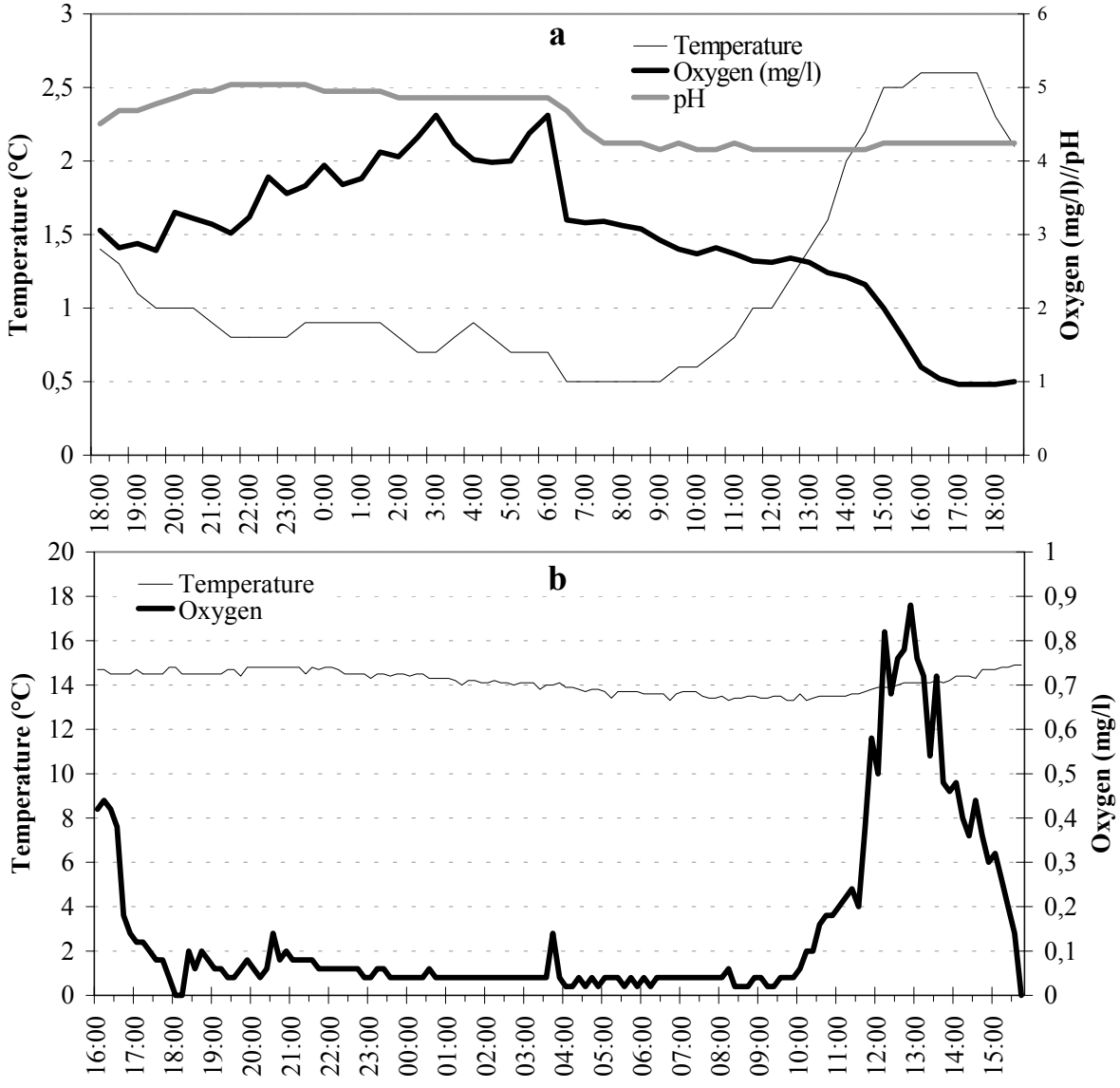

Figure 15: Day runs of oxygen, temperature and pH during (a) winter conditions in pool 3 (February 21-22, 2000); and (b) late spring conditions in pool 1 (May 27-28, 1999).

in the two temporary pools 1 (two runs) and 3 (3 runs) (Table 11). The record intervals were 30 minutes to the exception of the day run on May 27-28, 1999 in pool 1 (record interval 10 minutes). All measurements were taken about 5 cm above the pool's substrate layer near the emergence trap 2 (pool 1) and 7 (pool 3). The water depths during the runs were about 20 cm in pool 1 and 45 cm (21.-22.3. and 28.2.-2.3. 2000) or 16→9 cm (13.-15.5. 2000, remaining puddle just before drought) in pool 3. The highest contents of oxygen (8-35; 23 % of saturation) were measured during a run on February 21-22 (pool 3) with a range of temperatures of 0.5-2.6; 1.2 °C. This day run reflects winter conditions with low temperatures (see section 4.1.1.3.2.) (Figure 15a). No oxygen was detected (temperature range 3.6-7.1; 5.1 °C) during the February 28 - March 3 run and the oxygen levels were extremely low during the May/June runs (e.g. Figure 15b). This results show that low and even depleted oxygen levels are a characteristic feature of the pools investigated.

The ranges of values for all eight physicochemical factors measured show that the abiotic environment of the pools is highly variable, even during the aquatic phase.

4.1.1.3.2. Temperature

The recordings measured by the temperature data loggers on the pools' ground are summarized in Figure 16 (monthly arithmetic means and amplitudes). Seasonal temperature characteristics of the aquatic phases are listed in Table 12. Appendix 2 provides the daily means of water temperatures measured in pools 1-3.

Table 12: Temperature (°C) characteristics of the aquatic phases of pools 1 - 3.

Pool	Period	Minimum	Maximum	Mean (arithmetic)	Degree days*
Pool 1	25.11.1996 - 5.7.1997	-1.0	18.1	5.9	1323
	6.12.1997 - 5.12.1998	0.7	18.1	8.5	3124
	6.12.1998 - 18.7.1999	1.5	18.4	7.4	1608
Pool 2	6.12.1997 - 5.12.1998	1.9	15.6	8.7	3178
Pool 3	25.11.1996 - 15.5.1997	-1	11.7	4.2	728
	6.12.1997 - 17.6.1998	0.7	15.3	6.1	1192

* cumulative daily means of temperature above 0 °C for the given span of time.
See Appendix 2 for daily means of temperature.

To compare temperatures between pools, only readings that were done simultaneously in the three pools (aquatic phases of March 18 - April 30, 1997 and January 1 - May 31, 1998) were considered. The mean temperatures of pool 1 and pool 2 were almost identical but significantly lower in pool 3 (Table 13). The temperature amplitudes were the greatest in pool 1 and the lowest in pool 2 (Table 13).

The results of this section show that:

(a) due to the earlier drought, the mean temperatures during the aquatic phase of pool 3 were about 2°C lower than in pool 1 and 2;

(b) pools 1 and 3 are subjected to a higher risk of freezing down to the pools' ground; and

(c) due to exposure, water depth and later time of drought, pool 1 warms up faster during the

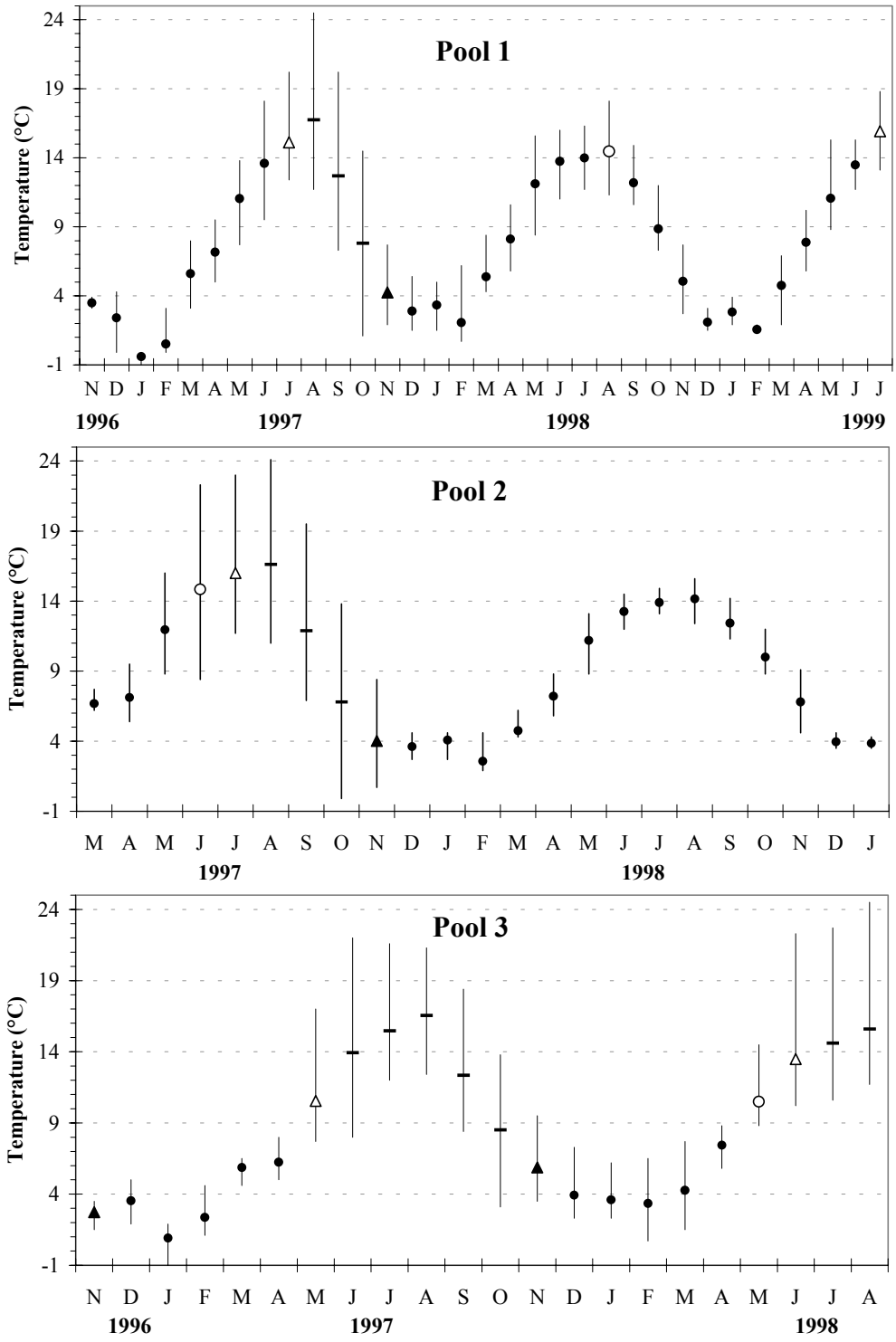

Figure 16: Monthly arithmetic means and amplitudes of temperature (°C) in pools 1-3 during the aquatic phase (black circles), months of drought/filling (open/black triangles) and the terrestrial phase (horizontal bar). An open circle symbolizes an intermediate drying up with subsequent refilling.

aquatic phase (higher maxima and amplitudes).

Measurements of ground temperature taken at one site per pool provide only a simplified picture of the real situation as temperature also varies in space and time following horizontal and vertical gradients. As an indication, the vertical gradients of temperature were measured in four day runs in

Table 13: Comparison of simultaneous recordings of temperature (°C) in pools 1 - 3 from March 18 - April 30, 1997 and January 1 - May 31, 1998.

min-max; mean ± std.	**Pool 1 (°C)**	**Pool 2 (°C)**	**Pool 3 (°C)**
	0.7-15.6; 6.4 ± 3.4	1.9-13.1; 6.2 ± 2.8	0.7-14.5; 5.9 ± 2.8
KRUSKAL-WALLIS-test	**N**	**H**	**p**
	3 x 2319	20.98	< 0.001
MAN-WHITNEY-U-test	**U**	**p**	**p_{corr}***
pool 1↔pool 2	2590927	0.032	0.096
pool 2↔pool 3	257948	0.004	0.012
pool 1↔pool 3	2512968	< 0.001	< 0.001

* adjusted p-value according to the BONFERRONI technique (k = 3) (see section 3.5.5.).

pools 1 and 3. In addition, the horizontal gradient of temperature was measured in pool 1 (Table 14, Figure 17). The results show that:

(a) the arithmetic mean on the ground of a sampling site can be clearly different (in the examples up to 2.7 °C) from those on the subsurface and other sites of the pool;

(b) the vertical stratification of temperature (indirect during winter, direct during the warm season)

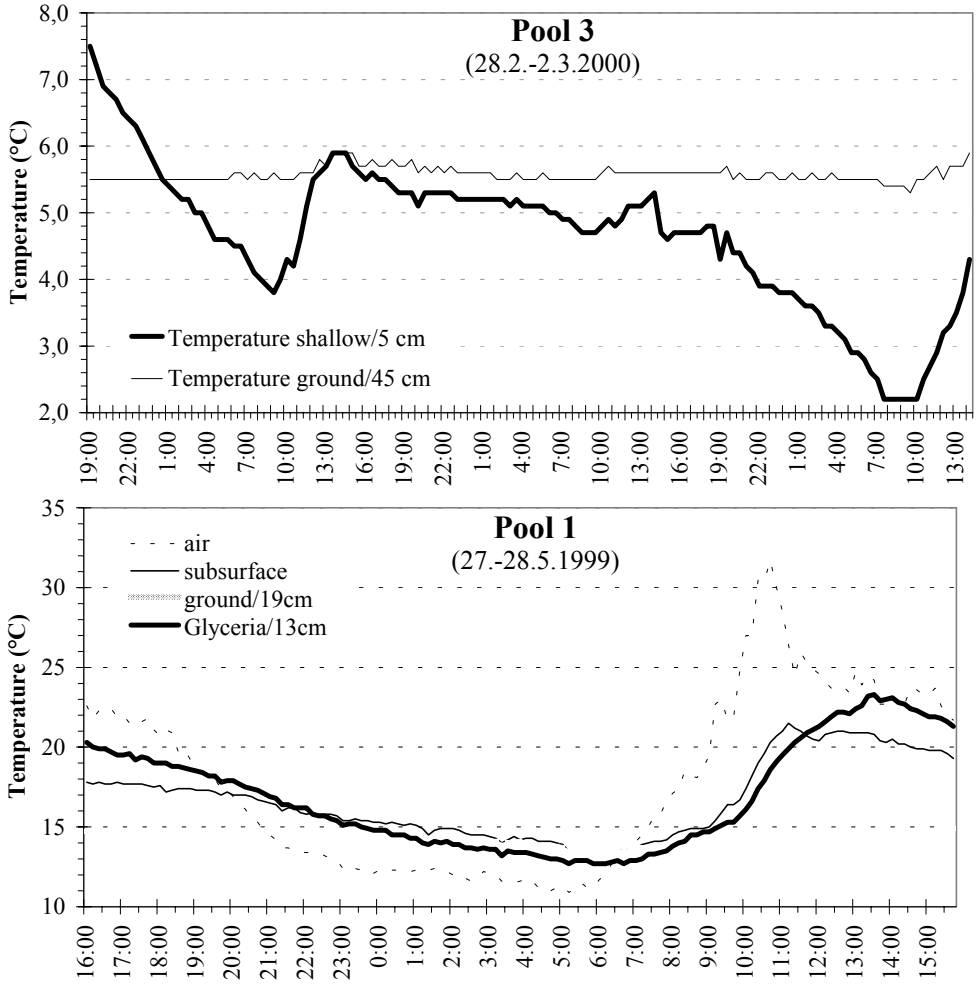

Figure 17: Day runs of temperature during late winter in pool 3 and late spring in pool 1 (labelling see Table 14).

slows down every day at least during the warm season of the year; and

(c) the daily variations of temperature during a warm day/night cycle are already low at a depth of about 20 cm.

Table 14: Summarized results of four day runs of temperature (°C) in pool 1 and 3.

Pool	Sampling period	sampling site	Minimum	Maximum	Mean (arithmetic)	N
3	28.2. - 2.3.2000	shallow/5cm	2.2	7.5	4.6	135
		ground/45cm	5.3	5.9	5.6	135
	13.5. - 15.5.2000	subsurface	11.2	27.0	15.0	77
		ground/16→9cm	11.6	18.1	14.2	82
		air	9.4	33.5	15.4	82
1	4.6. - 5.6.1997	subsurface	10.4	22.0	15.2	50
		middle/9cm	10.5	19.8	15.0	50
		ground/14cm	10.4	17.8	14.5	50
		Glyceria/5cm	8.8	24.3	14.8	50
	27.5. - 28.5.1999	subsurface	13.4	21.5	16.7	143
		ground/19cm	13.3	14.9	14.1	143
		Glyceria/13cm	12.7	23.3	16.8	143
		air	10.9	31.7	17.7	143

Abbreviations:

shallow = measurement taken on the ground of a shallow site near emergence trap 9 (all other measurements taken in pool 3 originate from the ditch near emergence trap 7 (Figures 13, 14 pp 45-46)); **subsurface** = measurement taken 1-2 cm below the water surface; **middle** = measurement taken in the middle of the water column; **ground** = measurement taken from the base of water column; **16→9** = water column shrank from 16 to 9 cm during the period of measurement; **air** = air temperature just above the water surface; ***Glyceria*** = measurement taken on a shallow site about 5 m to the east of site 2 (pool 1) within an area densely grown *by Glyceria fluitans* (all other measurements taken in pool 1 originate from site 2 (Figure 9, 10 pp 42-43)).

4.1.1.4. Water balance and precipitation

4.1.1.4.1. Pool 1

Figure 18 shows the duration of total drought (drought period at the deepest site of a pool, here site 2) of pool 1 from 1992 to 1999 in combination with the daily rates of precipitation and the monthly totals of precipitation and potential evaporation sensu HAUDE (WEISCHET 1991) with its monthly balances. Although pool 1 dried up every year, the duration and beginning of the drought period were very variable. In 1992 and 1998 the period of total drought lasted only a few days and the substrate on the deepest sites remained wet (Appendix 3). Contrastingly, the drought periods were long in 1993, 1995 and 1997. In 1993 and 1997, the drought period lasted about 3.9 months and in 1995 about 5 months. In years with long drought periods the substrate dried up intensely (Figure 19, Appendix 3). The years 1994, 1996 and 1999 showed an intermediate situation with respect to the length of the drought period (1.4-2.4 months) and the intensity of substrate drying (Appendix 3).

The pool may dry up from the beginning of June (see 1992 and 1993) to the end of August (1998), which are the months with the highest rates of potential evaporation. In five out of eight years, the pool dried up during July (first half of July only in 1997, the other years during the second half). Evaporation rates were low from September onwards, except in 1997. If the duration of drought periods was intermediate, stronger rainfalls in September/October lead to a refilling (precipitation –

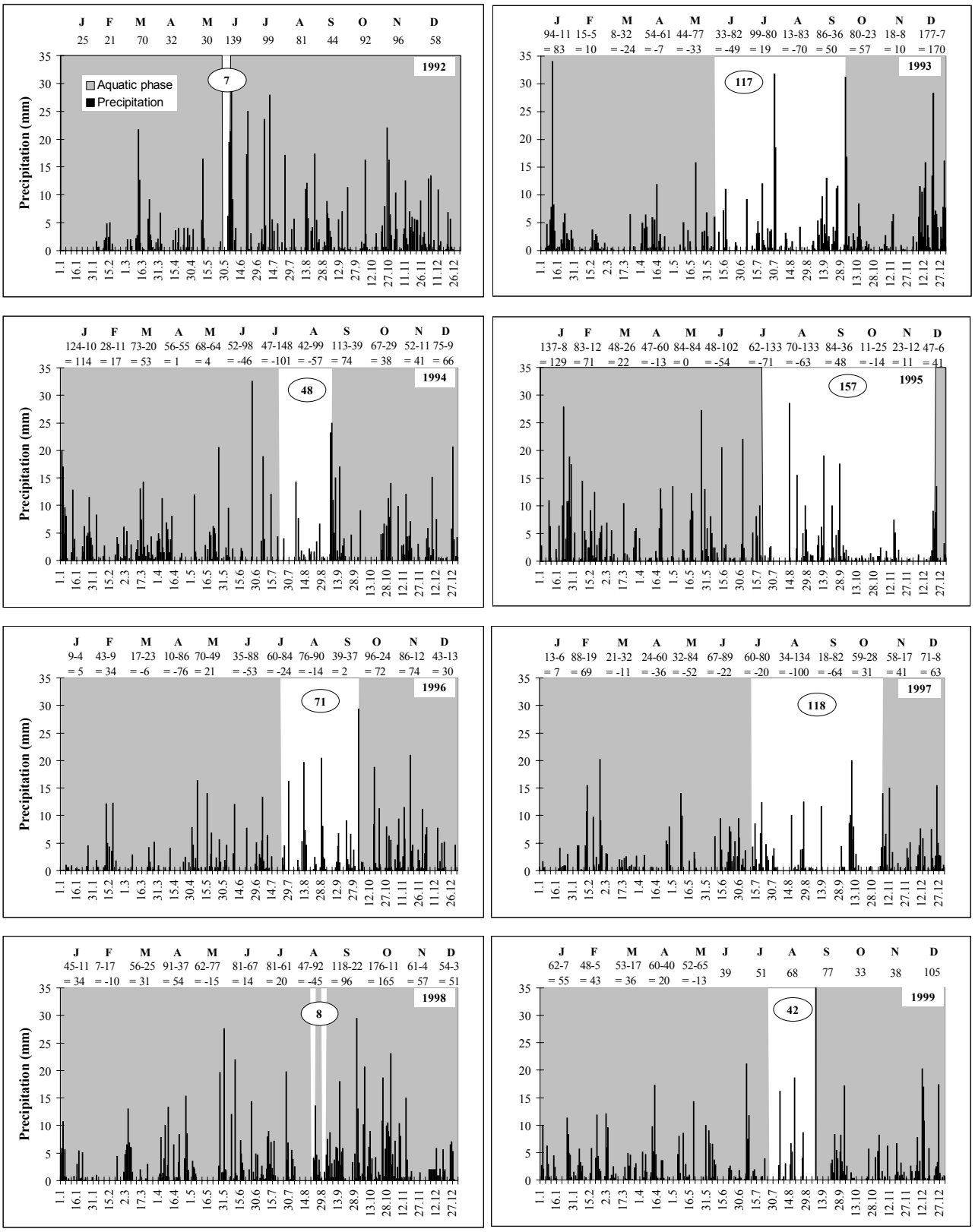

Figure 18: Rates of precipitation and potential evaporation on the 'Lahnberge' with the durations of the aquatic- and drought periods of pool 1 from 1992 - 1999.

Explanations:

The black bars represent the daily rates of precipitation; blue background shows the period of aquatic phase at the deepest site; white background shows the duration of total drought (values within the ellipses provide the duration of dry periods in days); x –y = xy at the top of the figures = monthly total of precipitation – monthly total of potential evaporation = xy (for 1992 and from June 1999 onwards no data of potential evaporation were available).

Table 15: Monthly totals of precipitation on the 'Lahnberge' from 1977-2000 with the observed (1992-1999) and predicted (1977-1991 and 2000) periods of total drought of pool 1.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Drought
1977	46	85	31	38	30	69↑	48	92	8	44	110↓	55	long
1978	18	26	75	18	82	39	45↑	21	59	24	7	149↓	long
1979	38	39	99	55	58	48	51↑	56	14	24	71↓	110	long
1980	35	41	44	30	35←	107	124	85	30	40	41	49	short
1981	80	17	93	44	82	122	54←	145	77	83	61	85	short
1982	45	13	62	31	63	67	28↑	52	22	118↓	41	94	intermediate
1983	67	44	54	91	117	30	54↑	24	63↓	30	40	54↓	intermediate?
1984	128	73	28	39	171	19	67↑	54	135↓	69	69	38	intermediate
1985	41	17	55	36	43←	115	82	57	↑49	23	63↓	39	intermediate
1986	77	7	99	46	84	31	48↑	50	53	88↓	29	82	intermediate
1987	46	33	84	22	85	90	57	53↑	40	72↓	57	35	intermediate
1988	81	80	105	21	41	12↑	74	18	66	41	52↓	71↓	long
1989	25	35	78	75	48	42←	107	42↑	58↓	68↓	37	105	short
1990	46	133	16	33	37←	86	43↑	56	51	54↓	76↓	74	intermediate?
1991	67	24	35	33	12←	104	36↑	6	44	36	83↓	60	long
1992	25	21	70	32	30←	139	99	81	44	92	96	58	short
1993	94	15	8	54	44	↑33	99	13	86	↓80	18	177	long
1994	124	28	73	56	68	52	47↑	42	↓113	67	52	75	intermediate
1995	137	83	48	47	84	48	62↑	70	84	11	23	47↓	long
1996	9	43	17	10	70	35	60↑	76	39	↓96	86	43	intermediate
1997	13	88	21	24	32	67	↑60	34	18	59	↓58	71	long
1998	45	7	56	91	62	81	81	47←	118	176	61	54	short
1999	62	48	53	60	52	39	51↑	68	↓77	35	38	105	intermediate
2000	46	69	53	33	68	47	126	44←	76	57	52	56	short
Min.	9	7	8	10	12	12	28	6	8	11	7	35	
Max.	137	133	105	91	171	139	126	145	135	176	110	177	
Mean	58	45	56	42	62	63	67↑	54	59↓	62↓	55	74	intermediate
SD	35	31	28	21	33	34	26	29	32	36	24	34	

Explanations:

The periods of drought from 1977-1991 as well as for 2000 were estimated from the observations covering 1992-1999. **Dark grey** = whole month dry; **lighter grey** = possibly whole month dry; ↑ = Month of drying (before/behind number = drying during the first/second half of the month); ↓ = Month of refilling (before/behind number = refilling during the first/second half of the month). The years for which the periods of drought were estimated, no differentiation of (re)filling in respect to first/second half of the month was made and all signs were placed behind the number of precipitation. Two signs of refilling in one year indicate two possible times of refilling; ← =possibility or actual occurrence of a short period (a few days) of total drought; **short** = no period of total drought or duration of drought only a few days long; **intermediate** = about 1-2 months of total drought; **long** = > 3 months of total drought; **Min., Max., Mean, SD** = minimum, maximum, arithmetic mean, standard diversity of monthly precipitation rates from 1977-2000.

potential evaporation = 30 to 50 mm). After long drought periods more rain was needed to refill the pool during September and October (precipitation – potential evaporation > 50 mm) and the time of refilling was therefore relatively late in 1997 and very late in 1995. The refilling always took place in the autumn and according to temporary pool terminology (section 5.1.1.) **pool 1 is an intermittent autumn-summer-pool**.

As there were precipitation data available for the years of 1977 to 1991 and 2000, drought periods of these years were extrapolated, following the assumption that the kind of water balance during these years was comparable with what had been observed in 1992 to 1999. The extrapolation (Table 15) shows that an intermediate duration of the drought period must be assumed as the most com-

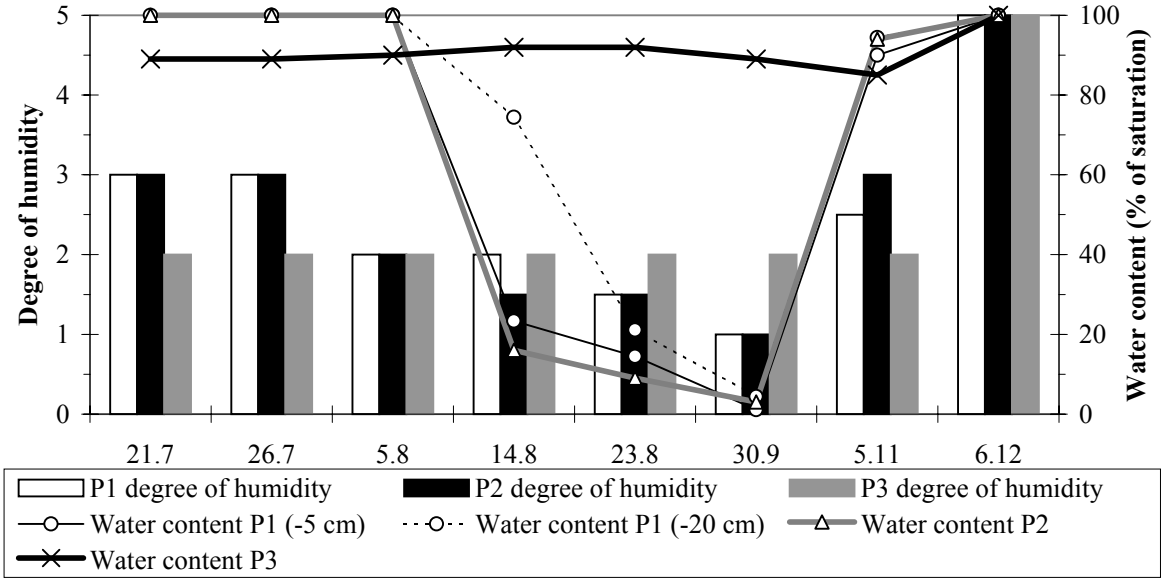

Figure 19: Water content (% of saturation) and grades of humidity during the dry periods of pools 1, 2 and 3 in 1997.

Abbreviations:

P1, 2, 3 = pool 1, 2, 3; **P1 (-5 cm/20 cm)** = values of substrate humidity for depths of 5 and 20 cm. There were no clear differences between the measurements taken at the two different depths in pools 2 and 3. Only the values for depths of 5 cm are therefore provided; **degree of humidity** see Table 1 p 16.

mon (11 cases), followed by years with a long drought period (7 cases) and finally by years with no or only a very short period of drought (6 cases).

In section 4.1.1.2.1., two different parts of pool 1 were described: the 'grass zone' and the 'helophyte zone'. The shrinkage of water starts from the western top of the 'grass zone' and ends with two remaining puddles in the 'helophyte zone', where emergence traps 2 and 3 had been placed. This pattern is illustrated in Figure 9 (p 42). As a result, the periods of total drought described above only reflect the situations around emergence traps 2 and 3. Table 16 allows a comparison of all trap sites with respect to the situations of water balance from 1993-1999. Because of their lower maximum depth of water, trap sites 1b and 1c were dry for longer periods than sites 1, 2 and 3. Site 1 dried up fastest of all three latter sites.

Table 16: Comparison of the dry periods between the trap sites of pool 1.

Site	1b and 1c	1	2	3
Maximum depth (cm)	9	24	35	30
Drought period 1993	mid of May - end of October (~ 5.5)	beg. of June – beg. of October (~ 4)		
Drought period 1995	**semiaquatic** from end of May – beg. of July, then **dry** from beg. of July onwards	2nd half of July – 2nd half of December(~ 5)		
Drought period 1996	mid of June – beg. of November (4.5)	2nd half of July – beg. of October (~ 2.4)		
Drought period 1997	mid of June to 2nd half of December (~ 6.5)	1st half of July – beg. of November (~ 4)		
Drought period 1998	**semiaquatic** from mid of May – end of July, then **dry** until 2nd half of September (~ 1.5)	mid of Aug. – mid of Sep. (~ 1)	two short periods in the end of August (~ 0.25)	
Drought period 1999	From mid of June onwards	1st half of July onwards	2nd half of July – 1st half of September (~ 1.4)	

Explanations:

The approximate length (months) of the drought period is presented in **brackets**. For 1992, 1994, 1995 and 1999 the time of drying and/or refilling was only stated for site 2 (Figure 18). In 1995 and 1998, there was a long **semiaquatic** phase on trap sites 1b and 1c (degree of humidity 3 + 4, for definition see Table 1 p 16) due to the expansion and shrinkage of water. **beg**. = beginning.

4.1.1.4.2. Pool 2

Table 17: Comparison of the dry periods between the trap sites of pool 2

Site	4	5 + 6
Maximum depth (cm)	34	59 + 44
Dry period 1993	1st half of June – 1st half of October (~4)	**semiaquatic** from end of June – beginning of August and end of August – mid of September
Dry period 1996	**semiaquatic** from 1st half of June – mid of August, then **dry** until the beginning of October (~2)	**semiaquatic** from 2nd half of July – 1st half of August
Dry period 1997	beginning of June – 2nd half of December (~7)	**semiaquatic** in the mid of June, **dry** from 1st half of July – 1st half of November (~4)
Dry period 1998	no drought	no drought

Explanations:
The approximate length (months) of the drought period is presented in brackets. For 1992, 1994, 1995 and 1999, the time of drying and refilling was only stated for site 5 and is illustrated in Figure 20. **Semiaquatic** = degree of humidity 3 + 4 (for definition see Table 1 p 16).

The lengths of the total drought observed for pool 2 are presented in Figure 20. The potential start of total drought is very similar to that of pool 1. But after stronger periods of rain there was a temporary water inflow coming in at the north-western top of pool 2. Pool 2 is also deeper (maximum depth of 59 cm) than pool 1 and the density of helophytes within the pool is much higher (Figure 12 p 45). Pool 2 therefore refilled quite fast after stronger rainfall and dried up quite fast if stronger rainfall did not appear for a longer period, especially during July and August. If there was little rain during May and June (as in 1993 and 1997), total drought could also start from mid of June up to the beginning of July. In two out of eight years, the pool did not dry up at all and in 5 other years the dry periods were short, with substrates remaining wet or very humid in the deepest sites (semiaquatic). **Pool 2 should therefore be called semi permanent** (section 5.1.1.). There was an exception in 1997 when strong rains failed in summer, causing the pool to dry up for about 4 months, which resulted in a strong desiccation of the mud (Figure 19). It is also most likely that long drought periods occurred in 1978, 1979, 1986 and 1988 (predicted from data in Table 15). Nevertheless it appears that long drought periods in pool 2 are rare and unpredictable. Table 17 presents a comparison of the dry periods in different sites of pool 2. The water level started shrinking in the north west of the pool and ended in a puddle around emergence trap 5 (Figure 11 p 43). Site 6 usually dried up one week earlier than site 5 (deepest site). In contrast to sites 5 and 6, site 4 regularly dried up for a longer period of time (except 1998).

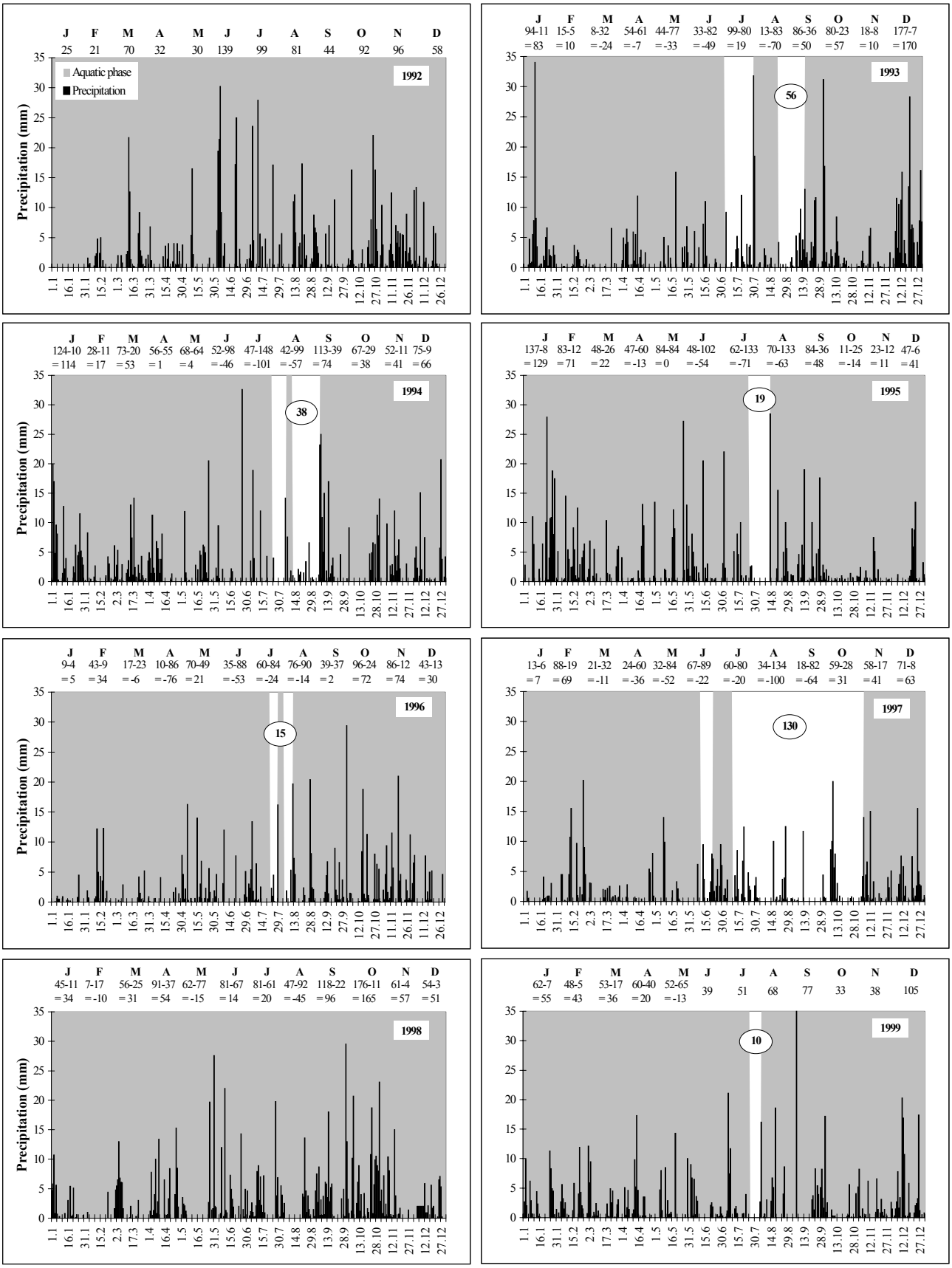

Figure 20: Rates of precipitation and potential evaporation on the 'Lahnberge' with the durations of the aquatic- and drought periods of pool 2 from 1992 - 1999.
Explanations see Figure 18.

4.1.1.4.3. Pool 3

In contrast to pool 1 and pool 2, which filled up to their maximum every year, the intensity of filling (inundation) of pool 3 varied strongly between the years (1993-2000), dependent on the intensity of rainfall in winter (Figures 13, 14 pp 45-46). The inundated area was large (= 'extensive flooding', Figure 14a-d p 46) in 1994, 1995, 1999, 2000 and probably in 1993 too (full extent of flooding not observed). In 1997 and 1998, the maximum extension of the water body was mainly restricted to the drainage ditches and the central part of pool 3 which was located between the two joining drainage ditches (= 'restricted flooding' = dark grey area in Figure 13 p 45, see also Figure 14e p 46). The pool did not refill at all in the winter of 1995/96 and therefore the duration of the terrestrial phase lasted about 16 months until the pool filled again in November 1996. Such a long terrestrial phase had probably not occurred further since 1977 (estimated from precipitation data in Table 15). At least for the aquatic phases of 1984/85 and 1988/89 it is supposed that there had been only a filling of the drainage ditches.

The trees burgeon in May and then start transpiring, which strongly accelerates the process of drying and leads to a relative good predictability of the time of the total drought. Pool 3 dried up between the 2nd half of May (1993, 1997, 1999, 2000) and the beginning of July (1995). The pool usually refilled in winter (November to January). The October of 1998 was however very wet and the pool also refilled in that month. A long terrestrial phase is therefore typical for pool 3. Due to the kind of water balance, **pool 3 is called an intermittent winter-vernal woodland pool** (section 5.1.1.).

Because there were long periods in the aquatic phase during which the water was restricted to the drainage ditches, Figure 21 distinguishes a 'ditch phase' (water restricted to the drainage ditches) and an 'inundation phase' (all situations with water exceeding the drainage ditches) (Figure 13 p 45). The 'ditch phase' and the 'inundation phase' therefore correspond to the aquatic phase of sampling sites 7 + 8 (both with a maximum depth of 55 cm) and the 'inundation phase' to the aquatic phase on sampling sites 9 + 10 (maximum depths of 30 cm and 20 cm) (Figures 13, 14 pp 45-46).

The extent to which the substrate dried out during the terrestrial phase on site 8 is illustrated in Figure 19. There were only low fluctuations of the water content and the substrate remained always humid (see also Figures 80, 81 pp 172 and 174, respectively).

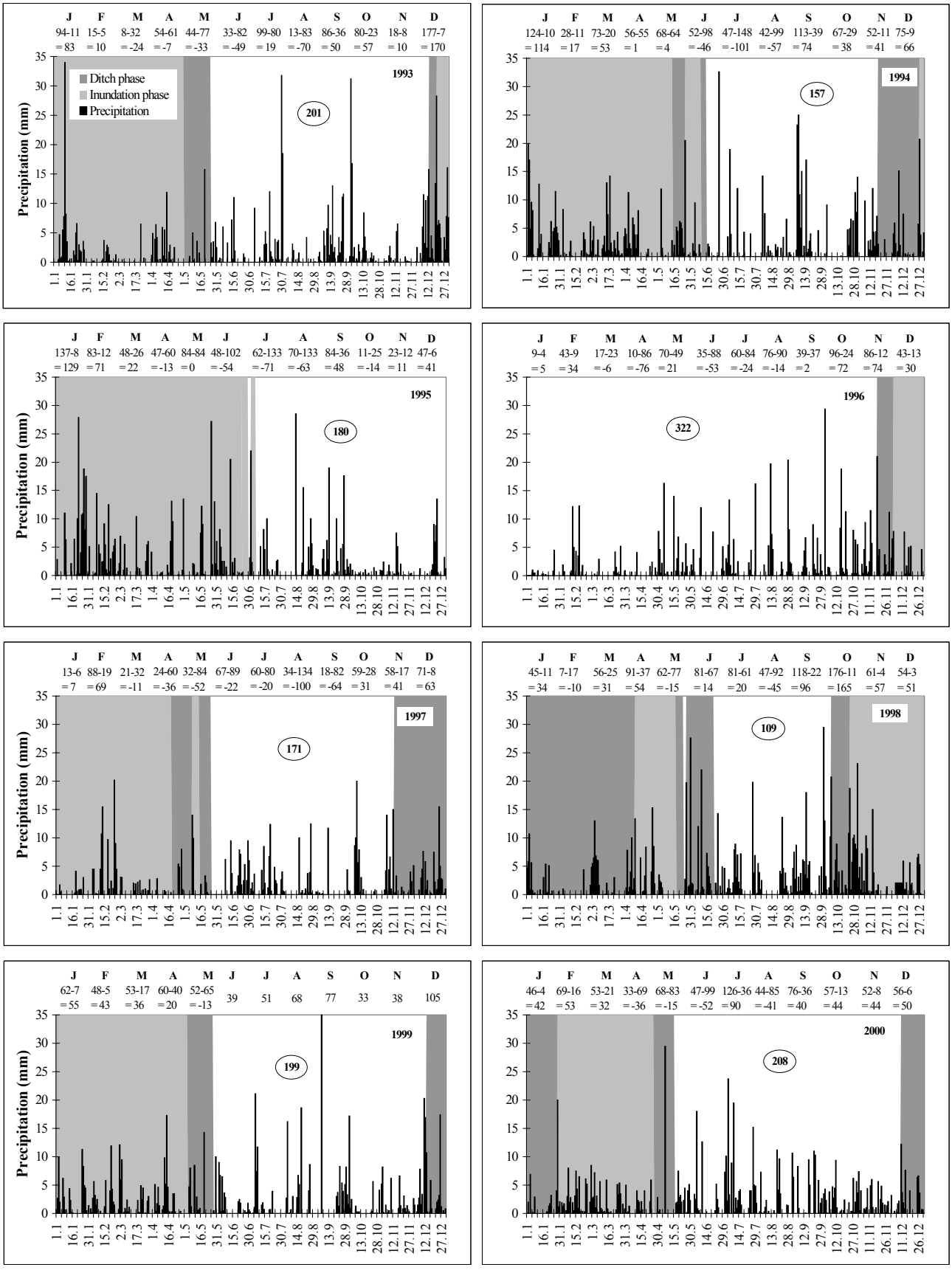

Figure 21: Rates of precipitation and potential evaporation on the 'Lahnberge' with the duration of the inundation phases (blue background), ditch phases (grey background) and drought periods (white background) of pool 3 from 1993–2000 (see text).
For further explanations see Figure 18.

4.1.2. Physicochemical characteristics of the experimental pools of the colonizing experiment

The protocol of the colonizing experiment was described in section 3.2.. The water of the colonizing pools was slightly acidic and the conductivity low (Table 18). There were no great differences between the pools, the ranges and mean values of conductivity found for boxes 1 and 6 were somewhat higher than in the remainder of boxes.

Table 18: pH, conductivity (min-max; mean) and water depths (mean) in the experimental boxes used for the colonizing experiment, 1998.

Box	pH	Conductivity (µS/cm)	Water depth (cm)*
1	6.1-6.4; 6.0	72-153; 134	14.3
2	5.3-6.4; 6.0	65-85; 75	13.5
3	5.9-6.3; 6.1	63-83; 73	11.7
4	5.9-6.2; 6.0	74-94; 84	14.1
5	5.8-6.6; 6.1	74-95; 85	12.3
6	5.1-6.1; 5.7	90-120; 105	8.2
7	5.7-6.1; 5.9	60-80; 70	14.5
8	5.2-5.9; 5.7	79-99; 89	13.3
9	5.8-6.2; 5.9	60-80; 70	13.9
10	5.8-6.4; 6.1	76-96; 86	11.8

*Because the variations of water depths were low, only the mean values are provided.

The level of oxygen was measured in Box 4 in a day run from August 11-12 (min-max; mean: 2.84-5.70; 3.98 mg/l and 32-79; 49 % of saturation). There was a clear day-night cycle in oxygen levels with the highest values occurring around 3 p.m. and the lowest values between 11 p. m. and 2 a.m. (Figure 22). Compared with the day runs for oxygen in pools 1 and 3, the oxygen levels in the experimental box was somewhat higher than those in the winter day run (February 21-22, 2000) done in pool 3 and much higher than in the other runs (Table 11 p 47, Figure 15 p 48).

From June 8 to July 16 data loggers recorded the water temperatures at intervals of 30 minutes in box 2 (shaded by bushes) and box 4 (not shaded) (Figure 23). The range and mean values of all measure-

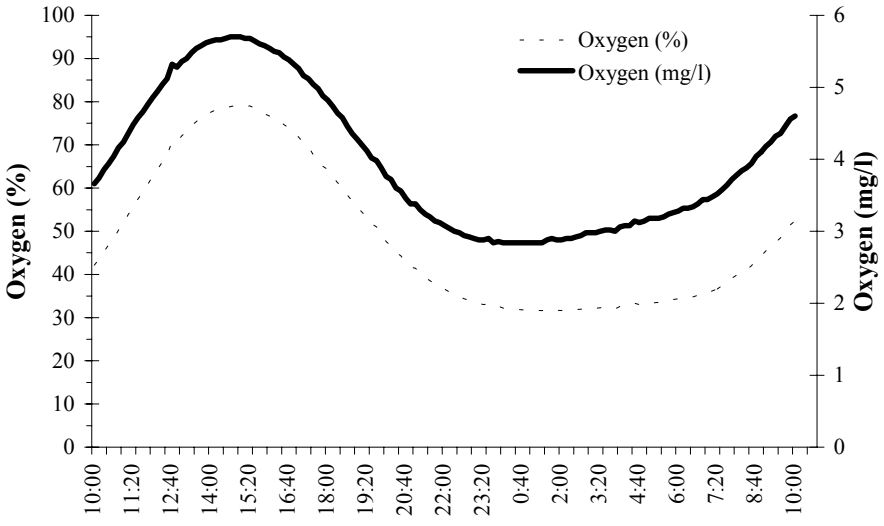

Figure 22: Day run of oxygen (mg/l and % of saturation) in the colonizing box 4 from 10:00 a.m. August 11 to 10:00 a.m. August 12, 1998.

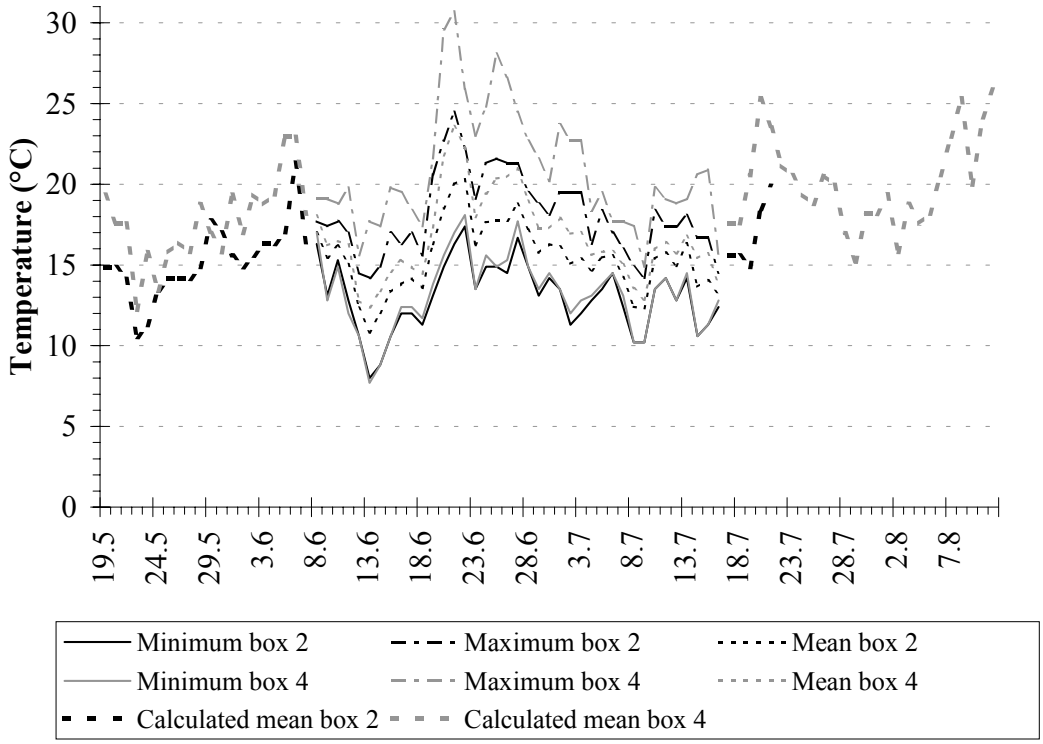

Figure 23: Calculated (May 19 - June 7 and July 17 - August 11) and measured (June 8 - July 16) water temperatures in the experimental boxes 2 and 4 used in the colonizing experiment, 1998 (for explanations see text).

ments were 8.0-24.5; 15.4 °C (box 2) and 7.7-30.7; 16.8 °C (box 4). There was a mean difference of temperature of 1.4 °C between the boxes. The daily maxima, minima and temperature averages of the two experimental boxes were compared with a MAN-WHITNEY-U-test. No significant differences were found in daily minima ($U = 712.5$, $p = 0.631$, $n = 39$), but there were significant differences in daily temperature averages ($U = 540.0$, $p = 0.028$, $N = 39$) and highly significant differences in daily maxima ($U = 408.0$, $p = < 0.001$). Because temperature loggers were only available for parts of the experiment (May 19-July 21 (box 2), May 19 - August 11 (box 4)), a calculation of the mean temperatures for the time without loggers was done using the temperature records of the meteorological station 'Am Stempel' (near Marburg, Hesse, Germany) (KÄMPF unpublished data), which was located not far away from the experimental boxes of the colonizing experiment. Daily temperature averages of the experimental boxes 2 and 4 for the whole experiment were calculated in three steps:

(1) The first step was to correlate the daily means of box 2 and 4 with the corresponding minima or maxima (the correlations with highest r^2 were taken for the calculations of the mean temperatures in boxes 2 and 4 (see 3)): (a) $\textit{mean temperature}_{box\ 2} = 0.9486 * \textit{minimum temperature}_{box\ 2} + 3.0397$ ($r^2 = 0.878$); (b) $\textit{mean temperature}_{box\ 4} = 0.6607 * \textit{maximum temperature}_{box\ 4} + 3.0131$ ($r^2 = 0.856$).

(2) The second step was to correlate the daily temperature maxima or minima measured by the meteorological station 'Am Stempel' with the maxima or minima measured in an experimental box: (a) $\textit{minimum temperature}_{box\ 2} = 0.7583 * \textit{minimum temperature}_{'Am\ Stempel'} + 6.3914$ ($r^2 =$

0.7565); (b) *maximum temperature* $_{box\ 4}$ *= 0.9017 * maximum temperature* $_{'Am\ Stempel'}$ *+ 6.7114* (r^2 = 0.8372).

(3) In the third step, the daily temperature averages measured in box 2 and 4 were calculated using the correlations obtained in (1) and (2) for May 19 - June 7 and July 16 - July 21 (box 4 until August 11): (a) *mean temperature* $_{Box\ 2}$ *= 0.9486 * ((0.7583 * minimum temperature* $_{'Am\ Stempel'}$*) + 6.3914) + 3.0397*; (b) *mean temperature* $_{box\ 4}$ *= 0.6607 * ((0.9017 * maximum temperature* $_{'Am\ Stempel'}$ *+ 6.7114) + 3.0131)* (Figure 23).

The deviations between the calculated and measured means of temperature were + 0.1 °C (box 2) and - 0.1 °C (box 4) for the period spanning from June 8 to July 16. The calculations therefore appear to satisfactorily reflect the actual temperature averages thus allowing an estimate of the mean temperature range and the degree-days for the whole length of the colonizing experiment (Table 19).

Table 19: Estimated characteristics of temperature for the whole length of the colonizing experiment, 1998 (for explanations see text).

	Temperature (°C)	Degree days*
Box 2 (May 19 - July 21)	10.5-21.3; 15.5	990
Box 4 (May 19 - July 21)	12.2-25.3; 17.4	1111
Box 4 (May 19 - August 11)	12.2.-25.9; 18.0	1528
* cummulative daily means of temperature above 0°C for the whole period of time.		

A day run of temperature in the experimental box 4 (Figure 24) indicated that the water temperatures at the different water depths (subsurface, middle (5 cm), ground (14 cm)) were almost identical (KRUSKAL-WALLIS-Anova: H = 1740390, df = 2 n = 447, p = 0.917) and followed with a slight delay, the rise and fall of the air temperature. The daily amplitude of temperature was large (15.4-33.4; 23.4 °C).

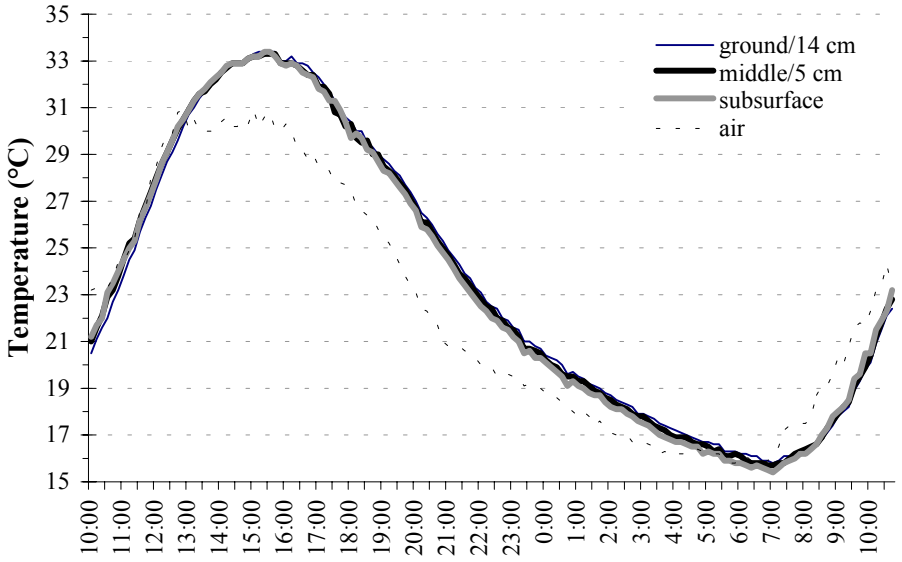

Figure 24: Day run of temperature in the colonizing box 4 from 10 a.m. August 11 to 10 a.m. August 12, 1998. The air temperature was measured in the shadow on the ground beside the box.

4.2. The chironomid community

4.2.1. The chironomid community of pools 1-3

2.2.1.1. General results

The results of the faunistical study on pools 1-3 are summarized in Tables 23-25. It is not the scope of this thesis to describe the full extent of information obtained (especially the emergence data for species others than *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* and the data on terrestrial chironomids). Nevertheless the Appendix 3 lists all the data obtained along with comments on determination, taxonomy, deposition of the material and literature used in the ecological classification and determination.

Altogether 51 species were found in pools 1-3 (33 in pool 1 and 2, respectively, and 23 in pool 3).

Limnophyes var. nov. and *Smittia* spec. A possibly are new species (see comments in the Appendix 3 and section 4.3.1.2.1.). It is the first record of *Pseudosmittia conjuncta* for Germany (see comments in the Appendix 3) and both *Limnophyes natalensis* and *Paratanytarsus tenellulus* are not listed for low mountain range regions of Germany (= Zone 2 in SAMIETZ 1996a).

Some species were found in only one pool (Table 20), but there were usually only a few individuals of such species. *Natarsia puntata* in pool 1, 1999, *Pseudosmittia conjuncta* in pool 3, 1996 and *Endochironomus tendens* in pool 2, 1993 however occurred in higher numbers and were therefore exceptions. Because of such species the cumulated frequencies of recorded species did not reach saturation, especially in pool 1 and 2, even after 8 and 6 years of sampling, respectively (Figure 25).

Table 20: List of species recorded in only one pool.

Pool 1	Pool 2	Pool 3
Monopelopia tenuicalar	*Limnophyes natalensis*	*Prodiamesa olivacea*
Natarsia punctata	*Limnophyes pumilio*	*Brillia modesta*
Cricotopus sylvestris	*Smittia* spec. B	*Bryophaenocladius ictericus*
Metriocnemus spec.	*Dicrotendipes lobiger*	*Bryophaenocladius* cf. *virgo*
Paratendipes albimanus	*Dicrotendipes notatus*	*Gymnometriocnemus* cf. *subnudus*
Polypedilum arundinetum	*Endochironomus tendens*	*Heleniella ornaticollis*
Tanytarsus usmaensis	*Synendotendipes lepidus*	*Limnophyes habilis*
		Orthocladius spec.
		Pseudosmittia conjuncta
		Tanytarsus eminulus

The chironomid community was documented over the whole or approximately whole period of emergence (aquatic and terrestrial phase) in two (pool 1) or three (pools 2 + 3) years of investigation. For these years it was possible to calculate the annual proportions of individuals representing different life forms (Table 21). Semiaquatic - terrestrial- and completely terrestrial species ranged between 27 and 58 % (pool 1), 39 and 69 % (pool 2) and 79 and 96 % (pool 3). The yield of chironomids (individuals/m² and year) ranged between 1,344 and 8,219 (pool 1), 181 and 4,525 (pool 2) and 2,360 and 45,175 (pool 3).

The quantitatively more important species (> 1% of the total yield) of the different life forms are

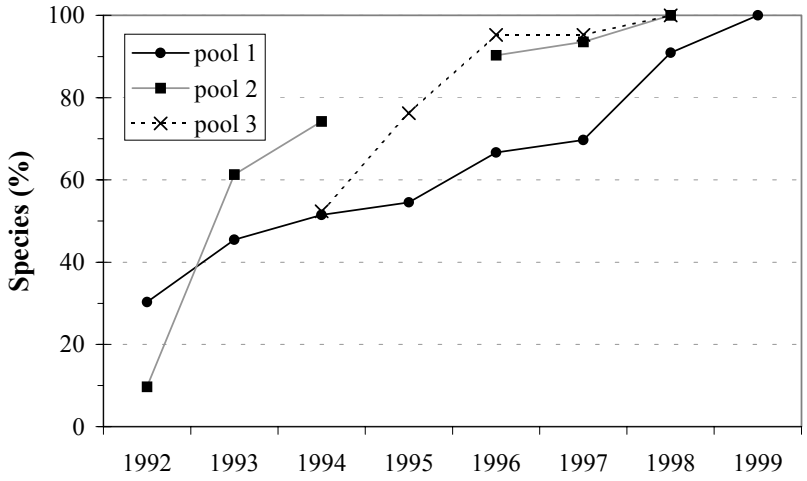

Figure 25: Cumulated frequencies of the recorded species (%) during the emergence study of pools 1, 2 and 3.

Table 21: Proportions of individuals (%) representing different life forms in pools 1, 2 and 3.

Life form	Pool 1		Pool 2			Pool 3		
	1993/94	1998	1993/94	1996	1998	1994	1996	1998
aquatic	21.7	64.6	29.5	30.5	49.9	0.6	0.0	0.1
aquatic - semiaquatic	19.7	8.4	1.8	0.7	10.0	8.1	0.2	2.3
semiaquatic	1.0	0.2	0.2	0.7	1.0	12.4	6.3	1.2
semiaquatic - terrestrial	40.9	23.8	66.4	65.6	39.0	52.7	11.4	13.4
terrestrial	16.8	3.1	2.3	2.6	0.1	26.3	82.1	83.0

Table 22: The chironomids of quantitative importance (percentage (individuals) of total yield in brackets).

Life form	Pool 1	Pool 2	Pool 3
aquatic	*P. tritum* (43.1 %) *C. scutellata* (5.1 %) *X. nigricans* (3.9 %) *P. varius* (3.3 %) *C. luridus* (2.3 %) *C. pseud./ulig.* (1.3 %) *X. falcigera* (1.2 %)	*C. scutellata* (14.0 %) *X. nigricans* (8.5 %) *X. falcigera* (7.9 %) *P. tritum* (2.4 %) *C. luridus* (1.8 %) *P. varius* (1.5 %) *C. pseud./ulig.* (1.1 %)	*P. tritum* (1.2 %)
aquatic - semiaquatic	*P. hydrophilus* (9.2 %)	*P. hydrophilus* (5.2 %)	*P. hydrophilus* (3.0 %)
semiaquatic			*L asquamatus* (4.2 %)
semiaquatic - terrestrial	*L. minimus*-agg. (19.6 %)	*L. minimus*-agg. (51.4 %)	*L. minimus*-agg. (17.3 %)
terrestrial	*Smittia* spec. A (7.0 %)		*P.* spec. A (70.9 %) *P. conjuncta* (2.2 %)

listed in Table 22. The aquatic and aquatic - semiaquatic species of quantitative importance were identical in pools 1 and 2 but their abundance greatly differed. *P. tritum* was the absolute dominant species in pool 1, followed by *P. hydrophilus* and *C. scutellata*. *X. nigricans* and *X. falcigera* were most abundant in pool 2. No semiaquatic species reached greater importance in pools 1 and 2. Contrastingly, pool 3 encountered only one aquatic species of quantitative importance (*P. tritum*), which was only abundant in 1995. The aquatic - semiaquatic *Paralimnophyes hydrophilus* and the

Table 23: The chironomid community of pool 1 (explanations and comments p 68).

	1992		1993					1994			1995		1996			1997			1998		1999					Total		
Site/method→	2	net	1	2	3	net	In	1	2	net	2	3	2	3	net	2	3	net	2	3	1b	1c[14]	2	3	net	∑	%	sex[1]
Tanypodinae																										761	9.5	-
1. *Monopelopia tenuicalar* **(s/a/se/Ule+po+poo (acidic))**																				1,0			1,0	0,1		2,1	<0.1	-
2. *Natarsia punctata* **(s/a/se/Ule+s)**																				1,0	5,4	18,29				24,33	0.7	0.727
3. *Procladius choreus* **(s/a/se/U)**	3,0			1,0									0,2	1,1		0,2				1,1				0,2		6,8	0.2	0.750
4. *Psectrotanypus varius* **(sd/a/se/po+poo)**	1,1				1,0								27,28	9,6	37L	51,67	1,1	4L	8,13	9,11	12,9		4,4		1P	122,140	3.3	0.871
5. *Xenopelopia falcigera* **(r/a/se/poo)**	11,0				1,0														1,0	11,0			19,0	7,0		50,0	0.6	
6. *Xenoelopia nigricans* **(sd/a/se/poo)**	2,0			1,0	1,0								1,0						68,0	22,0	10,0		20,0	26,0	3P	151,0	1.9	0.957
Xenopelopia spec.	0,14			0,1	0,1								0,4	0,3					0,85	0,21	0,6		0,37	0,38		0,210	2.6	
7. *Zavrelimyia* cf. *nubila* **(s/a/se/poo+p)**	0,1																		2,0				5,4			7,5	0.1	1.400
Tanypodinae gen. spec.													0,1			0,1										0,2	<0.1	-
Orthocladiinae																										3406	42.6	-
8. *Acricotopus lucens* **(s/a/se/Ule)**				4,0									1,0		1,0+Pex	1,0	1,0		0,1							7,1	0.1	-
9. *Corynoneura scutellata* **(d/a/p/Ule)**								0,1	0,3				0,10			0,9	1,61		0,157	0,86	0,1		0,64	0,19		1,411	5.1	0.002
10. *Cricotopus sylvestris* **(s/a/se/Ule)**													1,0		1,0											1,0	<0.1	-
11. *Limnophyes asquamatus* **(s/sa/p/m+w+tp)**								0,5	0,9		0,1									0,4						0,19	0.2	0.000
12. *Limnophyes minimus*-aggregate **(e/sa-t/pse/Ut)**			5,38	6,384	4,140			1,4	1,8		1,13		0,12	3,117		0,21	0,12		3,266	16,265	7,83	8,92	0,33	4,20		59,1508	19.6	0.039
13. *Limnophyes pentaplastus* **(s/a-sa/se/U)**																			0,1		0,1					0,2	<0.1	-
14. *Metriocnemus* spec. **(s/sa-t?/?/w?)**																					0,1					0,1	<0.1	-
15. *Paralimnophyes hydrophilus***(d/a-sa/se/tp)**	1,3			0,1		1L	1,0	49,23	133,78	3L			4,1	3,4	1,0; 22L, 1PLex	23,42	91,86	13L	38,26	69,61	0,1					411,326	9.2	1.260
16. *Paraphaenocladius impensus* **(s/sa-t/se/m+w)**																				2,3	3,1	7,6		0,1		12,11	0.3	1.090
17. *Psectrocladius* cf. *sordidellus* **(s/a/se/Ule)**																1,0		1L	1,0							2,0	<0.1	-
18. *Pseudosmittia* spec. A **(s/t/p/tp, S?)**											0,1		0,14						0,1		0,44	0,9		0,1		0,70	0.9	0.000
19. *Smittia* spec. A **(d/t/p/tp+?) new?**			0,12	0,178	0,53		0,3				0,108		0,19	0,100		0,2			0,6	0,65	0,4	0,6	0,4	0,4		0,561	7.0	0.000
Orthocladiinae gen. spec.				0,3																						0,3	<0.1	-
Chironominae/Chironomini																										3794	47.4	-
20. *Chironomus dorsalis* **(s/a/se/pu+p)**	3,2	1,0																								3,2	<0.1	-
21. *Chironomus longipes* **(s/a/se/po+poo)**																			0,1							0,1	<0.1	-
22. *Chironomus luridus* **(sd/a/se/poo)**	29,24	2,0	1,0		1,0	1,0					1,2		12,3			32,32			5,0	1,0	3,0	3,1	1,1	1,0		90,63	1.9	
23. *Chironomus piger/riparius* **(s/a/se/Ule)**													19,12	1,0	1,0+Pex			1L			2,2					22,14	0.5	1.055
24. *Chironomus pseudothummi/uliginosus* **(r/a/se/poo)**	12,4												4,3			9,8			31,11		3,3		0,1			59,30	1.1	
Chironomus spec.	0,22					1P							0,20	0,2			0,1	3L	0,6	0,4						0,55	0.7	
Chironomus luridus-aggregate															61L			7L										
25. *Microtendipes pedellus* **(s/a/se/Ule+po)**												1,0														1,0	<0.1	-
26. *Parachironomus parilis* **(s/a/se/Ule)**																			1,0							1,0	<0.1	-
27. *Paratendipes albimanus* **(s/a/se/U)**				1,0																						1,0	<0.1	-
28. *Phaenopsectra punctipes* **(s/a/se/po+l)**																				2,0						2,0	<0.1	-
29. *Polypedilum arundinetum* **(s/a/se/Ule)**																								1,0		1,0	<0.1	-
30. *Polypedilum tritum* **(e/a/se/tp+?)**	116,111	29L, 1P	1,0	4,0			23,13	38,38	105,115				9,9	9,9	6,5 + 3L	183,133	24,26		176,102	351,306	485,554	153,167	116,86	14,8		1784,1664	43.1	1.072
31. *Synendotendipes impar* **(s/a/se/Ule+po)**																								1,0		1,0	<0.1	-
Chironominae/Tanytarsini																										35	0.4	-
32. *Paratanytarsus tenellulus* **(s/a/se/poo)←**													0,1						4,4	1,0			5,6	6,5		16,16	0.4	1.000
33. *Tanytarsus usmaensis* **(s/a/se/l)**					1,0																					1,0	<0.1	-
Tanytarsus spec. **(s/a/se/?)**																			0,1	0,1						0,2	<0.1	-
Chironominae gen. spec.			0,1	0,1									0,1													0,3	<0.1	-
Total ∑	360[2]		58[3]	585[3]	202[3]			159	452		127[6]	1[6]	218[7]	268[7]		617[7]	305[7]		1019[8]	1315[8]	1244[7]	499[7]	411[7]	159[7]		7999*	100.0	-
Total year	-		-	-	-			215[4]	1030[4]		-	-	-	-		-	-		1019	1315	-	-	-	-		211**		
year m²	-		-	-	-			1344[4]	6437[4]		-	-	-	-		-	-		6369	8219	-	-	-	-		40***		
Total aquatic	-		-	-	-			154[5]	443[5]		-	-	173	48		594	293		743	964	1101	371	374	129		8250#		
aquatic m²	-		-	-	-			962[5]	2769[5]		-	-	1081	300		3712	1831		4644	6025	6881	2319	2337	806				

Table 24: The chironomid community of pool 2 (explanations and comments p 68).

	1992	1993					1994			1996			1997		1998			Total		
Site/method→	5	4	5	6	In	net	4	6	net	5	6	net	5	6	5	6	net	∑	%	sex[1]
Tanypodinae																		574	18.3	-
1. *Procladius choreus* **(s/a/se/U)**				1,0									1,1		0,2	2,0		4,3	0.2	-
2. *Psectrotanypus varius* **(r/a/se/po+poo)**	1,0		0,1			1,0+10L,5P,1Pex				1,1		3L	17,16	4,1	2,0	2,0		27,19	1.5	1.421
3. *Xenopelopia falcigera* **(d/a/se/poo)**			26,0	86,0	5,0	10,0										6,0		118,0	3.8	
4. *Xenopelopia nigricans* **(d/a/se/poo)**		1,0	6,0	59,0	1,0	10,0		1,0		1,0	1,0		1,0	3,0	16,0	40,0	1P	129,0	4.1	0.928
Xenopelopia spec.		0,6	0,58	0,141	0,7	0,25+6L, 32P/Pex					0,2			0,5	0,14	0,40		0,266	8.5	
5. *Zavrelimyia* cf. *nubila* **(s/a/se/poo+p)**						1P = *Z. nubila*	1,0									1,0		2,0	<0.1	-
Tanypodinae gen. spec.		0,2		0,2				0,1		0,1								0,6	0.2	-
Orthocladiinae																		2302	73.3	-
6. *Acricotopus lucens* **(s/a/se/Ule)**										1,0	0,1		0,1					1,2	0.1	-
7. *Corynoneura scutellata* **(e/a/p/Ule)**			0,2	0,9	0,8	0,1				0,13	0,2		0,18	0,15	0,218	0,163	1L	0,440	14.0	0.000
8. *Limnophyes asquamatus* **(s/sa/pse/m+w+tp)**								1,1		0,1				0,1	0,3	0,10		1,16	0.5	0.063
9. *Limnophyes minimus*-aggregate **(e/sa-t/pse/Ut)**		18,169	14,423	12,260	1,33	1,3	3,1	5,4		2,82	1,16		0,59	0,25	0,184	8,328		63,1551	51.4	0.041
Limnophyes minimus var. nov. **new?**														1,0				1,0	<0.1	-
10. *Limnophyes natalensis* **(s/sa-t/se/m+w (moss))** ←		0,1		0,1		0,1												0,2	<0.1	-
11. *Limnophyes pentaplastus* **(s/a-sa/se/U)**															2,1	1,0		3,1	0.1	-
12. *Limnophyes pumilio* **(s/a-sa?/se/?)**								1,1										1,1	<0.1	-
Limnophyes spec.						2P												0,0	0.0	-
13. *Paralimnophyes hydrophilus* **(d/a-sa/se/tp)**				1,0			1,3	8,9	1L	1,0			0,9	2,1	26,31	41,31		80,84	5.2	0.952
14. *Paraphaenocladius impensus* **(s/sa-t/se/m+w)**			1,0			0,1												1,0	<0.1	-
15. *Psectrocladius* cf. *sordidellus* **(s/a/se/Ule)**										5,0			0,3+1L					5,3	0.3	-
16. *Pseudosmittia* spec. A **(s/t/p/tp,S?)**										0,2	0,1							0,3	0.1	-
17. *Pseudosmittia curticosta* **(s/sa-t?/se/tp+r+?)**		1,0		1,0														2,0	<0.1	-
18. *Smittia* spec. A **(r/t/p/tp+?) new?**		0,6	0,25		0,1											0,1		0,32	1.0	0.000
19. *Smittia* spec. B **(s/t?/?/tp+?)**											0,1							0,1	<0.1	-
Orthocladiinae gen. spec.		0,4	0,1	0,1						0,1								0,7	0.2	-
Chironominae/Chironomini																		246	7.8	-
20. *Chironomus dorsalis* **(s/a/se/pu+p)**						9,4+2Pex												0,0	0.0	-
21. *Chironomus longipes* **(s/a/se/po+poo)**			2,0			6,7+1Pex												2,0	<0.1	-
Chironomus (cf. *Lobochironomus*) spec.												1L						0,0	0.0	-
22. *Chironomus luridus* **(r/a/se/poo)**	7,6	0,1				29,27+8Pex				6,3	3,1		2,1	1,1	14,3	5,1		38,17	1.8	
23. *Chironomus piger/riparius* **(s/a/se/U)**						2,0+1M	1,0											1,0	<0.1	
Chironomus piger/riparius/ Type "*lugubris*"										1,0								1,0	<0.1	1.355
24. *Chironomus pseudothummi*/uliginosus **(r/a/se/poo)**	2,1												1,0	0,1	13,13	3,1		20,16	1.1	
Chironomus spec.	0,2					0,4+23L, 19P/Pex				0,2			0,2		0,6	0,1		0,13	0.4	
Chironomus luridus-aggregate												50L						0,0	0.0	-
25. *Dicrotendipes lobiger* **(s/a/se/Ule)**										1,0								1,0	<0.1	-
26. *Dicrotendipes notatus* **(s/a/se/Ule+po)**					1,3	2P									1,0			1,0	<0.1	-
Dicrotendipes spec.															0,1			0,1	<0.1	-
27. *Endochironomus tendens* **(s/a/se/Ule+l)**			0,2	2,2														2,4	0.2	-
Endochironomus spec.						0,1+6L, 7P/Pex												0,0	0.0	-
28. *Parachironomus parilis* **(s/a/se/Ule)**													6,4	4,0		3,2		13,6	0.6	2.167
29. *Phaenopsectra punctipes* **(s/a/se/po+l)**			1,0											2,0	3,1	2,0		8,1	0.3	-
30. *Polypedilum tritum* **(sd/a/se/tp+?)**			2,2	5,0	1,0	0,1		1,1					0,2	1,0	19,17	15,10		43,32	2.4	1.344
31. *Synendotendipes impar* **(s/a/se/Ule+po)**				3,2	1,0	7,7	0,1							0,3	6,5	2,0		11,11	0.7	1.000
32. *Synendotendipes lepidus* **(s/a/se/Ule+l)**						1,0												0,0	0.0	-
Synendotendipes spec.												1L						0,0	0.0	-
Chironominae/Tanytarsini																		18	0.6	-
33. *Paratanytarsus tenellulus* **(s/a/se/poo)**←			2,0							1,0			1,1		3,4	4,1		11,6	0.5	1.833
Chironominae gen. spec.		0,1	0,1	0,2	0,1		1,0							0,1				1,5	0.2	-
Total ∑	19[9]	210	569	590			12	34		126[8]	29[8]		147[7]	72[7]	608[8]	724[8]		3140*	100.0	
Total year	-	-	-	-			222[4]	573[4]		126	29		-	-	608	724		343**		
Year m²	-	-	-	-			1388[4]	3581[4]		787	181		-	-	3800	4525		63***		
Total aquatic	-	-11[10]	105[10]	315[10]			8[5]	25[5]		39	10		87	46	424	387		3543#		
aquatic m²	-	-	656[10]	1967[10]			-	-		244	63		543	288	2650	2419				

Table 25: The chironomid community of pool 3 (explanations and comments p 68).

	1993	1994		1995			1996				1997				1998		Total		
Site/method→	In	7	9	7	9	10	7	8	Be	m	7	8	9	m	7	8	∑	%	sex[1]
Tanypodinae																	0,1	<0.1	-
1. *Zavrelimyia* spec. **(s/a/se/?)**								0,1									0,1	<0.1	-
Diamesinae																	0,0	0.0	-
2. *Prodiamesa ulivacea* **(s/a/se/r)**														1,0			0	0.0	-
Orthocladiinae																	2057,22209+2G+2L	98.7	-
3. *Brilia modesta* **(s/a/se/r)**						1,0											1,0	<0.1	-
4. *Bryophaenocladius ictericus* **(s/t?/se/S)**						1,0											1,0	<0.1	-
5. *Bryophaenocladius* spec.♀♀ (similar to *B. virgo*) **(s/t?/p?/S?)**							0,2										0,2	<0.1	-
6. *Corynoneura scutellata* **(s/a/p/Ule)**	0,1				0,2			0,1									0,3	<0.1	-
7. *Gymnometriocnemus* cf. *subnudus* **(s/t?/se/S)**										2,0							0,0	0.0	-
8. *Heleniella ornaticollis* **(s/a/se/r+s)**						0,1											0,1	<0.1	-
9. *Limnophyes asquamatus* **(sd/sa/pse/m+w+tp)**	69,945+1L	107,228	8,50	16,12	1,0	2,12	148,161	65,70	6,4+7L+2Pex		3,12		1,0		38,78	2,17	391,640	4.2	0.611
10. *Limnophyes habilis* **(s/sa-t?/se/w+m+?)**		0,1									0,1						0,2	<0.1	-
11. *Limnophyes minimus*-aggregate **(e/sa-t/pse/Ut)**	5,52	611,917	10,138	0,15	0,30	1,11	211,211	100,278	3,2+3L+2Pex		8,22	3,14	97,115		150,530+2G	160,632	1351,2913+2G	17.3	0.464
Limnophyes minimus var. nov. **new ?**							1,0										1,0	<0.1	-
12. *Limnophyes pentaplastus* **(s/a-sa/se/U)**															1,1		1,1	<0.1	-
Limnophyes spec.									2,2+2L								0,0	0.0	-
13. *Orthocladius* spec. **(s/a/se/?)**					1L												1L	<0.1	-
14. *Paralimnophyes hydrophilus* **(sd/a-sa/se/tp)**	247,413	63,122	31,40	49,30	9,20	3,1	2,4	1,8	2L		4,3	41,57			48,55	59,91	310,431	3.0	0.719
15. *Pseudosmittia* spec. A **(e/t/p/tp,S?)**		0,402	0,227	0,2	0,498	0,386	0,532	0,4701	0,15+4L+1P		0,17	0,803	0,785		0,2823	0,6258	0,17434	70.9	0.000
16. *Pseudosmittia conjuncta* **(sd/t/p/w,tp+?)←←**							0,547	0,2							0,1	0,1	0,551	2.2	0.000
17. *Pseudosmittia curticosta* **(s/sa-t?/se/tp,sb+?)**							1,0										1,0	<0.1	-
18. *Smittia* spec. A **(r/t/p/tp+?) new?**	0,2	0,125	0,81	0,3	0,1		0,4	0,2			0,1				0,8	0,8	0,233	1.0	0.000
Orthocladiinae gen. spec.				1L		0,3	0,2										0,5+1L	<0.1	-
Chironominae/Chironomini																	91,203	1.2	-
19. *Chironomus luridus* **(s/a/se/poo)**		0,1															0,1	<0.1	-
20. *Chironomus pseudothummi*-aggregate **(s/a/se/poo)**		1,1															1,1	<0.1	-
21. *Microtendipes pedellus* **(s/a/se/Ule)**		2,0															2,0	<0.1	-
22. *Polypedilum tritum* **(r/a/se/tp+?)**		2,1	2,3	70,186	8,7				1,0		1,2	2,0			3,2		88,201	1.2	0.438
Chironominae/Tanytarsini																	1,0	<0.1	-
23. *Tanytarsus eminulus* **(s/a/se/r)**		1,0															1,0	<0.1	-
Chironominae gen spec.		0,5		0,1		1,0											1,6	<0.1	-
Total ∑		2590	590	385	577	423	1826[8]	5229[8]			74[7]	920[7]	998[7]		3740	7228	24580*	100.0	
Total year		2590[11]	590[11]	-	-	-	1826	5229			-	-	-		3740[11]	7228[11]	58**		
year m²		10360[11]	2360[11]	-	-	-	11413	32681			-	-	-		23375[11]	45175[11]	1735***		
Total aquatic		534	134	364[12]	48[12]	21[12]	315	146			25	100	1		226	169	3****		
aquatic m²		2136	536	2275[12]	300[12]	131[12]	1969	913			156	625	6		1413	1056	26376#		

Explanations and comments on Tables 23-25 and 27:

General abbreviations :

aquatic m² = aquatic + semiaquatic individuals per year and m²; **Be** = extraction of the larvae by a Berlese funnel (in part with subsequent rearing into the adults); **CP** = colonizing pool; **Cu+Chim²** = density of mosquitoes + chironomids per m² during the colonizing experiment from May 19 – July 21, 1998; **G** = intersexes (gynander); **In** = inundation experiment 1993 (see DETTINGER-KLEMM & BOHLE 1996); **L** = larva(e); **Lex** = larval exuviae; **m** = net sampling of flying/swarming males; **m²** = density of chironomids or mosquitoes per m² during the colonizing experiment from May 19 – July 21, 1998; **M** = species reared from the egg mass; **net** = net samplings or specimens found in a water sample; **P** = pupa(e); **Pex** = pupal exuviae; **Pres.** = presence (number of boxes from which the species emerged); **sex** = sex ratio (males : females); **Site 1-10** = see section 4.1.1.2.; **Total** ∑ = total number of individuals per emergence trap and trapping period; **Total aquatic** = total number of aquatic + semiaquatic individuals per emergence trap and year; **Total year** = total number of individuals per emergence trap and year; **Year m²** = individuals per year and m²; ∑ = total number of all specimens caught by emergence traps;**%** = percentage of individuals of a taxon in relation to all specimens caught by emergence traps.

Abbreviations behind species name:

In parenthesis:

1st position: Dominance of species sensu PALISSA et al. (1979) : **e** = eudominant (>10%) ; **d** = dominant (5 - 10 %) ; **sd** = sub-dominant (2-5%) ; **r** = recedent (1-2%) ; **s** = sub-recedent (<1%).

2nd position: Main habitat of larva: **a** = aquatic; **a-sa** = aquatic-semiaquatic; **sa** = semiaquatic; **sa-t** = semiaquatic – terrestrial; **t** = terrestrial.

3rd position: Kind of reproduction: **p** = parthenogenetic; **pse** = parthenogenetic- and sexual; **se** = sexual.

4th position: Habitat preference: **l** = lakes; **m** = margins of different waters; **p** = pioneer habitats; **po** = ponds; **poo** = permanent small and/or shallow water bodies (pools); **pu** = rain puddles; **r** = running waters; **S** = terrestrial soils; **s** = springs; **sb** = spring brooks; **tp** = temporary pools; **U** = ubiquist in lenitic and lotic waters; **Ule** = ubiquist in lenitic waters (recordings from different kinds of lenitic waters and from slowly running waters); **Ut**= ubiquist in aquatic and terrestrial habitats; **w** = wet soils.

Not in parenthesis:

← not listed for the region of low mountain range (= zone 2) of Germany in SAMIETZ (1996a).

←←new species for Germany (see SAMIETZ 1999).

new? = undescribed species?

Comments:

-**Males and females are separated by a comma** (first position male(s), second position female(s)).

-[1] If the females of two or more related species were not or not in every cases separable, the sex ratio was determined together for all the species concerned.

-[2] Emergence trap without trap jar. Only larger chironomids were removed from the emergence funnel by an exhaustor (term thesis on culicids). The trap was exposed from April 23 - July 7 (only 7 days of drought in May). Hence the aquatic/semiaquatic chironomid community in 1992 is only partly known.

-[3] The emergence study started at the end of the aquatic phase on May 11, 1993 (total drought between June 6-9).

-[4] The total number of individuals from the beginning of June 1993 to the end of May 1994.

-[5] Emergence samplings until the end of May 1994. Hence the aquatic/semiaquatic chironomid community of 1994 is only partly known.

-[6] Only sporadic samplings by emergence traps in July and August 1995.

-[7] Emergence samplings until the beginning of the terrestrial phase (grade of humidity 1 + 2, see Table 1 p 16).

-[8] Emergence samplings over the whole period of emergence.

-[9] Emergence trap with trap jar was exposed from April 25 - July 7, 1992. Because the pool did not dry up in 1992, the chironomid community of this year is only partly known.

-[10] Emergence samplings started on May 11 (site 6) and June 4 (sites 4 + 5), 1993. Because during the present study the aquatic/semiaquatic chironomids of sites 5 + 6 usually did not emerge before mid May, the aquatic/semiaquatic chironomid communities of these sites are also ± quantitatively known for 1993.

-[11] Emergence samplings until August 10 (1998) and 23 (1994), respectively. Because chironomids continue to emerge until the beginning of October, the total number of individuals is not known.

-[12] Emergence samplings from May 5 - July 26, 1995 (until the beginning of the terrestrial phase). The total number of aquatic/semiaquatic individuals is therefore not fully known.

-[13] The values in brackets include the specimens that had emerged from July 21 – August 11, 1998 in CP4.

-[14] no floating emergence funnel, the funnel was pressed into the mud.

* Total number of individuals caught in emergence traps.

** Total number of specimens (L, P/Pex, (fe)males, M) caught by net sampling (pool 1 + 2) or by the Berlese technique (pool 3).

*** Total number of individuals obtained during the flood experiment (DETTINGER-KLEMM & BOHLE 1996).

**** total number of males caught by net sampling of flying/swarming males.

Total number of all specimens.

semiaquatic *Limnophyes asquamatus* dominated the aquatic and semiaquatic phase of pool 3. The ubiquitous *L. minimus*-agg. (comments see section 4.3.1.2.1.) was present in high numbers in all three pools. The terrestrial *Smittia* spec. A was frequent in pool 1 whilst *Pseudosmittia* spec. A reached very high densities in pool 3. The chironomid community of pool 3 was therefore dominated by terrestrial chironomids.

In the present study terrestrial and semiaquatic - terrestrial species are excluded from further analysis and closer examinations.

4.2.1.2. Emergence periods

Figure 26 shows the observed time spans of emergence for 26 species that emerged from pools 1, 2 and 3, from the colonization pools in 1993 and 1998 and from the flood experiment 1993 (see sections 4.2.2. and 4.3.1.1.1., DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996 and Appendix 3). Only species with ≥ 10 sampling dates were considered in Figure 26, the dates of emergence of the remaining species can be taken from the Appendix 3. Pools 1 and 3 usually dried up and the emergence of a species was usually either terminated by the drought or the first spring generation did not emerge from the pool because the species was first in need to colonize the habitat. But over the years and because of the variations of the hydrological regime (see section 4.1.1.4.), the whole period of emergence became well known, especially for those species, which were present in pool 1 and 2 as well and which were not rare. Aquatic/semiaquatic species for which the emergence period was well documented are *Psectrotanypus varius*, *Xenopelopia falcigera*, *Xenopelopia nigricans*, *Corynoneura scutellata*, *Limnophyes asquamatus*, *Paralimnophyes hydrophilus*, *Chironomus luridus*, *Polypedilum tritum* and *Paratanytarsus tenellulus*. The time of the first spring emergence is also quite well known for *Natarsia punctata*, *Procladius choreus*, *Zavrelimyia* cf. *nubila*, *Acricotopus lucens*, *Chironomus piger/riparius*, *Chironomus pseudothummi/uliginosus* and *Synendotendipes impar*. Some species (*Tanytarsus buchonius*, *Micropsectra lindrothi* and *Chironomus dorsalis*; *Chironomus dorsalis* on one occasion in pool 1 on June 14, 1992) emerged only in the colonization pools and must have been the offspring of at least one preceding generation that had emerged in May. The aquatic/semiaquatic species *Limnophyes pentaplastus* and *Psectrocladius* cf. *sordidellus* must have had a generation prior to the first half of June and second half of May respectively (FRITZ 1982, BECKER 1995, SCHNABEL 1999) and it is likely that these two species had appeared in pools 1-3 always as new colonizers.

4.2.1.3. Colonizer or aestivator?

My previous work (DETTINGER-KLEMM 1995a and DETTINGER-KLEMM & BOHLE 1996) demonstrated that *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* are able to aestivate the drought period in dry mud. These species are called aestivators. All other species are supposed to be unable to survive longer periods of drought and must therefore recolonize the pool after its refilling. These species are called colonizers (see section 5.3.5.3. for discussion).

That the colonizers actually disappeared after longer periods of drought and then recolonized the

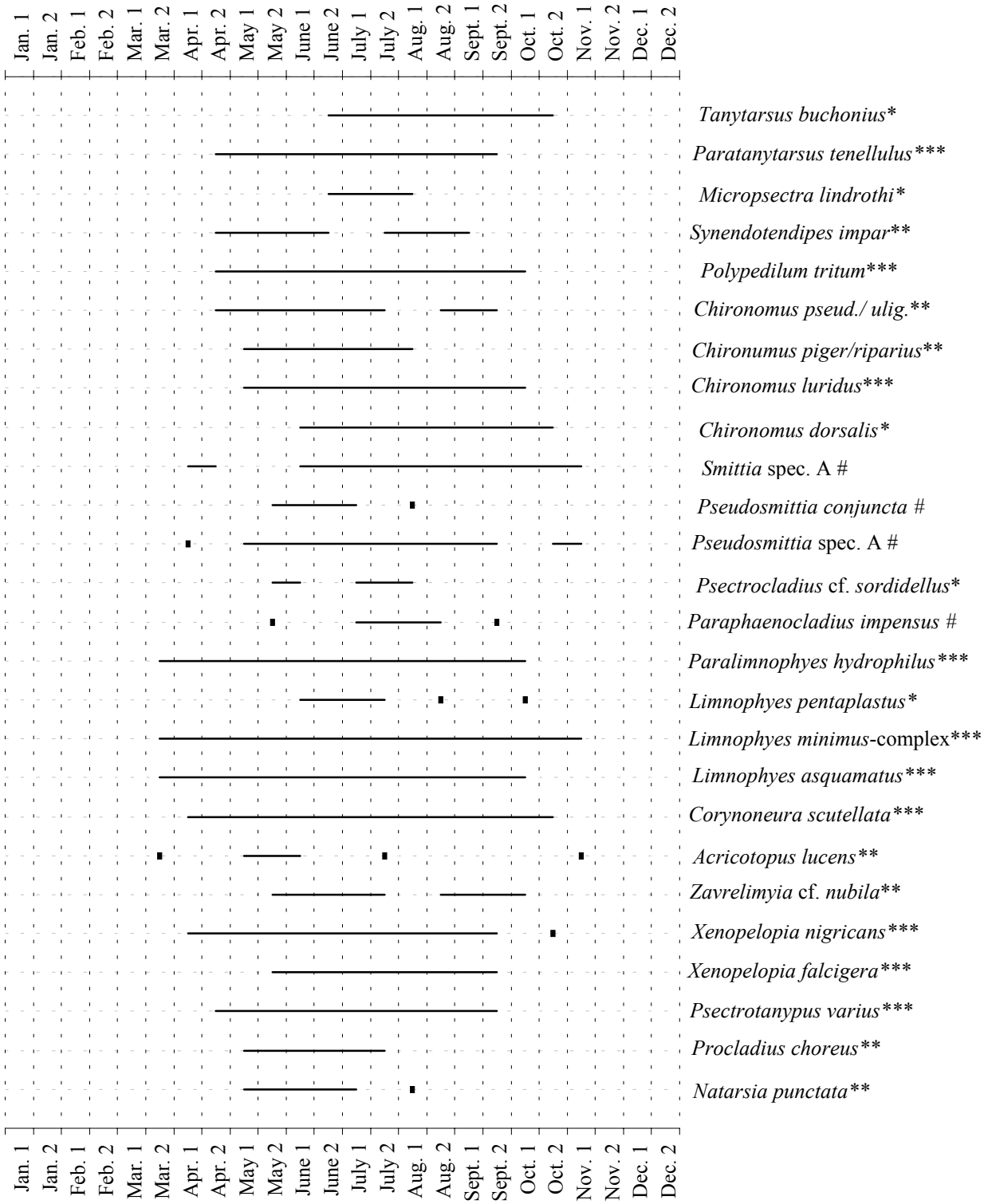

Figure 26: The observed emergence of the species with ≥ 10 sampling dates (see also Appendix 3).

Comments:

Jan. 1/2 etc. = first half/second half of the month.

* The species was only found as a colonizer, the emergence of the first spring generation from the hibernating habitat is therefore not known.

** The period of emergence shows gaps and/or is incomplete: a) too few observations, b) the emergence had been stopped by the drought period of the pool or c) by the end of the colonizing experiment.

*** The period of emergence is well known (precondition: hibernating in the habitat and no drought at least in one year).

In terrestrial species the occurrence is strongly dependent on the time of drought and the degree of humidity of the soil. This explains the gaps within the emergence period despite the high N.

Table 26: The emergence characteristics of aquatic/semiaquatic chironomids emerging from pool 1 in 1998 and 1999.

Species (rel. abundance in 1998)	1998			1999	
	First	Generation	Last	First	Generation
Monopelopia tenuicalar (< 0.1 %)	Aug. 3	S	Aug. 3	May 19	F?
Natarsia punctata (< 0.1 %)	Aug. 3	S	Aug. 3	May 7	F
Procladius choreus (0.1 %)	June 17	S	June 25	May 7	F
Psectrotanypus varius (2.4 %)	June 3	S	Sept. 21	April 2	F
Xenopelopia falcigera (1.4 %)	July 9	S	Sept. 11	June 9	F
Xenopelopia nigricans (10.8 %)	June 3	S	Oct. 19	April 16	F
Zavrelimyia cf. *nubila* (0.1 %)	Sept. 21	S	Sept. 21	June 18	F?
Acricotopus lucens (< 0.1 %)	Mar. 30	F	Mar. 30	-	-
Corynoneura scutellata (14.2 %)	May 5	S	Oct. 19	April 16	F
Limnophyes asquamatus (0.2 %)	Mar. 30	F	May 27	-	-
Limnophyes pentaplastus (< 0.1 %)	June 10	S?	June 10	June 25	S?
Paralimnophyes hydrophilus (11.4 %)	Mar. 30	F	Sept. 30	May 5	S
Psectrocladius sordidellus (< 0.1 %)	May 20	S?	May 20	-	-
Chironomus longipes (< 0.1 %)	Aug. 18	S?	Aug. 18	-	-
Chironomus luridus (0.5 %)	June 3	S	July 24	May 7	F
Ch. pseudothummi/uliginosus (2.9 %)	June 3	S	July 24	April 24	F
Parachironomus parilis (< 0.1 %)	June 17	S?	June 17	-	-
Phaenopsectra punctipes (0.1 %)	Aug. 3	S?	Aug. 18	-	-
Polypedilum tritum (54.8 %)	April 30	F	Sept. 21	April 24	F
Paratanytarsus tenellulus (0.5 %)	June 10	S	Sept. 11	April 30	F

Abbreviations:

First/Last = date of the first/last emergence; **Generation** = estimate (based on the data listed in the Appendix 3) of whether a species belonged to the first spring generation (**F**) or to any of the subsequent generations (**S**) (a **question mark** symbolizes estimates for species which emergence period is not well known (see section 4.2.1.2.); **rel. abundance** = percentage of the total aquatic/semiaquatic species that had emerged from pool 1 in 1998.

habitat after the refilling is demonstrated by the emergence of chironomids from pool 1 in 1998 and 1999 (Table 26). In 1997 pool 1 dried up from mid July to the beginning of November (see section 4.1.1.4.1.). For 1998 only the first emerging adults of *Acricotopus lucens* (only one specimen), *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* can be assigned to the first spring generation. These were aestivators, except for *Acricotopus lucens,* which must have colonized the habitat in November 1997. The first emergence of all other species must be assigned to generations succeeding the first spring generation, a strong hint that they had colonized the pool only in 1998. In 1998, pool 1 showed only a short period of total drought (19.8.-22.8. and 29.8.-1.9.) during which the mud remained wet on the sites that had dried up last. The colonizers could therefore have survived the short period of drought in the mud or colonized the habitat again after its refilling in September. The data of Table 26 show (column 'Last'), that at least the larvae of *Psectrotanypus varius*, *Xenopelopia falcigera*, *Xenopelopia nigricans*, *Zavrelimyia* cf. *nubila*, *Corynoneura scutellata*, *Paralimnophyes hydrophilus*, *Polypedilum tritum* and *Paratanytarsus tenellulus* were present in pool 1 after the short period of drought and it is most likely these larvae also hibernated in pool 1. It is therefore not surprising that, with the exception of *Limnophyes pentaplas-*

tus and *Paralimnophyes hydrophilus*, all the species encountered from pool 1 in 1998 and 1999 emerged during the period of the first spring emergence in 1999. It is likely that *Limnophyes pentaplastus* and *Paralimnophyes hydrophilus* had been overlooked during the first spring emergence in 1999 due to their low population densities.

In species with well-known emergence periods, the decision of whether a specimen can be assigned to the first spring generation or not was not problematic. In addition to the date of emergence, there were also often morphological peculiarities, which separate specimens of the first spring generation from such of the succeeding generations. The specimens of the first spring generation are often darker and larger (e.g. *Xenopelopia nigricans* (see comments in Appendix 3), *Chironomus luridus*, *Chironomus piger/riparius* and *Chironomus pseudothummi/uliginosus* (see Appendix 7), *Chironomus dorsalis*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* (see sections 4.4.2.2.1., 4.4.2.2.2. and 4.4.2.3.2.)) or there is a clear seasonal dimorphism in coloration as observed in *Paratanytarsus tenellulus* (see comments in Appendix 3). According to the emergence data all species must be polyvoltine. To estimate whether a species should be assigned to the first spring generation or to any of the succeeding generations, a minimum generation time of about 4 weeks was assumed (see sections 4.4.1.2.4.- 4.4.1.2.6., 4.4.2.1. and 4.4.2.3.1.). For example: in *Chironomus luridus* May 7 was the very first date of emergence during all the years of investigation. Specimens, which emerged from the beginning of June onwards, were assigned to the succeeding generations.

Though abundant, the emergence data of *Corynoneura scutellata* do not clearly show that the species is a colonizer that becomes extinct in periods of drought. The emergence of this species is therefore illustrated in Figure 27. There were long periods of drought in 1996 (pool 1) and 1997 (pool 1 and 2). In the succeeding years the first adults of *Corynoneura scutellata* appeared on May 6, 1998 (pool 1), May 10, 1997 (pool 1) and May 13, 1998 (pool 2). The first peaks of emergence in 1997 and 1998 were low and can be clearly separated from the second peaks, which were much more pronounced, especially in pool 1. As mentioned above, pool 1 dried up only for a very short period in 1998. But even this short period of drought had stopped the emergence of *Corynoneura scutellata* and only one female was recorded to emerge after the refilling. Some larvae therefore appear to have survived the drought period and it is most likely that some larvae hibernated in pool 1. In 1999 only one female was recorded to emerge within the sampling interval of April 4-16. This female is supposed to belong to the first spring generation of *Corynoneura scutellata*. In the current study, only a second female was recorded to emerge in April (April 11, 1994, pool 1). As a result the emergence of the first spring generation of *Corynoneura scutellata* is not well known, but is assumed to start at the beginning of April. The adults that had emerged within the first peaks of the emergence in May 1997 and 1998 must therefore be considered the offspring of colonizing females.

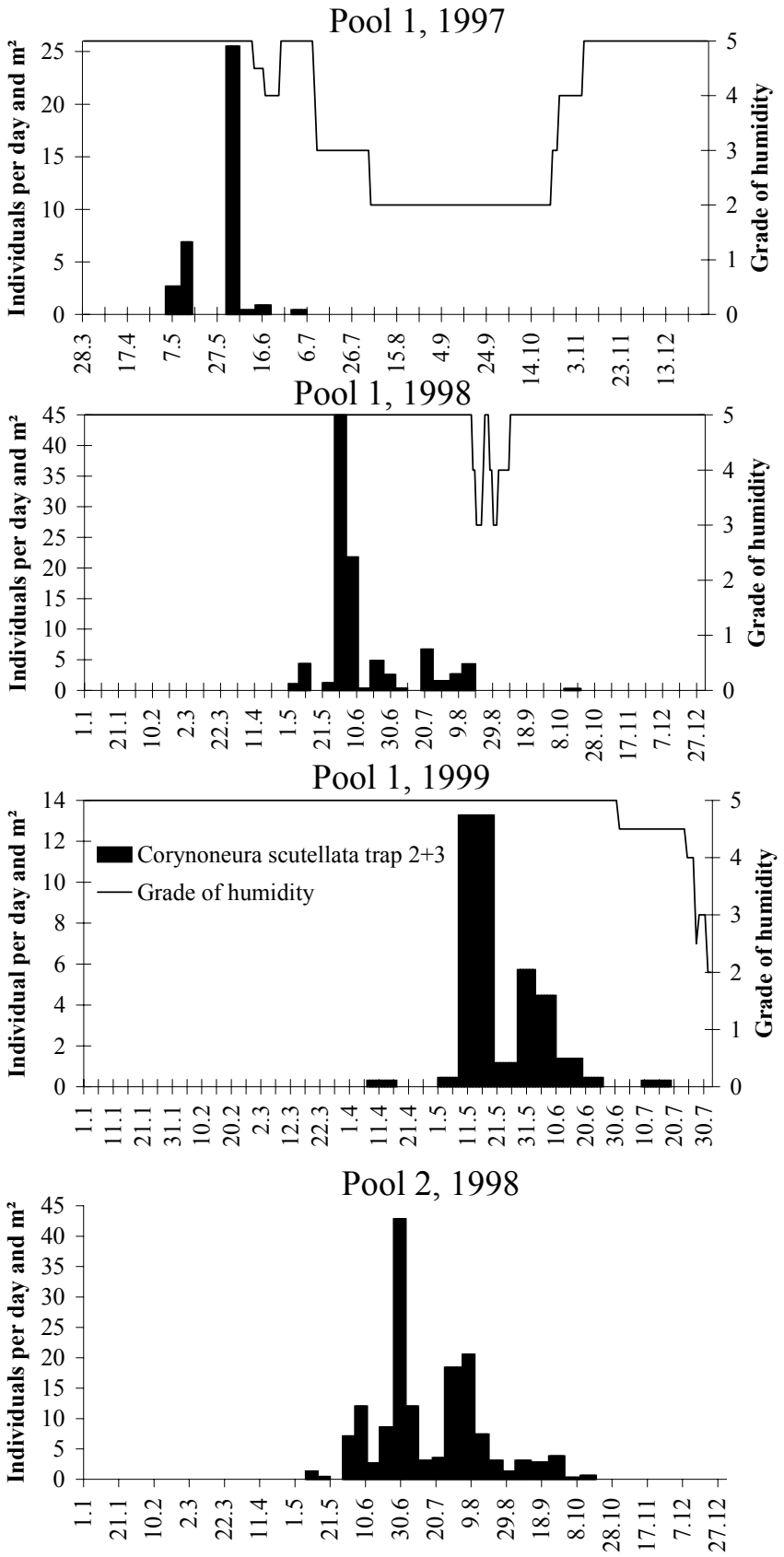

Figure 27: The emergence of *Corynoneura scutellata* from pool 1 (1997-1999) and pool 2 (1998).
Grade of humidity see Table 1 p 16.

4.2.1.4. Typical colonizers

The most abundant colonizers in pools 1-3 were typical species of small and/or shallow water bodies. They were represented by *Psectrotanypus varius*, *Xenopelopia falcigera*, *Xenopelopia nigricans*, *Chironomus luridus*, *Chironomus pseudothummi/uliginosus* and *Paratanytarsus tenellulus* (Table 22). In respect to the two species of *Xenopelopia* it is interesting that they clearly differed in respect to their period of emergence (Figure 26). *Zavrelimyia* cf. *nubila* is also typical for small and/or shallow water bodies but this species was only recorded in small numbers in pool 1 (12) and 2 (2). Only one colonizer of quantitative importance, *Corynoneura scutellata*, was an ubiquist. *Natarsia punctata* (more abundant only in pool 1, 1999), *Chironomus piger/riparius* (more abundant only in pool 1, 1996), *Synendotendipes impar* (more abundant only in pool 2, 1993 and 1998), *Parachironomus parilis* (more abundant only in pool 2, 1997) and *Procladius choreus* (regularly but small numbers of individuals present in pools 1 and 2) were other ubiquist colonizers of which more than 10 individuals had been recorded.

4.2.1.5. Main characteristics of the aquatic/semiaquatic chironomid communities

Figure 28 shows the relative composition of aestivators and colonizers of pool 1 and 2, respectively.

The share of aestivators in **pool 1** exceeded 60 % for the most part of the investigation. *Limnophyes asquamatus* was present in low numbers, *Paralimnophyes hydrophilus* and especially *Polypedilum tritum* were the characteristic aestivator species of the pool (Table 22). The share of aestivators was lower than 60 % in 1996 and 1999 on sites 2 and 3 and in 1998 on site 2. All these years showed peculiarities in the abiotic environment, especially in the water balance:

(1) In 1996 the numbers of emerging chironomids were the lowest for the period from 1996-1999 (for 1994, see comment Nr. 5 in 'explanations and comments on Tables 23-25 and 27' p 68): The previous year showed a drought period of unusual length (refilling in December, see Figure 18 p 53) and some of the physicochemical parameters seen in 1996 also differed from those observed in other years (section 4.1.1.3.1.).

(2) The pool had dried up for a long period in 1997, but for only a few days in 1998 (Figure 18 p 53). The number of emerging adults of the first spring generation of *Polypedilum tritum* (see section 4.4.2.1.1.) on trap sites 2 and 3 in 1998 was identical (81 individuals on site 2 and 80 on site 3) but the subsequent generations developed more successfully on site 3 (the share of the first spring generation on the species' total yield was 29 % on site 2 and 12 % on site 3). The number of emerging adults of the first spring generation of *Paralimnophyes hydrophilus* (see section 4.4.2.1.3.) was lower on site 2 (19 individuals) than on site 3 (40 individuals). On both trap sites the share of the first spring generation of *Paralimnophyes hydrophilus* on the total yield in 1998 was about 30 %.

(3) 1999 was an exception as it was preceded by the semi permanent hydroperiod in 1998. The pool dried up in July 1999 as in most of the other years (Figure 18 p 53). The relative abundance of the aestivators (except one specimen of *Paralimnophyes hydrophilus* only *Polypedilum tritum*)

and their density were strongly graded in pool 1 in 1999. On the very temporary sites 1b and 1c (Table 16 p 55) the relative abundance of *Polypedilum tritum* exceeded 80 % and the species density was extremely high (6494 individuals per m² and year on site 1b; because the trap on site 1c was pressed into the soil (no floating funnel trap) the density of this site was not compared with the other sites). On trap site 3, which was situated the furthest from the very tempo-

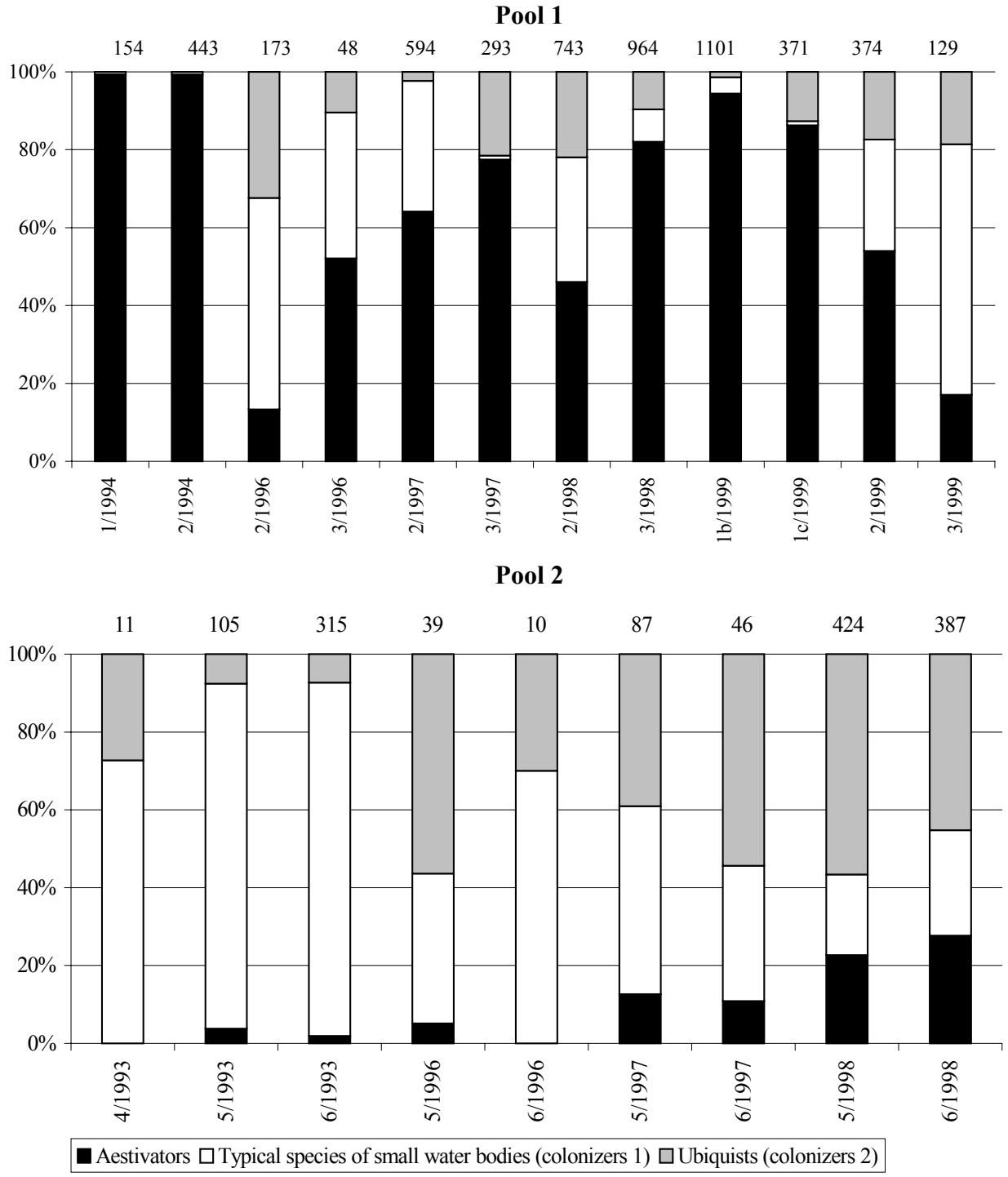

Figure 28: Relative abundances of aquatic/semiaquatic aestivators and colonizers in pools 1 and 2.

Comments:

- The numbers of aquatic/semiaquatic individuals are shown above the columns.
- Each column represents the annual crop of one trap site (e.g. 4/1993 = annual crop of aquatic/semiaquatic chironomids of trap site 4 in 1993).

rary part of pool 1 (Figure 9, p 41), the relative abundance and density of *Polypedilum tritum* were lowest. The results for site 2 were intermediate (Table 23).

The main characteristics of **pool 2** were a low number of emerging chironomids and a dominance of the colonizers (Figure 28). *Corynoneura scutellata* was the most abundant of the ubiquists. This species' relative abundances on the trap sites from 1994-1998 were: 4/1994: 0 %, 5/1993: 9 %, 6/1993: 3 %, 5/1996: 33 %, 6/1996: 20 %, 5/1997: 21 %, 6/1997: 33 %, 5/1998: 51 % and 6/1998: 42 %. The number of emerging chironomids was higher as in the other years in 1993 and 1998. The aestivators (*Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum*) were more numerous in 1998, the previous year showed a drought period of an unusual length.

Except some single records of colonizers, the aquatic/semiaquatic chironomid community of **pool 3** consisted of only three species of aestivators. The most abundant aestivator was *Limnophyes asquamatus* (1031 individuals) followed by *Paralimnophyes hydrophilus* (741 individuals) and *Polypedilum tritum* (289 individuals). The number of emerging adults of the semiaquatic *Limnophyes asquamatus* fluctuated strongly between the trap sites and years (Table 25). Because there was no aquatic phase in spring, only few specimens of the aquatic - semiaquatic *Paralimnophyes hydrophilus* emerged in 1996. In comparison with the other years, the number of emerging adults of *Paralimnophyes hydrophilus* was also unusually low on trap site 7 in 1997. Only few adults of the aquatic *Polypedilum tritum* were recorded every year, except in 1995. The pool dried up unusually late in 1995 (see section 4.1.1.4.3.) and a second generation of *Polypedilum tritum* was enabled to emerge from the pool (Figure 80 p 172).

Figure 29 summarizes the main characteristics of the aquatic/semiaquatic chironomid communities by help of a cluster analysis. Three main branches bifurcated primarily according to the predominance of *Limnophyes asquamatus* (branch 1), *Paralimnophyes hydrophilus* (branch 2) and *Polypedilum tritum* (branch 3). Trap sites of pool 1 and 2 were all united in branch 2, which also comprises four samplings in pool 3. The greater similarities were usually between the chironomid communities of pool 1 and 2, samplings of pool 3 being less similar to the others. As shown above the aquatic/semiaquatic chironomid community of pool 3 usually consisted only of two aestivator species (*Paralimnophyes hydrophilus* and *Limnophyes asquamatus*), except in 1995 when *Polypedilum tritum* was also frequent. For this year, the yield of trap site 7 was grouped into branch 3a together with three samplings of pool 1. Altogether, the chironomid community of pool 1 stands between those of pool 2 and 3. As mentioned above, *Polypedilum tritum* usually dominated within the chironomid communities of pool 1, followed by *Paralimnophyes hydrophilus*. But the chironomid community of pool 1 also contained higher proportions of colonizers (main species see section 4.2.1.4.), which caused the community of pool 1 to be quite similar to that of pool 2. Several colonizers (see above), the most important of which were *Psectrotanypus varius*, *Xenopelopia falcigera*, *Xenopelopia nigricans*, *Chironomus luridus* and *Corynoneura scutellata*, always dominated the chironomid communities of pool 2. The composition of the chironomid communities during the different years of investigation clearly reflects the different hydrological regimes of the three pools

investigated (see section 4.1.1.4.). The opposite habitats were pools 2 and 3, the first being semi permanent the second regularly dries up for several months. The water balance of pool 1 was in between pools 2 and 3. Therefore the cluster analysis arranged the samplings according to a gradient of habitat duration bottom up the ordinate (see sections 5.1.2. and 5.2.1).

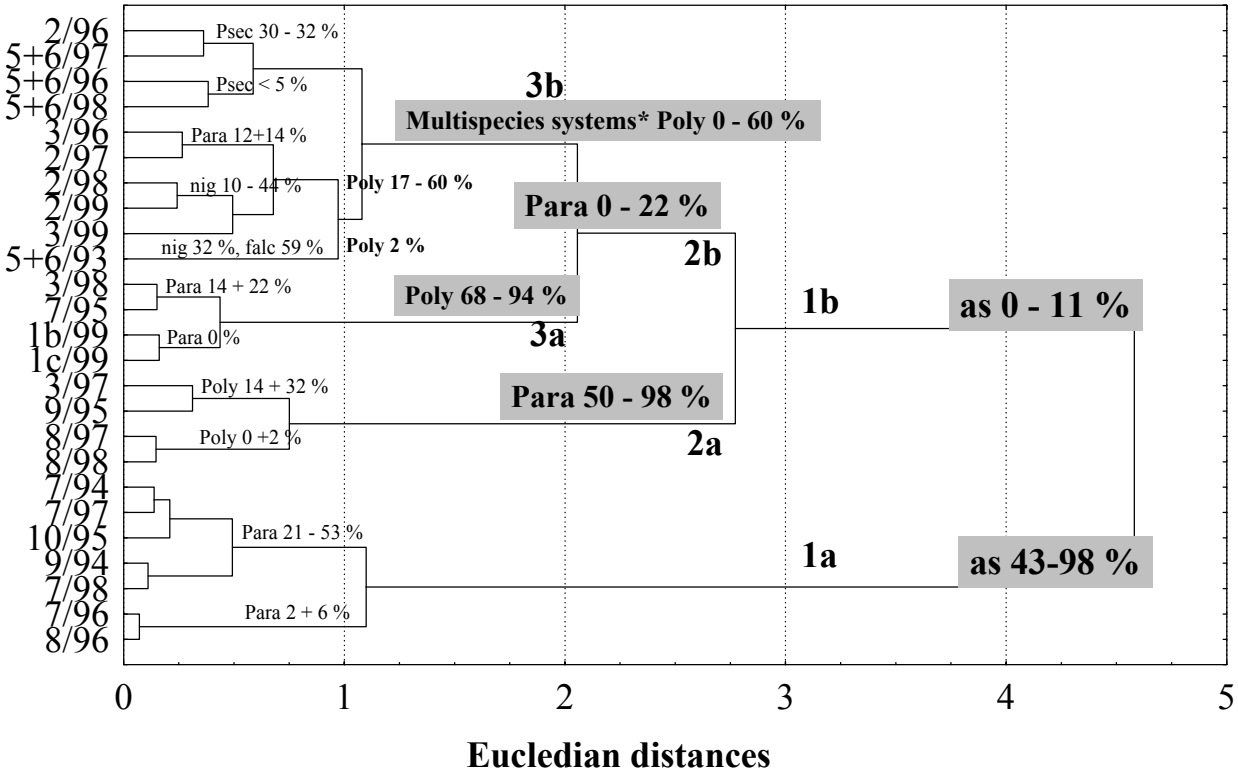

Figure 29: Cluster analysis (method sensu WARD 1963) of the aquatic/semiaquatic chironomid communities found in the trap sites of pools 1-3.

Comments:

The relative abundances of the species per trap site and year were used for the analysis. Because of the often-low N of emerging chironomids of trap sites 5 + 6, abundances were grouped in the analysis (the traps were standing close together, identical hydrological regime).

Only yields that recorded the aquatic/semiaquatic community at least almost quantitatively were considered in the analysis.

Main species for subdivision are written at the bases of the cluster branches: as = *Limnophyes asquamatus*, falc = *Xenopelopia falcigera*, Para = *Paralimnophyes hydrophilus*, Poly = *Polypedilum tritum,* Psec = *Psectrotanypus varius,* nig = *Xenopelopia nigricans.*

* Usually the following species were present and partly high abundant at the sampling sites (the number of sites without the species is set in brackets before the species name and the maximum abundance behind it): (1) *Corynoneura scutellata* (48 %), (2) *Paralimnophyes hydrophilus* (16 %), (1) *Polypedilum tritum* (60 %), (1) *Psectrotanypus varius* (32 %), (1) *Xenopelopia nigricans* (44 %).

2/96 etc. = trap site/year of recording; 1a - 3b = branch number.

4.2.2. The midge community of the colonizing experiment

4.2.2.1. General results

The emergence funnels of the colonizing experiment trapped 21 chironomid- and 2 mosquito species (Table 27). To the exception of seven species (*Bryophaenocladius illimbatus*, *Metriocnemus* cf. *eurynotus*, *Chironomus annularius*, *Cladotanytarsus* spec. *Micropsectra lindrothi*, *Paratanytarsus grimmii* and *Tanytarsus buchonius*), the majority of species (the mosquito species inclusively (see DETTINGER-KLEMM 1995a)) also occurred in pools 1-3. Contrasting with the situation in the three natural pools of the Lahnberge mountain range (section 4.2.1.), the proportion of Orthocladiinae was low (5 %) and the Chironomini predominated (76.9 %) the chironomid communities of the experimental pools. A further and characteristic difference with the chironomid communities of pools 1-3 is the relatively high proportion of Tanytarsini (16.7 %), which emerged from the colonizing pools. The latest column of Table 27 provides the number of experimental pools from which a given species had emerged (presence). *Chironomus dorsalis*, *Chironomus piger/riparius* and *Culex torrentium* were found in all experimental pools, *Tanytarsus buchonius* and *Culex pipiens* in 8 pools and *Corynoneura scutellata* in 6 pools. All other aquatic species were present in less than 5 experimental pools. The species with highest presence (to the exception of *Corynoneura scutellata*) accounted for the 96.5 % of the total number of individuals caught (*Chironomus dorsalis* 40.0 %, *Culex torrentium* 20.4 %, *Chironomus piger/riparius* 16.7 %, *Tanytarsus buchonius* 9.8 % and *Culex pipiens* 9.6 %). *Chironomus dorsalis* was therefore the most dominating midge species of the colonizing experiment, present in all experimental boxes and emerging with high numbers of individuals (Table 27).

4.2.2.2. Emergence

The first midges emerged on June 11 (boxes 4, 5 and 9) and on June 17 (remainder of boxes) (Figure 30). *Chironomus dorsalis*, *Culex pipiens* and *Culex torrentium* accounted for > 60 % of the midge species that emerged until June 24 and for < 50 % of those that had emerged until the end of the experiment on July 21. Generally the midge communities became more diverse towards the end of the experiment.

The time of the first emergence within an experimental box depends on the time a species needs for colonization and the duration of total development (development from egg until the adult). The very first adult midges had emerged after 15-23 days and belonged to the two mosquito species (Figure 31). *Chironomus dorsalis* showed a very low variance in respect to the first emergence: in seven experimental boxes the first individuals emerged after 23-29 days and in the remaining three after 29-36 days. Because the variance of the first emergence in *Culex pipiens* and *Culex torrentium* was higher than for *Chironomus dorsalis*, the median values of these three species were approximately the same. Though the time of the very first emergence of *Chironomus piger/riparius* and *Chironomus dorsalis* was the same, the median value was higher in the first species. The very first individuals of *Corynoneura scutellata* emerged after 23-29 days too. However, the variance was very high,

Table 27 : The chironomid/mosquito communities of the colonizing experiment (May 19 – July 21 (August 11), 1998) (for explanations and comments see p 68).

Colonozing pool→	CP1	CP2	CP3	CP4	CP5	CP6	CP7	CP8	CP9	CP10	∑	%	sex[1]	Pres.
Tanypodinae											87 (90)[13]	1.3	-	
1. *Procladius choreus* **(s/a/se/U)**								2,1			2,1	<0.1	-	1
2. *Psectrotanypus varius* **(s/a/se/po + poo)**				(2,1)[13]							(2,1)[13]	-	-	(1)
3. *Zavrelimyia* cf. *nubila* **(r/a/se/poo + p)**		18,20	19,23		2,2						39,45	1.3	0.867	3
Orthocladiinae											325 (363)[13]	5.0	-	
4. *Bryophaenocladius illimbatus* **(s/t/se/S?)**				(2,1)[13]					1,0		1,0 (3,1)[13]	<0.1	-	1 (2)
5. *Corynoneura scutellata* **(sd/a/p/Ule)**		0,64	0,4	(0,14)[13]	0,1			0,2	0,88	0,39	0,198 (0,212)[13]	3.0	0.000	6 (7)
6. *Cricotopus sylvestris* **(s/a/se/Ule)**	6,0						0,1		2,2	1,11	9,14	0.4	0.643	4
7. *Limnophyes asquamatus* **(s/sa/p/m+w+tp)**				0,3 (0,18)[13]			0,5		0,2	0,1	0,11 (0,26)[13]	0.2	0.000	4
8. *Limnophyes minimus*-aggregate **(s/sa-t/pse/Ut)**		2,5		0,1		0,1	1,0	1,0	0,1	0,3	4,11	0.2	0.364	7
9. *Limnophyes pentaplastus* **(s/a-sa/se/U)**		20,24						2,0	0,3		22,27	0.8	0.815	3
10. *Metriocnemus* cf. *eurynotus* **(s/a-sa/pse/m+s)**		6,1									6,1	0.1	-	1
11. *Paraphaenocladius* spec. **(s/sa-t?/ ?/ ?)**							0,2				0,2	<0.1	-	1
12. *Psectrocladius* cf. *sordidellus* **(s/a/se/Ule)**				13,5 (15,9)[13]						1,0	14,5 (16,9)[13]	0.3	1.778	2
Chironominae/Chironomini											4961 (5354)[13]	76.9	-	
13. *Chironomus annularius* **(s/a/se/po)**								1,0			1,0	<0.1	-	1
14. *Chironomus dorsalis* **(e/a/se/pu+p)**	122,83	153,116	245,199	166,145 (373,275)[13]	18,8	22,10	246,199	194,117	323,223	477,332	1966,1432 (2173,1562)[13]	52.9	1.391	10
15. *Chironomus piger/riparius* **(e/a/se/Ule)**	92,60	90,41	75,45	197,187+1G (215,225+1G)[13]	70,22	68,22	123,109	35,24	45,35	117,77	912,622 + 1G (930,660+1G)[13]	23.8	1.409	10
Chironomus piger/riparius/ Type "*lugubris*"	1,0	1,0									2,0	<0.1	-	
16. *Paratendipes albimanus* **(s/a/se/U)**									1,2		1,2	<0.1	-	1
17. *Polypedilum tritum* **(s/a/se/tp+?)**				(0,1)[13]			1,0	2,0	4,2		7,2 (7,3)[13]	0.1	-	3 (4)
Chironominae/Tanytarsini											1076 (1674)[13]	16.7	-	
18. *Cladotanytarsus* spec. **(s/a/se/ ?)**				8,10 (10,12)[13]			7,16				15,26 (17,28)[13]	0.6	0.607	2
19. *Micropsectra lindrothi* **(r/a/se/p + s)**			13,17	38,40 (45,47)[13]				5,1			56,58 (63,65)[13]	1.8	0.969	3
20. *Paratanytarsus grimmii* **(s/a/p/pu+poo, po, l)**				0,15 (0,309)[13]							0,15 (0,309)[13]	0.2	0.000	1
21. *Tanytarsus buchonius* **(e/a/se/pu,s,sb)**	1,0	325,241	28,22	48,83 (199,218)[13]			4,14	41,31	20,31	9,3	476,425 (627,560)[13]	14.0	1.120	8
Tanytarsus spec.				0,4							0,4	<0.1	-	
Chironominae gen spec.								0,1			0,1	<0.1	-	
Total∑	365	1127	690	964 (1997)[13]	123	123	728	460	785	1071	6436* (7482)[13]*	100.0		
m²	2281	7044	4319	6025 (12481)[13]	769	769	4625	2875	4906	6694				
Culicidae														
1. *Culex pipiens* **(e/a/se/pu, tp,poo)**	6,0			78,0	6,0	221,0	86,0	16,0	76,0	31,0	520,0	18.8		8
2. *Culex torrentium* **(e/a/se/pu,tp)**	315,0	48,0	20,0	85,0 (92,0)[13]	112,0	81,0	142,0	13,0	169,0	123,0	1108,0 (1115,0)[13]	40.2	1.439	10
Culex torrentium/pipiens	0,322	0,41	0,11	0,109 (0,114)[13]	0,54	0,176	0,127	0,34	0,176	0,81	0,1131 (0,1136)[13]	41.0		
Total∑	643	89	31	272 (284)[13]	172	478	355	63	421	235	2759 (2771)[13]*	100.0		
m²	4019	556	194	1700 (1775)[13]	1075	2988	2219	394	2631	1469				
Cu+Chi m²	6300	7600	4513	7725 (14256)[13]	1844	3756	6769	3269	7538	8163				

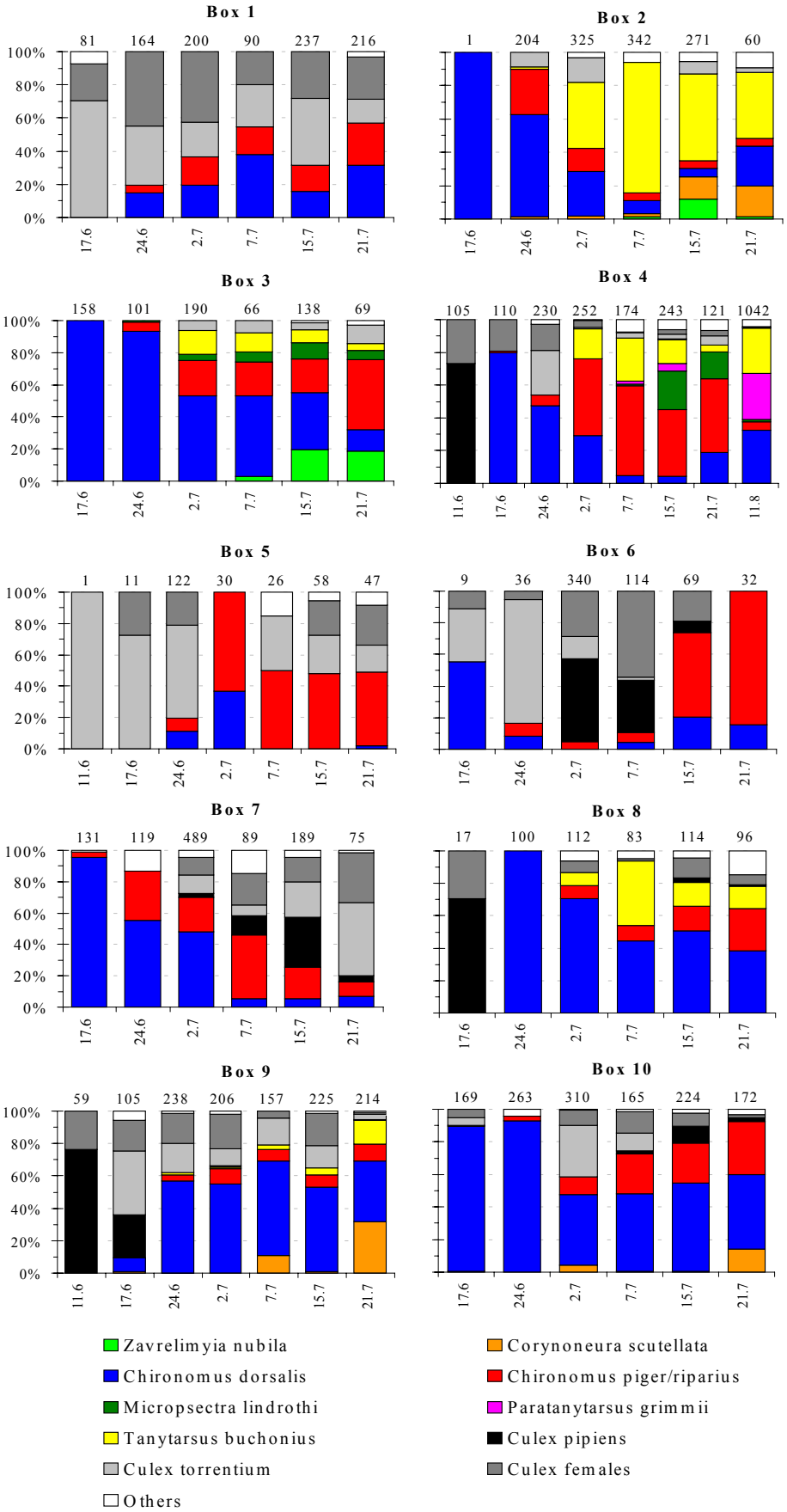

Figure 30: Relative abundances (%) of the emerging species of midges during the successive samplings in the colonizing experiment, 1998.
The numbers of emerged individuals are written above the columns.

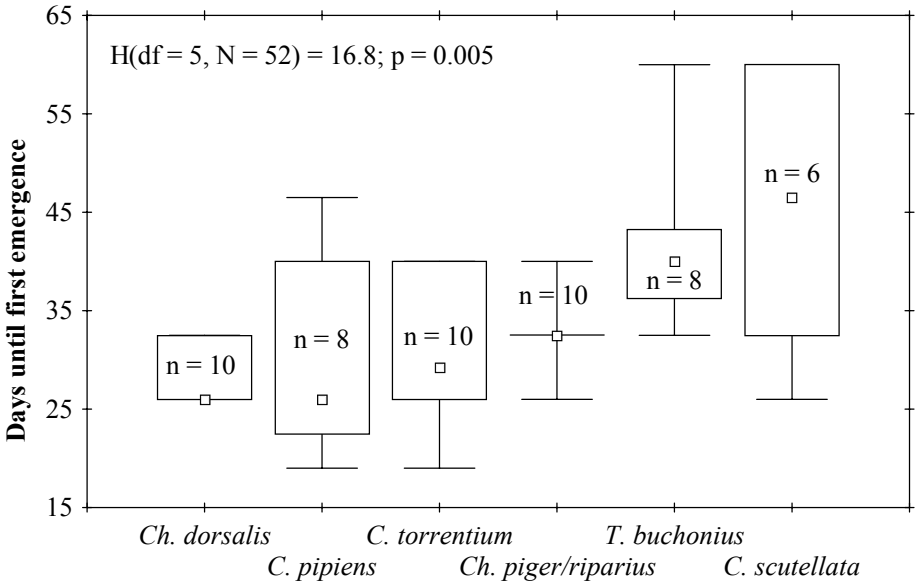

Figure 31: The first emergence of six species that occurred in more than 5 experimental boxes (numbers within the box plots) of the colonizing experiment until July 21, 1998.
H = H-statistics with p value of the KRUSKALL-WALLIS-ANOVA.

which resulted in a high median value of first emergence. The very first emergence of *Tanytarsus buchonius* was the latest (29-36 days) and its median value was located in between *Chironomus piger/riparius* and *Corynoneura scutellata*. The results of the first emergence were then compared by a KRUSKAL-WALLIS-ANOVA, which gave a significant result (Figure 31). When comparing the species' first emergence dates with a MAN-WHITNEY-U-test for matched pairs, the tests only showed significant differences for the following combinations:

C. dorsalis ↔ *T. bochonius* (U = 3.0; p = 0.001; p_{corr} = 0.005)

C. dorsalis ↔ *C. piger/riparius* (U = 23.5; p = 0.045; p_{corr} = 0.225)

C. dorsalis ↔ *C. scutellata* (U = 8.0; p = 0.017; p_{corr} = 0.085)

Cu. pipiens ↔ *T. buchonius* (U = 29.0; p = 0.032; p_{corr} = 0.160)

Cu. torrentium ↔ *T. buchonius* (U = 14.0; p = 0.021; p_{corr} = 0.105)

C. piger/riparius ↔ *T. buchonius* (U = 11.0; p = 0.010; p_{corr} = 0.05)

After applying the standard BONFERRONI-technique (Table 10 p 38), the only remaining differences of statistical significance were between *C. dorsalis* and *T. buchonius* and between *C. piger/riparius* and *T. buchonius*.

4.2.2.3. Did the distance to natural aquatic habitats cause differences in the colonization pattern of the experimental boxes?

To answer the headline question different correlations (Table 28) and a cluster analysis (Figure 32) were carried out.

Correlations: The distance to any of the three closest aquatic habitats (Figure 2 and Table 4 p 20)

Table 28: Colonizing experiment, 1998: correlations of the number of emerged species (Species), the time until the very first emergence of midges (First) and the mean value of first emergence of all midge species (Mean first) with distances to the three nearest potential colonization sources (ponds 1 and 2 and sewage plant (see Figure 2 and Table 4 p 20 and text)).

Distance from		Species	First	Mean first
	Normality	W = 0.95 p = 0.648	W = 0.59 p < 0.001	W = 0.94 p = 0.629
Mean distance	W = 0.944 p = 0.580	r = 0.304 F (1.8) = 0.81 p = 0.39	γ = 0.400 Z = 1.05 p = 0.289	r = 0.164 F (1.8) = 0.22 p = 0.651
Nearest aquatic habitat	W = 0.948 p = 0.633	r = 0.059 F (1.8) = 0.02 p = 0.870	γ = 0.524 Z = 1.44 p = 0.150	r = 0.197 F (1.8) = 0.32 p = 0.586
Pond 1	W = 0.889 p = 0.156	r = 0.519 F (1.8) = 2.95 p = 0.124	γ = -0.143 Z = -0.39 p = 0.694	r = 0.136 F (1.8) = 0.15 p = 0.708
Pond 2	W = 0.927 p = 0.402	r = 0.318 F (1.8) = 0.90 p = 0.370	γ = 0.048 Z = 0.13 p = 0.896	r = 0.172 F (1.8) = 0.24 p = 0.634
Sewage plant	W = 0.974 p = 0.919	r = 0.323 F (1.8) = 0.93 p= 0.362	γ = 1.000 Z = 2.75 p = 0.006 p_{corr} = 0.030	r = 0.051 F (1.8) = 0.02 p = 0.890

Explanations:

- If the SHAPIRO-WILK-W-test for normality (=Normality) did not reject the null hypothesis of normality, PEARSON´s r with F-statistics was used for correlations. If the null hypothesis of normality was rejected GOODMAN-KRUSKAL´s γ with t-statistics was applied for the analysis (multiple ties).
- The only significant correlation was that of the time of the first emergence with the distance to the sewage plant (shaded box). Because the same sample was used for five correlations the Standard BONFERRONI-technique was applied (see Table 10 p 38) and the p-value adjusted (= p_{corr}).

may have influenced the colonization of the experimental pools in two ways: (1) by causing differences in the number of emerged species (hypothesis: the more distant, the fewer species → negative values for r and γ); and (2) by altering the time of colonization by egg-laying females (hypothesis: the more distant, the later the very first emergence of midges or the higher the mean value of first emergence of all midge species present in a box, respectively → positive values for r and γ). Because the chironomid communities of the three nearest potential colonization sources were unknown, five different distance values were used for the correlations: (a) the mean distance of a box from all three potential colonization sources; (b) the distance to the next aquatic habitat; and (c) the distance to ponds 1 and 2 and to the sewage plant. Neither the species number nor the mean values of first emergence showed significant correlations to any of the distance values. There was one significant correlation between the very first emergence of midges and the distance to the sewage plant. The midges emerged earlier in experimental boxes 4, 5 and 9, which were situated next to the sewage plant (2 x *C. pipiens* (n = 164), 1 x *Culex torrentium* (n = 1), see Figure 30 p 80).

Cluster analysis: If any colonization source had affected the chironomid communities (species

composition and relative abundances of the species) of the experimental boxes this might have resulted in a regular pattern of similarity in the cluster analysis. Figure 32 shows that:

(a) the midge communities of all experimental boxes were very similar (Euclidean distances between the clusters < 0.7, compare with Figure 29 p 77);

(b) there are two main clusters, one with communities dominated by mosquitoes (boxes 1, 5 and 6), the other by chironomids (remainder of boxes). It is likely that the communities of experimental boxes 5 and 6 were greatly affected by pesticides applied in the adjacent rape fields at the end of June. The two main clusters do not reflect the spatial arrangement of the boxes;

(c) the arrangement of the sub clusters does not reflect the spatial arrangement of the experimental boxes either.

The results of this section show that the chironomid communities of the experimental boxes are very similar and that the differences observed cannot be explained by the spatial arrangement of the boxes in respect to the three closest aquatic habitats (except in the case of the first emergence of mosquitoes and the distance from the sewage plant).

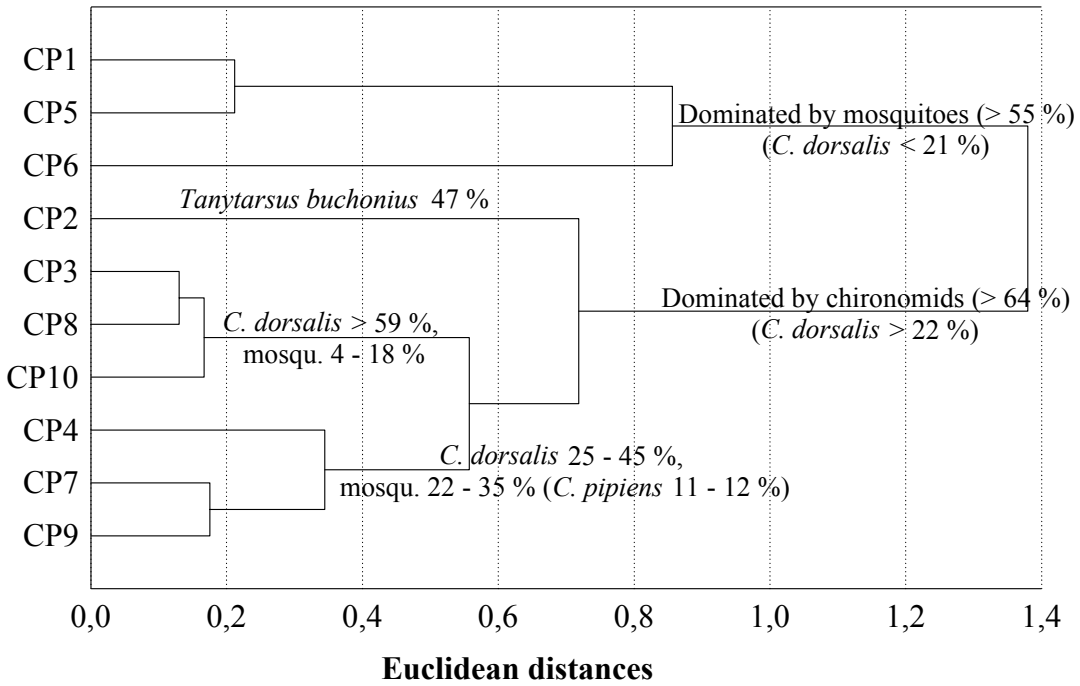

Figure 32: Cluster analysis (method sensu WARD 1963) of the aquatic/semiaquatic midge communities (relative abundances of the species were used for the analysis) emerging from the experimental boxes (CP) 1-10 of the colonizing experiment from June 11 - July 21, 1998.

4.3. Morphology and taxonomy

In section 4.2. it was shown that *P. tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* were the typical and specific chironomids of pools 1-3 and *Chironomus dorsalis* the most dominant midge species of the colonizing experiment. The autecology of these four species will be analysed in section 4.4.. The scope of the present section is to provide information on the four species' taxonomy, on some morphological aspects of the larvae as well as of the adults and to present illustrations of the species' metamorphosis. It was necessary to carry out an extensive morphological-taxonomical analysis for *Limnophyes asquamatus*.

4.3.1. *Limnophyes*

4.3.1.1. Taxonomy and parthenogenesis of Limnophyes asquamatus ANDERSEN, 1937

4.3.1.1.1. Introduction

This section is based on my earlier study on the biology of *L. asquamamatus* (see DETTINGER-KLEMM 1995a and DETTINGER-KLEMM & BOHLE 1996) and aims at elucidating the species' ecological role and mode of parthenogenesis. In DETTINGER KLEMM & BOHLE (1996) we interpreted the mode of parthenogenesis as being facultative, mainly based on figure 2e of this publication, which is also shown below (Figure 33). In this experiment a group sample of soil was taken from pool 3 about 60 days after the total drought. This soil sample was then transferred and flooded in a large plastic bucket, which had been exposed outdoors and connected with an emergence trap (see 'In' in Figure 4 p 23). During the first weeks of the experiment, the water surface was totally covered by a dense and thick layer of organic material, which then sunk to the bottom. Ten days after the flooding the first adults emerged and the emergence did not stop until the end of the experiment in October 25, 1993 . The emergence pattern showed three peaks. During the first peak, the share of males was 0.44 (n = 207). Only few males emerged during the second peak (sex ratio 0.02, n = 243)

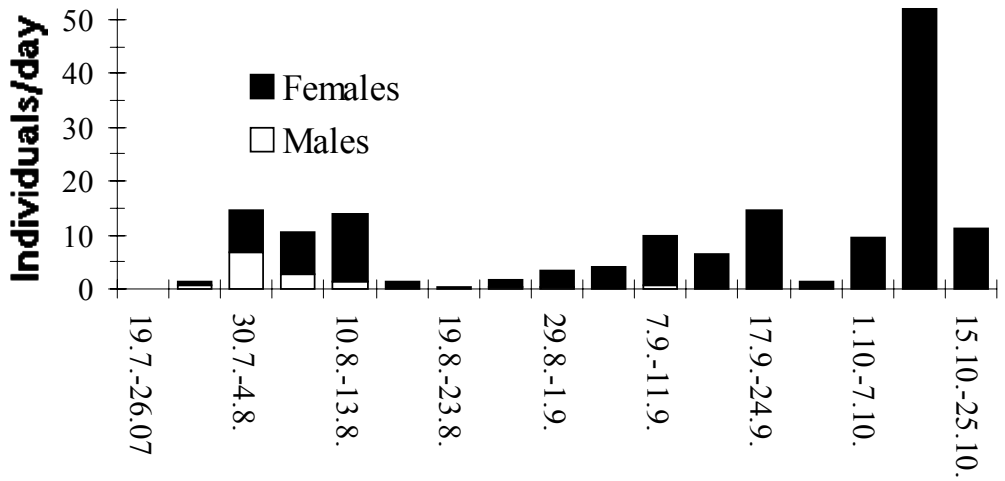

Figure 33: The emergence of *L. asquamatus* in the flood experiment 1993 (DETTINGER-KLEMM & BOHLE 1996).

and no males during the third (n = 555). We interpreted these results as an example of facultative parthenogenesis: after the emergence of the first generation, the species reproduced parthenogenetically within the experimental unit. The disappearance of males might have been caused by a failure to mate or by an environmental switch. I will come back to this experiment in section 4.3.1.1.7.. The task of this section is to test the validity of our previous assumption of facultative parthenogenesis.

4.3.1.1.2. Lab rearings

Figure 34: Habitus of a parthenogenetic female of *Limnophyes asquamatus* reared in a laboratory culture with specimens from pool 3.

In **1996**, the establishment of laboratory cultures with specimens taken from pool 3 failed (vessels 1-25 in Table 5 p 22). Twenty-one egg masses were laid in the culture vessels, which had been stocked with the number of adults exactly known (vessels 1-12, 13 (first run) and 14-17: 98♂♂, 61♀♀). None of these egg masses showed signs of development. Thirteen females, which had laid an egg mass, were mounted on slides as well as three females, which had laid none. Though the size of the culture vessels had varied from very small ('tube', see 'abbreviations and comments for tables 5 and 6' p 24) to very large ('T8', see 'abbreviations and comments and comments for Tables 5 and 6' p 25) the males did not swarm and no single observation of mating was done.

In **1997,** two further attempts at rearing the species were undertaken and parthenogenetic generations of *L. asquamatus* developed spontaneously in culture vessel 26 and 27, respectively (Table 5 p 22). Again, no mating or swarming was observed and no males occurred in any of the subsequent parthenogenetic generations.

The parthenogenetic individuals of vessels 26 and 27 were used to initiate parthenogenetic cultures with varying environmental conditions (Table 6 p 24). No male emerged from any of these cultures. One hundred and forty-one parthenogenetic females from these cultures were mounted on slides (Table 6 p 24).

On balance the results of the rearings of *L. asquamatus* are:

(1) there were females (called sexual in the subsequent study), which obviously laid non-developing

eggs without previous mating;

(2) parthenogenetic females produced only parthenogenetic females without mating;

(3) there seems to be no environmental switch inducing the development of males within the parthenogenetic lab cultures.

4.3.1.1.3. One or two species?

The results of the lab rearings arise the question whether *Limnophyes asquamatus* includes two species, a sexual and a parthenogenetic one. To clarify this question, five parthenogenetic females from culture vessel 28 (Nos 1512-1516 in Table 6 p 24) and 5 sexual females (Nos 1379-1383 in Table 5 p 22) were singly mounted on slides as explained in PINDER (1989) and described for taxonomic use (Table 29). Generally, the morphological parameters were measured only for one parthenogenetic and one sexual female, respectively. If a parameter seemed to show morphological differences, further specimens were measured in order to accept or reject the trend. The morphological analysis showed a very high correspondence of the morphological parameters between the parthenogenetic and sexual females. Figure 35 shows the results for two characteristic parameters (WL/ThL as parameters characterizing the species' size; LR_{p1} as an often used taxonomic character) for a greater number of females from different localities. The LR-value of the front leg showed no correlation with the body size and a range of 0.46-0.53; 0.50. As expected, the wing length (865-1334 µm) is highly correlated with the thorax length (450-750 µm). In both parameters there were absolutely no differences between the parthenogenetic and sexual females. There did seem to be clear differences between the parthenogenetic and sexual specimens only in the number of preepisternals (Pes) and the presence or absence of a lanceolate prescutellar bristle on each side of Prescutellum (Table 29).

The hypothesis that the parthenogenetic and the sexual specimens belong to two separate species which can be separated by the presence (sexual) or absence (parthenogenetic) of lanceolate prescutelars and the number of preepisternals (low number: sexual, high number: parthenogenetic) was then tested in a large scale comparison of specimens. Appendices 4 and 5 provide an overview of the material studied. Figure 36 shows the result of a comparison of females with and without lanceolate prescutellars. It is obvious that females with lanceolate prescutellars had significantly lower numbers of preepisternals (females from The Netherlands were an exception). Nevertheless, the number of preepisternals of females with- and without lanceolate prescutellars strongly overlapped. Females with lanceolate prescutellars were also found in culture vessels 28 and 32 of the parthenogenetic lab rearings (Table 6 p 24, Table 30). In respect to this character, all kinds of transitions between females with one lanceolate prescutellar on both sides of prescutellum and those without such bristles could be observed. However, between the parthenogenetic females with at least one lanceolate prescutellar and those with none, there was also a significant difference in the number of preepisternals (Figure 36). Because this result may be attributed to the different size of the specimens of the parthenogenetic lab cultures (see section 4.3.1.1.4.), the comparison was repeated for each culture vessel separately (Table 30). For the individuals raised in culture vessel 28 the p-value slightly exceeded the significance level ($\alpha = 0.05$), but the result was highly significant

Table 29: Description of the parthenogenetic and sexual females of *Limnophyes asquamatus*.

Part of body	Parameter	sex	Ind. Nr.	parth	Ind. Nr.	SÆTHER
Size	TL	**1366**	1381	**1839**	1516	**1888**
	WL	**1035**	1381	**1041**	1516	**1440**
	WW	**400**	1381	**411**	1516	
	TL/WL	1.32	1381	1.77	1516	1.24
	WL/WW	2.59	1381	2.53	1516	
Antenna	Fm	1+2,3,4,5	1381	1+2,3,4,5	1516	
	L Fm1	**43**	1379	**43**	1516	**45**
	L Fm2	**41**	1379	**37**	1516	**49**
	L Fm3	**46**	1379	**51**	1516	**49**
	L Fm4	**46**	1379	**47**	1516	**45**
	L Fm5	**97**	1379	**94**	1516	**96**
	AR	0.53	1379	0.53	1516	0.55-0.60
	b/SCh1*	4/1	1379	5/0	1516	
	b/SCh2*	5/2	1379	5/2	1516	
	b/SCh3*	5/2	1379	5/2	1516	
	b/SCh4*	5/2	1379	5/2	1516	
	b/SCh5*	5/>3	1379	5/9	1516	
	ApS	present	1379	present	1516	
Head	CS?**	no	1381	no	1516	yes
	IV	1	1381	1	1516	1
	OV	2	1381	2	1516	1
	Po	3	1381	2	1516	2
	Cls	17	1381	19	1516	12
	IoD***	**186**	1381	**191**	1516	
	L Pm1	**19**	1381	**20**	1516	**23-30**
	L Pm2	**30**	1381	**28**	1516	**38**
	L Pm3	**60**	1381	**58**	1516	**41-64**
	L Pm4	**57**	1381	**49**	1516	**45-60**
	L Pm5	**80**	1381	**95**	1516	**75-96**
	b Pm1	no	1381	no	1516	
	b Pm2	3	1381	2	1516	
	b Pm3	7/1SCl	1381	7/1SCl	1516	
	b Pm4	6	1381	6	1516	
	b Pm5	8	1381	7	1516	
	L tentorium	**107**	1381	**95**	1516	**116**
	W tentorium	**15**	1381	**13**	1516	**15**
	L stipes	**96**	1381	**95**	1516	**105**
	W stipes			**25**	1516	**30**
	shape CP	#	1381	#	1516	
Thorax	mAps	4-5	1379 + 1381	3	1516	3-4
	lAps	6-7	1379 + 1381	8	1516	4-5
	shape HP($^{1-4}$)	(1)-(4), see abbreviations	1379-1382	(4), see abbreviations	1512-1516	± (4)
	H+Dc	~12-15	1379 + 1381	13	1516	12-15
	Prs^{+}	1 lanc	1379 + 1381-1383	1 normal	1512, 1513-1515, 1516	0-1 lanc
	Ac	9^{++}	1379	9^{++}	1516	4-8
	Pa	6-7	1379 + 1381	7	1516	5-6
	Su	1	1379 + 1381	1	1512	1
	Pes	3-10	1379-1383	14-18	1512-1516	6-9
	b PA II	2-3	1379 + 1381	3-4	1512 + 1516	1-3
	b E II	7	1379	8	1516	4-5
	Scts	~5-6	1380 + 1383	7	1516	5-6
Wing	VR	1.30	1379	1.39	1516	1.25
	b Sq	2-5	1379-1382	2	1512 + 1516	3-4
	b R	10	1379	11	1516	~10
	b R_{1+2}	5	1379	5	1516	
	b R_{3+4}	12	1379	10	1516	
Leg	pulvilli?	no	1379	no	1516	
	L fe p_1	415	1379	386	1516	
	L tibia p_1	**455-496**	1379 + 1381	**465**	1516	
	L ta_1 p_1	**228-235**	1379 + 1381	**230**	1516	
	L ta_2 p_1	**146-158**	1379 + 1381	**138**	1516	
	L ta_3 p_1	**98-115**	1379 + 1381	**107**	1516	
	L ta_4 p_1	**58**	1381	**58**	1516	
	L ta_5 p_1	**67**	1381	**70**	1516	
	L TS p_1	**21-26**	1379 + 1381	20	1516	
	LR p_1	0.47-0.50	1379 + 1381	0.49	1516	
	BV p_1	2.91	1381	2.90	1516	
	SV p_1	3.71-3.87	1379 + 1381	3.70	1516	

Table 29 (continued).

Part of body	Parameter	sex	Ind. Nr.	parth	Ind. Nr.	SÆTHER
Leg continued	Ps p_1	no	1373	no	1516	
	SCh p_1	no	1373	no	1516	
	L fe p_2	**454**	1373	**437**	1516	
	L tibia p_2	**459**	1373	**429**	1516	
	L ta_1 p_2	**189**	1373	**180**	1516	
	L ta_2 p_2	**115**	1373	**98**	1516	
	L ta_3 p_2	**78**	1373	**76**	1516	
	L ta_4 p_2	**50**	1373	**46**	1516	
	L ta_5 p_2	**62**	1373	**64**	1516	
	L TS p_2°	**18/18**	1373	**17/16**	1516	
	LR p_2	0.41	1373	0.42	1516	
	BV p_2	3.61	1373	3.68	1516	
	SV p_2	4.83	1373	4.81	1516	
	Ps p_2	no	1373	no	1516	
	SCh p_2	no	1373	no	1516	
	L fe p_3	**436-475**	1379 + 1381	**432**	1516	**425**
	L tibia p_3	**474-507**	1379 + 1381	**487**	1516	**452**
	L ta_1 p_3	**248-280**	1379 + 1381	**255**	1516	**236**
	L ta_2 p_3	**134-143**	1379 + 1381	**127**	1516	**118**
	L ta_3 p_3	**123-135**	1379 + 1381	**128**	1516	**123**
	L ta_4 p_3	**53-57**	1379 + 1381	**53**	1516	**47**
	L ta_5 p_3	**67-69**	1379 + 1381	**67**	1516	**57**
	L TS p_3°	**40-49/16**	1379 + 1381	**37/14**	1516	**45/17**
	LR p_3	0.55	1379	0.52	1516	0.49
	BV p_3	3.12	1379	3.13	1516	3.32
	SV p_3	3.50	1379	3.60	1516	3.84
	Ps p_3	no	1379	no	1516	
	SCh p_3	no	1379	no	1516	
	TC	11	1379	8	1512	
	longest S°°	**~34**	1379	**39**	1512	
	shortest S°°	**~19**	1379	**20**	1512	
Abdomen	b T_I	~20	1381			8-16
	b T_{II}	~20	1381	18	1516	~17-20
	b T_{III}	~15	1381	24	1516	20-25
	b T_{IV}	~16	1381	27	1516	22-23
	b T_V	16-31	1381 + 1383	28	1516	23
	b T_{VI}	18	1381	28	1516	24-25
	b T_{VII}	24	1381	~30	1516	15-18
	b T_{VIII}	20	1381	~24	1516	17-19
	b S_I	~4	1381			0
	b S_{II}	~8	1381	~11	1516	3-4
	b S_{III}	10	1381	17	1516	7-13
	b S_{IV}	19	1381	26	1516	13-25
	b S_{5V}	~17	1381	26	1516	13-27
	b S_{VI}	23	1381	26	1516	16-27
	b S_{VII}	20	1381	23	1516	20-26
	b S_{VIII}	15	1381	14	1516	17-19
Genitalia	b T_{IX}	~17-~24	1381 + 1383	22-~24	1514 + 1516	14-24
	shape T_9	weakly bilobed	1381	weakly bilobed	1514	weakly bilobed
	L Gc IX	**53**	1380	**43**	1515	**68-75**
	W Gc IX	**30**	1380	**33**	1515	
	b Gc $IX^{(a-c)}$	a	1380	b	1515	9-14
	L Ce	**62**	1380	**62**	1515	**60-70**
	L No	**99**	1381	**92-101**	1512 + 1514	**101-113**

Abbreviations: The morphological terms and standard abbreviations used follow SÆTHER (1980), unless otherwise stated.
Column names: sex/parth = sexual/parthenogenetic females (see section 4.3.1.1.2.); Ind. Nr. = individual Nr. of measured specimen(s); SÆTHER = values according to SÆTHER (1990).
L = length**; W** = width**; b** = number of bristles; ~ = about; **bold** = measurements in µm; **not bold** = number of setae, ratio etc.
b/SCh1-5* = number of bristles/sensilla chaetica on flagellomeres 1-5.
CS?** = coronal suture complete?
IoD*** = interocular distance.
shape $HP^{(1-4)}$ = (1) = humeral pit ovoid, posterior ridge strongly sclerotisized, without additional depressions,
(2) =humeral pit ovoid on one side, on the other with two separate semicircular depressions,
(3) = humeral pit ovoid on one side, on the other with two separate small circular depressions,
(4) = humeral pit with posterior semicircular ridge and several cuticular depressions.
Prs^+ = number of lanceolate (lanc) or normal bristles on Prescutellum.
L TS $p_{2,3}$° = length of both tibial spurs are separated by a slash.
longest S/shortest S°° = length of longest/shortest spine on tibial comb.
= labial lonchus with stick-like sclerotisized process apically, bordered by four pores on each side.
$^{++}$ = anterior acrostichals only slightly and posterior clearly scalpellate.
a = four long basiomedial and six shorter and more slender apical bristles present.
b = two long basal and five shorter and more slender apical bristles present.

for the individuals from culture vessel 32. I observed also a transition in the shape of the lanceolate prescutellar bristles in the material from the inundation experiment (see section 4.3.1.1.1.). As a rule, lanceolate prescutellar bristles are clearly shorter (< 50 µm) than non-lanceolate bristles (> 70 µm). But in the inundation experiment there were also many specimens with prescutellars that clearly showed an intermediate shape. This transition is also reflected in the lengths (35-76; 51 µm) of prescutellars measured in 41 females originating from the inundation experiment.

The great overlap of the characters studied allows the rejection of the hypothesis of two separate species at least in a morphological point of view.

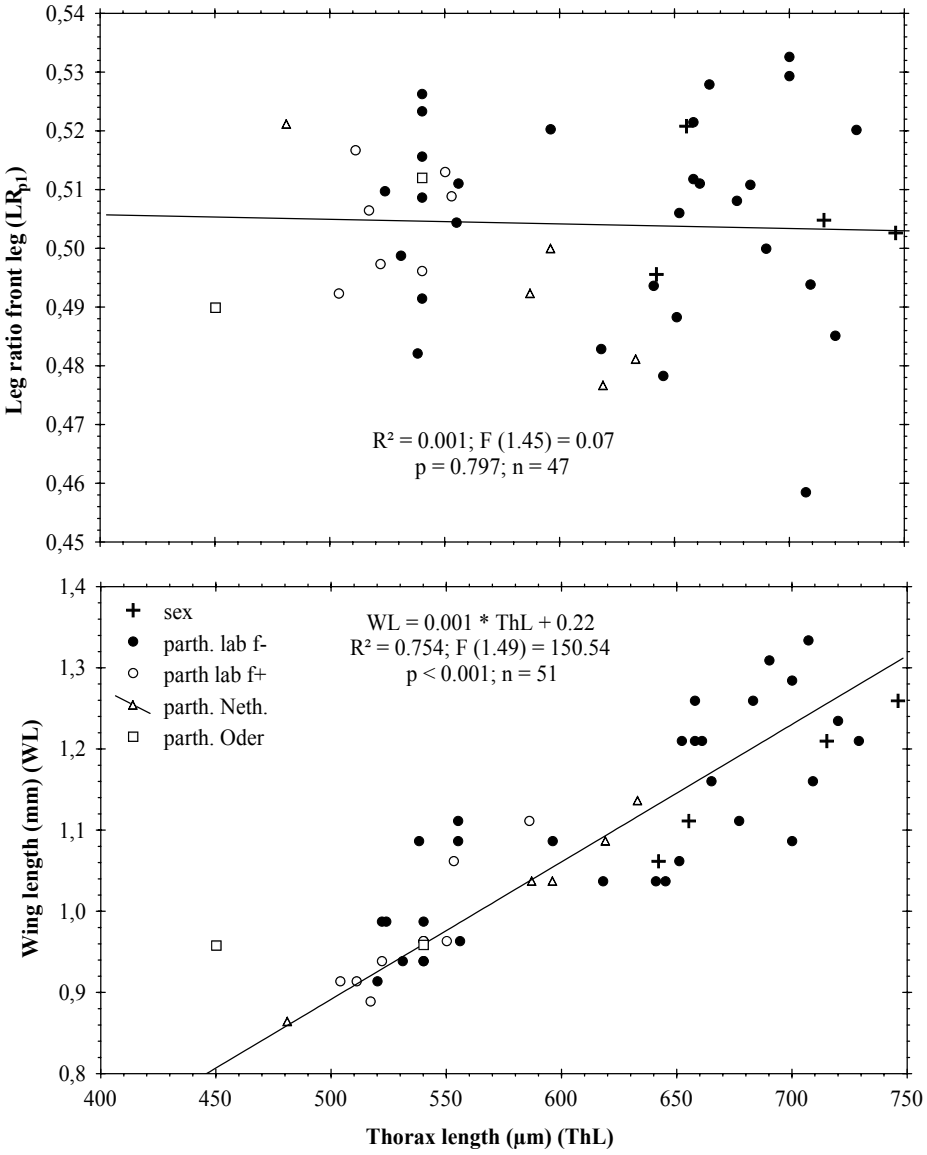

Figure 35: The (in)dependence of the wing length and leg ratio from body size (here characterized by the thorax length) in parthenogenetic and sexual females of *Limnophyes asquamatus*.

Abbreviations:

sex = sexual females from the laboratory (see section 4.3.1.1.2.);

parth. lab f+/- = females from the parthenogenetic lab rearings with (+) and without (-) lanceolate prescutellars (see section 4.3.1.1.2. and this section);

parth. Neth./Oder = parthenogenetic females from laboratory rearings from The Netherlands (Haarsteeg and s' Herzogenbosch, see Appendix 5) and the "Untere Odertal" (Germany, see Appendix 4).

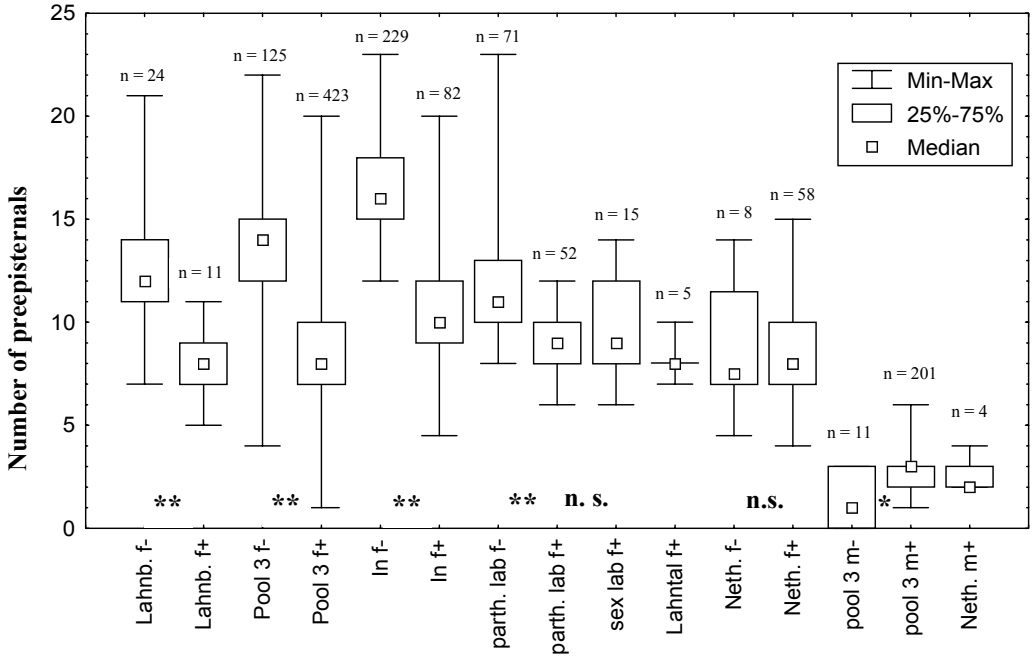

Figure 36: Comparison of the number of preepisternals in specimens of *Limnophyes asquamatus* with and without lanceolate prescutellars.

Abbreviations and comments:

-/+ = without/with lanceolate prescutellars; **In** = inundation experiment 1993 (DETTINGER-KLEMM & BOHLE 1996); **Lahnb.** = specimens from the Lahnberge mountain range others than from pool 3 (pool 1 + 2, colonizing experiments 1993 + 1998, see Appendix 4); **Lahntal** = females from two pools of the floodplain of the river Lahn near Marburg (SCHNABEL & DETTINGER-KLEMM 2000); **Neth**. = specimens from The Netherlands (see Appendix 5); **parth lab** = specimens from parthenogenetic lab rearings (Table 6 p 24); **sex** = sexual females from the lab (Table 5 p 22).

The **significance** of the differences was tested by MAN-WHITNEY-U-tests for matched pairs (* = $p < 0.01$; ** = $p < 0.001$; **n. s.** = not significant ($p > 0.05$)).

Tab. 30: The presence of lanceolate prescutellar bristles in the parthenogenetic females from the lab cultures.

Vessel/Temp/Density	0	0.5	1	?	MAN-WHITNEY-U-test
28/20 °C/low larval densities	**5**				
28/10 °C/high larval densities	**26**	**14**	**1**	**1**	**U = 100.5; p = 0.051**
29/10 °C/low larval densities	**8**				
30/15 °C/low larval densities	**4**			**1**	
31/15 °C/low larval densities	**3**				
32/20 °C/high larval densities	**30**	**12**	**27**	**9**	**U = 230.5; p < 0.001**

Abbreviations:

Vessel/Temp/Density = number of culture vessel/temperature at the time of preservation/larval density at the time of preservation (see Table 6 p 24).

0 = no lanceolate prescutellar; **0.5** = one lanceolate prescutellar on one side of prescutellum and none or a normal one on the other side; **1** = one lanceolate prescutellar bristle on both sides of prescutellum; **?** = prescutellar bristles broken off.

MAN-WHITNEY-U-test = comparison of the number of preepisternals between females with at least 0.5 lanceolate prescutellar and such without a lanceolate prescutellar (see text).

4.3.1.1.4. Is it possible to morphologically separate parthenogenetic from sexual females?

Figure 37 shows the results of two regressions for the number of preepisternals and body size for 41 parthenogenetic specimens of the different lab cultures (Table 6 p 24) and 31 sexual females, respectively. Fourteen of the sexual females originated from the lab (see section 4.3.1.1.2. and Table

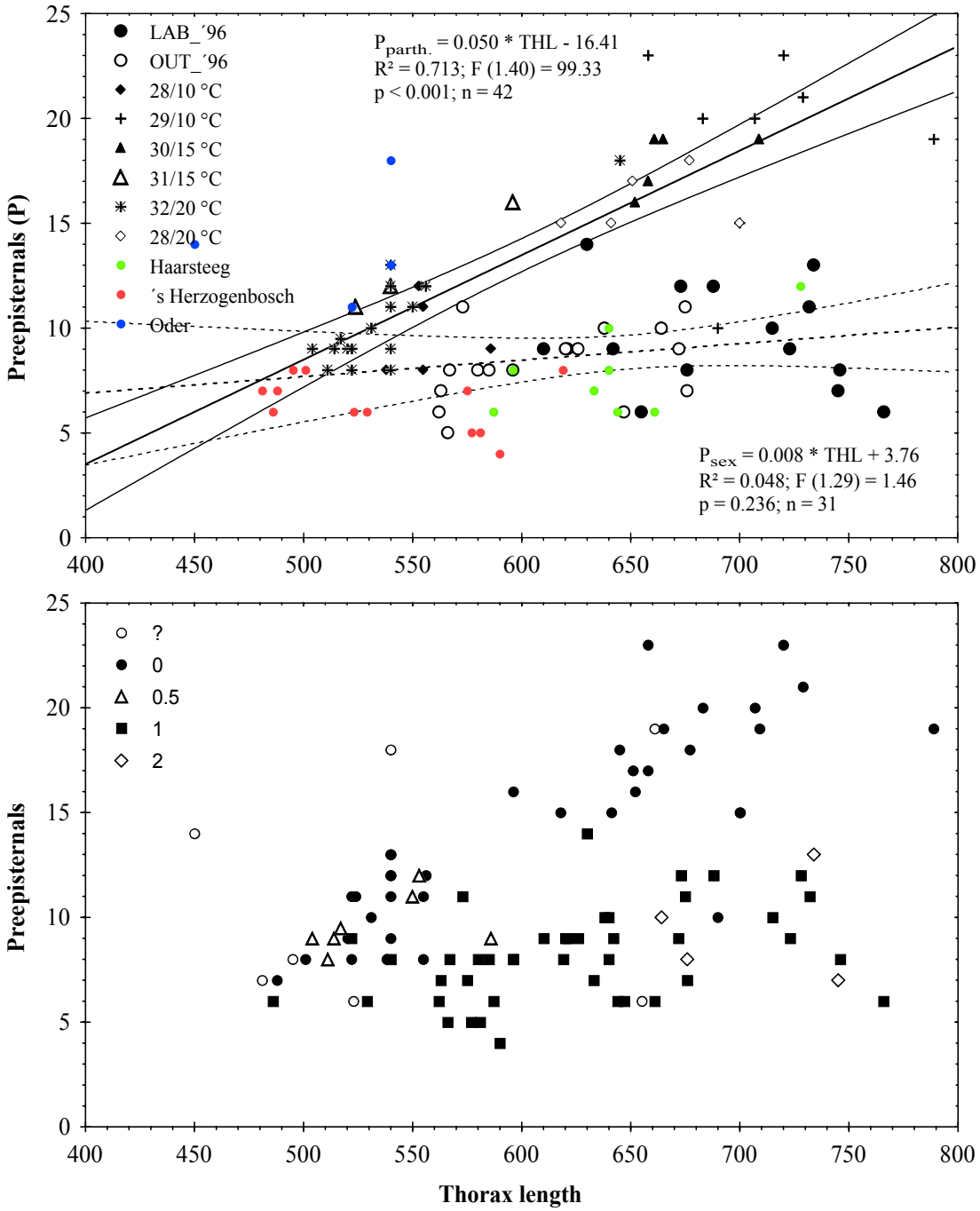

Figure 37: **Top:** Regression (inclusive 95 % confidence limits) for the number of preepisternals and the adult body size in the parthenogenetic and sexual females of *Limnophyes asquamatus*.

Bottom: This figure shows the same specimens as above, but the individuals were grouped according to their possession of 0, 0.5, 1 and 2 lanceolate prescutellars on each side of Prescutellum.

Abbreviatios and explanations:

28/10 °C etc. = parthenogenetic females: number of culture vessel and temperature during the time of preservation (see Table 6 p 24);

OUT ´96 = 'sexual' females caught by emergence traps in pool 3, 1996;

LAB ´96 = sexual females which had laid non-developing eggs in 1996 (see Table 5 p 22);

? = prescutellars broken off.

The results for the parthenogenetic individuals from the 'Untere Odertal' (= Oder), and from 'The Netherlands' (Haarsteeg and ´s Herzogenbosch, see Appendix 4 and 5) were also included in the figure but were excluded from the regression.

5 p 22) and 17 were collected in the emergence traps of pool 3 in 1996. The latter were assumed to also be sexual (section 4.4.2.1.2. Figure 81 p 174) and were taken from different samplings (19.4., 1.5., 15.5., 1.6. and 14.6.1996). The females from pool 3, 1996 were included into the regression to extend the size range of the sexual females. The analysis showed a highly significant correlation between body size and the number of preepisternals in the parthenogenetic specimens and no significant correlation in the sexual ones. Usually the parthenogenetic females from the lab cultures of pool 3 can be separated from the sexual females (which have always at least one lanceolate prescutellar bristle on each side of Prescutellum) by the number of preepisternals in relation to body size. However, small parthenogenetic females with one lanceolate prescutellar on each side of Prescutellum cannot be separated from the sexual females. The parthenogenetic females from The Netherlands usually had one lanceolate prescutellar bristle on each side of Prescutellum and correspond to the sexual females in respect to the number of preepisternals in relation to the body size. The parthenogenetic females from the "Untere Odertal" fit well with the parthenogenetic females from pool 3 which have no lanceolate prescutellar bristles but large numbers of preepisternals.

If there are parthenogenetic females, which can partly be separated from the sexual females by the absence of lanceolate prescutellars and higher numbers of preepisternals, there must be a correlation between the sex ratio and the share of females with lanceolate prescutellars and the mean number of preepisternals. Figure 38 shows that such correlations do exist for the population of *L. asquamatus* in pool 3.

The results of this section show that: (a) parthenogenetic females without lanceolate prescutel-

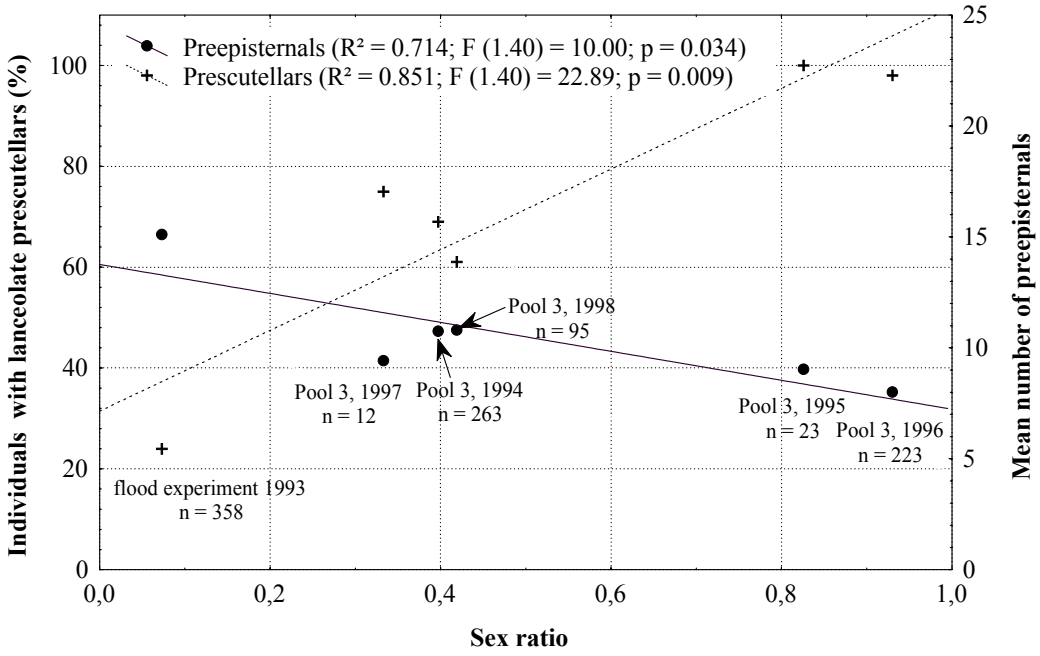

Figure 38: Correlation between the sex ratio of *Limnophyes asquamatus* and: (a) the mean number of preepisternals (continuous line); and (b) the share of females with lanceolate prescutellars (dotted line).

Pool 3, 1994-1998 = annual crop of individuals that had emerged from pool 3 from 1994-1998 (Table 25 p 67);
flood experiment 1993 = individuals that had emerged from flooded soil originating from pool 3 (see section 4.3.1.1.1.).

lars and high numbers of preepisternals can be morphologically separated from the sexual females; and (b) such a separation is not possible for the parthenogenetic females with lanceolate prescutellars.

4.3.1.1.5. Are there parthenogenetic ecotypes?

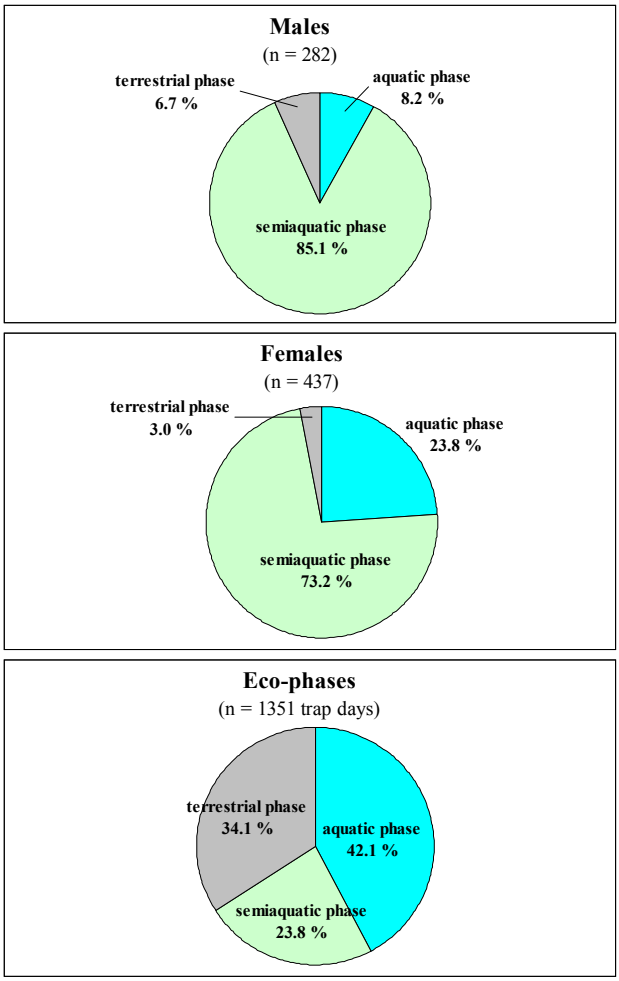

Figure 39: The emergence of males and females of *Limnophyes asquamatus* during the three eco-phases of pool 3, compared with the actual proportions of trap days within eco-phases throughout the emergence study (1994 - 1998).

It was then tested, whether the time of emergence of females with lanceolate prescutellars (predominantly sexual) and females without such bristles (parthenogenetic) differed. Figure 39 shows the emergence of all males and females from pool 3 during the different eco-phases (see Table 1 p 16) and also the proportions of trap days within eco-phases throughout the emergence study. The distribution of trap days and emerging adults (males + females) differed strongly between the levels of humidity (PEARSONS χ^2-test: $\chi^2 = 604.6$; df = 3; $p < 0.001$): *L. asquamatus* clearly prefers the semiaquatic phase. Figure 39 also shows that significantly more females than males emerged during the aquatic phase ($\chi^2 = 38.9$; df = 3; $p < 0.001$). The majority of females without lanceolate prescutellars (parthenogenetic) emerged during the aquatic phase, whereas females with lanceolate prescutellars (predominantly sexual) mostly emerged during the semiaquatic phase (predominantly from wet soils = grade 3, see Figure 40) ($\chi^2 = 132.1$, df = 3; $p < 0.001$). There were no significant

differences regarding the time at which females with lanceolate prescutellars (predominantly sexual) and males emerged ($\chi^2 = 6.1$; df = 3; p = 0.108) (compare Figures 39 and 40).

These results clearly show that within the population of pool 3 (a) the females without lanceolate prescutellars (parthenogenetic ecotype) were predominantly aquatic/semiaquatic; and (b) the sexual individuals of *Limnophyes asquamatus* clearly preferred wet soils and should be called terrestrial/semiterrestrial.

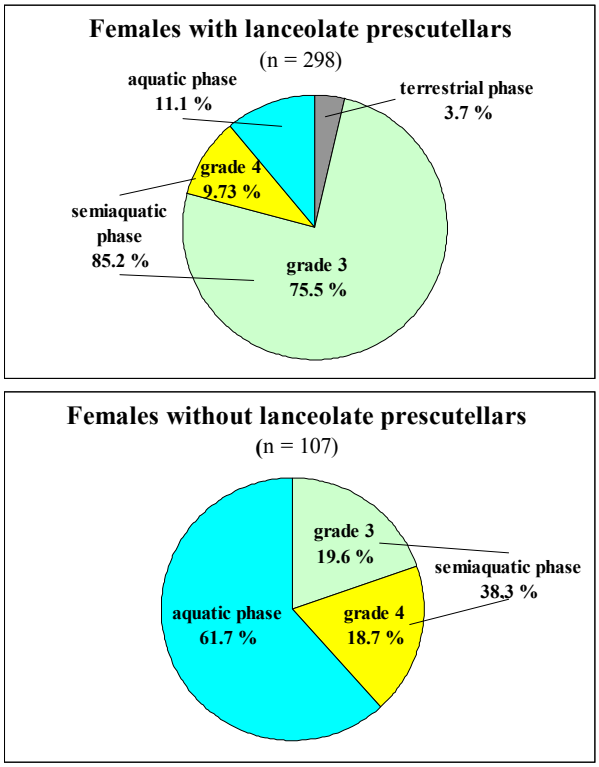

Figure 40: The emergence of *Limnophyes asquamatus* females with and without lanceolate prescutellars during the three eco-phases of pool 3.
The semiaquatic phase is subdivided into grade 3 (substrate like a wet sponge) and grade 4 (as grade 3, but very small puddles still present beneath the emergence trap) (see Table 1 p 16).

As shown above, there were also parthenogenetic females, which usually bare lanceolate prescutellars (especially parthenogenetic rearings from The Netherlands). The rearings conducted by HENK MOLLER PILLOT were done in culture vessels with wet soils and without a water-land-transition as in the rearings of the present study (see Appendix 5). It is therefore likely that there is also a second parthenogenetic ecotype, which prefers wet soils as does the sexual form of *L. asquamatus*.

4.3.1.1.6. Definition of the three ecotypes of *L. asquamatus*

The results presented above showed that there are obligatory sexual females of *L. asquamatus* and that there are probably two parthenogenetic ecotypes. These ecotypes are preliminary defined as follows:

Limnophyes asquamatus* forma *asquamatus is the sexual ecotype. The larvae are terrestrial/semiterrestrial and predominantly live in wet soils (Figures 39 + 40). The males normally bear one (n = 203) and sometimes no (n = 11) or two (n = 5) lanceolate prescutellars on each side of

Prescutellum. Two hundred and thirteen males had 1-6 preepisternals and these bristles were lacking in only three males (Figure 36). The females reproduce obligatory sexually and are undistinguishable from the parthenogenetic form *limosus* (see below).

Limnophyes asquamatus* forma *limosus is a parthenogenetic ecotype of *L. asquamatus*, which larvae are also assumed to prefer wet soils. The females of this ecotype are undistinguishable from *L. asquamatus* forma *asquamatus*. They usually bear (as the males) one, sometimes no (?), two (n = 16) or three (n = 1) lanceolate prescutellars on each side of Prescutellum (Figure 36). The number of preepisternals is not correlated with the body size (Figure 37). Specimens with a thorax length of ≥ 600 µm can be separated from the parthenogenetic forma *aquaticus* (see below) by the lower number of preepisternals (Figure 37).

Limnophyes asquamatus* forma *aquaticus is the second parthenogenetic ecotype. The adults often bear no lanceolate prescutellars. The number of preepisternals is higher as in the other two ecotypes and strongly dependent on body size (Figure 37). Therefore small specimens (≤ 600 µm) with lanceolate prescutellars are usually undistinguishable from the females of the ecotypes *asquamatus* and *limosus*. *L. as.* forma *aquaticus* is aquatic/semiaquatic (Figure 40).

4.3.1.1.7. The emergence of *L. asquamatus* from the flood experiment in 1993 (DETTINGER-KLEMM & BOHLE 1996) - a change of ecotypes?

Figure 41 shows the same data as described in section 4.3.1.1.1. and Figure 33. In addition, for each female it was noted whether lanceolate prescutellars were present or not. Within the first generation (26.7.-18.8.1993) there were only 6 females without lanceolate prescutellars. In the second generation (~23. 8.-30.9.) there were only 6 females with lanceolate prescutellars and none in the third

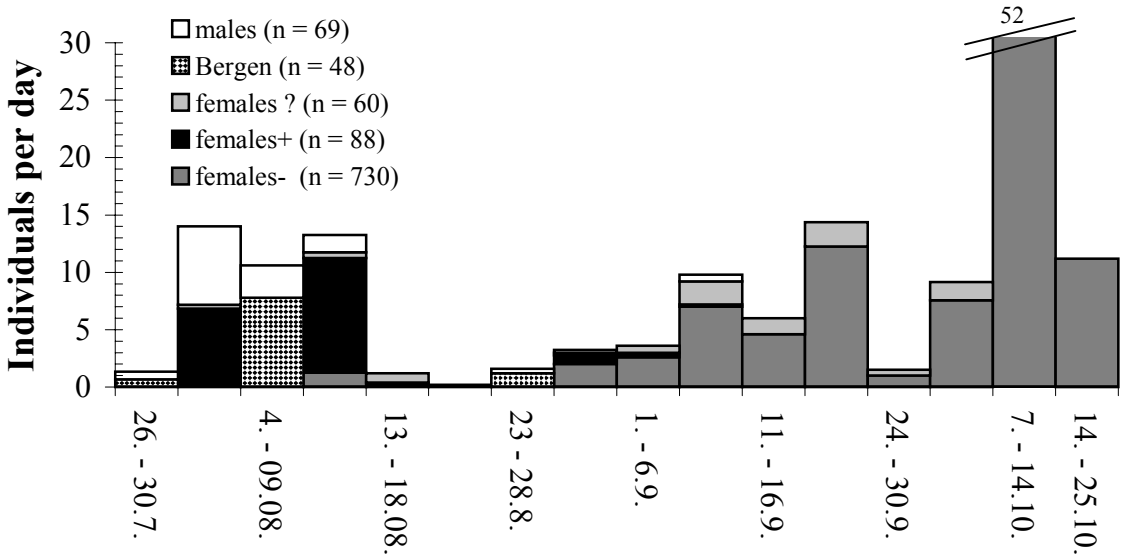

Figure 41: The emergence of ecotypes of *Limnophyes asquamatus* from the flood experiment in 1993 (DETTINGER-KLEMM & BOHLE 1996).

Abbreviations:
Bergen = females deposited in the Museum of Zoology in Bergen (not reinvestigated);
females ? = prescutellars broken off or not vissible;
females+/- = females with/without lanceolate prescutellars.

(beginning of October - end of the experiment). As mentioned in section 4.3.1.1.2., the sexual ecotype must have become extinct, because mating was not possible in the experimental unit of the flood experiment. If there were also parthenogenetic females with lanceolate prescutellars (forma *limosus* or the offspring of a sexual reproduction of the forma *aquaticus*) in the first generation, they were totally replaced by the typical forma *aquaticus* during the following generations.

4.3.1.1.8. Are there other undescribed species closely related to *L. asquamatus*?

(1) During the present study a total of 15 females were found, which were determined as *L. asquamatus* but had lanceolate humerals. These individuals had either one lanceolate prescutellar on each side of Prescutellum (n = 7) or these bristles were absent (n = 6) (in the two other specimens the prescutellars were broken off). All these specimens bore many preepisternals (10-18; 14.8). Fourteen such individuals were obtained from the flood experiment 1993 (DETTINGER-KLEMM & BOHLE 1996) (individuals number 3, 12, 13, 15, 20, 28, 40, 53, 57, 89, 117, 140, 153, 203) and one from an emergence trap in pool 3 in 1998 (individual number 1418). It is presently unclear whether these specimens are representatives of a new species or only extreme phenotypes of *L. asquamatus*.

(2) In the material from The Netherlands there was a morphologically unusual female and larva, respectively (Ospel, see Appendix 5 and also section 4.3.1.2.2.). These specimens could also be representatives of a new species.

(3) In the material from The Netherlands (Elslo, see Appendix 5) there were 2 ♂♂ and 1 ♀ of a new species, which will be named *Limnophyes mechthildae* spec. nov. The species is closely related to the nearctic *L. pilicistulus*. I had already recognized this new species in 1997 from material (36 ♂♂, 44 ♀♀) of three temporary pools in the floodplain of the river Lahn near Marburg (Hesse, Germany) (SCHNABEL 1999, SCHNABEL & DETTINGER-KLEMM 2000). HENK MOLLER PILLOT (pers. comm.) and OLE SÆTHER (pers. comm) confirmed the presence of a new species. A male and a female were deposited at the Zoological Museum Bergen as well as at the private collection of HENK MOLLER PILLOT. The remaining material is at present still in the authors' collection and awaiting description.

(4) There was also a morphologically unusual male from Great Britain that maybe belongs to a new species (SÆTHER 1990).

4.3.1.2. Description of the juvenile stages of L. asquamatus, L. minimus and L. natalensis

4.3.1.2.1. Introduction

It was not possible to determine the juvenile instars of the genus *Limnophyes* with the keys provided by SÆTHER (1990) and LANGTON (1991). This part of the present study therefore contributes to improving the taxonomy and determination of the juvenile instars of the genus *Limnophyes*.

***Limnophyes asquamatus*:** The larva of *Limnophyes asquamatus* has not been described yet; the

pupa was described in SÆTHER (1990). The definition of three eco-types in *Limnophyes asquamatus* (section 4.3.1.1.6.) called also for a reinvestigation of the pupa.

The *Limnophyes minimus*-complex: SCHNABEL'S (1999) Master's thesis showed that *L. minimus* and *L. punctipennis* are not separable at the moment and that there might be a third species, there called *L. minimus* var. nov., of which the males possess a simple virga (see also SCHNABEL & DETTINGER-KLEMM 2000). The taxonomic situation seems to be still more complex than shown for *L. asquamatus* in section 4.3.1.1., and as long as no further studies are undertaken *Limnophyes minimus* senso stricto, *Limnophyes minimus* var. nov. and *Limnophyes punctipennis* should be united under the *Limnophyes minimus*-complex. It is most likely that, comparably to what was seen in *L. asquamatus*, there is more than one parthenogenetic ecotype within the *L. minimus*-complex. In respect to the very complex situation, the juveniles should be only described from material unequivocally associated to the adults (single rearings of the larvae into the males and females, rearings from single egg masses, and from parthenogenetic lab cultures) and the descriptions presently available (SÆTHER 1990) should be replaced and supplemented by such descriptions. I therefore included the description of the larva and pupa of *Limnophyes minimus* senso stricto to this section.

Limnophyes natalensis: Only three females of *L. natalensis* were found in the habitats studied in the present investigation (Table 24 p 66). I nevertheless obtained many and unequivocally associated specimens (♂♂, ♀♀, larvae and pupae/pupal exuviae) originating from another locality of the Lahnberge mountain range (see comments in Table 31). The larvae clearly differed from the description of SÆTHER (1990) (Hordaland, Bergen, stream in Fjellveien, mature pupa reared from larva, 2 larvae) and there is no doubt that the larvae from Bergen belong to a new species and that the larva of *L. natalensis* has not been described yet. Accordingly, I added the description of the juvenile stages of *Limnophyes natalensis* to this section.

4.3.1.2.2. Description of the larvae

Table 31 shows a description of the instars IV of *L. asquamatus*, *L. natalensis* and *L. minimus* senso stricto. A description of the instars I-III of *L. asquamatus* and *L. minimus* senso stricto can be taken from Table 32. The head capsule size as well as the size of the flagellomere 1 can be used satisfactorily to separate the four larval instars from each other (Figure 44). The SE-micrographs and the drawings (Figures 42 and 43) illustrate different morphological aspects of the instar III of the *L. minimus*-complex and the instar IV of *L. asquamatus* and *Limnophyes minimus* senso stricto. Except the larvae, which were extracted from a soil sample of pool 3 in 1996 (most likely sexual, see sections 4.3.1.1.2. and 4.4.2.1.2.), the larvae of *L. asquamatus* were described from material obtained from the parthenogenetic laboratory cultures (Table 6 p 24 and Appendix 4). According to MOLLER PILLOT'S notes (Appendix 5) the larvae originating from Ospel (The Netherlands) must also, at least partly, belong to *L. asquamatus* forma *asquamatus*. There were absolutely no differences between the larvae of the parthenogenetic lab cultures and those thought to belong to the sexual type of *L. asquamatus*. In only one instar IV from Ospel (The Netherlands) (see also comments

in section 4.3.1.1.8. and Appendix 5) I did recognize a difference to the other *L. asquamatus* larvae. In this larva the flagellomere 1 was as broad as in the instar IV of *L. natalensis* (Figure 44).

4.3.1.2.3. Separation of the larva of *L. asquamatus* from the other known larvae of the genus, with additions to SÆTHER'S (1990) preliminary key

2. The setal marks of the antenna are somewhat distal to the ring organ and at about the same level (Figure 42m). The basal segment of the antenna is longer than in *Limnophyes minimus* senso stricto (lenghts in µm: instar I: 4-5; instar II: 9-14; instar III: 13-20; instar IV: 28-38; 33). A dark spot is present behind the base of the antenna (Figure 42f, not or only badly visible in macerated specimens). Anal tubules of the instar IV are relatively short (70-89 µm) and show no incisions pretending segmentation (Figure 42e). Anal setae long (lengths in µm: instar I: ± 50; instar II: ± 140; instar III: ± 203; instar IV: 243-370). S I with five branches, median branch about twice as long as first lateral branch (Figure 42b).....*Limnophyes asquamatus*

- The setal marks of the antenna are not at the same level on the flagellomere 1.....3

3. The distal setal mark of the antenna is close to the apical margin of flagellomere 1 and far from the basal mark (Figure 13 in SÆTHER 1990); flagellomere 1 is about 45 µm long. median chetulae laterales serrated.....*Limnophyes edwardsi*

- The basal setal mark of flagellomere 1 is at approximately the same level as the ring organ and the distal mark is somewhat above the ring organ (Figure 43h); flagellomere 1 shorter (until 35 µm).....4

4. Postmentum < 125 µm.....5

- Postmentum > 125 µm.....6

5. Length/width-ratio of flagellomere 1 of the instar IV (head capsule length ≥ 200 µm) < 2.5 (2.05-2.24), flagellomere 1 relatively short (lengths in µm: instar I: 3-4; instar II: 7 -8; instar III: 12-14; instar IV: 25-26); no dark spot behind the antennal base. Anal tubules of the instar IV long (± 95 µm), often with one or two incisions pretending segmentation (Figure 43e); anal setae relatively short (lengths in µm: instar I: ± 45; instar II: ± 80; instar III: ± 90; instar IV: ± 190). SI with seven branches, the median branch not twice as long as the first lateral branch. Two outer chaetulae laterales smooth, the two following (median) are fringed by fine setae (which may be broken off giving a serrated appearance). Size characteristics of the instar IV (in µm): head capsule length ± 239, length of postmentum ± 117, width of mentum ± 66, length of mandible ± 80. .....*L. minimus*-complex

- Median chaetulae laterales serrated (but see comment in 5, *Limnophyes minimus*-complex), mandible strongly bent apically (Figure 32C in SÆTHER 1990) ....'*Limnophyes natalensis*' sensu SÆTHER (1990)

6. (only instar IV): length/width-ratio of flagellomere 1 < 2.5 (2.06-2.11), length of flagellomere 1 ± 35 µm; no dark spot present behind the antennal base; anal tubules ± 120 µm long, at least at its base with an incision; anal setae until 250 µm; SI with seven branches, the median branch somewhat longer as the first lateral branch; median chetulae laterales with fringe of fine setae; head capsule length 280-290 µm, Postmentum ± 155 µm, width of mentum ± 85 µm and length of mandible ± 110 µm.....*Limnophyes natalensis* senso stricto

- *L. carolinensis* and *L. pentaplastus* ('median chetulae laterales apparently smooth') are not clearly separable from *L. natalensis* senso stricto following the data provided by SÆTHER (1990).

Table 31: Description of the instars IV of *Limnophyes asquamatus**, *Limnophyes minimus* senso stricto* and *Limnophyes natalensis***.

	Limnophyes asquamatus	***L. minimus* (n = 1-2)**	***L.* natalensis (n = 1-2)**
Body length (mm)	1.80-4.00; 2.56 (n = 38)	3.25	2.90-3.46
Head length (µm)	207-265; 230 (n = 37)	239	280-287
Head width (µm)	171-230; 200 (n = 31)	203	264
L/W-ratio of head	1.05-1.23; 1.16 (n = 31)	1.18	1.06
Head colour	Dark brown patch present behind the antennal base (Figure 42f) (clearly visible only in living and alcohol preserved larvae); apical half of mandible blackish; mentum somewhat darker as remainder of yellowish head capsule.	No dark brown patch present behind the antennal base; apex of mandible blackish (Fig. 43g); mentum dark brown anteriorly, becoming lighter posteriorly and only brownish between the setae submentalis; remainder of head yellowish.	As in *L. minimus*.
Mentum shape	See Figure 42i. The shape of mentum is approximately similar in the instars II and III, but clearly different in the instar I: middle tooth simple and pointed and somewhat lower than the first lateral teeth.	As in *L. asquamatus*.	As in *L. asquamatus.*
L Postmentum (µm)	123-140; 132 (n = 14)	117	155-156
W Mentum (µm)	56-77; 69 (n = 6)	66	84-89
D setae submentalis (µm)	40-49; 44 (n = 5)	44	52-59
Mandible shape	Figure 42h.	Figure 43g.	As in *L. minmus*.
L Mandible (µm)	81-105; 90 (n = 5)	79-81	107-112
Seta interna	Figure 42g. The main branches (I recognized 6) can be more pinnate than shown in the drawing.	As in *L. asquamatus*.	As in *L. asquamatus*, but I recognized 7 branches.
L Fm 1 (µm)	28-38; 33 (n = 29)	25-26	33-35
W Fm 1 (µm)	11-16; 13 (n = 23)	12	16-17
L/W-ratio of Fm 1	2.13-3.24; 2.56 (n = 23)	2.05-2.24	2.06-2.11
L Fm 2 (µm)	10-14; 11 (n = 6)	7-8	11-12
L Fm 3 (µm)	1-2 (n = 2)	1	2
L Fm 4 (µm)	6-7 (n = 2)	4.5	7
L Fm 5 (µm)	3 (n = 2)	2.5	3
AR	1.2-1.3 (n = 2)	1.3	1.3
D of RO from ab	10-12.5 (n = 2)	7	14
D basal setal mark from ab	15-16 (n = 2)	9	16
D distal setal mark from ab	16 (n =2)	12.2	20
Comment marks	In the instars II + III, the arragement of setal marks on Fm 1 is as in the instar IV.		
L Bl	26-27 (n = 2)		27
L Abl	14 (n = 1)		
Pecten epipharyngis	With 3 scales.	As in *L. asquamatus*.	As in *L. asquamatus*.

Table 31 (continued).

	Limnophyes asquamatus	***L. minimus* (n = 1-2)**	***L.* natalensis (n = 1-2)**
Chaetulae laterales	1st chaetulae laterales (Figure 42k) ± triangular and much broader as the teeth of the pecten epipharyngis (Figure 42b); 2nd clearly longer and more slender as the 1st; the following 3 inner chetulae still longer and more slender as the 2nd , they bear a fringe of long and fine hairs. The innermost chetulae laterales resemble the 2nd and have no fringe of setae.	As in *L. asquamatus*.	As in *L. asquamatus.*
Shape SI	With 5 branches, median branch about twice as long as first lateral branches (Figure 42b).	With 6 (?)-7 branches, median branch not twice as long as first lateral branches (Figure 43f).	As in *L. minimus*.
L SI	11-12.5 (n = 4)	-	14
L SII	13-17 (n = 2)	10	18-27
Premandible	PmB present, not visible in Figure 42j.	As in *L. asquamatus*.	As in *L. asquamatus.*
L anal tubules	70-89; 80 (n = 5)	95	120-122
W anal tubules	26-27 (n = 2)	18	33-35
Shape of anal tubules	Relatively short, without incisions (Figure 42e).	Long and slender, often with two incisions pre-tending a segmental structure (Figure 43e).	As in *L. minimus*.
L procercus	21-35; 28 (n = 6)	22	27
W procercus	14-23 (n = 2)	14	18
L proceral setae	30-47 (n = 2)		
L anal macrosetae	243-370; 306 (n = 15)	190	217-249
N anal macrosetae	7	7	7
L Supraanal setae	180-315; 250 (n = 12)	122	180-192 (n = 2)
L posterior parapods	102-110 (n = 2)	64	136
Hooks on post. parap. serrated ?	No (Figure 42d).	No	No
Hooks on ant. parap. serrated ?	Yes, with 2-3 toothlets apically, as in *L. minimus*.	Yes (Figure 43b).	Yes, as in *L. minimus*.
L longest L-seta on P IV	78-153; 107 (n = 8)	-	58

Abbreviations:

ab = base of flagellomere 1; **D** = distance; **Fm** = flagellomere of the antenna; **L** = length; **N** = number; **P** = pleura of the abdomen; **procercal setae** = two small setae on anterior surface of procercus; **W** = width; **other abbreviations** see SÆTHER (1980).

Comments:

*see comments on Table 32.

**The larvae of *L. natalensis* were found in huge numbers in wet moss within the open-air area of the animal house of the Department of Biology of the Philipps-University of Marburg (Hesse, Germany). The individuals were swept from swarms (♂♂: height of swarms 20-70 cm above the ground) and vegetation (♀♀) or were reared in the laboratory. The material was deposited at the following locations (addresses see the end of the Appendix 3):

a) Author's private collection: 133 ♂♂, 10 ♀♀, 20 larvae, 1 pupae and 2 pupal exuviae in alcohol or mounted on slides, 3 ♂♂ + associated pupal exuviae;
b) Peter Langton: 10 ♂♂, 4 ♀♀, 5 larvae in alcohol and 1 slide mounted ♂ + associated pupal exuviae;
c) Zoological Museum of Bergen (Norway): 1 ♂ + associated pupal exuviae, 2 larvae (all slide mounted);
a) Zoologische Staatssammlung München: 1 ♂ + associated pupal exuviae, 1 ♀ (all slide mounted).

Table 32: Some morphological parameters characterizing the instars I-III of *Limnophyes asquamatus** and *Limnophyes minimus* senso stricto** [and #].

Limnophyes asquamatus			
	Instar I	Instar II	Instar III
Body length (mm)	0.44-1.04; 0.68 (n = 14)	0.9-1.53; 1.21 (n = 17)	1.1-2.5; 1.50 (n = 47)
Head length (µm)	65-74; 70 (n = 17)	87-122; 106 (n = 17)	129-172; 152 (n = 44)
Head width (µm)	62-75; 70 (n = 14)	84-105; 95 (n = 13)	117-151; 132 (n = 39)
L/W-ratio of head	0.92-1.10; 1.0 (n = 14)	1.02-1.23; 1.12 (n = 13)	1.02-1.26; 1.15 (n = 39)
L anal tubules (µm)	15 (n = 1)	14-27; 23 (n = 4)	40-55; 46 (n = 3)
L procercus (µm)	4 (n = 1)	10-15; 12 (n = 4)	17-18; (n = 2)
L anal macrosetae (µm)	52 (n = 1)	140 (n = 1)	203 (n = 1)
L supraanal setae (µm)	-	105 (n = 1)	152-158; 156 (n = 3)
L postmentum (µm)	38 (n = 1)	61-67; 64 (n = 4)	78-97; 90 (n = 4)
W Mentum (µm)	20.3 (n = 1)	29-33; 31 (n = 4)	41-48; 46 (n = 4)
D setae submentalis (µm)	15 (n = 1)	17-22; 19 (n = 4)	26-31; 28 (n = 4)
L Mandible (µm)	29 (n = 1)	39-43; 41 (n = 4)	48-59; 54 (n = 4)
L Fm 1 (µm)	4-5; 4 (n = 8)	9-14; 11 (n = 14)	13-20; 18 (n = 22)
W Fm 1 (µm)	4-5; 5 (n = 8)	5-9; 6 (n = 13)	8-10; 9 (n = 22)
L/W-ratio of Fm 1	0.80-1.10; 0.92 (n = 8)	1.45-2.24; 1,69 (n = 13)	1.46-2.50; 2.00 (n = 22)
L Fm 2 (µm)	6 (n = 1)	7-8; 8 (n = 3)	7-12; 9 (n = 6)
L SII (µm)	7 (n = 1)	-	12 (n = 1)
Limnophyes minimus senso stricto			
Body length (mm)	0.25-0.33;0.30 (n = 3)	0.80-0.90 (n = 2)	1.00 (n = 1)
Head length(µm)	51-58; 54 (n = 3)	80-88 (n = 2)	122 (n = 1)
Head width (µm)	51 (n = 2)	93-94 (n = 2)	113 (n = 1)
L/W-ratio of head	1.14 (n = 1)	0.86-0.94 (n = 2)	1.08 (n = 1)
L anal tubules (µm)	17 (n = 1)	33 (n = 2)	48 (n = 1)
L Procercus (µm)	4.2 (n = 1)	9-10 (n = 2)	10 (n = 1)
L anal macrosetae (µm)	40-48 (n = 2)	76-85 (n = 2)	90 (n = 1)
L supraanal setae (µm)	38 (n = 1)	50 (n = 1)	61 (n = 1)
L postmentum (µm)		54-62 (n = 2)	84 (n = 1)
W Mentum (µm)	16 (n = 1)	30 (n = 2)	49 (n =1)
D setae submentalis (µm)		20-22 (n = 2)	27 (n = 1)
L Mandible (µm)	81-105; 90 (n = 5)	31-37 (n = 2)	57 (n = 1)
L Fm 1 (µm)	3-4 (n = 2)	7-8 (n = 2)	12-14 (n = 2)
W Fm 1 (µm)	2-3 (n = 2)	7-8 (n = 2)	11 (n = 1)
L/W-ratio of Fm 1	1.00-1.44 (n = 2)	0.94-1.03 (n = 2)	1.09 (n = 1)
L Fm 2 (µm)	6 (n = 1)	5 (n = 2)	7 (n = 1)
L SII (µm)		7 (n = 1)	

Abbreviations and comments:

Abbreviations see Table 31.

* 3 larvae of instars II and III, and 2 larvae of the instar IV were extracted from a soil sample taken in pool 3 by a Berlese funnel on May 2, 1996 (these larvae most likely belonged to the sexual ecotype, see section 4.3.1.1.2.) and did not differ from the rest of larvae, which were preserved from the parthenogenetic lab cultures (Appendix 4).

** The instars I (n = 5) and IV (n = 1 larva and 1 larval exuviae) were reared by the author from an egg mass (15 °C), which was deposited by a female caught whilst mating by ANDREA SUNDERMANN on June 21, 2000 (helocrene spring near Mardorf (Hesse, Germany), see SUNDERMANN 2001). The female was slide mounted after the egg mass had been lain. Five ♂♂, 4 ♀♀ and 17 pupal exuviae of the females' offspring were also preserved. The males clearly belonged to *L. minimus* senso stricto.

\# The instars II (n = 2) and III (n = 1) were extracted from a soil sample taken in pool 3 by a Berlese funnel on May 2, 1996, as well as the instar III which is shown in the SE-micrographs (Figure 43). Hence these larvae can be only assigned to the *L. minimus*-complex sensu meo (section 4.3.1.2.1.).

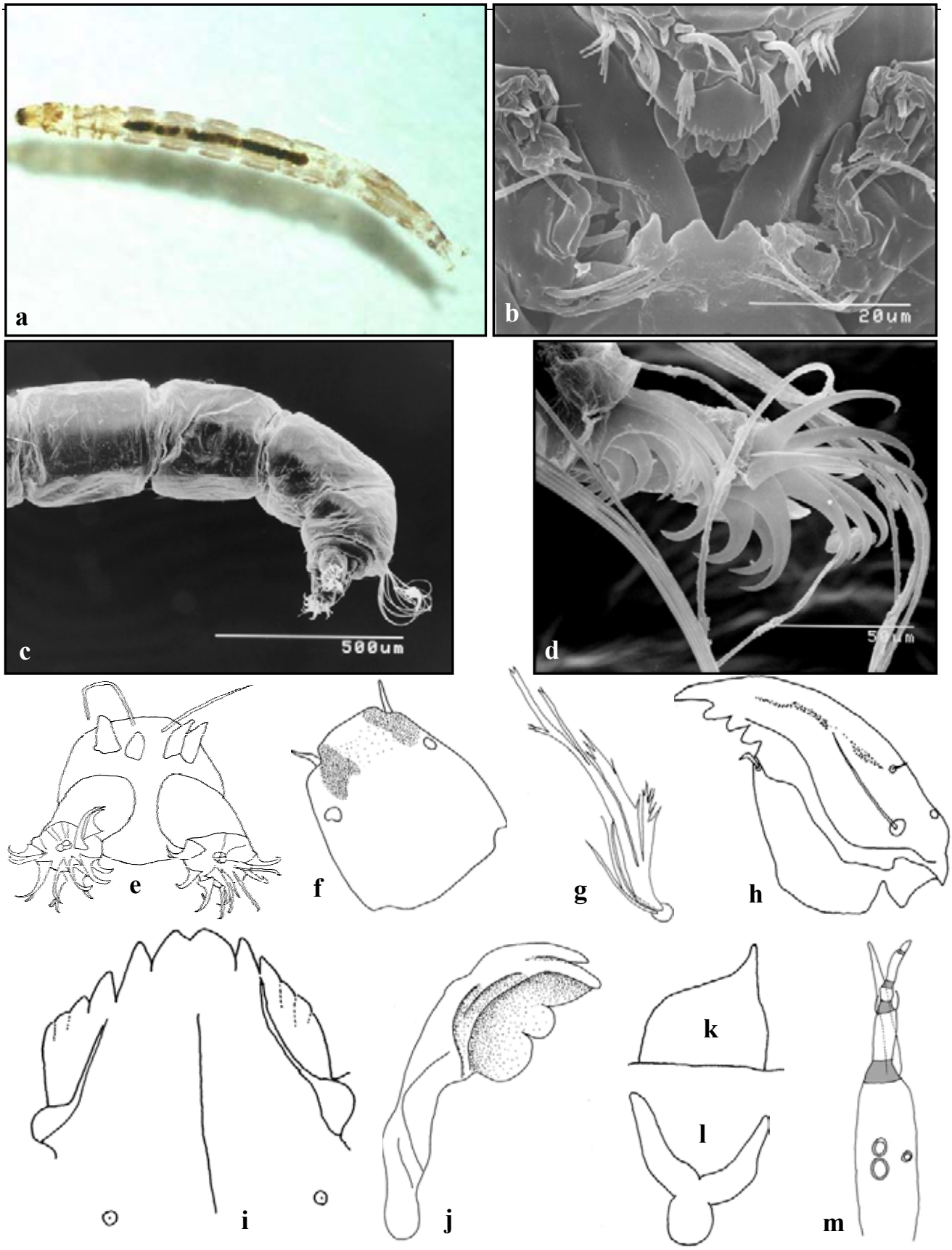

Figure 42: The larva of *Limnophyes asquamatus*: (a) habitus; (b) palatum with parts of mandible maxilla and mentum; (c) end of the abdomen; (d) hooks of the posterior parapods; (e) ventral view on anal segment; (f) colouration of the dorsal head capsule; (g) seta interna; (h) mandible; (i) mentum; j) premandible; (k) 1st chaetula laterales; (l) ungula with basal sclerite; (m) antenna.

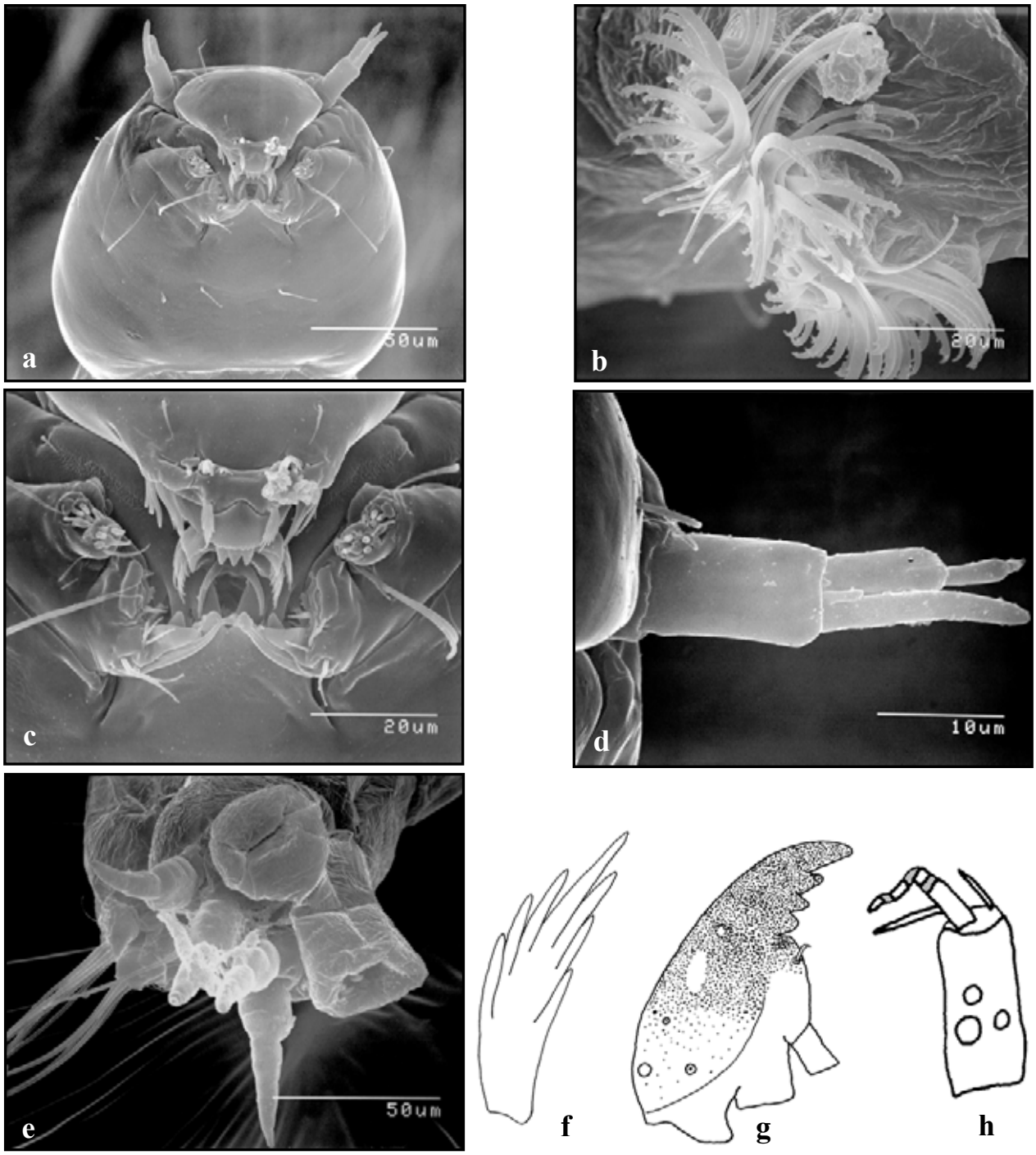

Figure 43: SE-micrographs of the instar III of the *Limnophyes minimus*-complex*: (a) head (frontoventral); (b) hooks of the anterior parapods; (c) palatum with parts of mandible, maxilla and mentum; (d) antenna; (e) end of the abdomen (caudoventral); (f) SI seta of palatum. Drawings of the instar IV of *Limnophyes minimus* senso stricto*: (g) pigmentation of the mandible; (h) antenna.

* see comments in Table 32 (** and #).

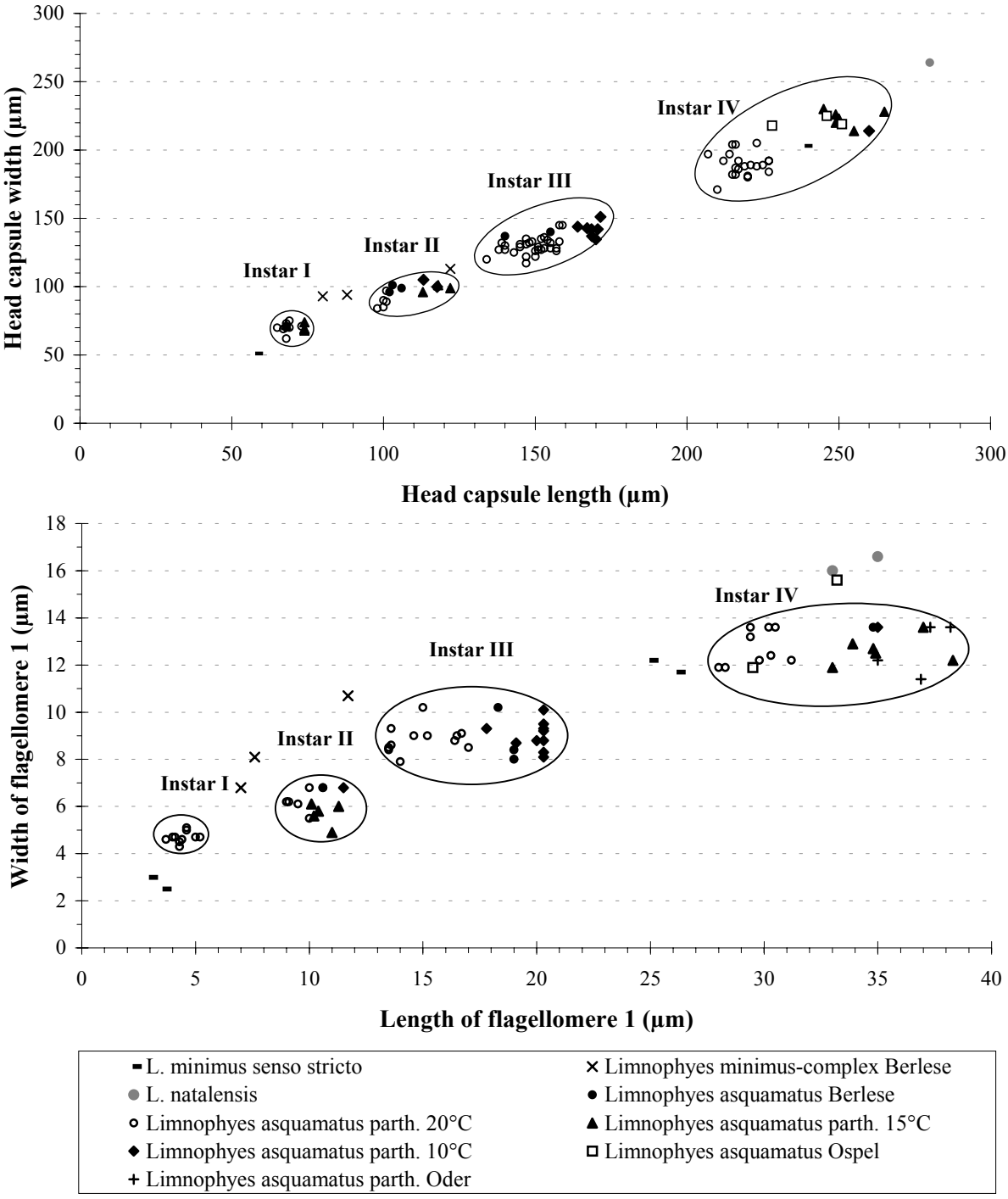

Figure 44: Variation in the size of head capsules and antennae of the different instars of *Limnophyes asquamatus* in comparison with single measurements on *L. minimus* and *Limnophyes natalensis*.

Explanations:

Limnophyes minimus senso stricto and *Limnophyes minimus*-complex see Table 32 and section 4.3.1.2.1.;
Berlese = extracted from a soil sample taken in pool 3 by a Berlese funnel on May 2, 1996;
parth = preserved from parthenogenetic lab cultures with different ambient temperatures (Table 6 p 24);
Oder = larval exuviae from parthenogenetic lab cultures of specimens from the Untere Odertal (see Appendix 4);
Ospel = larvae from Ospel (The Netherlands) (see Appendix 5).

4.3.1.2.4. Description of the pupae

From Table 33 a description of the pupae of *Limnophyes asquamatus* from different locatities can be taken.

It is most likely that one female pupal exuviae (obtained from a larva that had been extracted from a soil sample taken in pool 3 by a Berlese funnel on May 2, 1996 which was then singly reared into an adult) belongs to *L. asquamatus* forma *asquamatus* (section 4.3.1.1.2.). This female pupal exuviae correspond mostly to the description given by SÆTHER (1990). Tergite I and sternites IV-VIII however differed slightly with SÆTHER'S description, as they bore no spinules.

The pupae of the parthenogenetic lab cultures belong to *Limnophyes asquamatus* forma *aquaticus* and maybe also to *L. asquamatus* forma *limosus* (sections 4.3.1.1.4.-4.3.1.1.6.). A pupa from these lab rearings is illustrated in Figure 45. The pupae from the parthenogenetic lab cultures of the Untere Odertal clearly belong to *L. asquamatus* forma *aquaticus* (section 4.3.1.1.4.). The exuviae from Vogelenzang (The Netherlands, see Appendix 5) may belong to a parthenogenetic ecotype (females of the sample had no lanceolate prescutellars). As it is not clear if the parthenogenetic material also includes *L. asquamatus* forma *limosus*, the separation of the sexual and parthenogenetic material presented below was only done tentatively.

A comparison of some morphological characteristics of unequivocally associated material of *Limnophyes asquamatus*, *Limnophyes minimus* senso stricto and *Limnophyes natalensis* can be taken from Table 34, the following key facilitates the separation of these three species.

1. Anal macrosetae (AM) long[1] (200-276 (*300* [2]) µm), with apical hook[3] and strongly bend dorsoventrally (Figures 38c, f). Anal lobe (AL) 191-263 µm, AM/AL-ratio 1.08 (*0.96*)-1.23 (*1.5*). Abdominal segment VIII with 5 L-setae, L_4 90 (*64*)-140 (*150*) µm. Paratergites with spinulae anteriorly (Figure 45b). Apical spines on tergites II-VIII no longer than 65 µm (normally ± 50 µm). Length of wing sheaths[3] (SL) of female pupae 558-751 µm and corresponding ratio of SL/SW[3] 3.11-3.34; 3.23 (length and width of male wing sheaths[3] are not available at the moment) .....*Limnophyes asquamatus*. 2
- Anal macrosetae short (< 180 µm) and apparently without apical hook[3].....3

2. Sternites II-IV without and sternites V-VIII eventually with weak shagreen (spinulae)..*L. asquamatus* f. *asquamatus.*
- Sternites II-VIII with clear shagreen (spinulae) (Figure 45d).....*L. asquamatus* cf. forma *aquaticus.*

3. Anal macrosetae (AM) straight to slightly bend dorsoventrally (Figure 45h), short (122-143 µm) and without apical hook[3]. Anal lobe (AL) 165-196 µm, AM/AL-ratio 0.66-0.80. Abdominal segment VIII with 5 L-setae, L_4 50-70 µm. Length of male wing sheaths[3] (SL) 688-751 µm and of female wing sheaths[3] 643-713 µm; corresponding ratios of SL/SW[3] are 3.51-3.72 (males) and 2.86-3.17 (females).....*L. minimus* senso stricto (= sexual, male virga with 3-5 spines, see section 4.3.1.2.1.).
- Anal macrosetae (AM) slightly bend dorsoventrally (Figure 45g), longer (155 (*131*)-179 (*169*) µm) and without apical hook[3]. Anal lobe (AL) 229 (*169*)-239 (*225*) µm, AM/AL-ratio 0.69 (*0.63*)-0.75 (*0.94*). Abdominal segment VIII with 5 (*4*) L-setae, L_4 (*20*)-61 (*97*) µm. Length of male wing sheaths[3] (SL) 868-911 µm; corresponding ratios of SL/SW are 3.80-4.09 (data on length and width of female wing sheaths are not available at the moment)..... .....*L. natalensis*

[1] The wide range of length is at least partly caused by imprecise measurements due to the strong dorsoventral bend.

[2] Italic values in parenthesis are taken from SÆTHER (1990) and LANGTON (1991).

[3] These characters have not been used in descriptions yet.

Table. 33. Measurements of the pupae of *Limnophyes asquamatus* from different localities and cultures.

	Pool 3			Oder	Nether.
	***L. as.*f. as. ♂[1]**	***L. as.*cf. f. *as.* ♀[1]**	***L. as.* parth.[2]**	***L. as.* f. *aquaticus*.[3]**	***L. as.* ♀[4]**
L Abd. (mm)	2,00	1,50	1,52-2,08; 1,85 (n = 7)	1,33-1,74; 1,45 (n = 5)	1,6
L P (mm)	-	-	2,50-3,03; 2,71 (n = 3)	2,00-2,62; 2,23 (n = 5)	2,23
L AL (µm)	213	213	175-240; 213 (n = 9)	147-224; 187 (n = 8)	199
L G (µm)	-	50	31-65; 45 (n = 7)	-	49
L AM (µm)	256	250	200-276; 240 (n = 15)	220-270; 247 (n = 8)	245
L AM/L AL	1,20	1,17	1,04-1,22; 1,15 (n = 9)	1,09-1,51; 1,34 (n = 8)	1,23
W AM (µm)	-	4,4	6 (n = 3)	-	5
L FS(µm)	-	60	43-52 (n = 3)	-	42
SL (µm)	-	684	558-751; 653 (n = 8)	-	587
SW (µm)	-	218	175-225; 208 (n = 6)	-	189
SL/SW	-	3,14	3,18-3,34; 3,27 (n = 6)	-	3,11
L AS (µm)	-	340	308-380; 338 (n = 8)	-	353
L Dc_1 (µm)	-	52	70-80 (n = 2)	-	45
L Dc_2 (µm)	-	52	52-60 (n = 2)	-	41
L Dc_3 (µm)	-	42	32-52 (n = 2)	-	34
L Dc_4 (µm)	-	52	52 (n = 1)	-	41
D Dc_1-Dc_2 (µm)	-	8	0-6; 3 (n = 8)	-	7
D Dc_2-Dc_3 (µm)	-	2	0-9; 3 (n = 8)	-	2
D Dc_3-Dc_4 (µm)	-	29	10-34; 19 (n = 8)	-	49
L Pc (µm)	-	45	52-70; 59 (n = 3)	-	30
N lAps	-	1	1		1
L lAps (µm)	-	52	40-74; 52 (n = 3)	-	-
N mAps		2	2	-	2
L mAps (µm)	-	-	23-88; 51 (n = 3)	-	-
N L-setae T I-VIII	-	-	?/4/4/4/4/4/4/5	-	-
L L_1 Pl VIII (µm)	-	93	100-175; 146 (n = 4)	-	137
L L_2 Pl VIII (µm)	-	70	110-175; 134 (n = 5)	-	108
L L_3 Pl VIII (µm)	-	50	70-150; 103 (n = 5)	-	118
L L_4 Pl VIII (µm)	-	-	70-140; 107 (n = 4)	-	121
L L_5 Pl VIII (µm)	-	136	123-135, 129 (n = 3)	-	130
dar T I	-	no	no	no	no
dar T II-IX	-	intensive	intensive	intensive	intensive
var S I	-	no	no	no	no
var S II-VIII	no	no	yes	yes	S II-V ? weak
N spines T IV	67	66	35-74; 58 (n = 6)	37-70, 52 (n = 7)	-
N spines T VI	45	45	48-75; 55 (n = 8)	37-53; 43 (n = 7)	65
N spines T VIII	-	47	25-55; 44 (n = 6)	-	55
lo spine T IV	50	43	50-67; 59) (n =9)	50-62; 61 (n = 7)	54
lo spine T VI	50	48	44-73; 62 (n = 9)	53-67, 62 (n = 7)	49
lo spine T VIII	-	40	40-53; 47 (n = 3)	-	53

Comments:

[1] The larvae had been extracted from a soil sample taken in pool 3 by a Berlese funnel on May 2, 1996 and were then singly reared into an adult (female exuviae belongs most likely to *L. asquamatus* f. *asquamatus* as the male (see section 4.3.1.1.2.).

[2] It is possible that both parthenogenetic ecotypes were present within the parthenogenetic laboratory cultures (see Figure 36 and sections 4.3.1.1.4. and 4.3.1.1.6.). If this was the case, forma *aquaticus* was much more numerous.

[3] From parthenogenetic laboratory culture of specimens from the 'Untere Odertal' (see Appendix 4)

[4] The exuviae from Vogelenzang (The Netherlands) is associated to a female without lanceolate prescutellars. The female was probably parthenogenetic (see Appendix 5).

Abbreviations:

Abd = abdomen; **AS** = antennal sheath; **D** = distance; **dar** = dorsal armament of points; **L GS** = distance between apex of the genital sheath and apex of the anal lobe (♂: genital sheath > anal lobe; ♀: genital sheath < anal lobe); **L** = length; **lo** = longest; **N** = number; **P** = pupae; **Pl** = pleura; **S** = sternite; **SL** = sheath lenght; **SW** = sheath width; **T** = tergite; **var** = ventral armament of spinulae; **W** = width; for **further abbreviations** see SÆTHER (1980).

Table 34: Morphological comparison of the pupae of *Limnophyes asquamatus*, *Limnophyes minimus*[1] and *Limnophyes natalensis*[2].

	L. asquamatus	*L. minimus* senso stricto		*L. natalensis*
	Females	Males	Females	Males
L Abd. (mm)	1,33-2,08; 1,67 (n = 14)	1,51	1,96	1,97
L P (mm)	2,00-3,03; 2,39 (n = 9)	1,96	2,71	2,92
L AL (µm)	147-240; 201 (n = 19)	178-196; 187 (n = 5)	165-186 (n = 2)	223-239; 231 (n = 5)
L GS (µm)	31-65; 46 (n = 9)	18-38; 30 (n = 5)	27-32 (n = 2)	35-38; 36 (n = 5)
L AM (µm)	200-276; 243 (n = 25)	122-143; 134 (n = 5)	126-132 (n = 2)	155-179; 170 (n = 5)
L AM/L AL	1,04-1,51; 1,24 (n = 19)	0,66-0,80; 0,72 (n = 5)	0,76-0,79 (n = 2)	0,69-0,78; 0,74 (n = 5)
W AM (µm)	4-6; 5 (n = 5)	5	5	7
L FS(µm)	42-61; 51 (n = 5)	44	44	65
SL (µm)	558-751; 650 (n = 10)	688-751; 706 (n = 5)	643-713 (n = 2)	868-911; 882 (n = 5)
SW (µm)	175-225; 207 (n = 8)	189-202; 196 (n = 5)	225 (n = 2)	216-240; 226 (n = 5)
SL/SW	3,11-3,34; 3,23 (n = 8)	3,51-3,72; 3,60 (n = 5)	2,86-3,17 (n = 2)	3,80-4,09; 3,90 (n = 5)
L AS (µm)	308-380; 340 (n = 10)	776	378	758
L Dc_1 (µm)	45-80; 62 (n = 4)	52	64	75
L Dc_2 (µm)	41-60; 51 (n = 4)	40	-	35
L Dc_3 (µm)	32-52; 40 (n = 4)	-	30	30
L Dc_4 (µm)	41-52; 48 (n = 3)	32	30	35
D Dc_1-Dc_2 (µm)	0-8; 4 (n = 10)	8	7	9
D Dc_2-Dc_3 (µm)	0-9; 2 (n = 10)	2	0	0
D Dc_3-Dc_4 (µm)	10-49; 23 (n = 10)	32	38	39
L Pc (µm)	30-70; 51 (n = 5)	68	62	63
L lAps (µm)	40-74; 52 (n = 4)	-	68	63
L mAps (µm)	23-88; 51 (n = 3)	-	51	70
N L-setae T I-VIII	?/4/4/4/4/4/4/5	-	4/4/4/4/4/4/4/5	4/4/4/4/4/4/4/5
L L_1 Pl VIII (µm)	93-175; 136 (n = 6)	105	100	125
L L_2 Pl VIII (µm)	70-175; 123 (n = 7)	105	64	87
L L_3 Pl VIII (µm)	50-150; 98 (n = 7)	70	76	98
L L_4 Pl VIII (µm)	70-140; 110 (n = 5)	52-70; 63 (n = 5)	52-55 (n = 2)	61
L L_5 Pl VIII (µm)	123-136; 131 (n = 5)	105	96	116
dar T I	no	no	no	no
dar T II-IX	intensive	intensive	intensive	intensive
var S I	no	no	no	no
var S II-VIII	no or yes	yes	yes	yes
N spines T IV	35-74; 55 (n = 14)	80-90 (n = 1)	90-100 (n = 1)	~120 (n = 1)
N spines T VI	37-75; 50 (n = 17)	50-60 (n = 1)	70-80 (n = 1)	80-90 (n = 1)
N spines T VIII	25-55; 46 (n = 8)	30-40 (n = 1)	50-60 (n = 1)	60-70 (n = 1)
lo spine T IV	43-67; 58 (n = 18)	57	50	54
lo spine T VI	44-73; 61 (n = 18)	50	52	50
lo spine T VIII	40-52; 47 (n = 5)	56	54	58

Comments:

[1] see comments in Table 32.

[2] see comments in Table 31.

Abbreviations see Table 33.

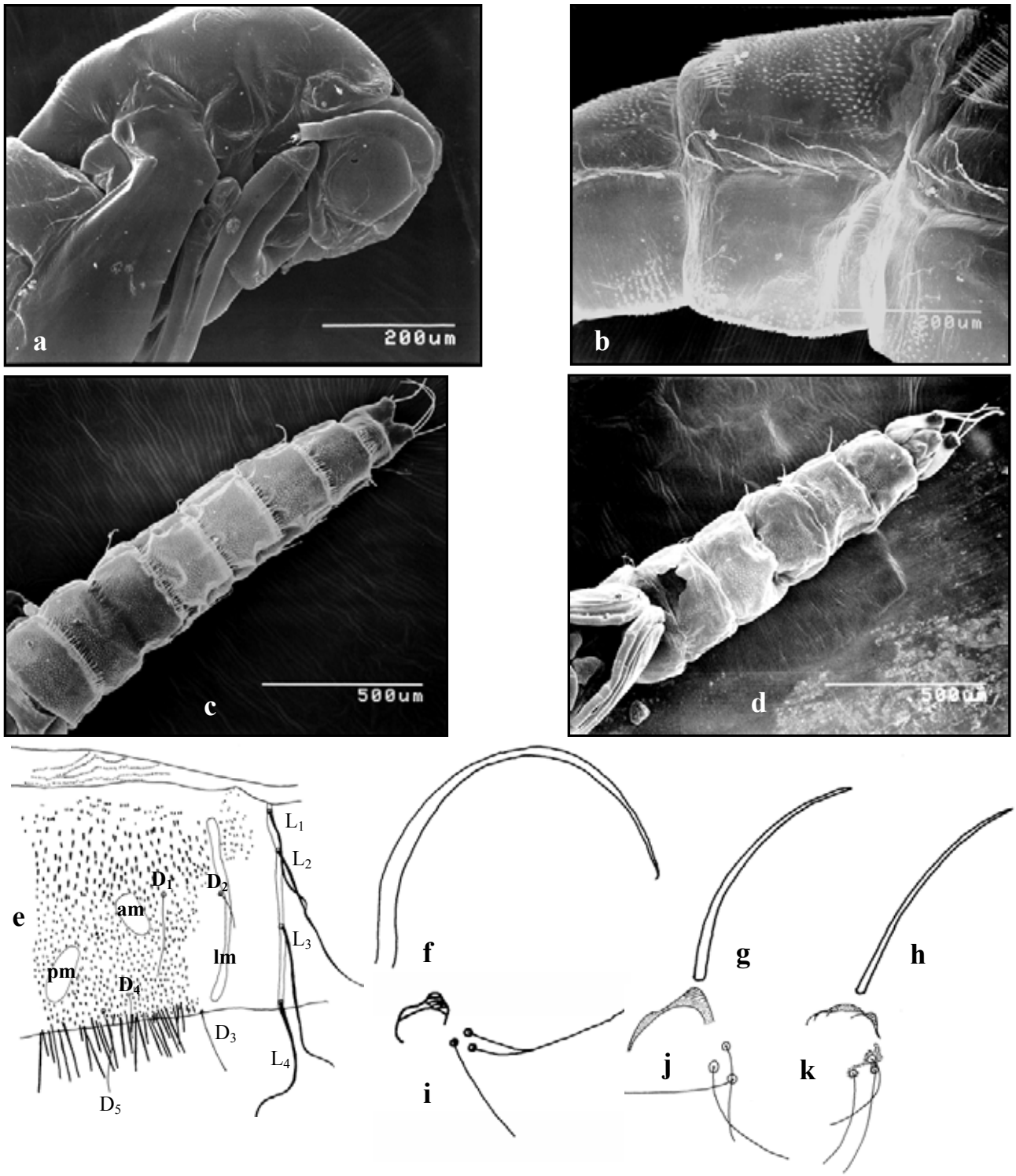

Figure 45: The pupa of *Limnophyes asquamatus* cf. f. *aquaticus**: (a) Cephalothorax (lateral); (b) abdominal segment VII (lateral); (c) abdominal segments II - IX (dorsal); (d) abdominal segments III - IX (ventral); (e) dorsal armament of abdominal segment IV (D_1-D_5 = D-setae; L_1-L_5 = L-setae; am, lm, pm = anterior-, lateral- and posterior muscle marks). Megaseta: (f) *L. asquamatus* cf. f. *aquaticus**; (g) *L. natalensis***; (h) *Limnophyes minimus* senso stricto***. Precorneal region: (i) *L. asquamatus* cf. f. *aquaticus**; (j) *L. natalensis***; (k) *L. minimus* senso stricto***.

* see comments on Table 33; ** see comments on Table 31; *** see comments on Table 32.

4.3.2. *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*

4.3.2.1. Taxonomy & determination

4.3.2.1.1. *Chironomus dorsalis sensu* STRENZKE (1959) and KEYL & KEYL (1959)

Taxonomy: Although the species is usually called *Chironomus dorsalis*, there is a controversy as to its name (MARTIN 2001). WÜLKER (cit. in LINDEBERG & WIEDERHOLM 1979) examined the type of *C. dorsalis* MEIGEN, 1818, which proved to be an *Einfeldia* species. STRENZKE (1959), who redescribed both the adult male and female, as well as KEYL & KEYL (1959), who described the karyotype from larvae of the 'STRENZKE-material', used the name as it was given by EDWARDS (1929). However, *C. nigroviridis* MACQUARD, 1834 and *C. sordidatus* KIEFFER, 1913 may also be senior synonyms of EDWARDS' *C. dorsalis*. The species taxonomic situation therefore remains unclear until its identity is confirmed from the type material after which the oldest available synonym may be used as the species' name (ASHE & CRANSTON 1990).

Determination of the adult: The adult male of *C. dorsalis* is relatively well separable from the other known species of the genus by the shape of the appendage 1 (not strongly expanded distally (LINBEBERG & WIEDERHOLM 1979), band-shaped to sickle-shaped (STRENZKE 1959)), the beard ratio (BR) of Ta_2 on P_1 (2.7 ± 0.35 (STRENZKE 1959), < 3.0 (LINDEBERG & WIEDERHOLM 1979)) and the high value of the length/width-ratio of the 5^{th} tarsal segment on P_1 (7.97 ± 0.40 (STRENZKE 1959) ~ 8.0 (LINDEBERG & WIEDERHOLM (1979)). In the present study the latter two characters were measured on 20 males from the lab cultures that had been subjected to different ambient temperatures (Appendix 8). The various temperatures applied resulted in different adult body sizes (section 4.4.1.2.9. and Table 64 p 195). A correlation of the BR and the body size (characterized here by the thorax length, see section 4.3.2.2.) was not significant ($r = 0.285$, $F = 1.59$, $df = 1.18$, $p = 0.220$), the range measured (1.77-3.30; 2.31) was greater than provided by both STRENZKE (1959) and LINDEBERG & WIEDERHOLM (1979). There was a significant negative correlation between the length/width-ratio of Ta_5 P_1 and the body size ($r = -0.694$, $F = 16.70$, $df = 1.18$, $p < 0.001$), the range measured was also greater than provided in the literature (6.14-9.40; 7.44). The range of wing length was also much higher as provided by STRENZKE (1959) (see section 4.3.2.2.). Nevertheless, the combination of characters allows a good identification of the adult male.

Determination of the larva: The larva of *C. dorsalis* is well separable from the other known species of Western Europe by the presence of ventral and lateral tubules (Figure 46a), the gula that is at least partly pigmented, the pigmented frontal apotome, the shape of mentum (Mentumtype III: fourth lateral tooth tiny and smaller as its neighboured teeth (Figure 46e)), and the relatively small head capsule (≤ 650 µm) (VALLENDUUK & MOLLER PILLOT 1999). In some cases, the mentum was abraded and the colouration of the head was only weak (development at high water temperatures) and the separation of the fourth instar larva from other species was therefore not possible. Because no thorough morphological description is available, many details of the larval morphology are shown in the SE-micrographs of Figures 46 and 47.

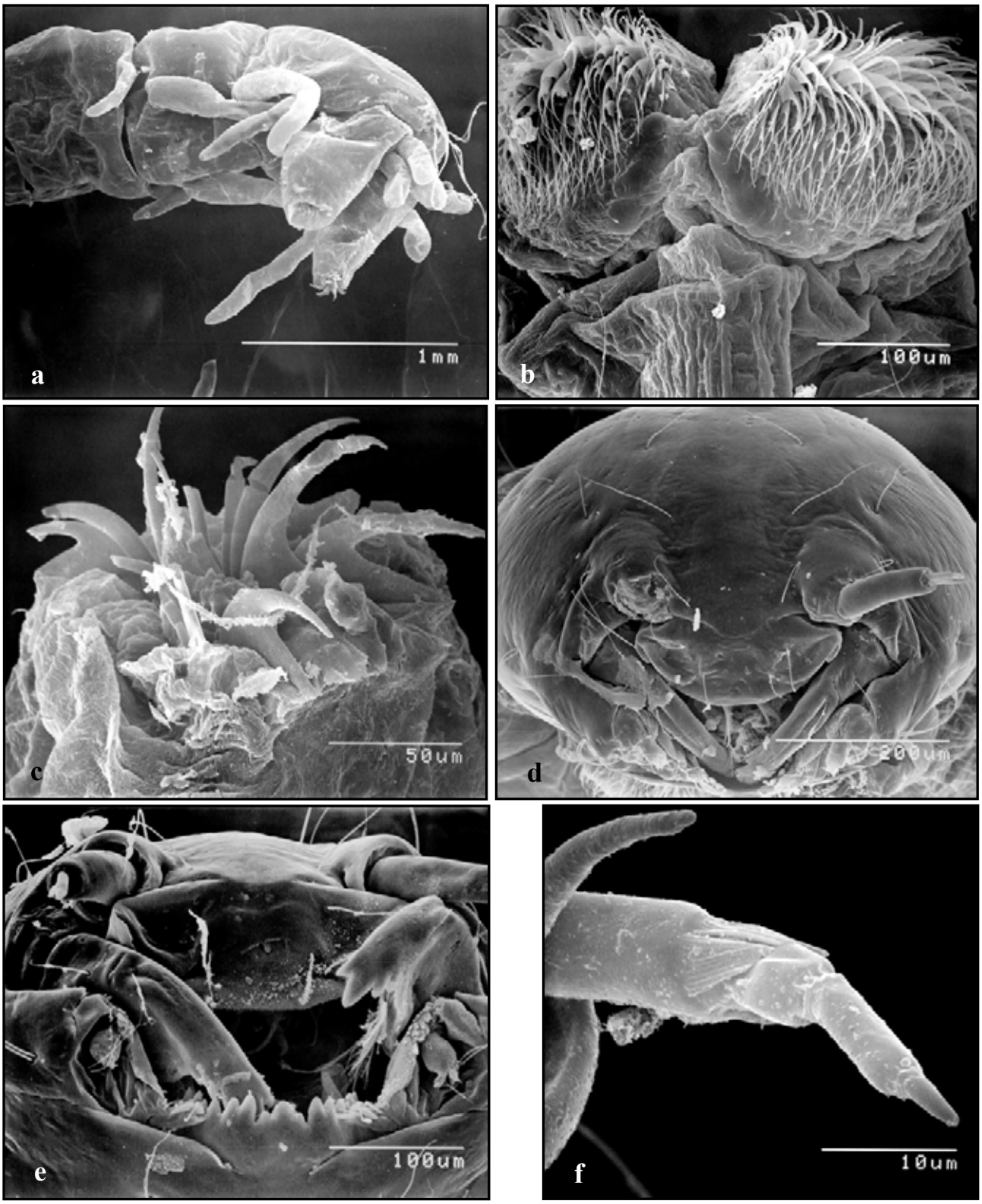

Figure 46: SE-micrographs of the instar IV of *Chironomus dorsalis* I: (a) end of the abdomen; (b) hooks of the anterior parapods; (c) hooks of the posterior parapods; (d) frontodorsal view on head; (e) frontoventral view on head; (f) antennal segments 2 - 5.

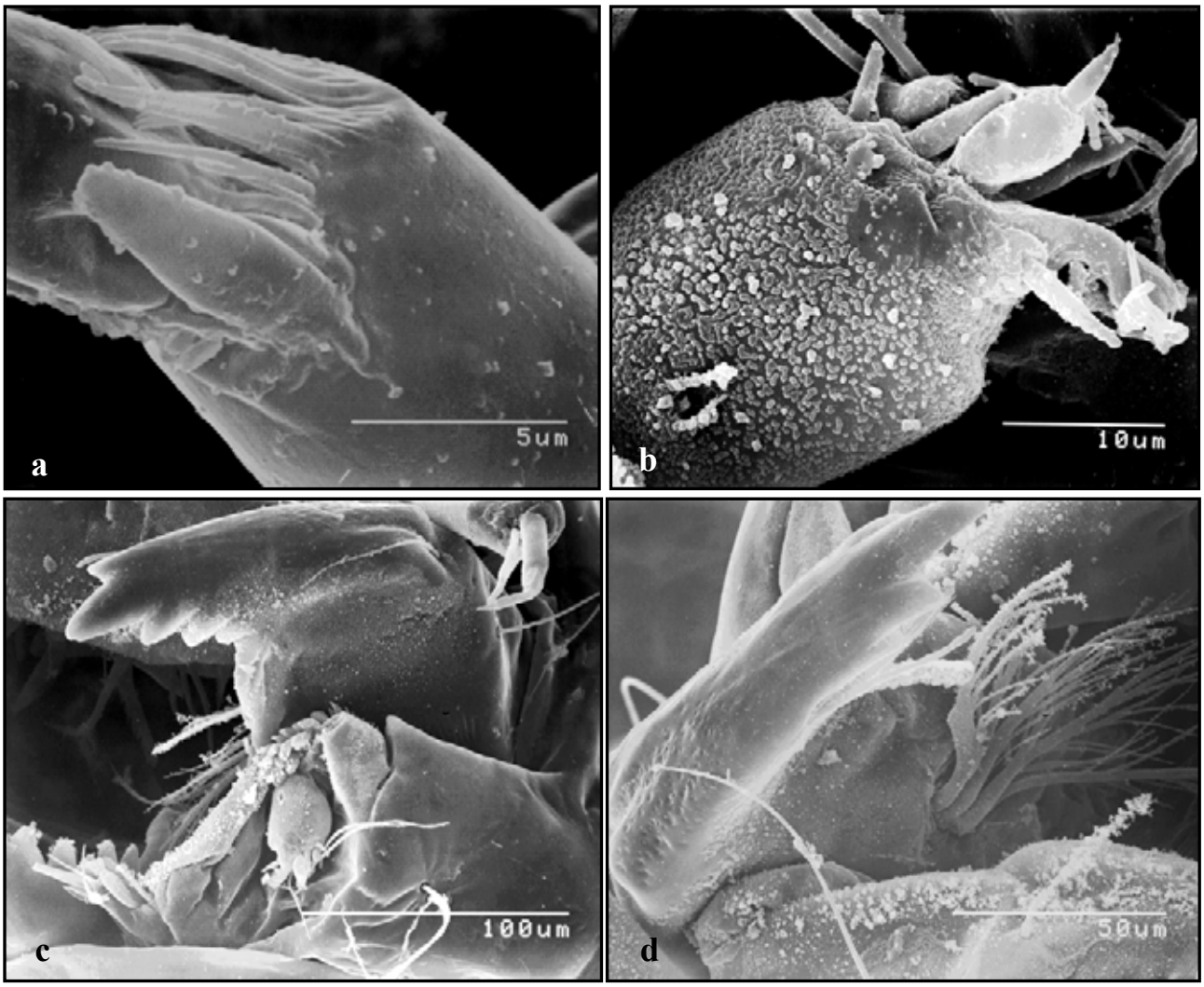

Figure 47: SE-micrographs of the larva of *Chironomus dorsalis* II: (a) Lauterborn organ and style; (b) maxillary palp; (c) outer view on mandible; (d) innerview on mandible.

4.3.2.1.2. *Polypedilum tritum* (WALKER, 1856)/*Polypedilum uncinatum* GOETGHEBUER, 1921

Taxonomy: In the Palaearctic region the genus *Polypedilum* KIEFFER is currently subdivided into 5 subgenera *Polypedilum* s. str., *Pentapedilum* KIEFFER, *Tripodura* TOWNES, *Uresipedilum* SASA ET KIKUCHI and *Cerobregma* SÆTHER ET SUNDAL (SÆTHER et al. 2000). The male genitalia of *Polypedilum sordens*, *Polypedilum tritum* and *Polypedilum uncinatum* are quite similar and these species are all placed within the subgenus *Pentapedilum*. This subgenus is however still in need of revision. *Polypedilum sordens* is well separable by the broad gonostylus, the typical colouration of the abdomen (living specimens with olive-green thorax and black vittae, abdominal segments black-brown with light apical bands) and its greater size (one male (determination confirmed by F. REISS) from an inundation pool in the floodplain of the river Lahn (near Marburg, Hesse, Germany) (SCHNABEL 1999), had a wing length of 2.67 mm and a thorax length of 1.24 mm (compare with Table 35 p 117)). I was not able to separate the species *P. tritum* and *P. uncinatum* by following the descriptions given by PINDER (1978) and GOETGHEBUER (1937-1954). The following characters are supposed to separate the species:

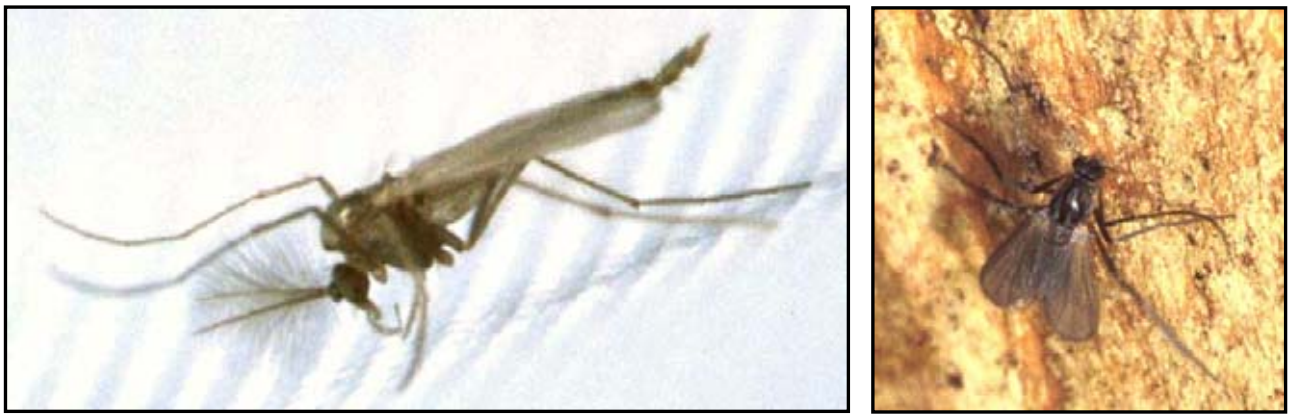

Figure 48: Habitus of male (left) and female (right) of *Polypedilum tritum*.

(a) Lateral seta inserted halfway along appendage 1. Anal point slightly expanded distally and broadly rounded at apex. Alive yellow-brown, vittae darker and well separated from remainder of the thorax. Abdominal segments uniformly greenish-brown. LR = 1.4-1.6 and AR = 2 ..... *P. tritum*

(b) Lateral seta inserted about two-thirds of the way along appendage 1. Anal point not expanded distally, more pointed at tip. Colouration of vittae merges into the colouration of the remainder of thorax. LR ~ 1.5 and AR = 1.62-1.75 ..... *P. uncinatum*

The habitus of a living male and female is shown in Figure 48. These correspond with GOETGHEBUER's description of colouration for *P. uncinatum*. The colouration of the thorax of freshly emerged specimens however resembles the description of *P. tritum*. Unfortunately, GOETGHEBUER (1921 and 1937-1954) did not mention the colouration of the abdomen in *P. uncinatum*. In my collection there are two males, collected in the same spot (Stelle I) of a temporary cut-off of the river Lahn on June 27, 1997 (Altarm Süd Sichertshausen) (SCHNABEL 1999). F. REISS inspected these two specimens and determined one as *P. tritum* (label entry LR = 1.40) and the other as *P. uncinatum* (label entry LR = 1.57). Nevertheless, the separation of the species remained unclear to me. I therefore studied the characters thought to be of diagnostic value of a greater number of specimens (Appendix 6). These characters were (a) the position of the lateral seta on appendage 1; (b) the shape of the anal point; (c) the leg-ratio; and (d) the antennal ratio:

(a) The appendage 1 was bent evenly or seemed to be straight, sometimes it seemed to be angled (strongly dependent on view), a fold or a knob could either be present or absent. In some specimens the appendage was constricted on the insertion of the lateral seta and then evenly narrowed towards its tip. The position of the lateral seta was expressed by a ratio (distance of lateral seta from the base of the appendage 1/length of appendage 1), which I called the appendage ratio. The appendage ratio showed a range of 0.45-0.71; 0.54, a correlation with the body size (expressed here by the thorax length, see section 4.3.2.2.) was not significant (Figure 49a). The results show that this character cannot be used as a separation character between *P. tritum* and *P. uncinatum*.

(b) The apex of the anal point was generally rounded at its apex and, in some specimens, somewhat expanded distally. If the anal point is seen in the lateral view it appeared to be pointed at tip.

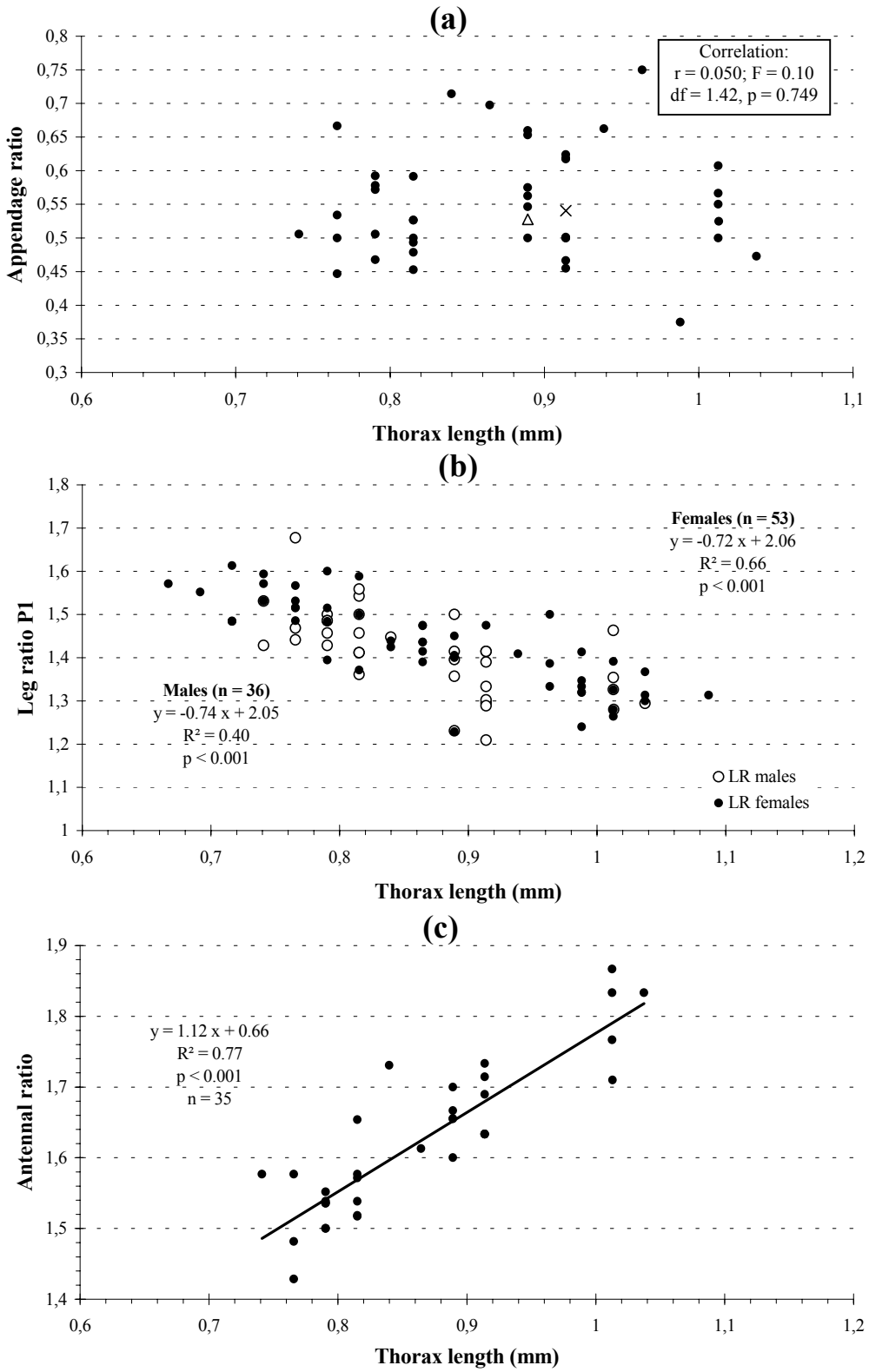

Figure 49: Variation of the (a) appendage ratio; (b) leg ratio; and (c) the male antennal ratio in *P. tritum*.

Explanations:

(a): Δ = specimen determined as *P. uncinatum* by F. REISS; x = specimen determined as *P. tritum* by F. REISS. The remaining specimens derived from (1) laboratory cultures originating from pool 1 and (2) field samplings taken in pool 1, pool 2, Altarm 1 Sichertshausen (SCHNABEL 1999) and Lake Borken (HEINMÜLLER et al. 1998) (Appendix 6). For further explanations see text.

(b) + (c): these regressions were only done with specimens of the different lab cultures.

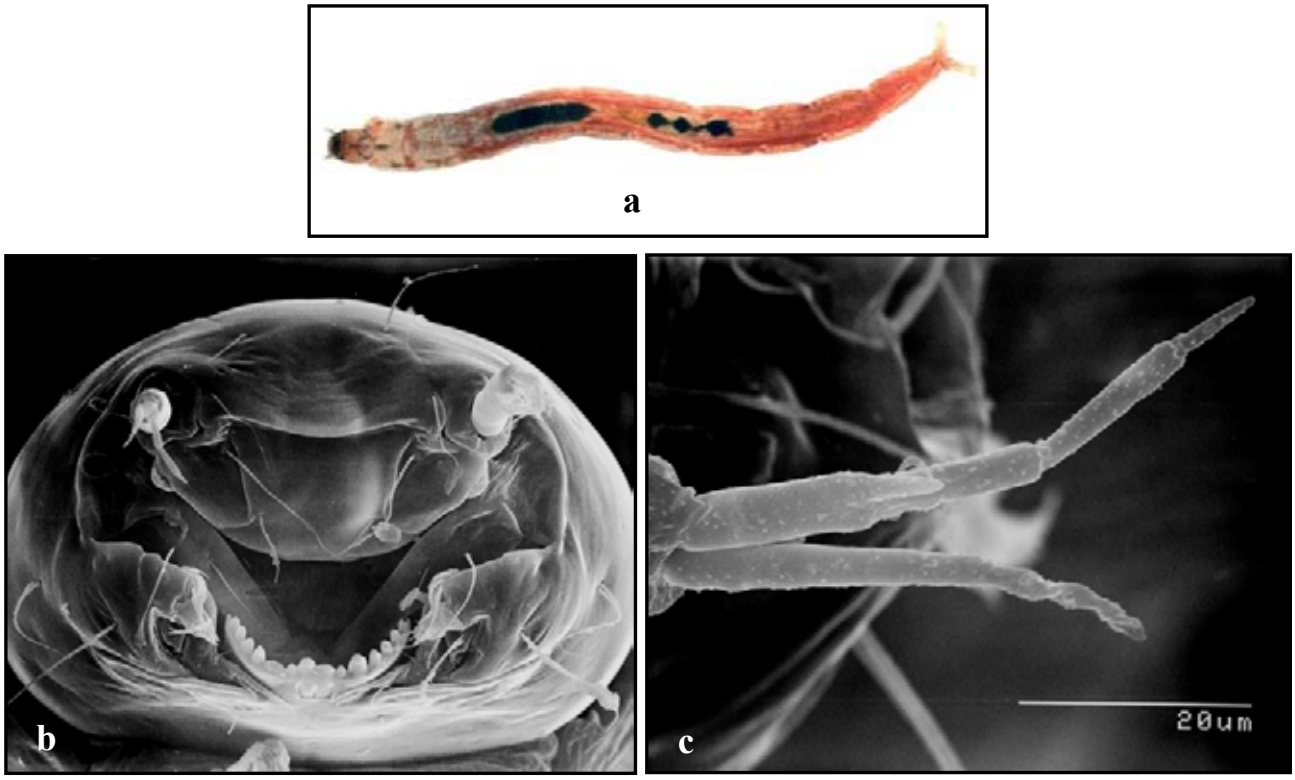

Figure 50: The larva of *Polypedilum tritum*: (a) habitus; (b) frontal view of head; (c) flagellomeres 2-5 of the antenna.

(c) The **leg ratio** is dependent on body size in males as well as in females (Figure 49b). This ratio ranged between 1.21-1.68; 1.41 in males (n = 36) and 1.23-1.61; 1.44 in females. Again, this character cannot serve as a separation feature.

(d) The **antennal ratio** of the adult male is also strongly dependent on body size (Figure 49c). It ranged between 1.43-1.87; 1.63 and is therefore not an appropriate separation feature either.

The results presented above show that it is not possible to separate *Polypedilum tritum* and *P. uncinatum* with the separation features available. Probably *Polypedilum uncinatum* is a junior synonym of *Polypedilum tritum*, but this still requires investigation of the type material. Nevertheless, the species is named as *Polypedilum tritum* during the present investigation, instead of the more correct term *Polypedilum tritum/uncinatum*.

Determination of the larva: The most important larval characters of *P. tritum* are shown in Figure 50. By following the key compiled by KLINK et al. (2002), one ends up with *P.* cf. *uncinatum*: the gula is not darkened, the first side teeth neighbouring the two middle teeth are tiny (Figure 50b) and the flagellomeres 2-4 are about equal in length (Figure 50c). The range of head capsule length of *P. tritum* in the present study (299-412; 354 µm; n = 63, see Table 36 p 120) is much wider than provided in KLINK et al. (2002) (391-469; 425 µm; n = 10) for *Polypedilum* cf. *uncinatum*. MOLLER PILLOT (1984) mentioned that the larvae he identified as *P.* cf. *uncinatum* belong to the group *nubeculosum* and that he was not sure about where to place *Polypedilum tritum* larvae that following the descriptions of BRYCE (1960) and ROBACK (1957), belong to group *nubeculosum* but according to BURTT (1940) belong to the group *sordens*. There are therefore problems associated with the identi-

fication of *Polypedilum tritum/uncinatum* larvae. The *P. uncinatum* sensu BEATTIE (1978a) has larvae, which belong to the group *bicrenatum* (MOLLER PILLOT 1984), another case of misidentification!

4.3.2.1.3. *Paralimnophyes hydrophilus* (GOETGHEBUER, 1921)

Fortunately, there are hitherto no taxonomic problems known in *Paralimnophyes hydrophilus* (WANG & SÆTHER 2002). In Germany there is only one species of the genus. The habitus of a male, female and larva is shown in Figure 51. In contrast to the diagnosis found in CRANSTON et al. (1983), the SI seta of palatum may also be bifid with a large main branch and a weak side branch (Figure 52g). The larva is very characteristic and easily recognized by its purple body colour (Figure 51c), the long lateral setae on the body segments (Figure 51d) and a mandible with 4 inner teeth (Figure 52b). Further morphological aspects are illustrated in Figure 52.

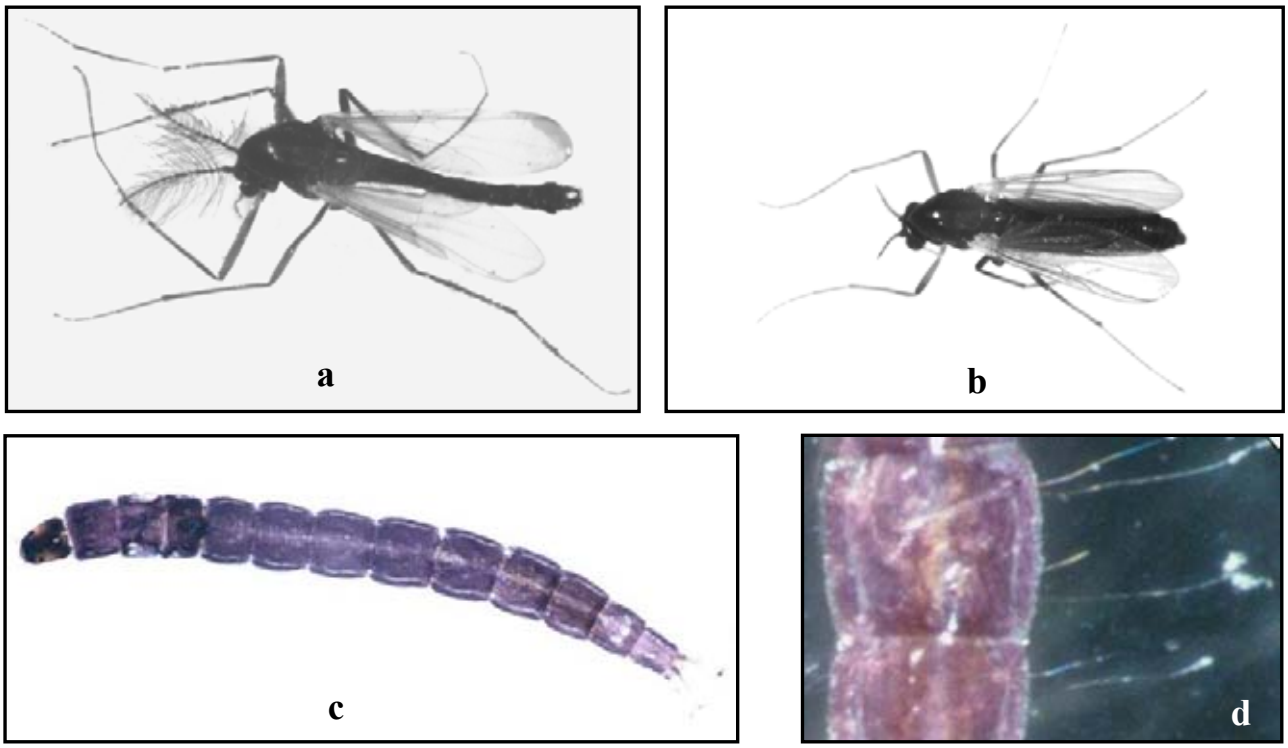

Figure 51: The habitus of *Paralimnophyes hydrophilus*: (a) male; (b) female; (c) larva; (d) body segments of larva with long lateral setae.

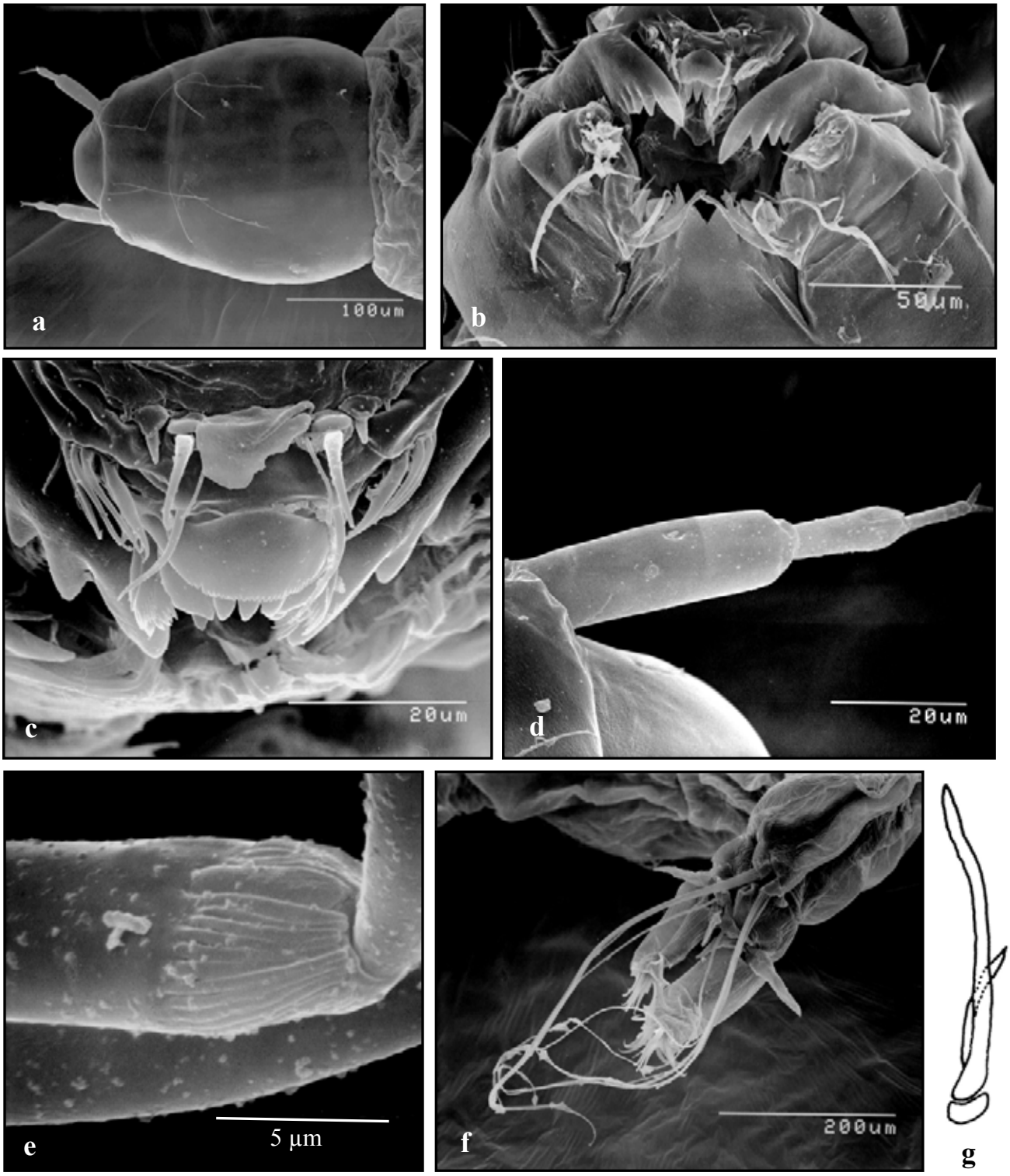

Figure 52: SE-micrographs of the larva of *Paralimnophyes hydrophilus*: (a) dorsal view of head; (b) ventral view of anterior part of head; (c) palatum; (d) antenna; (e) Lauterborn organ; (f) dorsal view of the end of the abdomen; (g) bifid SI seta of palatum.

4.3.2.2. Size characteristics of the adults

The body size of adults, especially of females is considered to be an important indirect parameter of biological fitness. The total length of alcohol preserved specimens is not a good indicator as the abdomen may shrink or swell (lower values of r^2 in the regressions of Figures 53 + 54). Fortunately, wing length as well as thorax length are strongly and significantly correlated with the body length and are not influenced by the preservation medium (higher values of r^2 in the regressions of Figures 53 + 54). The wing- and thorax lengths therefore characterize better the adult body size of alcohol preserved specimens. Since thorax length measurements are faster to take, the thorax length was usually used to characterize the adult body size in the present study. The range of the three parameters (wing-, thorax- and total length) for adult individuals of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* are listed in Table 35.

Table 35: Size characteristics (min.-max.; mean) of the adults of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*.

	♂♂	♀♀
Chironomus dorsalis		
Wing length lab (mm)	2.55-3.60; 3.14 (n = 59)	2.65-4.00; 3.24 (n = 47)
Wing length col. (mm)	2.40-3.65; 2.91 (n = 233)	2.5-3.85; 3.05 (n = 225)
Thorax length lab (mm)	1.25-1.70; 1.48 (n = 60)	1.40-1.85; 1.58 (n = 47)
Thorax length col. (mm)	1.10-1.70; 1.35 (n = 252)	1.20-1.75; 1.44 (n = 242)
Total length lab (mm)	4.70-6.55; 5.75 (n = 40)	4.15-6.50; 5.22 (n = 30)
Total length col. (mm)	4.60-6.75; 5.50 (n = 185)	3.80-6.60; 4.96 (n = 189)
Polypedilum tritum.		
Wing length 'lab' (mm)	1.43-2.32; 1.91 (n = 78)	1.31-2.47; 1.87 (n = 60)
Thorax length 'lab' (mm)	0.74-1.04; 0.87 (n = 80)	0.67-1.09; 0.87 (n = 62)
Thorax length field (mm)	0.64-1.09; 0.87 (n = 116)	0.54-1.14; 0.86 (n = 91)
Total length 'lab' (mm)	2.49-3.71; 3.03 (n = 36)	1.68-3.16; 2.36 (n = 59)
Paralimnophyes hydrophilus.		
Wing length lab (mm)	1.04-1.56; 1.35 (n = 38)	0.99-1.78; 1.35 (n = 35)
Thorax length lab (mm)	0.54-0.79; 0.68 (n = 39)	0.54-0.86; 0.68 (n = 35)
Thorax length field (mm)	0.49-0.89; 0.68 (n = 129)	0.49-0.87; 0.65 (n = 112)
Total length lab (mm)	1.85-2.09; 2.27 (n = 28)	1.48-2.72; 1.99 (n = 30)

Abbreviations and comments:

C. dorsalis: lab = individuals from the different lab cultures (see section 4.4.1.2. and Appendix 8): 9.5 °C 10♂♂ 7♀♀; 13.8 °C SD/LD 10♂♂ 10♀♀; 16.0 °C 10♂♂ 8♀♀; 20.0 °C 10♂♂ 8♀♀; 25.0 °C 10♂♂ 4♀♀; 30.2 °C 7♂♂ 7♀♀.
col. = individuals from different sampling dates of the colonizing experiment (section 4.4.2.3.).

P. tritum: 'lab' = individuals from the different lab cultures (see section 4.4.1.2. and Appendix 8) and in addition 9 males from different locations in the field (individuals no. I135-I143 in the Appendix 6): 9.5 °C 10♂♂ 10♀♀; 13.8 °C SD/LD 10♂♂ 10♀♀; 14.6 °C 11♂♂ 9♀♀; 19.3 °C 11♂♂ 9♀♀; 25.0 °C 10♂♂ 10♀♀; 29.1 °C 9♂♂ 7♀♀; 30.2 °C 10♂♂ 7♀♀.
field = individuals from pool 1 in 1998 and 1999 (section 4.4.2.2.1.).

P. hydrophilus: lab = individuals from the different lab cultures (see section 4.4.1.2. and Appendix 8): 4.5 °C 1♂ 1♀; 9.5 °C 10♂♂ 11♀♀; 14.6 °C 9♂♂ 10♀♀; 19.3 °C 8♂♂ 7♀♀; 25.0 °C 10♂♂ 7♀♀.
field = individuals from pool 1 in 1997 and 1998 (section 4.4.2.2.2.).

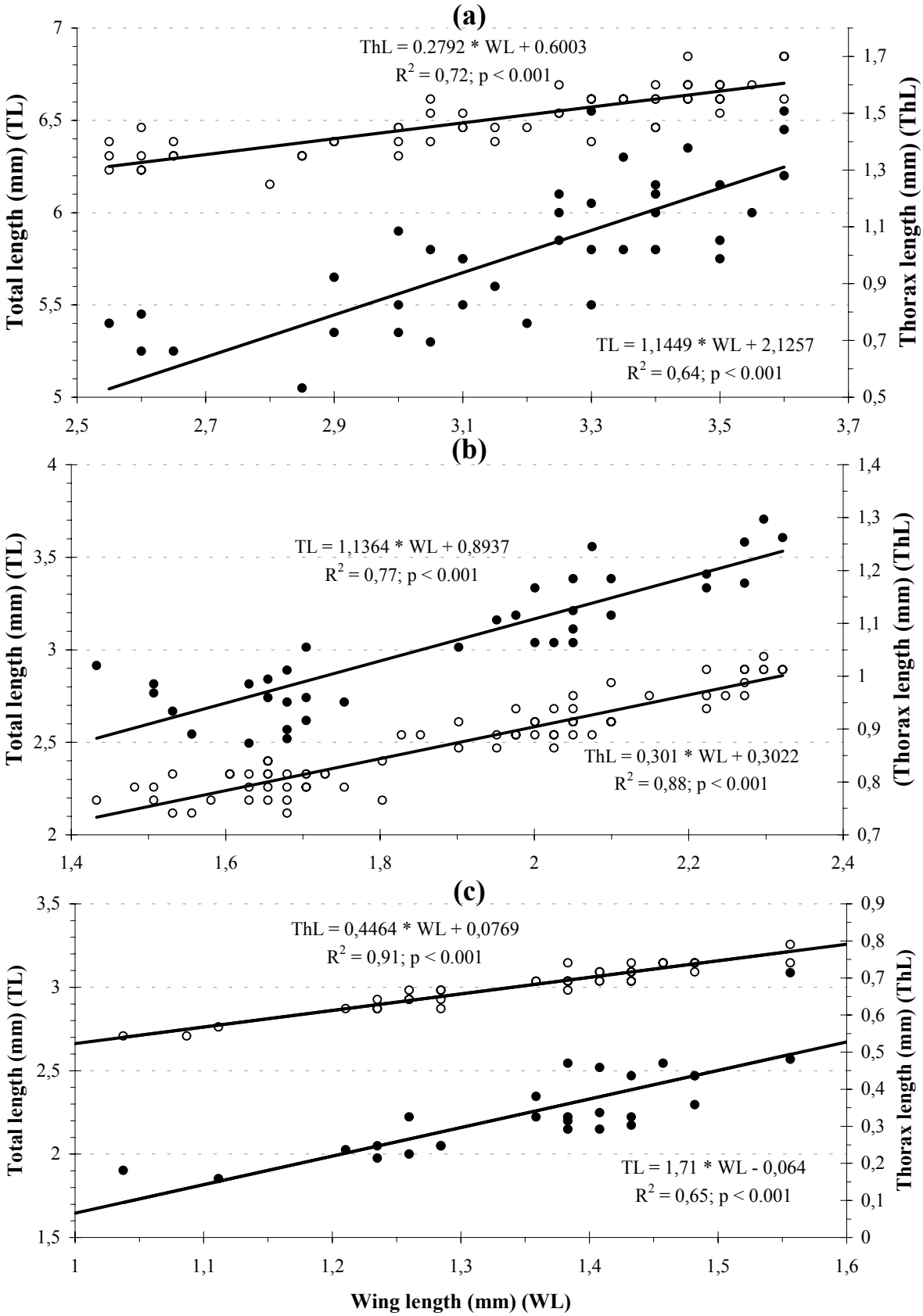

Figure 53: Regressions between wing length and total length (●) and between wing length and thorax length (○) for adult males of (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*.

For the regressions only lab- or 'lab' individuals (see Table 35) were used.

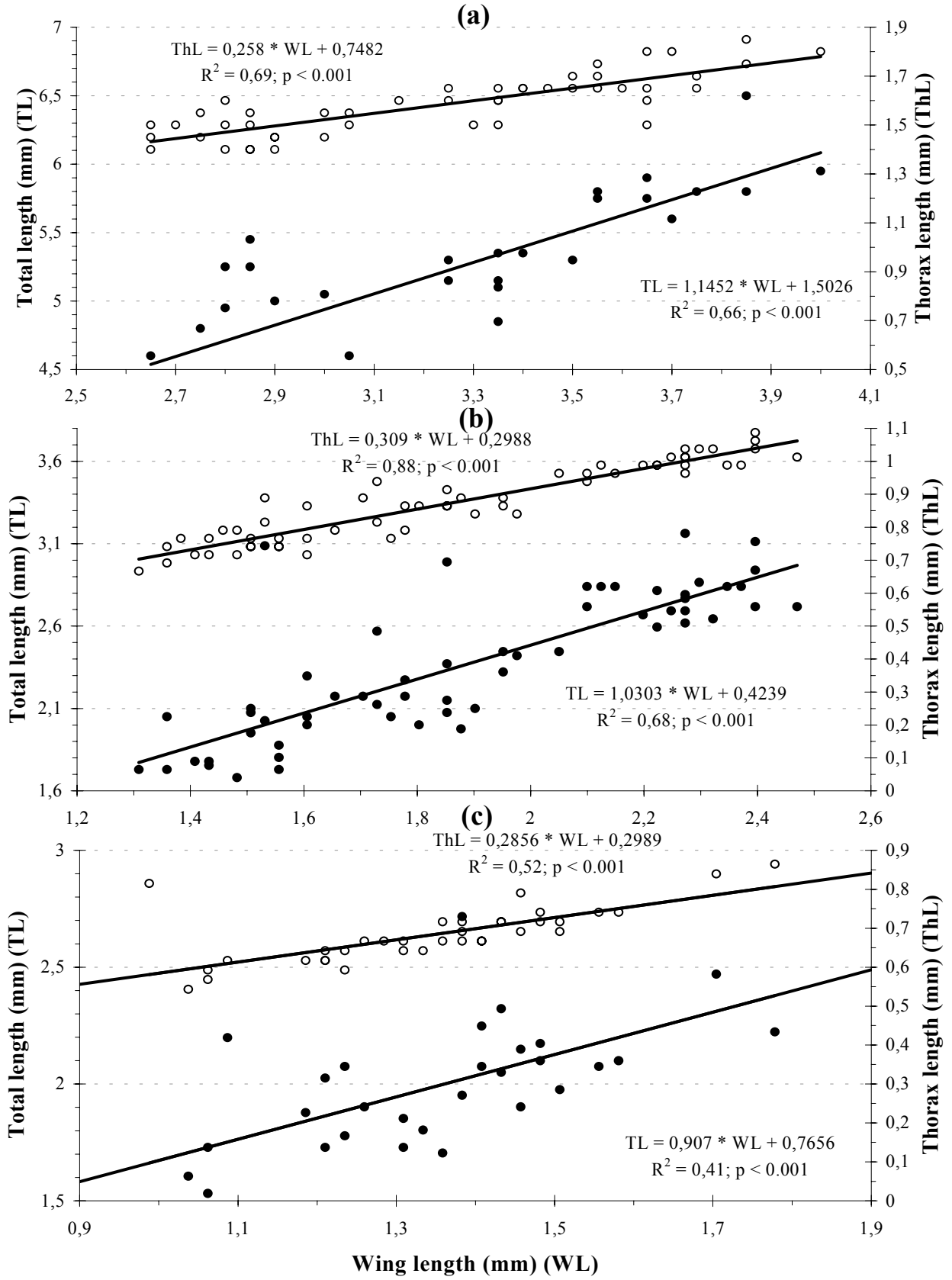

Figure 54: Regressions between wing length and total length (●) and between wing length and thorax length (○) for adult females of (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*.

For the regressions only lab- or 'lab' individuals (Table 35) were used.

4.3.2.3. Size characteristics of the juvenile stages

The larval instars of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* are clearly separable from each other by their head capsule size (Figure 55). The range of head capsule length, head capsule width, body length, body width and thorax width is presented in Table 36.

Table 36: Size characteristics (min.-max.; mean ± 1 sd) of larval instars and pupae of *Chironomus dorsalis*, *Polypedilum tritum and Paralimnophyes hydrophilus*.

Instar	Head L (µm)	Head W (µm)	Body L (mm)	Body W (µm)	Thorax W (µm)
		Chironomus dorsalis			
I	105-184; 123 ± 10.9 n = 53	101-184; 112 ± 11.2 n = 51	0.7-2.0 n = 161	40-201 n =162	
II	182-224; 199 ± 10.7 n = 48	159-208; 190 ± 9.9 n = 48	1.7-3.8 n = 106	102-347 n = 106	
III	270-405; 355 ± 29.7 n = 54	245-356; 311 ± 22.3 n = 52	3.0-7.5 n = 138	161-564 n = 140	
IV	494-649; 585 ± 40.3 n = 65	409-592; 510 ± 37.1 n = 64	4.7-12.8 n = 316	353-1128 n = 316	367-1241 n = 314
		Polypedilum uncinatum			
I	77-105; 87 ± 4.2 n = 60	68-85; 74 ± 3.5 n = 47	0.4-1.4 n = 130	35-133 n = 127	
II	120-154; 138 ± 6.5 n = 49	99-123; 114 ± 5.1 n = 43	1.2-2.6 n = 87	70-127 n = 87	
III	194-247; 221 ± 12.4 n = 66	151-205; 175 ± 11.4 n = 55	1.7-3.8 n = 126	92-315 n = 121	
IV	299-412; 354 ± 28.5 n = 63	237-333; 287 ± 25.8 n = 60	2.7-6.8 n = 261	160-509 n = 261	180-613 n = 240
P			2.9-5.4 n = 13		
		Paralimnophyes hydrophilus			
I	70-81; 75 ± 3.0 n = 72	68-82; 76 ± 3.1 n = 63	0.4-1.1 n = 265	30-111 n = 264	
II	102-129; 115 ± 5.1 n = 46	91-123; 104 ± 5.7 n = 44	0.8-2.3 n = 116	60-150 n = 116	
III	151-196; 171 ± 9.8 n = 50	120-160; 147 ± 8,7 n = 48	1.4-2.8 n = 114	71-257 n = 114	
IV	222-316; 260 ± 20.0 n = 67	190-257; 222 ± 13.4 n = 61	2.1-5.1 n = 278	132-430 n = 276	135-450 n = 232
P			2.3-3.4; 2.8 n = 14		

Abbreviations and comments:
I, II, III, IV, P = instars 1-4 and pupae.
All larvae measured were taken from the different lab cultures (section 4.4.1.2. and Appendix 9).

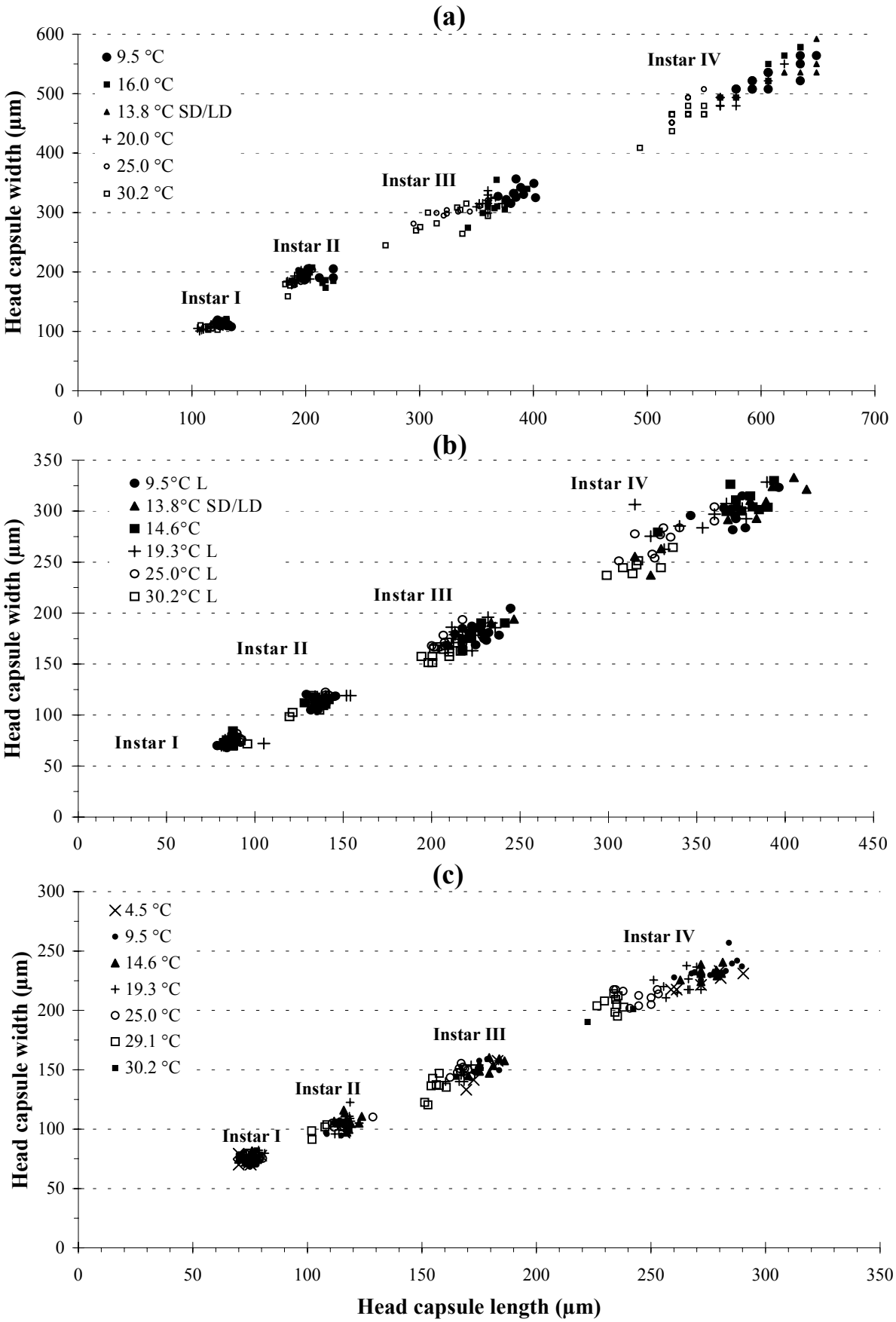

Figure 55: Separation of the larval instars using head capsule size in (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*.
The larvae were taken from lab cultures with different ambient temperatures (Appendix 8).

4.3.3. Comparison of two parameters of flight capacity in four species of *Chironomus* MEIGEN

MCLACHLAN (1986) stated a sexual dimorphism for *Chironomus imicola* KIEFFER, an inhabitant of ephemeral rain-pools in tropical Africa. Males of that species have relatively narrow, short and fast-beating wings with a shorter stroke and a lower ability for sustained flight than females. In addition males are smaller than females. The females have a greater ability for sustained flight, relatively long and broad wings that are slow-beating and have a large amplitude of beat. MCLACHLAN explained this sexual dimorphism by the different flight necessities: females fly primarily in order to disperse and lay eggs whereas males fly primarily in order to mate in the aerial swarm and therefore require a higher aerobatic ability. In section 4.2.2. it was shown that *Chironomus dorsalis* was the most dominant midge species of the colonizing experiment and colonized all boxes quickly. *C. dorsalis* is thought to be a specific inhabitant of ephemeral rain-puddles, a habitat which spatio-temporal persistence is unpredictable. *C.piger/riparius* was the second most abundant chironomid species of the colonizing experiment. This species was also present in all experimental boxes but colonized the pools more slowly. *C. luridus* and *C. pseudothummi/uliginosus* were typical colonizers of pool 1 and 2 (section 4.2.1.). They prefer permanent and/or shallow water bodies,

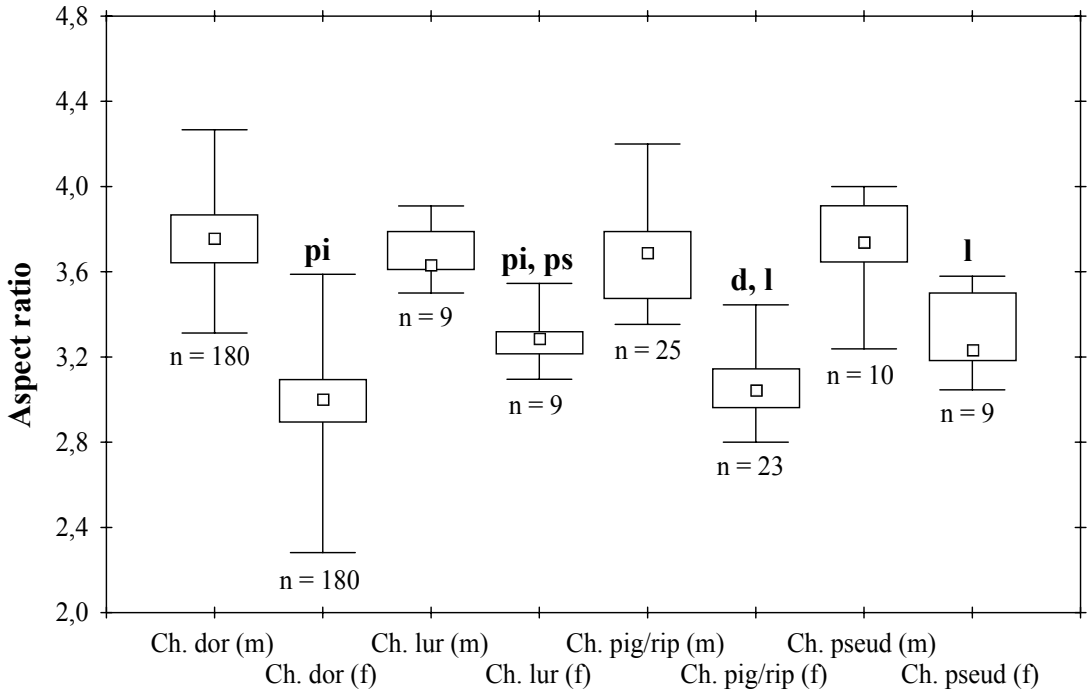

Figure 56: Comparison of the wing aspect ratios of *Chironomus dorsalis*, *Chironomus luridus*, *Chironomus piger/riparius* and *Chironomus pseudothummi/uliginosus*.

Explanations:

- Comparisons were done with an ANOVA ($F = 303.0$, $df = 7$, $p < 0.001$) and a TUKEYS honest significant difference test for unequal N in multiple comparisons. The variance values were not significantly different (LEVENE'S test: $F = 1.8$, $df = 7.4$, $p = 0.089$). All wing aspect ratios in males were not significantly different ($p > 0.05$) and all intraspecific differences between males and females were highly significant ($p < 0.001$). Species for which females there was no significant difference are marked in bold above the box-and-whisker-plots (d = *Ch. dorsalis*; l = *Ch. luridus*; pi = *Chironomus piger/riparius*, ps = *Ch. pseudothummi/uliginosus*).
- m/f = males/females.

which may dry up, but are not specialized to temporary waters. I hypothesize that *C. dorsalis* and *C. piger/riparius* are specific colonizers, which have a higher dispersal ability than *C. luridus* and *C. pseudothummi/uliginosus*. Based on MCLANCHLAN'S paper (1986), I compared the four species' wing aspect ratio (wing length : wing width) expecting the females of the better colonizers to have a lower wing aspect ratio (higher wing area in comparison to the body size, see section 4.3.2.2.). All species showed a strong sexual dimorphism of the wing aspect ratio (Figure 56). The dimorphism was great in *C. dorsalis* (d = 0.78) and low in *C. luridus* (d = 0.41) and *C. pseudothummi/uliginosus* (d = 0.43). *C. piger/riparius* (d = 0.61) was in between *C. dorsalis* and *C. luridus* and *C. pseudothummi/uliginosus*. The males of the four species did not differ significantly from each other. As expected, wing aspect ratio in *C. dorsalis* females was lowest and significantly different from those of *C. luridus* and *C. pseudothummi/uliginosus*. The wing aspect ratio of *C. piger/riparius* females was intermediate and not significantly different from that seen in *C. dorsalis* and *C. luridus* as well. Finally, the female wing aspect ratio of *C. pseudothummi/uliginosus* females was the only one that was not significantly different to that of *C. luridus*.

In addition to the wing aspect ratio, the 'thorax ratio' sensu meo was used in comparisons between species and sexes. The thorax ratio is defined as the ratio of wing length to thorax length. I hypothesized that sustained flight requires a greater muscular system and therefore a greater thorax in relation to the remainder of the body. The thorax ratio should therefore be lower in the better coloniz-

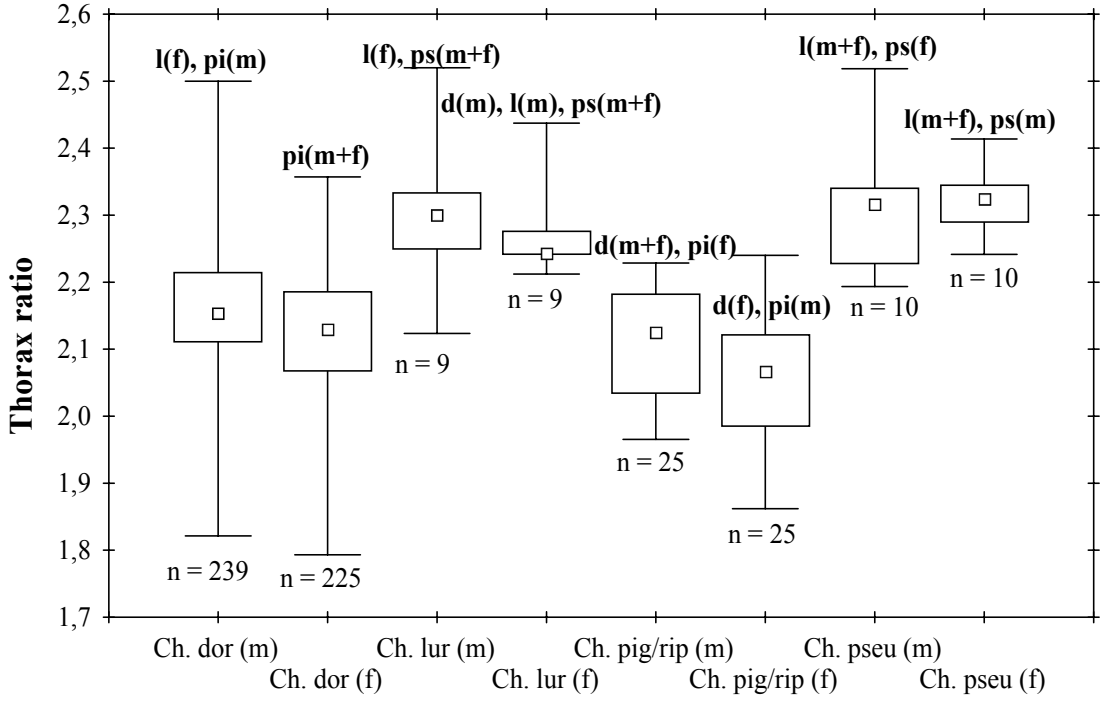

Figure 57: Comparison of the thorax ratio of *Chironomus dorsalis*, *Chironomus luridus*, *Chironomus piger/riparius* and *Chironomus pseudothummi/uliginosus*.

Explanations:

Comparisons were done with an ANOVA ($F = 23.6$, $df = 7$, $p < 0.001$) and a TUKEYS honest significant difference test for unequal N in multiple comparisons. The variance values were not significantly different (LEVENE´S test: $F = 1.0$, $df = 7.54$, $p = 0.409$). Groups for which there were no significant differences ($p > 0.05$) are marked in bold above the box-and-whisker-plots (m = males; f = females; d = *C. dorsalis*; l = *C. luridus*; pi = *C. piger/riparius*; ps = *C. pseudothummi/ uliginosus*).

ers. *C. dorsalis* females had a somewhat lower thorax ratio than males of the species (Figure 57). *C. luridus* and *C. piger/riparius* also present this tendency although the difference between males and females was not significant. Contrasting to the situation for the wing aspect ratio, there were interspecific differences in the thorax ratio of males as well as females. The thorax ratios of both sexes of *C. dorsalis* and *C. piger/riparius* and of *C. luridus* and *C. pseudothummi/uliginosus* were significantly different. *Chironomus dorsalis* and *Chironomus piger/riparius*, which had been assumed to have the highest dispersal ability, had the lower thorax ratios.

The material and individual values of measurements are listed in the Appendix 7.

4.4. Autecology

This section presents basic information on the autecology of the most specific aquatic/semiaquatic chironomids of temporary pools 1 and 3 (see section 4.2.1.) - *Polypedilum tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* - and of the experimental puddles of the colonizing experiment (see section 4.2.2.) - *Chironomus dorsalis*. The scope of this section is to concentrate on the question of whether a species' characteristics are a result of a specific adaptation to temporary pools or of a preadaptation common in Chironomidae. To help clarifying this question, species that are typical of small but permanent standing waters were also included in the investigation program.

4.4.1. Laboratory studies

4.4.1.1. Mating and oviposition

Mating was not observed in *Chironomus dorsalis* (see section 3.3.1.2.) and *Limnophyes asquamatus* (see sections 3.3.1.1. and 4.3.1.1.2.). The males of *Polypedilum tritum* swarmed a few centimetres above the water surface up to a maximum height of about 1.5 meters. While swarming,

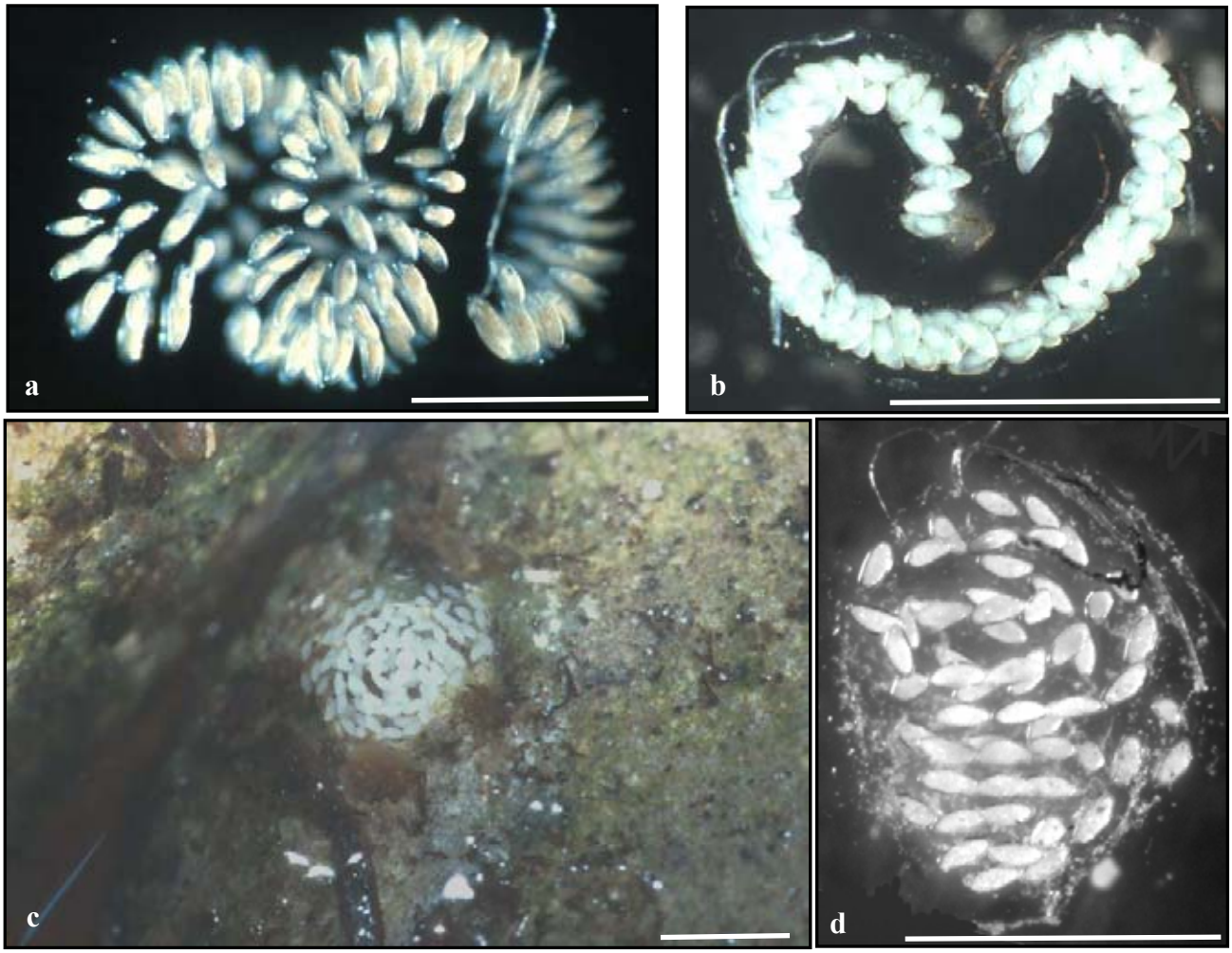

Figure 58: The egg masses of: (a) *Polypedilum tritum*; (b) *Paralimnophyes hydrophilus*; (c) *Limnophyes asquamatus* forma *aquaticus*; and (d) *Limnophyes asquamatus* forma *aquaticus or limosus*. A scale of 1 mm is marked by the white bars.

males flew just above the water surface in more or less eight-shaped horizontal loops (< 1m circumference). Swarming usually occurred at dusk. During daytime, adults were usually resting in the vegetation just above the water surface and on the pool's edge. If very many adults were present, temporary and small swarms occurred spontaneously, even during daytime. When females entered the swarm they were grasped by the males and mating took place within the swarm with the male and female obviously in face-to-face position. Mating lasted about 2-3 seconds and couple lost some height. After mating, the males continued swarming and the females usually flew to a resting point. Swarming of *Paralimnophyes hydrophilus* has not been observed in the field. In the lab, swarming males usually hit the top of the cage, regardless of its height (see section 3.3.1.2.). While swarming the males performed small and fast movements up and down. On entering a swarm females danced a few seconds with the males before being grasped. The couple then sank to the ground. Copulation in *Paralimnophyes hydrophilus* lasted about 3 minutes and was done in the end-to-end position. In small vessels coupling could even be induced without swarming, as a male that came into contact with a female tried to 'rape' her, which often resulted in mating.

Egg masses and oviposition: The adults of *Chironomus dorsalis* are short-lived. At ambient temperatures of 5 °C they have a life span (min.-max.; mean) of 11-30; 17.9 days (n = 92). The egg masses of *Chironomus dorsalis* were deposited on firm substrata at the water's edge or on floating material. They were attached to the substrate with a stalk, which is typical in *Chironomus*. The egg mass of *Chironomus dorsalis* is illustrated on plate 2 (Figure n) in STRENZKE (1959). The number of eggs of twelve egg masses counted varied from 150 to 631 (mean = 371). The egg masses of *Polypedilum tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* have not yet been described. The terms used in the following descriptions of the egg masses follow NOLTE (1993).

Polypedilum tritum (Figure 58a): The females sat on the water's surface or on the water's edge to lay their eggs. During oviposition the abdomen is bent ventrally, the apices of the hind tibiae touch each other. The females needed about 1 minute to lay the eggs, pressing movements of the abdomen could be seen. After the egg mass had been pressed out, it remained either attached to the abdomen or was held with the hind legs. If a female had laid her eggs at the water's edge it then flew to the open water where the egg mass was released. The egg masses swelled within a minute and while floating they finally became attached to any structure. The number of eggs within an egg mass ranged from 50 to 180 (mean = 106.6, n = 143). The elliptical eggs had a length of about 270 µm, their length/width-ratio was ± 3.0. The egg mass (maximum length observed was about 3 mm) was club-shaped, which cannot be observed in Figure 58a because of the transparent gelatine. The eggs were lined up in a single row and arranged ± vertically to line axis. The egg line was first folded into loops which then formed a spiral.

Limnophyes asquamatus (Figure 58c+d): The sexual females were alive for 3-8 days (20.0 °C). Females that were fed sugared water lived significantly longer (5-9; 6.8 days, n = 7) than females that were not fed (3-6; 3.8 days, n = 9) (MANN-WHITNEY-U-test: U = 2.0, p = 0.003). In 1996, several observations of egg deposition in *Limnophyes asquamatus* forma *asquamatus* were made during the

attempts at establishing laboratory cultures (see sections 3.3.1.1. and 4.3.1.1.2.). The oviposition seemed to be hindered by captivity. However, the females obviously preferred humid to wet soils as oviposition sites. The females died after the oviposition and in many cases became stuck to the egg mass. Interestingly, sexual females were not able to crawl on water: if a female landed on the water's surface it was unable to leave it again. The egg masses of the parthenogenetic females (Figure 58c: *L. asquamatus* forma *asquamatus*; Figure 58d: parthenogenetic ecotype not possible to determine (the offspring females had 0.5-1 lanceolate prescutellars and 8-10 preepisternals, the thorax was 504-522 µm long, see section 4.3.1.1.6. and Figure 37 p 91)) were often laid on the water's edge. The parthenogenetic females were also unable to crawl on water. The number of eggs per egg mass in *Limnophyes asquamatus* ranged between 55 and 100 (n = 6). The eggs showed a length/width-ratio of ± 2.5, were ± 170 µm long and shaped ± elliptical. The eggs were lined up horizontally in a single row, the line was then folded into loops. The egg mass was club-shaped (maximum length observed was about 1.5 mm), possibly with hair-like stalks (Figure 58d).

Paralimnophyes hydrophilus (Figure 58b): The egg masses were usually laid on the water's edge and sometimes also directly on the water's surface. Females became often stuck to the egg mass and lay dead or still alive beside it. The number of eggs per egg mass ranged between 10 and 100 (mean = 36.7, n = 245). The eggs (elliptical, ± 190 µm long, length/width-ratio ± 2.1) were lined up in two rows and arranged diagonally to ± vertically to line axis. The eggs of the two rows alternated and their diagonal/vertical position to line axis slightly differed. The egg mass was more or less rope-shaped (diameter of rope ± 0.3 mm) and often wound to a ring (diameter of the ring up to 1.5 mm). This ring-shape was however not constant and the egg mass could also be pretzel-shaped as shown in Figure 58b.

4.4.1.2 The impact of temperature and photoperiod on development

4.4.1.2.1. Mortalities in the experiments

The number of eggs of *Polypedilum tritum* and *Paralimnophyes hydrophilus* was counted at the beginning of the experiment and the percentage of emerging adults was therefore exactly known. The percentage of emerging adults in relation to the number of eggs at the beginning of the experiment was estimated on a scale of 1 to 5 (1 = 0.1-15.0 %, 2 = 15.1-30.0 %, 3 = 30.1-45.0 %, 4 = 45.1-60.0 %, 5 = 60.1-100 %) in all other species (*Limnophyes asquamatus*, *Chironomus annularius*, *Chironomus dorsalis*, *Chironomus luridus*) reared during the present study, (for detailed results and further explanations see Appendix 8).

MANN-WHITNEY-U-tests were applied to determine whether the type of culture vessel (plastic aquaria against crystallizing dishes) affected the percentage of emerging adults of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*. Only temperatures that were used with both plastic aquaria and crystallizing dishes were taken into account for the comparison. The survival rates of *Chironomus dorsalis* (range and median value of grade of survival in (a) the aquaria: 1-5; 2 (n = 20); and (b) the crystallizing dishes: 1-2; 1 (n = 10) (U = 31.5, p = 0.003)) and *Paralim-*

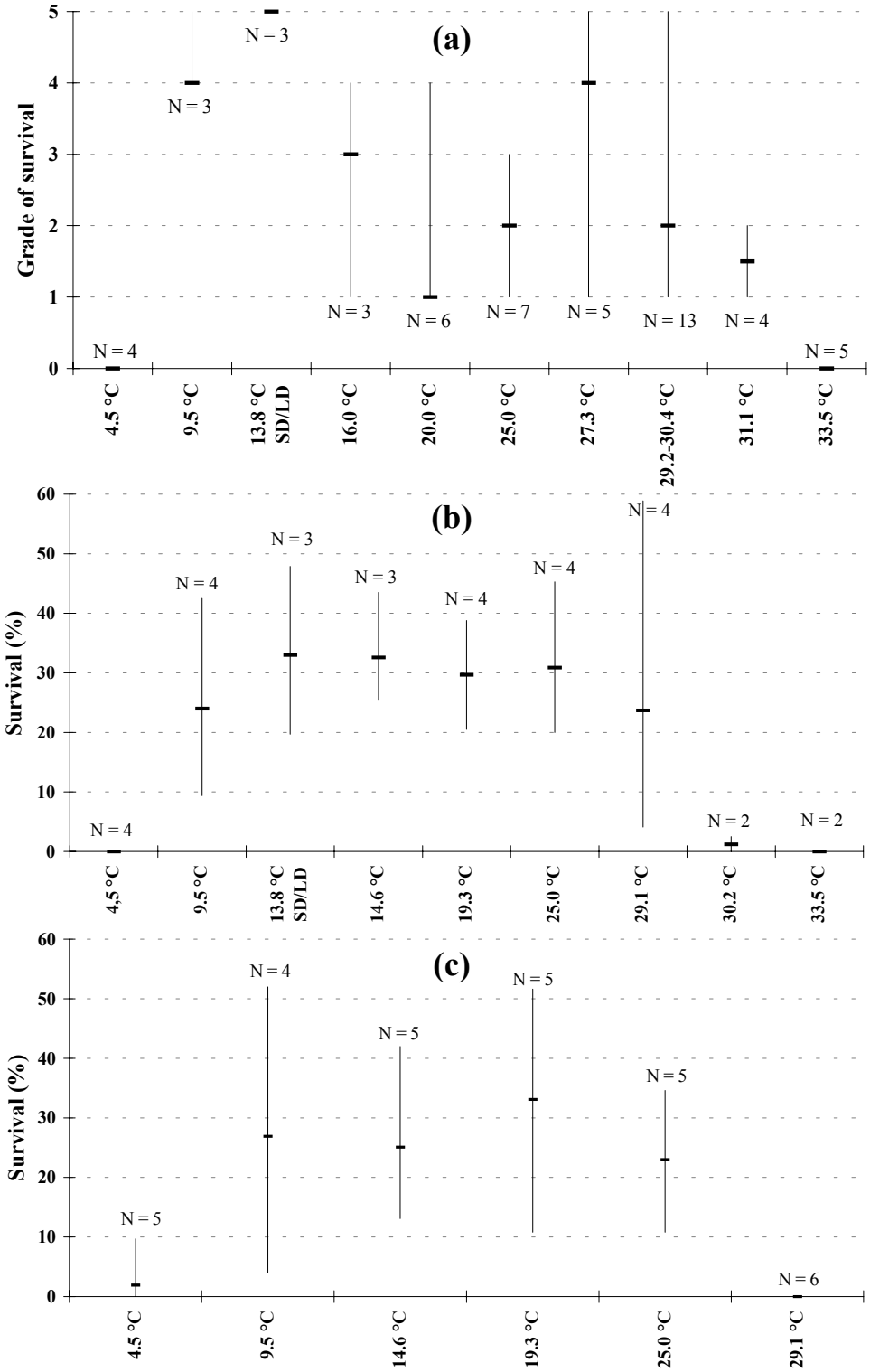

Figure 59: Survival (range and median[1]/mean[2]-values) from egg until the adult emergence in the laboratory cultures of (a) *Chironomus dorsalis*[1]; (b) *Polypedilum tritum*[2]; and (c) *Paralimnophyes hydrophilus*[2].

N = number of replicates. For further informations see Appendix 8 and text.

nophyes hydrophilus (range and mean value of survival in (a) the aquaria: 26.6-52.6; 43.8 % (n = 5); and (b) the crystallizing dishes: 3.7-43.9; 22.2 (n = 14) (U = 7, p = 0.010)) were significantly higher in the plastic aquaria. This does not apply for *Polypedilum tritum* (range and mean value of survival in (a) the aquaria: 4.1-47.5; 28.8 (n = 7); and (b) the crystallizing dishes: 12.4-58.9; 29.2 (n = 15) (U = 47; p = 0.689)).

A further analysis investigated a correlation between temperature and survival (Figure 59). Temperatures between 16.0 °C and 31.1 °C did not affect the survival rates of *Chironomus dorsalis* (γ = -0.042, Z = -0.293, p = 0.769). The survival rate at temperatures between 9.5 °C and 13.8 °C SD was however always greater than 45 % and thus significantly higher than in the other experiments (MANN-WHITNEY-U-test: U = 17.0, p = 0.002 (only the experiments with the plastic aquaria were considered)). There were no correlations between the temperatures between the lethal limits (see below) and the survival of *Polypedilum tritum* (γ = -0.085, Z = -0.514, p = 0.607) and *Paralimnophyes hydrophilus* (γ = 0.00, Z = 0.00, p = 1.000).

The upper lethal limit for total development was highest in *Chironomus dorsalis* (between 31.1 and 33.5 °C), intermediate in *Polypedilum tritum* (± 30.2 °C) and lowest in *Paralimnophyes hydrophilus* (between 25.0 and 29.1 °C). The lower lethal limit was not reached in *Paralimnophyes hydrophilus* (< 4.5 °C) and lay between 4.5 °C and 9.5 °C in *Chironomus dorsalis* and *Polypedilum tritum*. For the latter two species, a temperature of 4.5 °C resulted in increased mortality during embryonic development whilst larvae that did hatch did not grow and eventually died. Further information on lethal temperatures can be taken from the Appendix 8.

4.4.1.2.2. Larval growth

The larvae of *Chironomus dorsalis* and *Polypedilum tritum* build tubes and those of *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* are free living. Both Chironomini species were truly aquatic. The larvae of *Paralimnophyes hydrophilus* lived under water and within the water film of the water-land interface and thus the species is aquatic-semiaquatic. The larvae of the parthenogenetic laboratory cultures of *Limnophyes asquamatus* were also aquatic-semiaquatic (see section 4.3.1.1.5.) but mostly fed in the water-land interface and in wet substrata. The impact of temperature on larval growth was only investigated for *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*. Figure 60 illustrates the larval growth in relation to the different ambient temperatures applied and Table 37 provides diverse functions of growth. More information on the database is listed in the Appendix 9. The larval growth was best described by logistic model functions, but when ignoring the slowing down in growth towards the end of the larval development, exponential- and linear regressions also provided high goodness of fit. Since larval growth of all three species can be satisfactorily described by exponential and linear model functions, body length proceeds at approximately constant rates and a direct relationship between the (specific) growth rates and temperature (section 4.4.1.2.8.) can be established without respect to body size (OSTROVSKY 1995). Thus K´ of the linear model function (Table 37) is the specific growth rate at a given ambient temperature (OSTROVSKY op. cit.). At temperatures of 4.5 °C no larval growth oc-

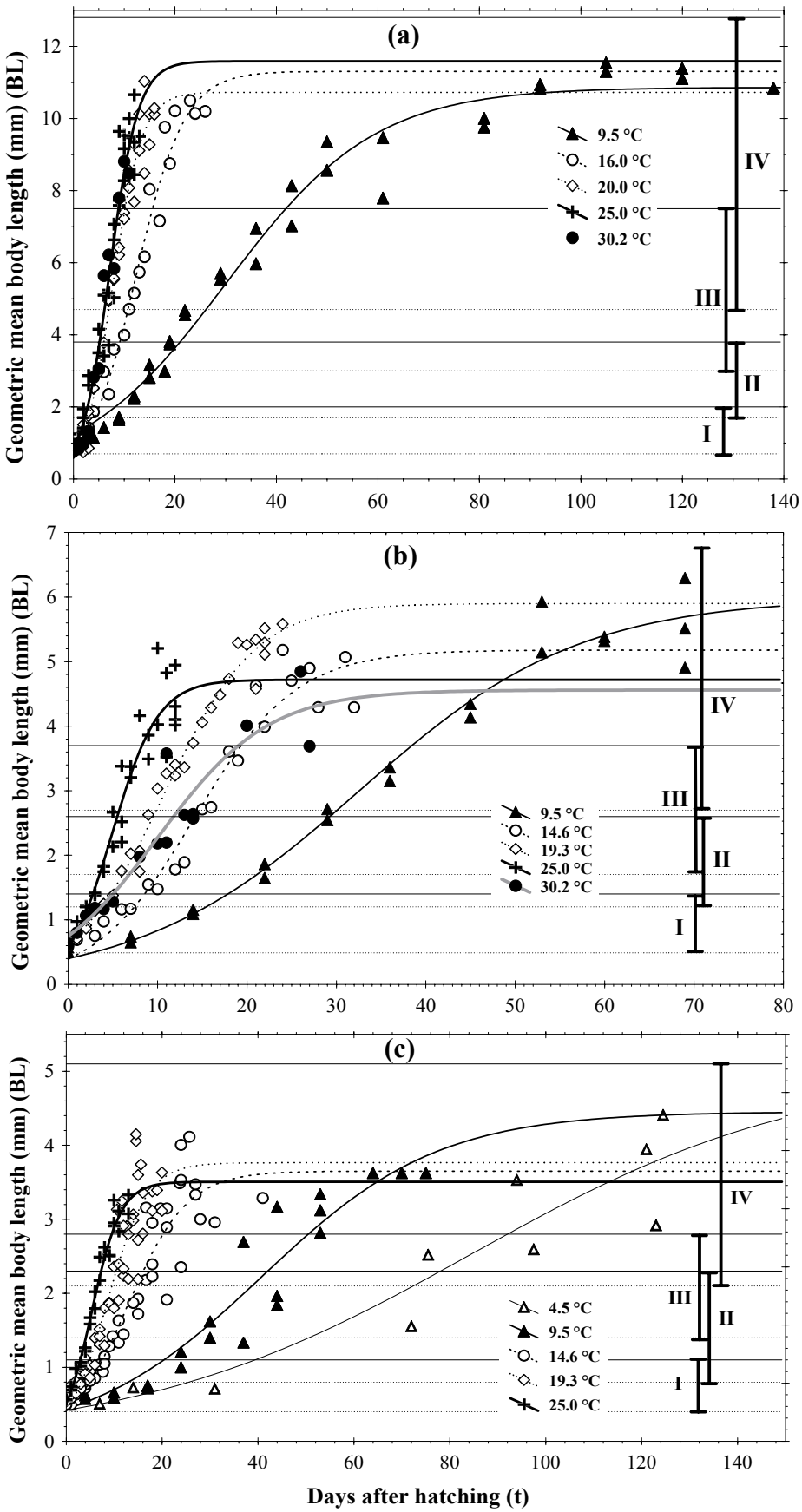

Figure 60: The larval growth in relation to different temperatures applied: (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*.
I, II, III, IV = range of body length of the instars I - IV (minimum values: interupted lines; maximum values: complete lines).

Table 37: Logistic, exponential and linear model functions[1] of regressions for mean larval body lengths (BL) vs. duration of development (t) (days), with statistical values.

[2]Logistic model ($BL = K/(D * e^{(-p * t)} + 1)$)				Exponential model ($BL = e^{(p * t + bo)} + c$)				[3]Linear model ($BL = K' * t + a$)	
Function	R^2	N 1	N 2	Function	R^2	N 1	N 2	Function	R^2
Chironomus dorsalis									
$BL(9.5\ °C) = 10.87/(7.77 * e^{(-0.068 * t)} + 1)$	0.98	35	169	$BL(9.5\ °C) = e^{(0.002 * t + 4.502)} - 89.596$	0.98	24	114	$BL(9.5\ °C) = 0.157*t + 0.84$	0.98
$BL(16.0\ °C) = 11.31/(13.44 * e^{(-0.210 * t)} + 1)$	0.98	21	114	$BL(16.0\ °C) = e^{(0.045 * t + 1.888)} - 6.036$	0.97	18	90	$BL(16.0\ °C) = 0.399*t + 0.84$	0.93
$BL(20.0\ °C) = 10.73/(14.88 * e^{(-0.349 * t)} + 1)$	0.98	36	163	$BL(20.0\ °C) = e^{(0.053 * t + 2.278)} - 9.451$	0.98	31	138	$BL(20.0\ °C) = 0.629*t + 0.84$	0.94
$BL(25.0\ °C) = 11.59/(13.02 * e^{(-0.358 * t)} + 1)$	0.95	32	126	$BL(25.0\ °C) = e^{(0.116 * t + 1.291)} - 2.821$	0.95	27	106	$BL(25.0\ °C) = 0{,}732*t + 0.84$	0.91
$BL(30.2\ °C) = 9.45/(19.24 * e^{(-0.492 * t)} + 1)$	0.98	17	128	$BL(30.2\ °C) = e^{(0.058 * t + 2.327)} - 10.069$	0.96	17	128	$BL(30.2\ °C) = 0.682*t + 0.84$	0.90
Polypedilum tritum									
$BL(9.5\ °C) = 5.99/(13.94 * e^{(-0.081 * t)} + 1)$	0.97	21	100	$BL(9.5\ °C) = e^{(0.225 * t + 0.805)} - 1.829$	0.99	16	75	$BL(9.5\ °C) = 0.079*t + 0.61$	0.92
$BL(14.6\ °C) = 5.18/(12.28 * e^{(-0.177 * t)} + 1)$	0.96	23	100	$BL(14.6\ °C) = e^{(0.053 * t + 0.536)} - 1.196$	0.97	19	80	$BL(14.6\ °C) = 0.154*t + 0.61$	0.91
$BL(19.3\ °C) = 5.90/(8.12 * e^{(-0.195 * t)} + 1)$	0.99	30	147	$BL(19.2\ °C) = e^{(0.022 * t + 2.182)} - 8.370$	0.97	23	107	$BL(19.3\ °C) = 0.224*t + 0.61$	0.97
$BL(25.0\ °C) = 4.72/(7.03 * e^{(-0.392 * t)} + 1)$	0.92	27	135	$BL(25.0\ °C) = e^{(0.056 * t + 1.644)} - 4.558$	0.93	21	105	$BL(25.0\ °C) = 0.369*t + 0.61$	0.91
$BL(30.2\ °C) = 4.56/(5.09 * e^{(-0.162 * t)} + 1)$	0.90	16	74	$BL(30.2\ °C) = e^{(0.009 * t + 2.603)} - 12.649$	0.87	16	74	$BL(30.2\ °C) = 0.152*t + 0.61$	0.87
Paralimnophyes hydrophilus									
$BL(4.5\ °C) = 5.051/(10.991 * e^{(-0.028 * t)} + 1)$	0.91	13	32	$BL(4.5\ °C) = e^{(0.016 * t - 0.364)} - 0.241$	0.91	10	21	$BL(4.5\ °C) = 0.023*t + 0.54$	0.85
$BL(9.5\ °C) = 4.454/(9.246 * e^{(-0.054 * t)} + 1)$	0.90	22	104	$BL(9.5\ °C) = e^{(0.030 * t - 0.380)} - 0.231$	0.88	21	99	$BL(9.5\ °C) = 0.041*t + 0.54$	0.81
$BL(14.6\ °C) = 3.650/(7.812 * e^{(-0.161 * t)} + 1)$	0.90	45	175	$BL(14.6\ °C) = e^{(0.033 * t + 0.862)} - 1.908$	0.89	39	144	$BL(14.6\ °C) = 0.107*t + 0.54$	0.87
$BL(19.3\ °C) = 3.765/(7.980 * e^{(-0.242 * t)} + 1)$	0.88	52	210	$BL(19.2\ °C) = e^{(0.074 * t + 0.389)} - 0.990$	0.90	45	182	$BL(19.3\ °C) = 0.174*t + 0.54$	0.86
$BL(25.0\ °C) = 3.507/(5.825 * e^{(-0.331 * t)} + 1)$	0.98	27	124	$BL(25.0\ °C) = e^{(0.043 * t + 1.542)} - 4.168$	0.97	23	108	$BL(25.0\ °C) = 0.237*t + 0.54$	0.96
$BL(29.0\ °C) = 2.596/(7.113 * e^{(-0.425 * t)} + 1)$	0.80	29	87	$BL(29.0\ °C) = e^{(0.248 * t - 1.186)} + 0.170$	0.84	19	63	$BL(29.0\ °C) = 0.186*t + 0.54$	0.71

Abbreviations:

R^2 = percentage of explained variance; N 1 = number of mean values used for the regressions ; N 2 = number of larvae measured;

[1] see section 3.5.6. for explanation of model functions;

[2] regression lines see Figure 60;

[3] N1 and N2 as in the exponential regressions.

curred in *Chironomus dorsalis* and *Polypedilum tritum*, but slow growth was still observed in *Paralimnophyes hydrophilus*. At temperatures of 9.5 °C, the larval growth was strongly delayed in the instar IV of *Chironomus dorsalis*.

4.4.1.2.3. The impact of temperature and photoperiod on larval growth and adult emergence in *Chironomus dorsalis* and *Polypedilum tritum*

The impact of short-days (SD: 8:16 hours) on larval growth and adult emergence of *Chironomus dorsalis* and *Polypedilum tritum* was investigated in three replicates (Appendix 8). The results of

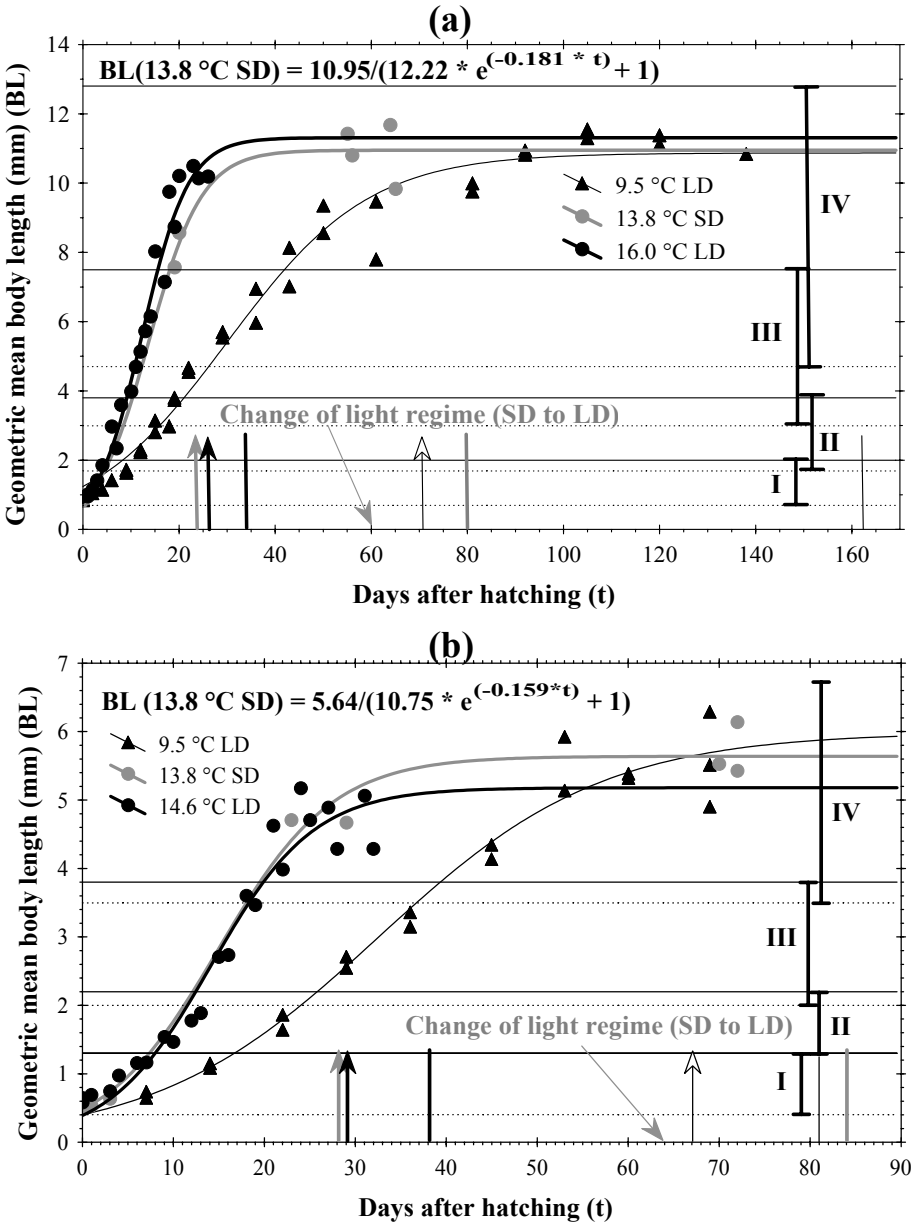

Figure 61: The influence of temperature and photoperiod on larval growth and adult emergence in (a) *Chironomus dorsalis*; and (b) *Polypedilum tritum*.

The results of the LD/SD experiments are shown in black/grey. The arrows that point to the top indicate the time of first emergence (bold black: 14.6/16.0 °C LD; bold grey: 13.8 °C SD; narrow black with open arrow: 9.5 °C). The vertical bars indicate the 50 %-emergence in the same manner as described for the first emergence. I, II, III, IV = range of body lengths of the instars I - IV (see Figure 60). N of the SD-experiment: *C. dorsalis* N = 36 larvae + 1383 adults, *P. tritum* N = 38 larvae + 833 adults. N of the other experiments see Table 37 and Appendix 9.

these experiments are summarized in Figure 61.

The results of the larval growth of *Chironomus dorsalis* as well as the main characteristics of the adult emergence at temperatures of 9.5 °C and 16.0 °C were added to Figure 61a for purpose of comparison. The regulation of temperature in the SD-experiment was not as strict as in the long-day experiments (LD: 16:8 hours, see Appendix 8). The spot checks of larval size in the SD experiment show that larval growth was nearly identical with the 16.0 °C LD experiment. This applies to the first emergence as well. But the pattern of emergence following the first emergence was very different in the SD- and 16.0 °C LD experiments: 50 % of emergences occurred up to 34 days after hatching in the 16.0 °C LD experiment, while only 9.4 % of the adults emerged until 60 days after hatching in the SD experiment. Sixty days after hatching, the light regime in the SD experiment was changed into LD and the 50 %-emergence was then reached 20 days later (80 days after hatching). The first emergence in the 9.5 °C LD experiment (71 days after hatching) started about ten days before the 50 %-emergence in the SD experiment was reached. Comparably, to what was seen in the SD experiment, the majority of adults emerged with a strong delay (50 %-emergence: 163 days after hatching). The results summarized by Figure 61a show that short-days delayed development into pupae in the majority of fourth instar larvae. The same applies to the 9.5 °C LD experiment. Hence short-days as well as low temperatures induce an oligopause sensu MÜLLER (1992) in the instar IV of *Chironomus dorsalis*.

Polypedilum tritum (Figure 61b) presented similar trends for short days to *Chironomus dorsalis*. Larval growth and the first emergence in the SD- and the 14.6 °C LD experiments were quite similar. But on short-days, only 6.1 % of the adults had emerged in the 64 days following hatching. The light regime was then switched to long-days resulting in a 50 %-emergence 20 days later (84 days after hatching). No strong delay of the 50 % emergence was observed in the 9.5 °C LD experiment. The results show that short-days induced an oligopause (MÜLLER 1992) in *Polypedilum tritum*, but that contrasting to what was seen for *Chironomus dorsalis* no such pause was seen at low temperatures (9.5 °C).

4.4.1.2.4. Total development in *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*

Table 38: F-statistics of the log-linearized formulae in Figure 62 (log D = -p * log T +log a).

	First emergence	Median values	Last emergence
C. dorsalis	F (df = 1.27) = 588.9 p < 0.001	F (df = 1.22) = 595.6 p < 0.001	F (df = 1.22) = 460.9 p < 0.001
P. tritum	F (df = 1.13) = 1370.5 p < 0.001	F (df = 1.13) = 566.7 p < 0.001	F (df = 1.13) = 201.4 p < 0.001
P. hydrophilus	F (df = 1.18) = 381.8 p < 0.001	F (df = 1.17) = 242.9 p < 0.001	F (df = 1.17) = 143.5 p < 0.001

Figure 62 illustrates the duration of total development (development from oviposition up to the adult emergence) of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* in relation to the different temperatures applied. The Potential regressions ($D = a * T^{-p}$) for the first-,

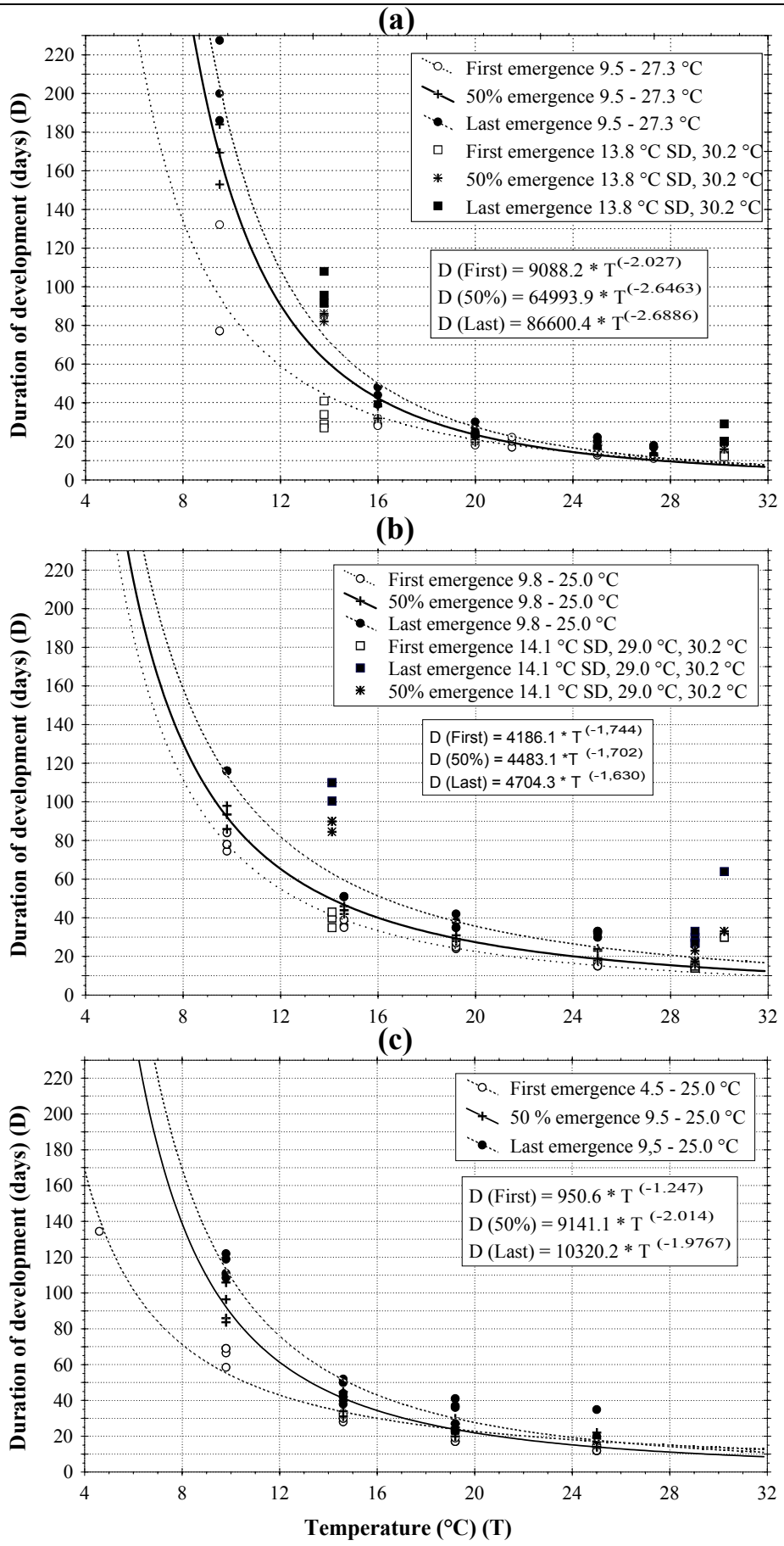

Figure 62: Influence of temperature on the total development of (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*. For explanations see text.

last- and 50 %-emergence were calculated (for single results see Appendix 8). The percentages of explained variance of the potential model functions were high (*Chironomus dorsalis*: first emergence $R^2 = 0.887$ (n = 29), median values $R^2 = 0.986$ (n = 24), last emergence $R^2 = 0.984$ (n = 24); *Polypedilum tritum*: first emergence $R^2 = 0.990$ (n = 15), median values $R^2 = 0.990$ (n = 15), last emergence $R^2 = 0.970$ (n = 15); *Paralimnophyes hydrophilus*: first emergence $R^2 = 0.950$ (n = 20), median values $R^2 = 0.960$ (n = 19), last emergence $R^2 = 0.960$ (n = 19)). Only those temperatures that clearly lay below the species upper sublethal limits were used for the regressions (< 30.2 °C in *Chironomus dorsalis* and < 29.0 °C in *Polypedilum tritum* and *Paralimnopphyes hydrophilus*, see Figure 62). The results of the SD-experiments were also excluded from the regressions. The F-statistics for the log-linearized model functions (log D = -p*log T + log a) are listed in Table 38. Although mortality was very high (Figure 59 p 128), seven adults of *Paralimnophyes hydrophilus* did emerge at temperatures of 4.5 °C. Because all adults emerged over the same time period, only data on the first emergence can be provided. For further comparisons between the species see section 4.4.1.2.6..

4.4.1.2.5. Total development in *Chironomus annularius* - a typical species of permanent ponds

The development of seven egg masses of *Chironomus annularius* was investigated in 12 treatments at five temperature levels and at short- and long-days. Survival (emerging adults in relation to the number of eggs present at the beginning of the experiment) was low (≤ grade 2, for definition see section 4.4.1.2.1. or Appendix 8) in the experiments with temperatures ≥ 19.6 °C and lay between 2 and 4 in the experiments with temperatures of 11.0 °C and 13.8 °C. First emergence usually occurs without a pronounced delay even if development into the adult is retarded (section 4.4.1.2.3.). It was therefore possible to calculate a regression to illustrate the dependence of first emergence on temperature (Figure 63). This regression's percentage of explained variance was high ($R^2 = 92.1$ (n

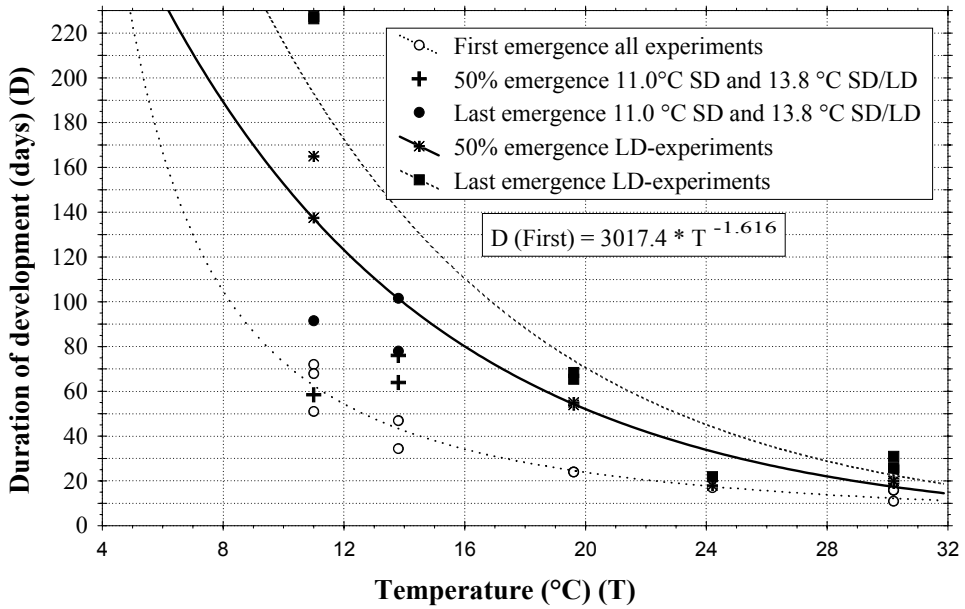

Figure 63: Influence of temperature on the total development of *Chironomus annularius*.
For explanations see text.

= 11); F-statistics of the log-linearized formula for first emergence: F (df = 1.9) = 141.3, p < 0.001). The treatments at 11.0 °C with long-days or alternatively short-days clearly showed total development in *Chironomus annularius* to be delayed by long-days (median value short-days: 51 d, median values long-days: 227.5 and 226.5). In the experiment at 13.8 °C, the light regime was switched from SD to LD 36 d after oviposition and the median values of total development (64 and 76 days) lay in between the results for SD and LD at 11.0 °C (Figure 63). The first emergence in the 13.8 °C SD→LD treatments occurred 34.5 and 47 days after oviposition. The majority of larvae were therefore instars IV when the light regime was switched and as a result long-days postponed the development of instars IV into adults. It is however likely that high temperatures (> 19.6 °C) cancelled the effects of long-days on larval development (Figure 63).

4.4.1.2.6. Further data on total development of additional species and a comparison with *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*

It is often claimed that species of temporary water bodies develop faster than those living in permanently inundated areas. To check whether this applies in *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*, I originally intended to also investigate the development of *Chironomus luridus*, a species typical of small standing water bodies (pools, see section 4.2.1.). But I could only obtain and rear three egg masses of *Chironomus luridus*. *Chironomus annularius* was therefore included in the investigation program (section 4.4.1.2.5.), although it is a species more typical of larger standing waters, especially of ponds (MATĚNA & FROUZ 2000). Figure 64 shows a comprehensive comparison of the duration of total development at four temperature levels (~10 °C, ~15 °C, ~20 °C and ~25 °C). The test statistics of this comparison can be taken from Table 39. In this comparison, I also included the results for the total development of *Limnophyes asquamatus* at 21.5 °C (Appendix 8). Only the results of the experiments of *Chironomus annularius* at 11.0 °C (SD normal development, LD delayed development) and 25.0 °C (at this level of temperature the LD-delay of development was probably totally cancelled out) were included in the comparisons (section 4.4.1.2.5.). The main results of these comparisons can be summarized as follows:

(a) (~10 °C): The development of *Chironomus annularius* was the fastest of the four species, provided that long-days did not delay development. *Chironomus luridus* and *Chironomus dorsalis* were both thermophilous with high (≥ 9.5 °C) cue temperatures for oligopause sensu MÜLLER (1992) (sections 4.4.1.2.3. and 4.4.1.2.7.) and therefore had the slowest total development times. *Paralimnophyes hydrophilus* and *Polypedilum tritum* showed a development of intermediate length and no thermal oligopauses (sections 4.4.1.2.2. and 4.4.1.2.3.).

(b) (~15 °C): *Chironomus dorsalis* was the fastest developing of all the four species at temperatures of ± 15 °C. The development in *Chironomus luridus* and *Polypedilum tritum* was equal in length and comparatively slow. The position of *Paralimnophyes hydrophilus* was intermediate. Mean ambient temperatures around 15 °C were typical in the natural habitats during summertime (sections 4.1.1.3.2. and 4.1.2.).

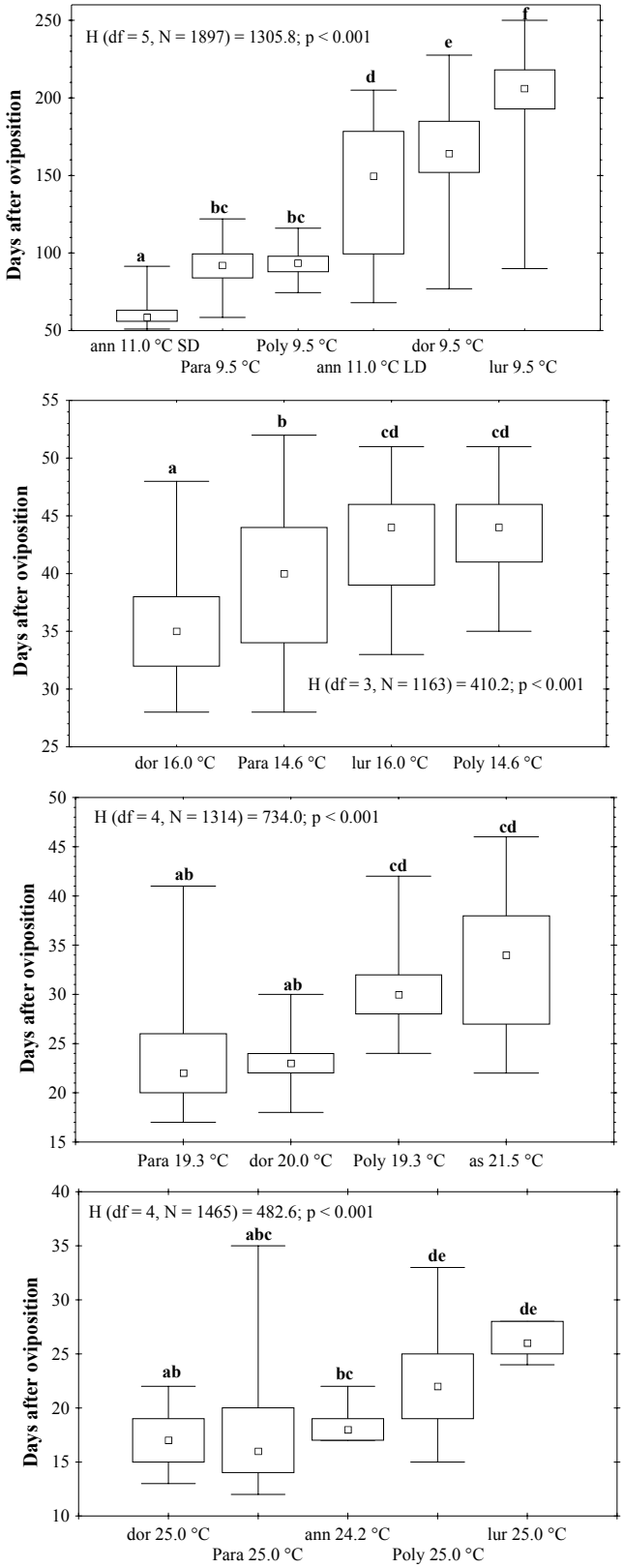

Figure 64: Comparison of the development times of different species at similar levels of temperature.
Abbreviations and explanations:
ann = *Chironomus annularius*; **as** = *Limnophyes asquamatus* (parthenogenetic lab culture); **dor** = *Chironomus dorsalis*; **lur** = *Chironomus luridus*; **Para** = *Paralimnophyes hydrophilus*; **Poly** = *Polypedilum tritum.*
The results of the KRUSKAL-WALLIS-ANOVA are shown in each figure, the different characters above the box-plots marking significant differences in mean values (see Table 39 and Appendix 8).

(c) (~20 °C and ~25 °C): *Chironomus dorsalis* and *Paralimnophyes hydrophilus* were the fastest developing at temperatures of 20 °C and 25 °C. Interestingly, at temperatures of ~25 °C the duration of development was (i) equal in *Chironomus annularius*, *Chironomus dorsalis* and *Paralimnophyes hydrophilus*; and (ii) also not significantly different for *Polypedilum tritum* and *Chironomus luridus*.

Table 39: Test statistics (MANN-WHITNEY-U-tests for matched pairs) for comparing the duration of development of different species at similar levels of temperature (see Figure 64).

About 10 °C (k = 15)					
	P. hydrophilus	*P. tritum*	*C. annularius* LD	*C. dorsalis*	*C. luridus*
C. annularius SD	$p_{new} < 0.001$ U = 1087	$p_{new} < 0.001$ U = 599	$p_{new} < 0.001$ U = 195	$p_{new} < 0.001$ U = 91	$p_{new} < 0.001$ U = 4
P. hydrophilus		$p_{new} = 0.057$ U = 68424	$p_{new} < 0.001$ U = 13238	$p_{new} < 0.001$ U = 5842	$p_{new} < 0.001$ U = 421
P. tritum			$p_{new} < 0.001$ U = 17332	$p_{new} < 0.001$ U = 7595	$p_{new} < 0.001$ U = 606
C. annularius LD				$p_{new} < 0.001$ U = 54415	$p_{new} < 0.001$ U = 2618
C. dorsalis					$p_{new} < 0.001$ U = 7984
About 15 °C (k = 6)					
	P. hydrophilus	*C. luridus*	*P. tritum*		
C. dorsalis	$p_{new} < 0.001$ U = 35353	$p_{new} < 0.001$ U = 2286	$p_{new} < 0.001$ U = 15061		
P. hydrophilus		$p_{new} < 0.001$ U = 13339	$p_{new} < 0.001$ U = 37812		
C. luridus			$p_{new} = 2.908$ U = 11612		
About 20 °C (k = 6)					
	C. dorsalis	*P. tritum*	*L. asquamatus*		
P. hydrophilus	$p_{new} = 0.196$ U = 70479	$p_{new} < 0.001$ U = 15888	$p_{new} < 0.001$ U = 1772		
C. dorsalis		$p_{new} < 0.001$ U = 4795	$p_{new} < 0.001$ U = 1211		
P. tritum			$p_{new} = 0.221$ U = 9958		
About 25 °C (k = 10)					
	P. hydrophilus	*C. annularius*	*P. tritum*	*C. luridus*	
C. dorsalis	$p_{new} = 1.941$ U = 76833	$p_{new} = 0.003$ U = 5388	$p_{new} < 0.001$ U = 445387	$p_{new} < 0.001$ U = 0	
P. hydrophilus		$p_{new} = 1.533$ U = 3286	$p_{new} < 0.001$ U = 36832	$p_{new} = 0.002$ U = 177	
C. annularius			$p_{new} < 0.001$ U = 3698	$p_{new} < 0.001$ U = 0	
P. tritum				$p_{new} = 0.055$ U = 787	

Non-significant differences are indicated by a grey background;
p_{new} = adjusted p value according to the standard BONFERRONI-technique (see Table 10 p 38).

The data show the hypothesis of faster development of the temporary pool dwellers to be not confirmed.

In the course of the present study nine additional species were reared (Table 40). The permanent lentic water species *Acricotopus lucens* and *Paratanytarsus grimmii* (see sections 4.2.1. and 4.2.2. and Appendix 3) have also very short generation times. The data additionally indicate that short

Table 40: Data on total development time of nine additional species.

Species	Temperature	Days from oviposition until (first) emergence*	Comments
Acricotopus lucens	21.5 °C LD	15	Lab rearing of a photographed egg mass. Only the first emergence was noticed. 5 ♂♂, 2 ♀♀, 3 Pex, 5 L coll. ADK.
Limnophyes minimus	15.0 °C LD	28-34; 28.5 (n = 17)	Sexual form. Lab rearing of a photographed egg mass (Table 32 p 101). 9 ♂♂, 8 ♀♀, 16 Pex, 7 L (instars I and IV) coll. ADK.
Parametriocnemus stylatus	10.1 °C**	72-155; 146 (n = 288)	Rearing of an egg mass. Probably thermal Parapause sensu MÜLLER (1992) in the instar III, similar as in *H. lugubris* (instar II, see STEINHART 1999) or *Stempellina* cf. *montivaga* (instar III, see SUNDERMANN & DETTINGER-KLEMM 2002). 2 ♂♂, 2 ♀♀, 12 Pex, 1 P, 3 L ZSM, 2 ♂♂, 2 ♀♀, 3 Pex, 4 L ZMB many ♂♂, ♀♀, Pex, and L (all instars) coll. ADK.
Chironomus cf. nuditarsis	19.6 °C LD 24.2 °C LD 30.2°C LD	30-105; 79.5 (n = 92) 23-105; 52.5 (n = 124) 17-55; 34.8 (n = 77)	The egg mass was divided into three parts before rearing. Most likely high densities prolonged development of most larvae (see REIST & FISCHER 1987). 148 ♂♂, 155 ♀♀, many Pex, 158 L (all instars) coll. ADK..
Chironomus plumosus-agg.	11.0 °C SD 11.0 °C LD	137.5 (n = 6) 78-271; 214.1 (n = 64)	High larval mortalities due to unsuited rearing conditions. Short-days induce an oligopause as in *C. dorsalis* (FISCHER 1974). 41 ♂♂, 29 ♀♀ 1Pex, 54 L (all instars) coll. ADK.
Dicrotendipes notatus	19.6 °C LD	34-44; 36.8 (n = 143)	Lab rearing of a photographed egg mass. 52 ♂♂, 91 ♀♀, 45 L (all instars) and 1 Pex coll. ADK.
Glyptotendipes foliicola	24.2 °C 30.2 °C	33-84; 45.0 (n = 45) 34-41 (n = 3)	The egg mass was first photographed and then divided into two parts before rearing. 26 ♂♂, 22 ♀♀, 74 L (all instars) coll. ADK.
Glyptotendipes pallens	19.6 °C LD	47 (n = 7)	Lab rearing of a photographed egg mass. Only the first emergence was noticed. 3 ♂♂, 4 ♀♀, 32 larvae (all instars) coll. ADK.
Paratanytarsus grimmii	24.2 °C LD	13	Parthenogenetic lab rearing. Only the first emergence was noticed. 7 ♀♀, 6 Pex, 1 P, 2 L coll. ADK

Comments and explanations:

* If the adult emergence was fully documented, the data are provided in the min-max; mean standard.

** Three first adults emerged 72 d after oviposition (10 °C), but no further eclosion was then noticed until day 90. At this time, the majority of the larvae were still in the instar III. The temperature was then degraded to 5.0 °C for 20 days and after this period switched back to 10 °C. About 20 days later (130 days after oviposition) an explosive adult emergence was observed (N = 155♂♂ and 133 ♀♀).

- For abbreviations see Appendix 3.
- Sampling sites of the species see Table 7 p 28.

generation times are widespread amongst Chironomidae.

4.4.1.2.7. Emergence patterns

Figure 65 illustrates the emergence of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* at different temperatures. The emergence pattern of all three species can be described as unimodal and the period of emergence was clearly longer at 9.5 °C. At 9.5 °C, the number of emerging adults of *Polypedilum tritum* and *Paralimnophyes hydrophilus* grew more or less continuously until the peak (50 %-emergence) was reached. Contrastingly, the increase in adults of *Chironomus dorsalis* emerging after the first emergence was strongly delayed (~ 70 days). As explained in section 4.4.1.2.3., the delay of emergence in *Chironomus dorsalis* has to be understood as a thermal oligopause sensu MÜLLER (1992). No such pause occurs in *Polypedilum tritum* and

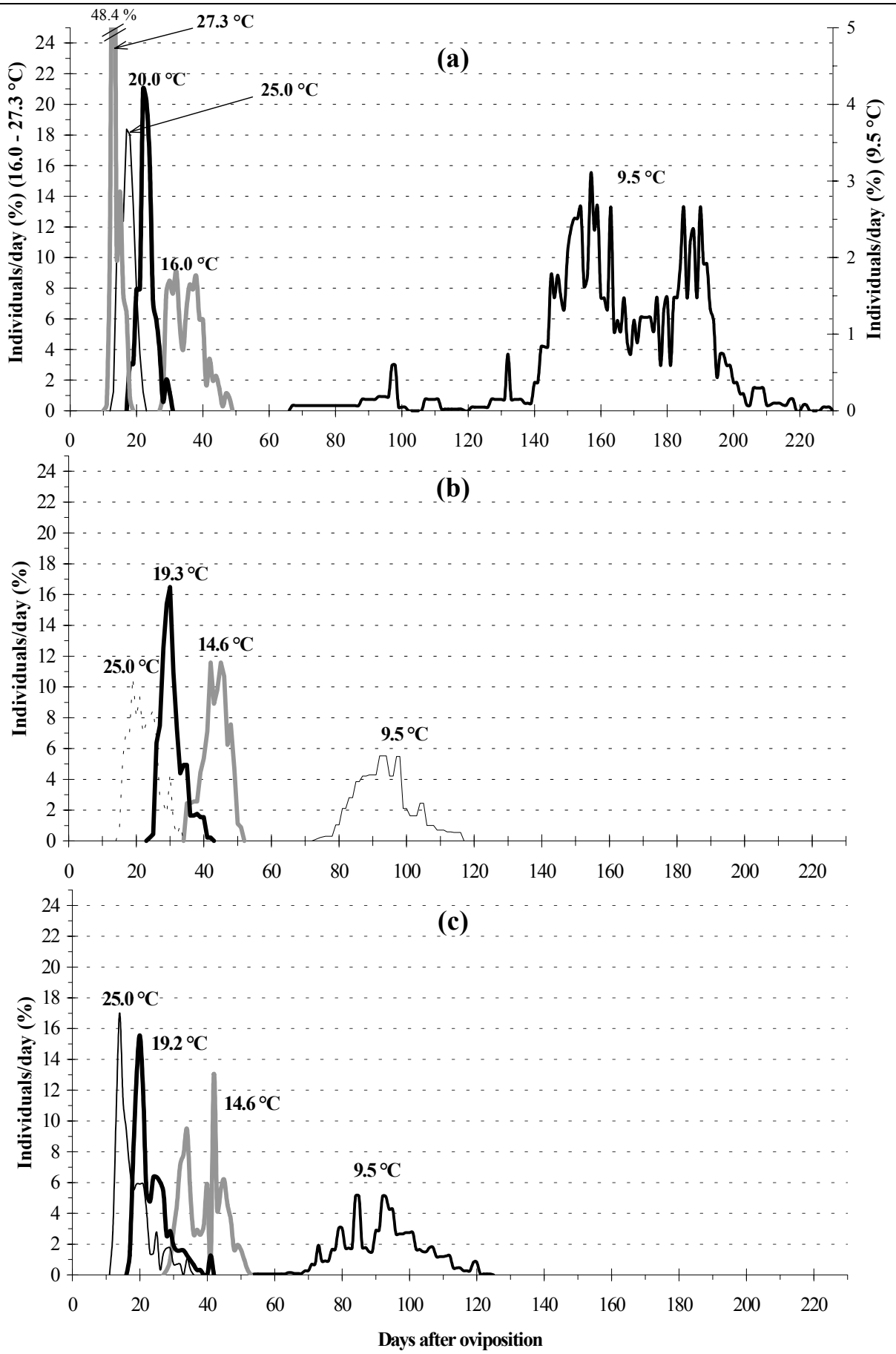

Figure 65: The emergence of (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus* at different temperatures and long-days.

Paralimnophyes hydrophilus. The emergence pattern of *Chironomus luridus* at 9.5 °C and 16.0 °C was similar to what was observed in *Chironomus dorsalis* (Figure 66b). *Chironomus luridus* is therefore also subjected to a thermal oligopause, the cue temperature of which is assumed to lie between 9.5 and 16.0 °C. The emergence patterns of *Chironomus annularius* (Figure 66a) emphasise what was shown in section 4.4.1.2.5: Long-days greatly delayed the emergence at 11.0 °C, but higher temperatures progressively cancelled the delay until it was completely absent at 24.2 °C.

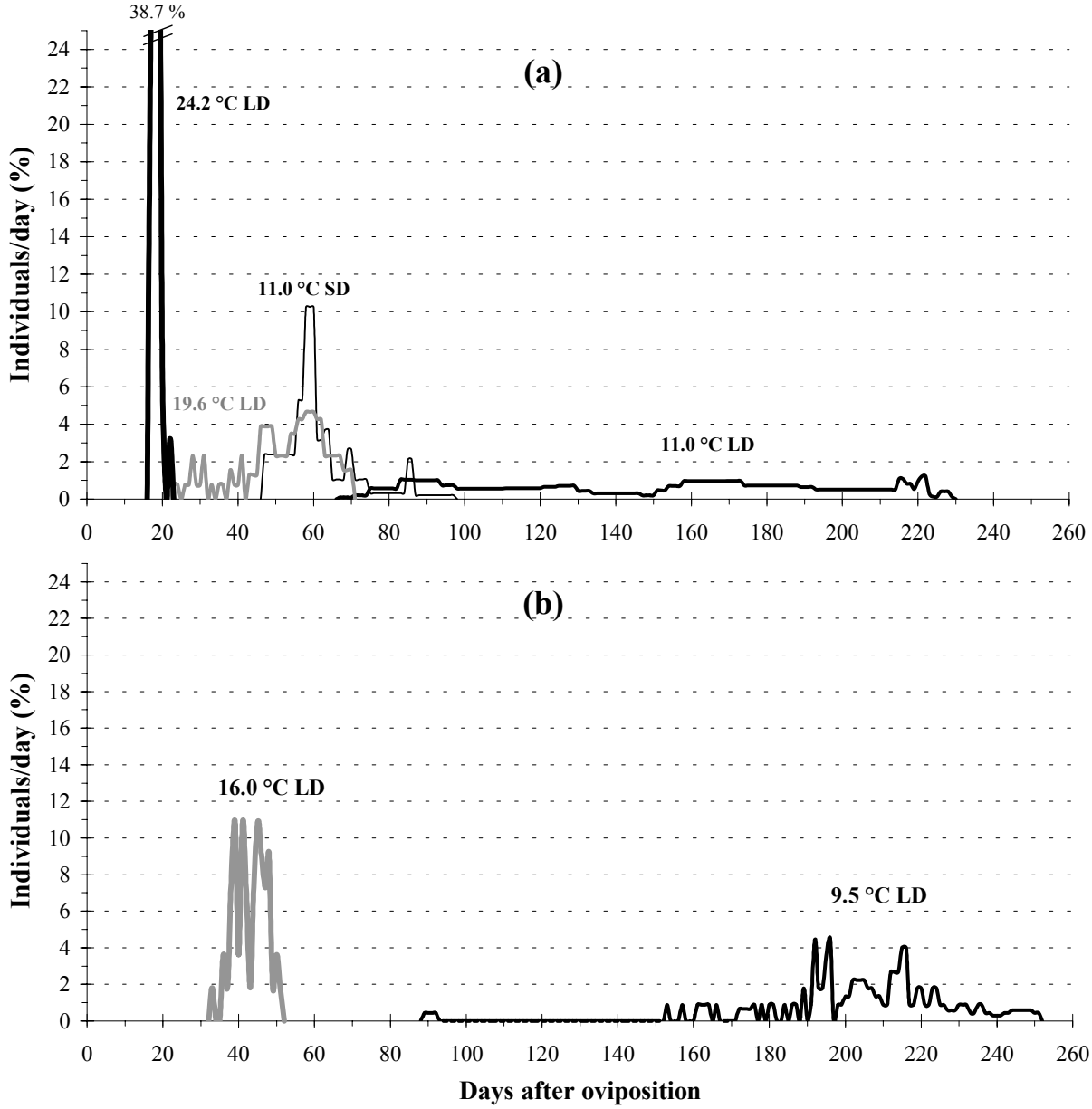

Figure 66: The emergence of (a) *Chironomus annularius*; and (b) *Chironomus luridus* at different temperatures and day lengths.

4.4.1.2.8. Developmental zero, thermal constant and Q_{10}-values

Developmental zero: The larval growth of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* can be satisfactorily described by exponential and even linear model functions (Table 37 p 131). In the latter case, K´ represents the specific growth rate at a given temperature.

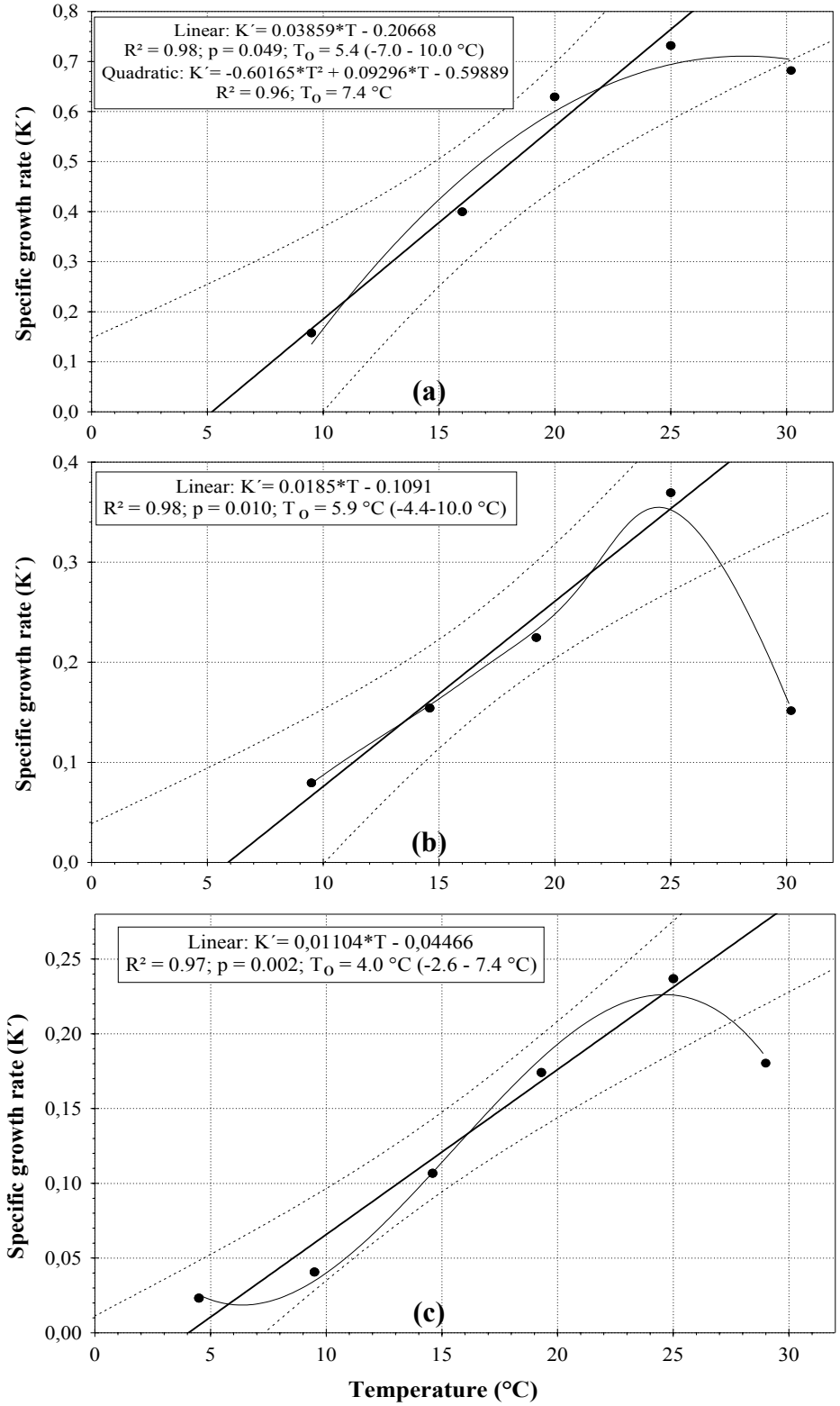

Figure 67: Regressions of specific growth rate (K´) vs. temperature (T) of (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*.

Linear = equation with percentage of explained variance (R^2), p-value and developmental zero (T_0) with 95 % confidence lobe (in brackets) of the linear regression line;

Quadradtic = equation with percentage of explained variance (R^2) and dev. zero (T_0) of the quadratic regression line;

- No equations were provided for the other non-linear regression lines;
- The specific growth rates obtained at temperatures ≥ 29 °C were excluded from linear regressions;
- The broken lines mark the 95 % confidence limits of linear regressions.

Table 41: Developmental zero growth of *Paralimnophyes hydrophilus*, *Chironomus annularius*, *Chironomus dorsalis* and *Polypedilum tritum*: regressions of mean growth rates (mGr) and mean rates of development (Rd) versus temperature (°C) (T).

	Mean growth rates versus T	Rates of development versus T		
		First emergence	Mean emergence	Last emergence
		Chironomus annularius		
Function		Rd = 0.0029 * T - 0.0156		
N		11		
Residuals		W = 0.89; p = 0.154		
R^2		0.89; df = 1.9; F = 83; p < 0.001		
intercept		df = 9; t = -2.3; p = 0.046		
slope		df = 9; t = 9.1; p < 0.001		
T_0		5.3 °C (0.1-8.7 °C)		
		Chironomus dorsalis		
Function	mGr = 0.0117 * T – 0.0538	Rd = 0.0037 * T -0.0240	Rd = 0.0035* T - 0.0262	Rd = 0.0030 * T - 0.0234
N	9 means à 437 larvae	24	19 means à 2085 adults	19
Residuals	W = 0.98; p = 0.935	W = 0.97; p = 0.714	W = 0.97; p = 0.782	W = 0.93; p = 0.218
R^2	0.95; df = 1.7; F = 125; p < 0.001	0.93 (df = 1.2; F = 295; p < 0.001	0.95; df = 1.2; F = 305; p < 0.001	0.94; df = 1.2; F = 266; p < 0.001
intercept	df = 7; t = -2.7; p = 0.033	df = 22; t = -5.5; p < 0.001	df = 17; t = -6.5; p < 0.001	df = 17; t = -6.22; p < 0.001
slope	df = 7; t = 11.2; p < 0.001	df = 22; t = 17.2; p < 0.001	df = 17; t = 17.5; p < 0.001	df = 17; t = 16.3; p < 0.001
T_0	4.6 °C (0.6-7.3 °C)	6.6 °C (4.6-8.1 °C)	7.6 °C (5.8-9.0 °C)	7.7 °C (5.8-9.3 °C)
		Polypedilum tritum		
Function	mGr = 0.0092 * T – 0.0485	Rd = 0.0033 * T - 0.0218	Rd = 0.0024 * T - 0.0125	Rd = 0.0015 * T - 0.0041
N	7 means à 300 larvae	15	15 means à 1906 adults	15
Residuals	W = 0.90; p = 0.327	W = 0.95; p = 0.490	W = 0.97; p = 0.806	W = 0.88, p = 0.044
R^2	0.97; df = 1.5; F = 161; p < 0.001	0.97; df = 1.1; F = 472; p < 0.001	0.97; df = 1.1; F = 366; p < 0.001	0.93, df = 1.1; F = 176; p < 0.001
intercept	df = 5; t = -3.7; p = 0.014	df = 13; t = -7.8; p < 0.001	df = 13; t = -5.5; p < 0.001	df = 13; t = -2.0; p = 0.069
slope	df = 5; t = 12.7; p < 0.001	df = 13; t = 21.7; p < 0.001	df = 13; t = 19.1; p < 0.001	df = 13; t = 13.3; p < 0.001
T_0	5.3 °C (2.0-7.5 °C)	6.5 °C (5.2-7.7 °C)	5.2 °C (3.5-6.6 °C)	2.7 °C (-0.3-5.0 °C)
		Paralimnophyes hydrophilus		
Function	mGr = 0.0069 * T - 0.0214	Rd = 0.0036 * T - 0.0175	Rd = 0.0032 * T - 0.0202	Rd = 0.0025 * T - 0.0156
N	14 means à 522 larvae	20	19 means à 1279 adults	19
Residuals	W = 0.96; p = 0.740	W = 0.92; p = 0.130	W = 0.95; p = 0.400	W = 0.92; p = 0.110
R^2	0.90; df = 1.1; F = 110; p < 0.001	0.92; df = 1.2; F = 202; p < 0.001	0.89; df = 1.2; F = 133; p < 0.001	0.82; df = 1.2; F = 80; p < 0.001
intercept	df = 12; t = -2.1; p = 0.061	df= 18; t = -3.9; p = 0.001	df = 17; t = -4.0; p < 0.001	df = 17, t = -3.0; p = 0.008
slope	df = 12; t = 10.5; p < 0.001	df = 18; t = 14.2; p < 0.001	df = 17; t = 11.5; p < 0.001	df = 17; t = 8.9; p < 0.001
T_0	3.1 °C (-0.1-5.5 °C)	4.9 °C (2.6-6.7 °C)	5.3 °C (4.7-5.7 °C)	6.2 °C (2.4-8.7 °C)

Abbreviations:

intercept + slope = t-statistics of the regression coefficients**; R^2** = percentage of explained variance with F-statistics; **Residuals** = SHAPIRO-WILK-W-test for normality of residuals;; **T_0** = temperature of developmental zero growth with 95% confidence lobe (in brackets). A grey background marks the T_0-values used for the calculation of degree-days. For further information see text and the Appendices 8 and 9.

The dependence of K´ on temperature can be described by a linear regression (Figure 67), provided temperatures are within the species' favourable range (OSTROVSKY 1995). The developmental zeroes (T_0) of larval growth of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* were determined by help of the linear equations given in Figure 67. Accuracy of these values was however not very high (wide 95 % confidence lobes). The calculations of the developmental zeroes of larval growth were therefore repeated, yet based on an exponential growth model the growth rates of which can be computed by the equation of OSTROVSKY (1995) (section 3.5.8.). Mean growth rates (mGr) were calculated using only the data of the quasi-exponential growth period (section 4.4.1.2.2.). The geometric means of larval body lengths, growth rates between samplings, number of larvae measured and the mean growth rates appear in Appendix 9. The linear regressions of mGr versus temperature and the corresponding T_0-values are presented in Table 41. The 95 % confidence lobes of these T_0-values were much closer than of the T_0-values obtained by the linear models and therefore used for further considerations. The rates of development (section 3.5.8.) were also dependent on temperature, which can be described by linear regressions (Table 41). There is no single value for the rate of development as the period of emergence varied. The first and last emergence mark extremes whereas the mean values are best suited to estimate the average tendency of emergence, provided that the N is high enough (central limit theorem and law of large numbers, LORENZ 1996). The regressions of rates of development versus temperature are therefore separately provided for the first-, mean- and last emergence. The developmental zeroes with 95 % confidence lobes of total development were determined as previously described for larval growth (Table 41). Four estimates of the developmental zero are therefore given for each species (three for total development and one for larval growth), except in *Chironomus annularius* for which the developmental zero could only be calculated for the first emergence (Table 41). It was impossible to determine the developmental zero of *Chironomus luridus* as only one replicate was done for temperatures of 9.5 °C, 16.0 °C and 25.0 °C (Appendix 8). The developmental zeroes of larval growth were lower as those of total development in *Chironomus dorsalis* and *Paralimnophyes hydrophilus*. In *Chironomus dorsalis*, this difference was clearly caused by a cue temperature to oligopause in the instar IV (section 4.4.1.2.3.), the situation in *Paralimnophyes hydrophilus* remains however unclear. There were no differences in the developmental zeroes of larval growth and total development of *Polypedilum tritum* and therefore there obviously is no cue temperature to oligopause in this species.

Thermal constant: The thermal constants (Table 42) were calculated using the developmental zeroes for larval growth in *Chironomus dorsalis* (4.6 °C) and *Paralimnophyes hydrophilus* (3.1 °C) and the developmental zero calculated from the mean rates of development in *Polypedilum tritum* (5.2 °C). The mean thermal constants of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* were compared with a KRUSKAL-WALLIS-ANOVA ($H (df = 2, N = 59) = 21.4$; $p < 0.001$) and with multiple MANN-WHITNEY-U-tests with adjusted p-values according to the standard BONFERRONI-technique ($k = 3$, see Table 10 p 38). The differences between *Chironomus dorsalis* and *Polypedilum tritum* ($U = 33$, $p_{new} = < 0.001$) and *Chironomus dorsalis* and

Table 42: The thermal constants of *Chironomus annularius*, *Chironomus dorsalis, Polypedilum tritum* and *Paralimnophyes hydrophilus*

	First emergence	Last emergence	Median	Mean
		Chironomus annularius		
°C	11.0-30.2 °C (+SD)	-	-	-
Range	274-410	-	-	-
Mean (CL)	351 (317-385)	-	-	-
Normality	W = 0.89; p = 0.123	-	-	-
N	11	-	-	-
		Chironomus dorsalis		
°C	16.0-30.2 °C (+SD)	16.0-27.3 °C (-SD)	16.0-27.3 °C (-SD)	16.0-27.3 °C (-SD)
Range	248-377	295-547	295-467	284-458
Mean (CL)	308 (295-320)	406 (380-432)	344	347 (327-367)
Normality	W = 0.96; p = 0.266	W = 0.96; p = 0.484	W = 0.88; p = 0.013	W = 0.931; p = 0.140
N	33	21	21	21
		Polypedilum tritum		
°C	9.5-29.1 °C (+SD)	9.5-19.3 °C (-SD)	9.5 °C-29.1 °C (-SD)	9.5-29.1 °C (-SD)
Range	297-381	479-592	356-550	374-547
Mean (CL)	339 (328-349)	503	416	425
Normality	W = 0.95; p = 0.316	W = 0.69; p < 0.001	W = 0.87; p = 0.011	W = 0.89; p = 0.031
N	22	11	19	19
		Paralimnophyes hydrophilus		
°C	9.5-25.0 °C	9.5-25.0 °C	9.5-25 °C	9.5-25.0 °C
Range	263-441	373-781	307-678	313-639
Mean (CL)	347 (220-373)	560 (493-626)	443 (392-494)	446 (398-495)
Normality	W = 0.94; p = 0.305	W = 0.91; p = 0.081	W = 0.95; p = 0.365	W = 0.94; p = 0.308
N	19	19	19	

Abbreviations and explanations:

Column names: First emergence/Last emergence/Median/Mean = degree-days from oviposition until the first-/last-/ 50 %-/mean emergence.

Line names: °C = temperature range taken into account inclusive/exclusive of the short-day experiments (±SD); **Range** = range of thermal constant; **mean (CL)** = arithmetic mean (95% confidence lobe) for the thermal constants of total development; **Normality** = result of SHAPIRO-WILK-W-test for normality: if the result was significant ($p < 0.05$) the null hypothesis (the data fulfil normality) was rejected and no 95 % CL was calculated in addition to the arithmetic mean of the thermal constants; **N** = number of values taken into account.

The thermal constants were calculated from the results listed in the Appendix 8.

Paralimnophyes hydrophilus ($U = 74$, $p_{new} = 0.002$) were significant, whilst differences between *Polypedilum tritum* and *Paralimnophyes hydrophilus* were not significant ($U = 168$, $p_{new} = 2.145$). The short durations of development, which had been stated for total development ≥ 15 °C in *Chironomus dorsalis* and *Paralimnophyes hydrophilus* (section 4.4.1.2.6.), are therefore the result of a lower thermal constant in the first- and of a lower developmental zero in the latter species. A comparison with the thermal constants of *Chironomus annularius* (developmental zero 5.3 °C) was only possible for total development until the first emergence (see section 4.4.1.2.5.). A KRUSKAL-WALLIS-ANOVA was significant (H ($df = 3$, $N = 85$) $= 14.9$, $p = 0.002$), the multiple comparisons by MANN-WHITNEY-U-tests (if p values were significant, they were adjusted (p_{new}) according to the standard BONFERRONI-technique ($k = 6$)) showed the following results:

C. annularius ⇔ *C. dorsalis*: $U = 87.0$, $p_{new} = 0.063$;

C. annularius ⇔ *P. tritum*: $U = 99.0$, $p = 0.401$;

C. annularius ⇔ *P. hydrophilus*: U = 98.0, p = 0.780;

C. dorsalis ⇔ *P tritum*: U = 169.0, p_{new} = 0.005;

C. dorsalis ⇔ *P hydrophilus*: U = 178, p_{new} = 0.060;

P. tritum ⇔ *P. hydrophilus*: U = 184.0, p = 0.513.

The thermal constants for total development until the first emergence of *Chironomus annularius*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* were not significantly different, but the level of significance ($\alpha = 0.05$) was only slightly exceeded for the combinations *C. annularius* ⇔ *C. dorsalis* and *C. dorsalis* ⇔ *P. hydrophilus*, whilst the thermal constants of *Chironomus dorsalis* and *Polypedilum tritum* were significantly different. The comparison of the thermal constants show that the heat gain necessary for the total development of *Chironomus dorsalis* was lower than in the other species. A comparison with *Chironomus luridus* was not possible because the developmental zero was unknown.

The thermal constants of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* were also estimated for the different stages of development using the data listed in Appendix 9 (Table 43). The data show that about 40 % of the development from egg to the adult was spent in the instar IV (and much longer during an oligopause!) and that the length of the pupal stage (only observed in *Paralimnophyes hydrophilus*) was the shortest of all development stages. At 4.5 °C (not listed in Table 42) the embryonic development lasted 10 or 11 days in *Chironomus dorsalis* and 23 or 24 days in *Paralimnophyes hydrophilus*, whilst *Polypedilum tritum* embryos died before hatching. At 4.5 °C, the small larvae of *Chironomus dorsalis* did not grow after hatching and eventually died, slow development into adulthood was observed for *Paralimnophyes hydrophilus* (section 4.4.1.2.4.).

Q_{10}-values: The Q_{10}-values of *Chironomus annularius*, *Chironomus dorsalis*, *Chironomus luridus*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* (Table 44) confirm the previous results. VAN'T HOFF's theory (section 3.5.8.) helps with determining the species' favourable- and suboptimal temperatures. The Q_{10}-values of *Chironomus annularius* indicate that temperatures (a) between 11 and 24 °C were favourable; and (b) between 24 and 30 °C were suboptimal. The Q_{10}-values of *Chironomus dorsalis* suggest (a) the cue temperature to thermal oligopause to lie between 10 and 14 °C (see Q_{10} First 9.5-13.8 °C SD and 13.8 °C SD-16.0°C); (b) the favourable temperatures (Q_{10}-values >1.5 < 4) to lie between the lower cue temperature to oligopause (~12 °C) and 27 °C; and (c) the suboptimal temperatures to lie between 27 and 30 °C. *Chironomus dorsalis* may therefore be termed thermophilous. Temperatures (a) between 10 °C and 25 °C were favourable; (b) between 25-29 °C were suboptimal; and (c) above 29 °C were sublethal to lethal to *Polypedilum tritum* (eurythermous to thermophilous). *Paralimnophyes hydrophilus* showed high Q_{10}-values (between 4 and 6) over a wide range of temperatures (probably from > 3.1 (T_0) -15 °C). For temperatures >15 °C, the Q_{10}-values ranged from 1.8 to 2.6. Temperatures of 29 °C were lethal to *Paralimnophyes hydrophilus* (section 4.4.1.2.1.). These data probably indicate that (a) temperatures ≤ 20 °C were

Table 43: Estimates of the duration of development and of the thermal constants for the different development stages.

Development stage	9.5°C		14.6°C/16.0 °C		19.3°C/20°C		25.0°C		Mean D-days ± Std.
	D-days	Days	D-days	Days	D-days	Days	D-days	Days	
Chironomus dorsalis									
Egg	2 x 29; 34/**31**	2 x 6; 7/**6.3**	39	3.5	2 x 39; 46/**41**	2 x 2.5; 3/**2.7**	4 x 51; 31/**47**	4 x 2.5; 1.5/**2.3**	41 ± 9
Instar I	2 x 51	2 x 10.5	44; 56/**50**	4; 5/**4.5**	2 x 54	2 x 3.5	41; 51/**46**	2; 2.5/**2.3**	50 ± 5
Instar II	2 x 49	2 x 10	2 x 44	2 x 4	39; 46/**43**	2.5; 3/**2.8**	41; 71/**56**	2; 3.5/**2.8**	48 ± 10
Instar III	59; 76/**68**	12; 15.5/**13.8**	56; 83/**70**	5; 7.5/**6.3**	39; 46/**43**	2.5; 3/**2.8**	2 x 71	2 x 3.5	63 ± 15
Instar IV+P	561; 625/**593**	114.5; 127.5/**121.0**	189; 211/**200**	17; 19/**18.0**	162; 185/**174**	10.5; 12/**11.3**	2 x 153	2 x 7.5	176 ± 23*
Polypedilum tritum									
Egg	2 x 52	2 x 12	2 x 56	2 x 6	2 x 56	2 x 4	2 x 59	2 x 3	56 ± 3
Instar I	2 x 77	2 x 18	71; 80/**76**	7.5; 8.5/**8**	1 x 71	1 x 5	1 x 59	1 x 3	73 ± 8
Instar II	2 x 32	2 x 7.5	2 x 56	2 x 6	2 x 42	2 x 3	40; 59/**50**	2; 3/**2.5**	45 ± 11
Instar III	2 x 65	2 x 15	2 x 56	2 x 6	1 x 71	1 x 5	40; 59/**50**	2; 3/**2.5**	59 ± 10
Instar IV+P	144; 196/**170**	33.5; 45.5/**39.5**	155; 183/**169**	16.5; 19,5/**18**	169; 183/**176**	12; 13/**12.5**	139; 238/**189**	7; 12/**9.5**	176 ± 32
Paralimnophyes hydrophilus									
Egg	2 x 64	2 x 10	35; 46; 69/**50**	3;4; 6/**4.3**	3 x 32; 2 x 49/**39**	3 x 2; 2 x 3/**2.4**	2 x 44	2 x 2	47 ± 13
Instar I	131; 179/**155**	20.5; 27.9/**24.2**	81; 92; 115/**96**	7; 8; 10/**8.3**	89; 65; 97/**84**	5.5; 4; 6/**5.2**	2 x 77	2 x 3.5	100 ± 34
Instar II	150; 86/**118**	23.5; 13.5/**18.5**	2 x 69; 75/**71**	2 x 6; 6.5/**6.2**	32; 49; 57/**46**	2; 3; 3.5/**2.8**	44; 55/**50**	2.0; 2.5	69 ± 33
Instar III	29; 51/**40**	4.5; 8/**6.3**	23; 2 x 109/**80**	2; 2 x 9.5/**7.0**	49; 81; 130/**87**	3; 5; 8/**5.3**	2 x 44	2 x 2	67 ± 38
Instar IV+P	162; 294; 304/**253**	25.3; 46; 47.5/**39.6**	138; 155; 173/**155**	12; 13.5; 15/**13.5**	105; 203; 243/**184**	6.5; 12.5; 15/**11.3**	2 x 164	2 x 7.5	191 ± 64
Pupae			12-35; **18** (N = 17)	1-3; **1.6** (N = 17)	16 (N = 2)	1.0 (N = 2)	22 (N = 14)	1.0 (N = 14)	20 ± 5

Abbreviations and explanations:

Columns: **D-days** = degree-days; **Days** = estimated duration (days) of development until 50 % of moulting into the subsequent stage of development; **Mean D-days ± Std.** = means of estimated thermal constants ± standard deviation.

Signs: **P** = pupal stage; * = the mean value ± standard deviation was calculated by exclusion of the results of the 9.5 °C experiments.

Comments: **1.** The temperature of a column may be somewhat different between the species, which is indicated by the corresponding values being separated by a slash (Appendix 8 and 9). **2.** Different single values are separated by a semicolon and separated from the corresponding mean value (in bold print) by a slash. When the single values are identical, the number of values collected is separated from the actual value by a multiplication sign. The duration of the pupal stage was estimated from individual observations and therefore provided in the min.–max.; mean standard with number of observations in brackets.

favourable to *Paralimnophyes hydrophilus*; and (b) temperature fluctuations between > 3 and 15 °C can be effectively exploited for larval growth. The species may therefore be termed psychrophilic to eurythermous. The two Q_{10}-values of *Chironomus luridus* show that temperatures of 9.5 °C lay below the species threshold for oligopause and that temperatures of 25 °C were probably already suboptimal.

Table 44: Q_{10}-values of total development for *Paralimnophyes hydrophilus*, *Chironomus annularius*, *Chironomus dorsalis, Chironomus luridus* and *Polypedilum tritum*.

Temperature	Q_{10} First	Q_{10} Mean
Chironomus annularius		
11.0 °C SD-13.8 °C SD/LD	2.228	-
11.0 °C LD - 13.8 °C SD/LD	6.905	-
13.8 °C SD/LD - 19.6 °C LD	2.491	-
19.6 °C LD - 24.2 °C LD	2.116	-
24.2 °C LD - 30.2 °C LD	1.329	-
Chironomus dorsalis		
9.5 °C LD - 16.0 °C LD	6.025	9.941
9.5 °C LD - 13.8 °C SD	11.999	4.650
13.8 °C SD - 16.0 °C LD	1.567	43.896
16.0 °C LD - 20.0 °C LD	2.680	3.527
20.0 °C LD - 21.5 °C LD	1.313	-
20.0 °C LD - 25.0 °C LD	1.812	1.686
21.5 °C LD - 25.0 °C LD	2.081	-
25.0 °C LD - 27.3 °C LD	2.723	2.704
27.3 °C LD - 30.2 °C LD	0.716	0.446
Chironomus luridus		
9.5 °C LD - 16.0 °C LD	4.681	10.891
16.0 LD - 25.0 °C LD	1.4	1.753
Polypedilum tritum		
9.5 °C LD - 14.6 °C LD	4.463	4.488
9.5°C LD - 13.8 °C SD	5.007	1.148
13.8 °C SD - 14.6 °C LD	2.405	6842.103
14.6 °C LD - 19.3 °C LD	2.166	2.166
19.3 °C LD - 25.0 °C LD	2.329	1.839
25.0 °C LD - 29.1 °C LD	1.276	1.295
29.1 °C LD - 30.2 °C LD	0.001	0.002
Paralimnophyes hydrophilus		
4.5 °C LD - 9.5 °C LD	4.247	-
9.5 °C LD - 14.6 °C LD	4.480	5.663
14.6 °C LD - 19.3 °C LD	2.580	2.444
19.3 °C LD - 25.0 °C LD	1.760	1.920

Explanations:

Q_{10} First/Q_{10} Mean = Q_{10}-values based on the arithmetic mean of all replicates for the minimum and mean duration of development. For further explanations see text.

4.4.1.2.9. Adult body size

The results of measurements of the adult body size of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* during the experiments on temperature and photoperiod are presented in Figure 68, Table 59 (p 183), Table 61 (p 187) and Table 64 (p 195). The thoraces of *Chironomus dorsalis* females were significantly larger than those of males, with one exception at 20.0 °C (t-tests for matched pairs: 13.8 °C SD: df = 18, t = -2.3, p = 0.037; 9.5 °C: df = 15, t = -4.0, p = 0.001; 16.0 °C: df = 16, t = -3.12, p = 0.007; 20.0 °C: df = 16, t = -0.39, p = 0.70; 25.0 °C: df = 12, t = -2.78, p = 0.017; 30.2 °C: df = 18, t = -6.02, p < 0.001). MANN-WHITNEY-U-tests for matched pairs were carried out for *Polypedilum tritum* and *Paralimnophyes hydrophilus* but none of the comparisons showed a statistically significant difference ($p \leq 0.050$) of thorax size between the sexes. In all three species, correlations between temperature and thorax length were negative and highly significant (Figure 68). The few adults of *Paralimnophyes hydrophilus*, which had emerged at 4.5 °C, were much larger than adults of the other temperature treatments (U = 1.0, p < 0.004). The body size of *Chironomus dorsalis* males was greater in the 13.8 °C SD- than in the 9.5 °C LD treatments (df = 18, t = 3.88, p = 0.001); this tendency was however not significant in females (df = 15, t = 0.58, p = 0.577). *Polypedilum tritum* adults that were reared in the 13.8 °C SD treatments were significantly larger than those reared during 9.5 °C LD experiment (U = 73.5, p < 0.001).

It was only intended to compare the adult body size of *Chironomus annularius* for the 11.0 °C LD- and SD experiments (Table 45). The mean values of female thorax lengths were greater than those of males, the difference was however only significant for individuals of the SD experiment. Using the table of random numbers found in LORENZ (1996), an equal number of males and females (LD: 14 ♂♂ + 14 ♀♀; SD: 12 ♂♂ + 12 ♀♀) was chosen and their adult body size in the LD- and SD experiments compared. The individuals which had emerged from the LD experiment were significantly larger (U = 165.0, p = 0.0015). As observed in *Chironomus dorsalis* and *Polypedilum tritum*, a photoperiodically delayed development resulted in larger adults.

Table 45: Comparison of the adult thorax length of *Chironomus annularius* in the 11.0 °C LD- and the 11.0 °C SD experiment.

	♂♂	♀♀	MAN-WHITNEY-U-test
11.0 °C SD	1.750-2.000; 1.895 ± 0.060 (n = 20)	1.750-2.400; 2.054 ± 0.185 (n = 12)	U = 31.5, p = 0.006
11.0 °C LD	1.600-1.950; 1.815 ± 0.079 (n = 17)	1.750-2.000; 1.886 ± 0.097 (n = 14)	U = 72.5, p = 0.065

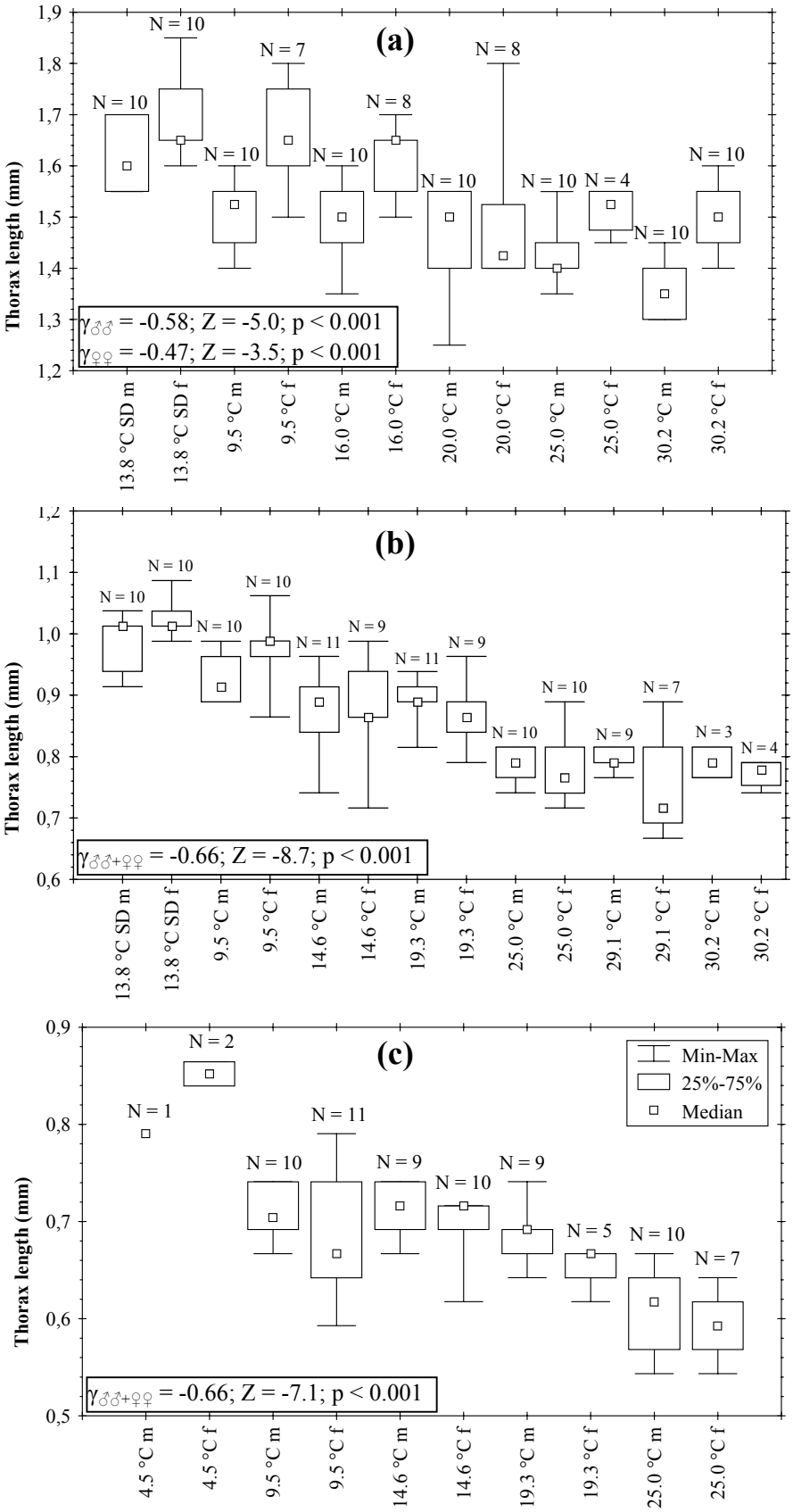

Figure 68: The depencence of body size on temperature and photoperiod in (a) *Chironomus dorsalis*; (b) *Polypedilum tritum*; and (c) *Paralimnophyes hydrophilus*.

The statistical values of correlations between body size and temperature (GOODMAN-KRUSKALS-γ) are provided within the boxes. If there were significant differences of size between males and females (*C. dorsalis*), the correlation coefficients with statistical values were calculated for males and females separately. m = ♂♂; f = ♀♀.

4.4.1.2.10. Protandry and sex ratio

Table 46: Emergence statistics for males and females.

Experiment	♂♂ First	♂♂ Med	♂♂ Mean	♂♂ sd	♂♂ N	♀♀ First	♀♀ Med	♀♀ Mean	♀♀ sd	♀♀ N	U	p	Δ
Chironomus annularius													
11.0 °C SD	51	58.5	57.6	6.5	51	51	63	65.8	10.8	41	513	<0.001	-8.2
11.0 °C LD	72	141.5	141.9	42.9	139	68	165	158.3	47.5	107	5887	0.005	-16.4
13.8 °C SD	34.5	72	70.5	12.0	151	47	72	73.5	11.2	200	13256	0.048	-3.0
19.6 °C LD	24	51	49.1	13.3	43	26	54	53.3	9.5	86	1587	0.188	-4.2
24.2 °C LD	17	19	18.5	1.2	18	17	18	18.2	1.1	13	104	0.57	+0.3
30.2 °C LD	11	19	19.2	3.3	121	15	21	21.1	3.5	134	5795	<0.001	-1.9
Chironomus dorsalis													
9.5 °C LD	77.0	161.0	161.5	24.7	351	88	170.0	169.0	24.6	326	46717	<0.001	-7.5
13.8 °C SD	27.0	84.0	80.7	12.9	682	28.0	84.0	81.7	11.5	701	233429	0.447	-1.0
16.0°C LD	28.0	33.0	34.0	4.4	191	30.0	37.0	37.1	4.4	162	9233	<0.001	-3.1
20.0 °C LD	18.0	22.0	22.1	2.2	229	19.0	23.0	23.7	2.2	262	18780	<0.001	-1.6
25.0 °C LD	13.0	17.0	17.0	2.1	284	14.0	17.0	17.2	1.9	280	38483	0.505	-0.2
27.3 °C LD	11.0	13.0	13.4	1.3	261	12.0	14.0	14.3	1.5	200	16484	<0.001	-0.9
30.2 °C LD	12.0	16.0	16.6	2.3	473	14.0	18.0	18.2	2.8	417	65477	<0.001	-1.6
Chironomus luridus													
9.5 °C LD	90	206	204.5	29.1	67	161	204	202.4	19.7	45	1313	0.247	+2.1
16.0 °C LD	33	40	40.8	3.9	29	41	45.5	45.6	2.8	26	127	<0.001	-4.8
Polypedilum tritum													
9.8 °C LD	78.0	92.0	92.6	8.0	202	74.5	93.5	95.2	8.0	226	18240	<0.001	-2.6
13.8 °C SD	34.0	90.0	86.3	12.6	409	37.0	90.0	88.4	10.6	424	71978	<0.001	-2.1
14.6 °C LD	35.0	43.0	43.1	3.5	218	35.0	44.0	43.9	3.6	230	21390	<0.008	-0.8
19.2 °C LD	25.0	29.0	29.9	3.2	226	24.0	30.0	31.4	3.5	229	18907	<0.001	-1.5
25.0 °C LD	15.0	21.0	21.5	3.9	279	15.0	22.0	22.8	4.2	296	34641	<0.001	-1.3
29.0 °C LD	14.0	20.0	20.6	4.2	193	14.0	23.0	22.3	4.6	196	14840	<0.001	-1.7
Paralimnophyes hydrophilus													
9.8 °C LD	58.5	90.0	89.1	12.1	195	71.0	94.0	94.8	9.9	168	11484	<0.001	-5.7
14.6 °C LD	28.0	39.0	38.4	5.8	184	30.0	40.0	39.9	5.7	123	9634	0.027	-1.5
19.2 °C LD	17.0	20.0	22.5	4.7	173	18.0	23.5	24.5	4.8	142	8282	<0.001	-2.0
25.0 °C LD	12.0	16.0	17.5	4.5	171	12.0	16.0	18.4	5.4	117	9325	0.326	-0.9

Abbreviations and explanations:

First/Med/Mean/sd/ = First emergence/median value of emergence/arithmetic mean of emergence/standard diversity (days after oviposition); **N** = number of emerged ♂♂ and ♀♀.

U/p/Δ = U-value/p-value of the MANN-WHITNEY-U-test for matched pairs/Δ = difference (days) between the mean values of male and female emergence (- = males developed faster; + = females developed faster).

Generally males emerged earlier than females, exceptions were rare and mainly observed in cultures with suboptimal ambient temperatures or light regimes which delayed development (Table 46). On average, development in males was 4-7 % faster than in the females (*C. annularius* 7 %, *C. dorsalis* 5 %, *C. luridus* 5 %, *P. tritum* 4 %, *P. hydrophilus* 6 %).

The sex ratio (♂♂/♀♀) was calculated for each replication if the number of emerged adults exceeded 10 (see Appendix 8). The mean values of all sex ratios and the 95 % confidence lobes were then calculated (Table 47). The data show that the sex ratio did not differ significantly from 1:1 in *Chironomus annularius* and *Polypedilum tritum* but significantly exceeded 1:1 in *Chironomus dorsalis* and *Paralimnophyes hydrophilus*.

Table 47: Sex ratio.

	Experiments	Mean	95 % CL	N
Chironomus annularius	11.0-30.2 °C +SD	0.94	0.68-1.20	11
Chironomus dorsalis	9.5-31.1 °C +SD	1.25	1.05-1.46	44
Polypedilum tritum	9.5-25.0 °C +SD	1.0	0.87-1.14	18
Paralimnophyes hydrophilus	9.5-25.0 °C	1.36	1.16-1.57	16

Abbreviations:
Experiments = temperature range taken into acount (+SD = inclusively the short-day experiments);
Mean/95 % CL/N = mean sex ratio/95 % confidence lobe of mean value/number of replicates taken into acount.

4.4.1.3. Competition

This experiment was a pilot study and its results are therefore preliminary. The following hypotheses were tested:

Hypothesis 1: Large larvae are better competitors than small ones.

Hypothesis 2: Species of permanent pools/ponds are better competitors than those of temporary pools.

Table 48: The emergence of adults from the experiments on competition.

Competitor	Target species		Competitor	
	♂♂,♀♀+L	Survival (%)	♂♂ + ♀♀	Survival (%)
Instars I of *Chironomus dorsalis*				
0	36,40	95.0		
0	32,32	80.0		
annularius 1	30,35	81.3	1,2	3.8
annularius 1	37,32	86.3	8,14	27.5
annularius 2	10,6	20.0	5,4	11.3
annularius 2	7,8	18.8	6,1	8.8
tritum 1	40,32	90.0	27,27	33.8
tritum 1	36,38	92.5	22,34	35.0
tritum 2	44,15	73.8	49,45	58.8
tritum 2	28,28	70.0	61,41	63.8
Instars I of *Chironomus plumosus*-aggregate				
0	7,6	16.3		
dorsalis 2	15,14+3	40.0	40,40	100.0
dorsalis 2	12,12+1	31.3	29,45	92.5
tritum 2	17,16	41.3	54,62	72.5
tritum 2	18,19	46.3	52,47	61.9
Instars I of *Polypedilum tritum*				
0	39,39	97,5		
0	29,22	63.8		
annularius 1	14,21	21.9	2,3	6.3
annularius 1	6,14	12.5	3,8	13.8
annularius 2	3,5	10.0	2,10	15.0
annularius 2	8,8	20.0	3,3	7.5
dorsalis 1	27,27	33.8	40,32	90.0
dorsalis 1	22,34	35.0	36,38	92.5
dorsalis 2	13,20	41.3	43,37	100.0
dorsalis 2	7,16	28.8	37,43	100.0

Explanations:
0 = no competitor present = control;
annularius 1, dorsalis 1, tritum 1 = newly hatched larvae of the competitors *C. annularius*, *C. dorsalis* and *P. tritum*;
annularius 2, dorsalis 2, tritum 2 = a mix of larger instars II to small instars IV of the competitor species;
♂♂,♀♀+L = number of males, females (emerged and partly preserved) + larvae (preserved).

Table 48 provides an overview of the number of emerging adults and their survival (%) within the experimental units. The impact of a competitor on the duration of development of newly hatched larvae of the target species is illustrated by Figures 69 and 70, the corresponding test statistics can be taken from Table 49. In addition, the adult body size was measured in *Chironomus dorsalis* for those treatments with newly hatched larvae at the beginning of the experiment (Figure 71). Unfortunately the vial with preserved adults of *Chironomus dorsalis* that had emerged in the experiment with larger larvae of *Chironomus annularius* (annularius 2) was lost.

The results can be summarized as follows:

I. *Chironomus dorsalis*:

(a) Survival of newly hatched larvae until adulthood was not reduced (80-95 %) if the competitors (*Chironomus annularius* and *Polypedilum tritum*) were newly hatched as well (Table 48);

(b) Larger larvae of *Polypedilum tritum* somewhat reduced- (74 and 70 %) and larger larvae of *Chi-*

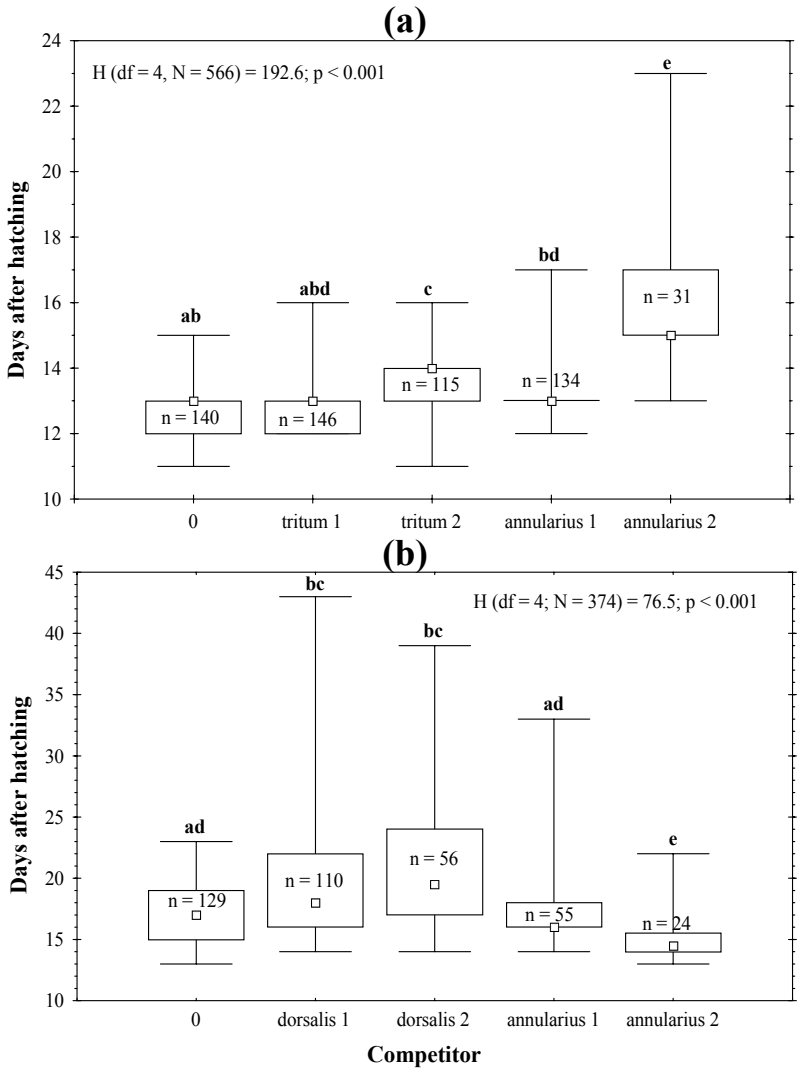

Figure 69: The duration of development (20.5 °C) of instars I into adults of (a) *Chironomus dorsalis*; and (b) *Polypedilum tritum* with and without competitors present.
The results of the KRUSKAL-WALLIS-ANOVA are shown in each figure, the different characters above the box-plots mark significant differences in mean values (see Table 49). For abbreviations see Table 48.

ronomus annularius strongly reduced (19 and 20 %) survival of newly hatched *Chironomus dorsalis* larvae until adulthood (Table 48);

(c) Survival of larger larvae of *Chironomus dorsalis* was always high (93-100 %) if the competitors were newly hatched (Table 48).

(d) If the competitors were small the duration of development did not differ or differed slightly from the control (replicates without competitors = 0) (Figure 69a);

(e) If larger larvae of *Polypedilum tritum* were present the duration of development was slightly prolonged. A distinct prolongation of development was observed when larger larvae of *Chironomus annularius* were the competitors (Figure 69a);

(f) Newly hatched competitor larvae had a negative impact on the adult body size of *Chironomus dorsalis*. This impact was significant in the experiment with small larvae of *Chironomus annularius* as competitors (Figure 71).

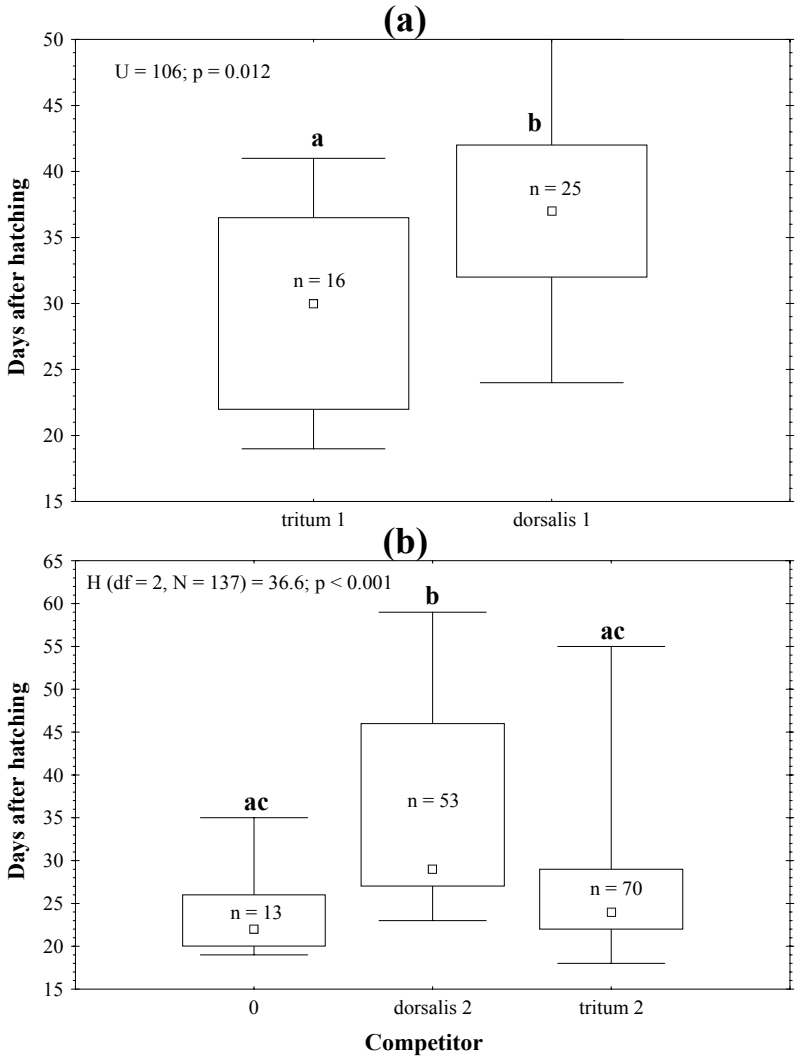

Figure 70: The duration of development (20.5 °C) of first instar larvae into adults of (a) *Chironomus annularius*; and (b) *Chironomus plumosus*-aggregate with and without competitors present.
See Figure 69 for comments.

Hypothesis 1 and 2 were confirmed for newly hatched larvae of *Chironomus dorsalis*: the negative impact of larger competitor larvae was greater than that of small larvae (hypothesis 1) and the negative impact was more pronounced if the permanent pond species was the competitor (hypothesis 2).

II. *Polypedilum tritum*:

(a) Survival of newly hatched larvae until adulthood was strongly reduced in presence of *Chironomus annularius* larvae (10-22 %) and clearly reduced in presence of *Chironomus dorsalis* larvae (29-41 %) (control 64 and 98 %) irrespective of the competitor's larval size (Table 48);

(b) There was no prolongation of development if *Chironomus annularius* larvae were present, but a significant lengthening was observed in presence of *Chironomus dorsalis* larvae, irrespective of its larval size (Figure 69b);

(c) Survival of larger larvae of *Polypedilum tritum* in presence of newly hatched competitors was always high (59-73 %), regardless of the competitor species.

Irrespective of their larval size, both competitor species had a very negative influence on newly hatched larvae of *Polypedilum tritum* (hypothesis 1). There were no strong differences of the negative influence of the pond- (*Chironomus annularius*) and the colonizing species (*Chironomus dorsalis*) on the target species *Polypedilum tritum*, although *Chironomus annularius* caused the higher mortalities (hypothesis 2). The experiment also showed that the impact of newly hatched competitors on larger larvae of *Polypedilum tritum* was low (hypothesis 1). Therefore, hypothesis 1 was partly- and hypothesis 2 weakly confirmed.

III. The pond species (*Chironomus annularius* and *Chironomus plumosus*-aggregate):

(a) Survival of newly hatched *Chironomus plumosus*-aggregate larvae until adulthood was low in the control (16 %) and higher in presence of larger larvae of *Polypedilum tritum* (41 and 46 %) and *Chironomus dorsalis* (31 and 40 %). Duration of development was prolonged if large lar-

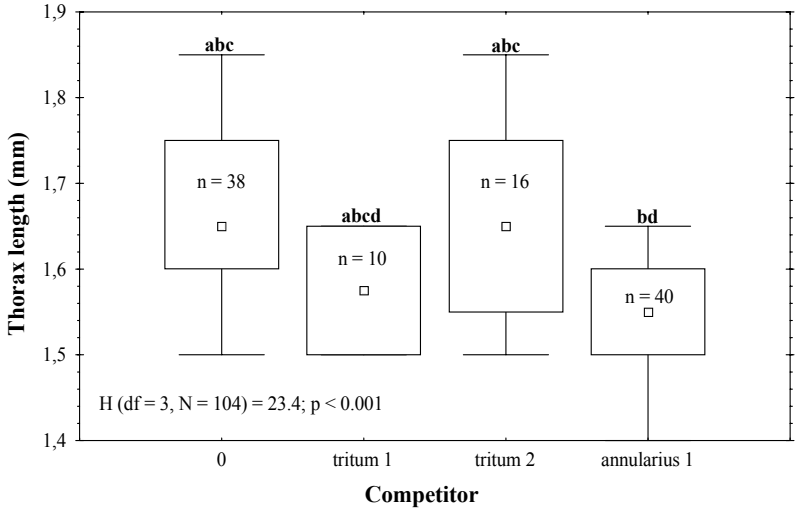

Figure 71: The impact of competitors on the adult body size of *Chironomus dorsalis* reared (20.5 °C) from instars I.
See Figure 69 for comments.

vae of *Chironomus dorsalis* were present (Figure 70 b);

(b) Survival of newly hatched and larger *Chironomus annularius* larvae was always low (6-28 %). The duration of development was longer if small larvae of *Chironomus dorsalis* were present (Figure 70a).

Unintentionally two species were used in the experiment as representatives of a pond species. The comparisons are therefore incomplete. It was originally intended to use only *Chironomus plumosus* in the experiment (remember: the development of *Chironomus annularius* is delayed by long-days, see section 4.4.1.2.5.).

Table 49: Statistical values for the multiple comparisons done with MANN-WHITHNEY-U-tests (Figures 69 - 71).

Length of development of instars I of *Chironomus dorsalis* into adults (Figure 69a) (k = 10)				
	tritum 1	tritum 2	annularius 1	annularius 2
0	U = 9931; p = 6.12	U = 3059; p < 0.001	U = 7658; p = 0.020	U = 78; p < 0.001
tritum 1		U = 3406; p < 0.001	U = 8269; p = 0.093	U = 108; p < 0.001
tritum 2			U = 3997; p < 0.001	U = 465; p < 0.001
annularius 1				U = 167; p < 0.001
Influence of competitors on the adult body size of *Chironomus dorsalis* reared from instars I (Figure 71) (k = 6)				
	tritum 1	tritum 2	annularius 1	
0	U = 101; p = 0.129	U = 292; p = 4.864	U = 311; p < 0.001	
tritum 1		U = 53; p = 0.928	U = 150; p = 1.352	
tritum 2			U = 166; p = 0.031	
Length of development of instars I of *Chironomus plumosus*-aggregate into adults (Figure 70b) (k = 3)				
	dorsalis 2	tritum 2		
0	U = 90; p < 0.001	U = 323; p = 0.250		
dorsalis 2		U = 850; p < 0.001		
Length of development of instars I of *Polypedilum tritum* into adults (Figure 69b) (k = 10)				
	dorsalis 1	dorsalis 2	annularius 1	annularius 2
0	U = 5256; p < 0.001	U = 1713; p < 0.001	U = 3087; p = 1.580	U = 619; p < 0.001
dorsalis 1		U = 2354; p = 0.127	U = 2022; p = 0.005	U = 322; p < 0.001
dorsalis 2			U = 585; p < 0.001	U = 69; p < 0.001
annularius 1				U = 224; p < 0.001

- Non-significant differences are marked by a grey background;
- The p value was adjusted according to the standard BONFERRONI-technique (Table 10 p 38);
- For abbreviations see Table 48, for further explanations see text.

4.4.1.4. Larval density

Table 50: The survival (%) of emerged adults in the experiments on larval density.

Density	Larvae/vessel	5	10	20	40	80	160	320	640	1,280	2,560
	Larvae/m²	786	1,572	3,144	6,288	12,575	25,150	50,301	100,602	201,203	402,406
Survival *C. dorsalis*		100	100	95	100	95	94	70	4	0	0
Survival *P. tritum*		100	70	35	23	98	64	62	43	0	0

This pilot experiment was concerned with the influence of overcrowding on development (indicated by the rates of survival, body size and duration of development) in the typical colonizer *Chironomus dorsalis* and the typical aestivator *Polypedilum tritum*. I hypothesized that, at least in the colonizing species, high densities (especially characteristic towards habitat extinction) accelerate development into adulthood in order to avoid desiccation.

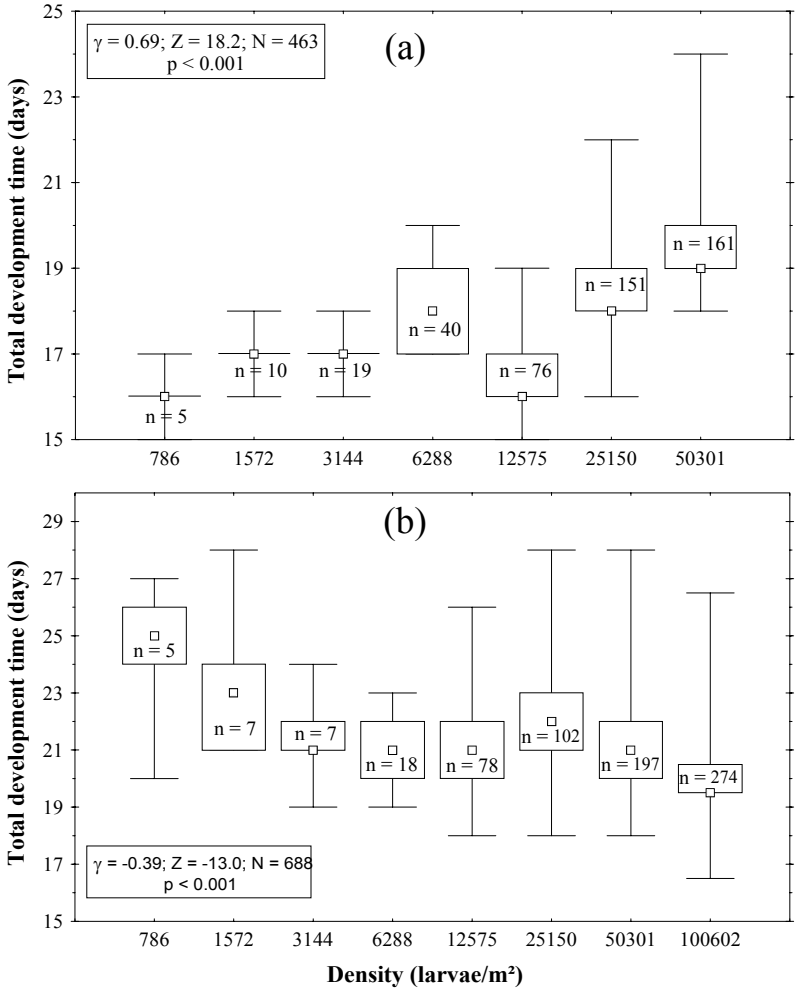

Figure 72: The impact of larval density on total development time (days after oviposition at 20.5 °C) of (a) *Chironomus dorsalis*; and (b) *Polypedilum tritum*.
The results of the correlations between the duration of total development and larval density (GOODMAN-KRUSKAL'S-γ) are provided in each figure; n = number of emerged adults.

Survival of *Chironomus dorsalis* was high (≥ 94 %) up to a density of 25,150 larvae per m², a significant decline of mortalities then occurred up to a density of 50,300 larvae per m² (GOODMAN-KRUSKAL'S-γ: γ = -0.882, Z = -2.5, p = 0.012). At densities of ≥ 100,600 larvae per m² the conditions in the culture vessels became toxic (Table 50).

Survival of *Polypedilum tritum* greatly fluctuated and no significant decline in the survival was observed up to a density of 100,600 larvae per m² (SPEARMAN'S-ρ: ρ = -0.36, t = -0.9, p = 0.385). The conditions in the vessels with ≥ 201,200 larvae per m² became toxic (Table 50).

The time of total development was positively correlated with larval densities in *Chironomus dorsalis* and negatively correlated in *Polypedilum tritum* (Figure 72). A Kruskal-Wallis ANOVA revealed that larval density had a significant impact on the adult body size of *Chironomus dorsalis* but not on that of *Polypedilum tritum* (Figures 73a,b). A repeated KRUSKAL-WALLIS-ANOVA showed that there were no significant differences of the adult body size of *Chironomus dorsalis* (a) up to densities of 12,575 larvae/m²; and (b) between the three treatments with ≥ 25,150 larvae/m². The adult body size of the treatments with ≤ 12,575 larvae/m² and ≥ 25,150 larvae/m² was then com-

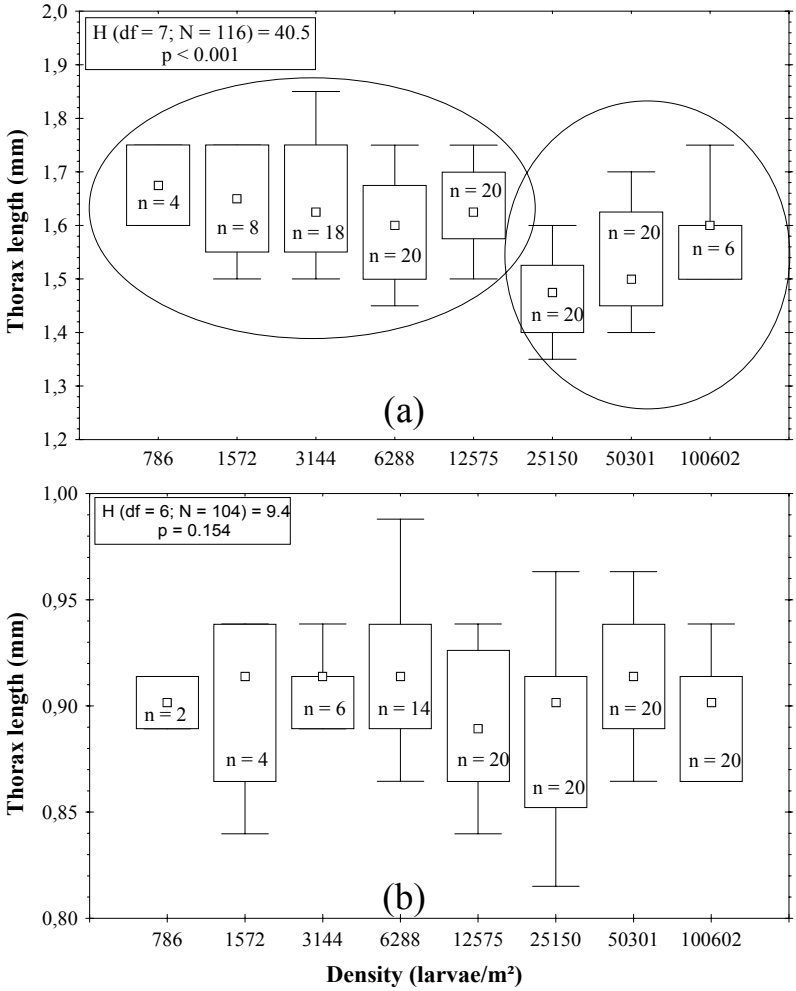

Figure 73: The impact of larval density on the adult body size (20.5 °C) of (a) *Chironomus dorsalis;* and (b) *Polypedilum tritum*.

The results of a KRUSKAL-WALLIS-ANOVA are provided in each figure; repeated KRUSKAL-WALLIS-ANOVA's showed no significant results for the circled box-plots in the figure of *Chironomus dorsalis*; n = number of adults (males and females in equal proportions) measured for the thorax length; for further explanations see text.

pared with a MANN-WHITNEY-U-test, which showed the average size of adults to be smaller in the high density treatments ($U = 653$, $p < 0.001$).

The experiment on larval density showed that high larval densities accelerated development in *Polypedilum tritum* but not in *Chironomus dorsalis*. If in the latter species there is an accelerated development towards habitat extinction, factors others than larval density trigger it.

4.4.1.5. Predation

The aim of this experiment was to test whether geophilous dragonfly larvae (here *Libellula depressa*) effectively prey on sediment-living chironomids. A further aim was to determine whether there are differences in predation on species that are typical of temporary pools and those typical of permanent ponds/pools. The results of the experiment are listed in Table 51. The end of the emergence of the *Chironomus plumosus*-aggregate was reached about two months later than in *Chironomus dorsalis* and *Polypedilum tritum*. In replicates with a predator, only one male of the *Chironomus plumosus*-aggregate emerged and the dragonfly larvae were dead at the end of the experi-

ment, probably because of the long absence of prey. The dragonfly larvae had doubled their weight until the end of the experiment with larvae of *Chironomus dorsalis* and had eaten nearly all larvae before these were able to emerge. The predator larvae also fed on the larvae of *Polypedilum tritum* (only one valid replicate (+2)) and their weight was the same at the end as in the beginning of the experiment. Greater quantities of *Polypedilum tritum* larvae are therefore necessary for the adequate feeding to meet the nutritional requirements of dragonfly larvae. The experiment showed the geophilous dragonfly larvae to prey effectively on sediment-living and tube-building chironomids. Further research would be necessary to answer the question of whether there are differences between the temporary pool- and the pond species.

Table 51: Results of the predation experiment.

Experiment	♂♂,♀♀	%	L_{begin} (gram)	L_{end} (gram)	Date 1	Date 2
Chironomus plumosus-aggregate						
0	54,45	33.0			16.9.1997	28.11.1997
+1	0,0	0.0	0.063	† (3.11.'97)		
+2	1,0	0.3	0.079	† (3.11.'97)	27.10.1997	
Chironomus dorsalis						
0	64,68	85.2			8.9.1997	18.9.1997
+1	4,0	1.3	0.081	0.160 (18.9.'97)	8.9.1997	12.9.1997
+2	5,6	3.7	0.084	0.173 (18.9.'97)	9.9.1997	13.9.1997
Polypedilum tritum						
0	92,91	61.0			8.9.1997	22.9.1997
(+1)*	54,64	39.3	0.058	††	9.9.1997	19.9.1997
+2	0,0	0.0	0.068	0.069 (17.9.'97)		

Abbreviations and explanations:
Experiment: 0 = without dragonfly larva, **+1/+2** = replicates with dragonfly larva;
♂♂,♀♀ = number of emerged males, females;
% = percentage of survival;
$\mathbf{L_{begin}}$ = weight of dragonfly larva at the beginning of the experiment (30.8.1997);
$\mathbf{L_{end}}$ = weight of dragonfly larva at the end of the experiment (date of end in parenthesis);
Date 1 = beginning of the emergence;
Date 2 = end of the emergence;
* and †† = the dragonfly larva died before the first adults emerged;
† = dragonfly larva found dead at the end of the experiment.
Except in the experiment 0 of *Chironomus dorsalis* (only 155 larvae), 300 chironomid larvae were always present at the beginning of the experiment (= 13,734 larvae/m²).

4.4.1.6. Drought-tolerance

4.4.1.6.1. *Polypedilum tritum* and *Paralimnophyes hydrophilus*

As explained in section 3.3.6., the water content of the mud within the larval trays at the end of the drought period was classified into five classes of humidity (class 1: 0-19.9 %, class 2: 20-39.9 %, class 3: 40-59.9 %, class 4: 60-79.9 %, class 5: 80-90 %). The water contents measured in the mud trays and the corresponding classification into classes of humidity within the larval trays, can be taken from the Appendix 10.

Figure 74 shows the results of the experiment on drought-tolerance for instars I, III and IV in *Polypedilum tritum*. The data were arranged according to (a) the tray's moisture level; and (b) the length of desiccation. Survival of the larvae was not observed in very dry mud (water content 0-19.9 %)

except in 11 instars IV, which had survived 3 days of drought. Instars III and IV survived up to 180 days whenever the water content exceeded 20 % of the mud weight. There was a negative correlation between the duration of the drought period and survival of instars III in mud with water contents ≥ 20 % (GOODMAN-KRUSKALS-γ: H_0: γ = 0; H_1: γ < 0; γ = -0.42, Z = -2.45, p = 0.007, N = 20 larval trays). A portion of instars IV developed into adults after the mud had dried up (Figure 78, section 4.4.1.6.4.) and therefore no survival rates could be calculated (the adults emerging from the different larval trays were all collected in the same experimental box (Figure 6 p 33)). The adult emergence caused a very irregular pattern of survival in the instar IV and made further statistical analysis of these results impossible. Instars I were more sensitive to the drying up of mud. Survival in mud with water contents between 20-39.9 % was low even after a short period of drought, and no survival was observed after 180 days. Survival of instars I was very irregular in trays with water

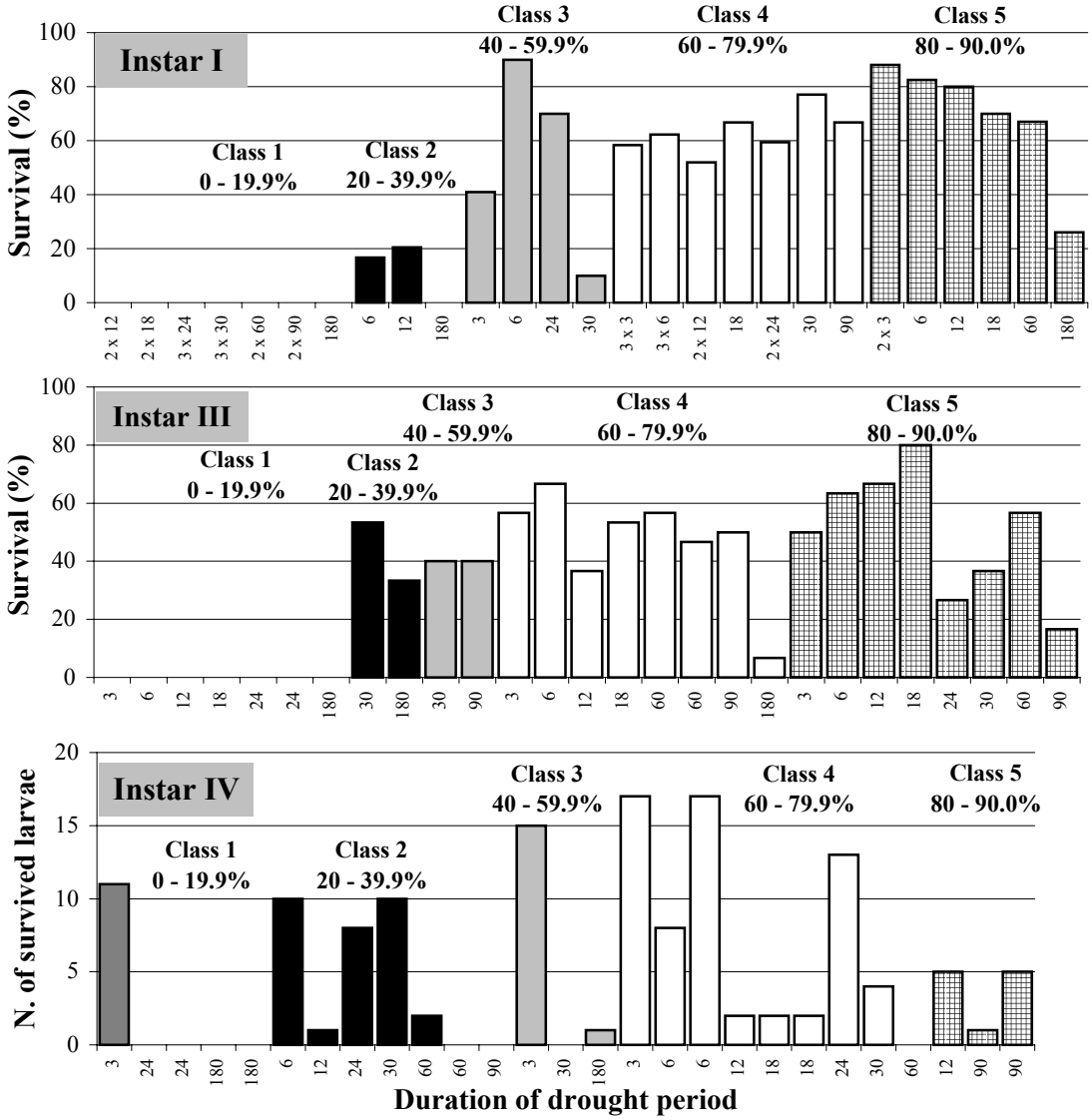

Figure 74: Results of the experiment on drought-tolerance of *Polypedilum tritum*.
For instar I, mean survival rates were calculated if more than one tray was within the same class of humidity after the same period of time (e.g. 3 x 3 within humidity class 4 = three larval trays showed a mean survival of 58 % after a drought period of 3 days). The results of all larval trays are shown individually for instars III and IV. No survival rate could be calculated for instars IV because a high number of larvae developed into adulthood (see Figure 78). For further explanations see text.

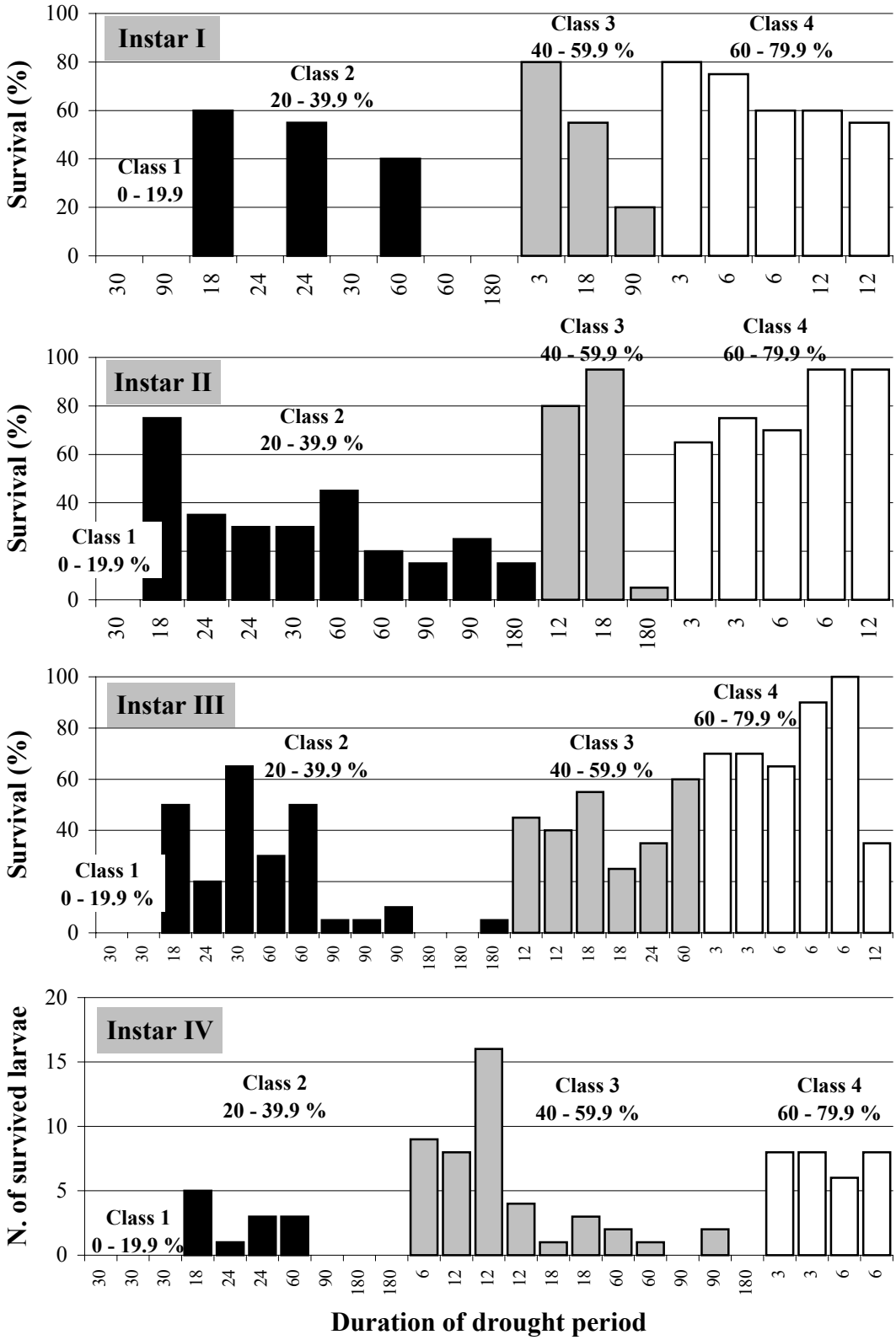

Figure 75: Results of the experiment on drought tolerance of *Paralimnophyes hydrophilus*.
No survival rate could be calculated for instar IV, because a high number of larvae went on to develop into adulthood (see figure 78). For further explanations see Figure 74 and text.

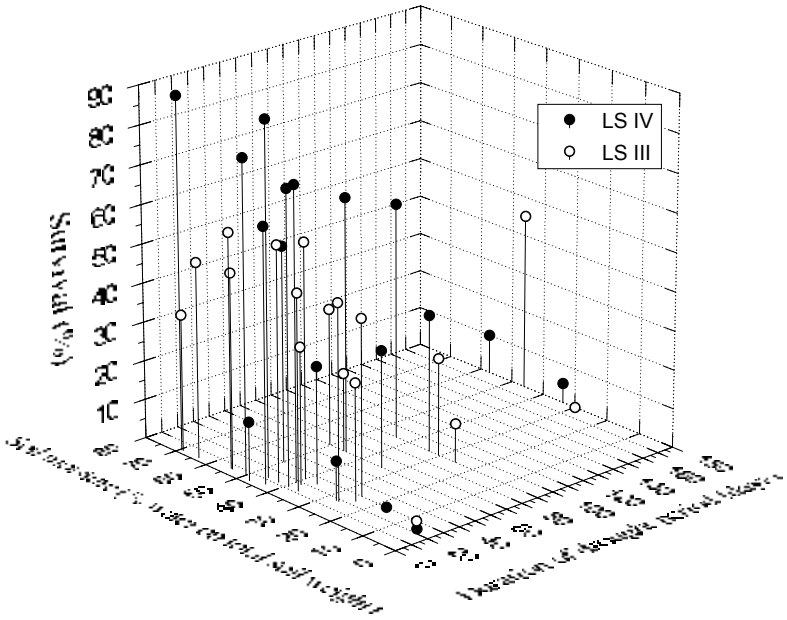

Figure 76: Survival of the instars III and IV of *Limnophyes asquamatus* (parthenogenetic lab rearings) in relation to the duration and intensity of drought.

contents between 40-59.9 %, which indicates that the threshold for survival of instars I lies between these limits. If water contents were ≥ 60 % at the end of the drought period, a survival of instars I up to 180 days was possible and there was a negative correlation between survival and the duration of the drought period (GOODMAN-KRUSKALS-γ: H_0: $\gamma = 0$; H_1: $\gamma < 0$; $\gamma = -0.33$, $Z = -1.89$, $p = 0.029$, $N = 20$ larval trays).

The results of the experiment on drought-tolerance of *Paralimnophyes hydrophilus* are illustrated by Figure 75. Similarly to what was seen for *Polypedilum tritum*, no survival occurred within substrates with water contents attributed to class 1. Instars I could survive over long time periods in substrates of classes 2-4. The irregular pattern of survival within substrates of class 2 indicates that the critical content of substrate humidity for the instar I probably lies between 20 and 39.9 %. Therefore instars I of *Paralimnophyes hydrophilus* are most likely more tolerant to drying up than those of *Polypedilum tritum*. There was a significant correlation between survival of instars I and the length of the drought period, in experiments in which at least some larvae survived (GOODMAN-KRUSKALS-γ: H_0: $\gamma = 0$; H_1: $\gamma < 0$; $\gamma = -0.96$, $Z = -3.72$, $p < 0.001$, $N = 11$ larval trays). Instars II survived for up to 180 days whenever the substrate's water content exceeded class 1. No differences of survival were visible between classes 2, 3 and 4 until 18 days of drought. Survival of instars II was significantly correlated with the duration of the drought period (GOODMAN-KRUSKALS-γ: H_0: $\gamma = 0$; H_1: $\gamma < 0$; $\gamma = -0.69$, $Z = -3.65$, $p < 0.001$, $N = 17$ larval trays). Survival of instars III seemed to be not different to that of instars II. There were no differences in survival rates up to 60 days of desiccation of instars III at humidity levels 2 and 3 (MANN-WHITNEY-U-test: $U = 15$, $p = 1.0$, $N_{class\ 2} = 5$, $N_{class\ 3} = 6$). Survival of instars III at humidity levels 2-4 was significantly correlated with the duration of the drought period (GOODMAN-KRUSKALS-γ: H_0: $\gamma = 0$; H_1: $\gamma < 0$; $\gamma = -0.69$, $Z = -4.42$, $p < 0.001$, $N = 23$ larval trays). The drought-tolerance of instars IV seemed be similar to that seen in

the instar III, but due to the adult emergence (Figure 78, section 4.4.1.6.4.) no further statistical analysis could be done. Instars III and IV of *Polypedilum tritum* and *Paralimnophyes hydrophilus* obviously have a comparative ability to survive desiccation.

4.4.1.6.2. *Limnophyes asquamatus*

Table 52: Double regressions with statistical values for the dependence of larval survival of *Limnophyes asquamatus* (parthenogenetic lab rearings) on the water content of the mud (Humidity) and the duration of drought period (Duration) (see also Figure 76).

	Humidity & Duration	Humidity	Duration
	Instars III + IV		
Function (1)	S = -0.19 * t + 0.92 * h + 12.66		
R²/r (2)	R² = 0.453	r = 0.567	r = -0.464
F-statistics/T-statistic (3)	F = 13.67, df = 2.33, p < 0.001	t = 3.96, df = 33, p < 0.001	t = -3.01, df = 33, p = 0.005
N	36	36	36
R² independent (4)	0.0097		
F-statistics independent (4)	F = 0.34, df = 1.34, p = 0.567		
	Instar III		
Function (1)	S = -0.14 * t + 0.52 * h + 22.95		
R²/r (2)	R² = 0.419	r = 0.470	r = -0.466
F-statistics (3)	F = 5.41, df = 2.15, p = 0.017	t = 2.07, df = 15, p = 0.057	t = -2.04, df = 15, p = 0.059
N	18	18	18
R² independent (4)	0.049		
F-statistics independent (4)	F = 0.82, df = 1.16, p = 0.379		
	Instar IV		
Function (1)	S = -0.26 * t + 1.43 * h - 0.82		
R²/r (2)	R² = 0.590	r = 0.705	r = -0.576
F-statistics (3)	F = 10.80, df = 2.15, p = 0.001	t = 3.85, df = 15, p = 0.002	t = -2.728, df = 15, p = 0.016
N	18	18	18
R² independent (4)	0.0012		
F-statistics independent (4)	F = 0.017, df = 1.16, p = 0.897		

Abbreviations and comments:

(1) function for the multiple regression (S = survival (%), t = duration of drought period (days), h = humidity of soil (% of water on total weight);

(2) R² = coefficient of total determination, r = partial correlation coefficient;

(3) F-statistics and t-statistics for the multiple regression and partial correlation, respectively

(4) coefficient of determination and F-statistics for the relation between humidity of soil and the duration of drought in the experiments (independent variables).

In the experiments on drought-tolerance done for *Limnophyes asquamatus*, the water content of the mud at the end of the drought period was exactly known (section 3.3.6.). These data were therefore analysed differently to those of *Polypedilum tritum* and *Paralimnophyes hydrophilus*. Only instars III and IV had been tested for their ability to survive periods of drought (Figure 76). In contrast to *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* (section 4.4.1.6.4.), only 13 out of 720 instars III and IV of *Limnophyes asquamatus* developed into adults after the start of the drought period (= 2.4 %). As observed in *Polypedilum tritum* and *Paralimnophyes hydrophilus*, no survival occurred in substrates with water contents < 20 %. Larvae survived up to 180 days of drought in substrates with water contents of 20-40 % (= class 2), which again matches the results of *Polypedilum tritum* and *Paralimnophyes hydrophilus*. In one larval tray with instars III and a moisture level of 46 % (= class 3), survival of 45 % occurred even after 180 days of desiccation.

This may indicate that the ability to survive long periods of drought is higher in *Limnophyes asquamatus* than in *Polypedilum tritum* and *Paralimnophyes hydrophilus*. Because the substrate's water content in the experiments was not correlated with the duration of the drought period (R^2 independent and F-statistics independent in Table 52), a double regression of survival in relation to substrate humidity and the duration of the drought period was carried out. It was also possible to calculate partial correlations for survival and substrate humidity on the one hand and survival and the duration of the drought period on the other. The results presented in Table 52 show that survival was dependent on the intensity of drying up as well as on the duration of the drought period. If instars III and IV were included into the same analysis (Instars III + IV in Table 52), this result was highly significant. If the instars III and IV were analysed separately, the dependence of survival on substrate humidity and the duration of the drought period was significant in the instar IV and the level of significance ($\alpha = 0.05$) was slightly exceeded in the instar III.

4.4.1.6.3. *Chironomus dorsalis* and *Chironomus pseudothummi*-aggregate

In contrast to the experiments on drought tolerance of *Polypedilum tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus*, only one run with 50 % potassium hydroxide as hygroscopic medium was done for *Chironomus dorsalis* and the *Chironomus plumosus*-aggregate. The larvae of

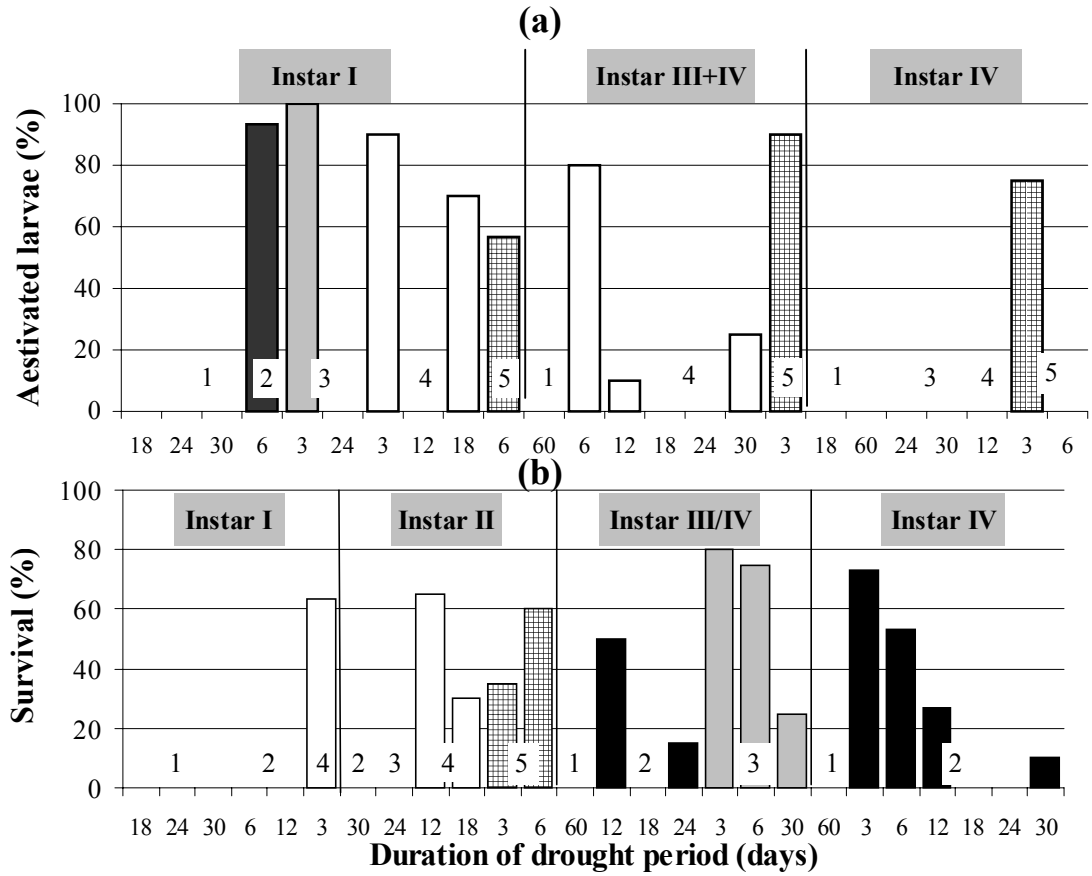

Figure 77: Results of the experiments on drought tolerance of (a) *Chironomus dorsalis*; and (b) the *Chironomus plumosus*-agg.

The data were arranged according to (a) the instar; (b) to the class of humidity at the end of the experiment (numbers above the abscissa); and (c) to the duration of the drought period. The signatures of the columns are used as in Figures 74 +75.

both species, especially those of the *Chironomus plumosus*-aggregate, were assumed to exhibit no unusual ability to endure periods of drought. These experiments were therefore conducted with the intention to get an impression of the preadaptation of Chironomidae to survive desiccation.

Chironomus dorsalis instars I survived up to 18 days of drought (Figure 77a). In contrast to *Polypedilum tritum* and *Paralimnophyes hydrophilus*, where survival was always observed in substrates with water contents of classes 3, 4 and 5, survival of the instars I in *Chironomus dorsalis* was very irregular, even within these classes of humidity. The majority of larval trays in the experiment with instars III and very small instars IV (Instar III+IV in Figure 77a) showed a substrate humidity of class 4 at the end of the drought period. But despite this high level of humidity survival was very irregular and low if the duration of drought was ≥ 12 days. However, 25 % of survival occurred in a larval tray with substrate humidity of class 4 after 30 days of drought. In the experiment with larger instars IV, aestivated larvae were only found in one larval tray with substrate humidity of class 5 after 3 days of drought. The percentage of emerging adults was similar to that observed in *Polypedilum tritum* and *Paralimnophyes hydrophilus* (section 4.4.1.6.4.). It therefore appears that the instars III and IV of *Chironomus dorsalis* have a much lower ability to survive long periods of drought than *Polypedilum tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus*. *Chironomus dorsalis* larvae only survived longer periods of drought in substrates with high water contents (classes 4 and 5). The instars III and IV of *Chironomus dorsalis* also behave differently than those of *Polypedilum tritum*. While *Polypedilum tritum* larvae usually stayed in their tubes when drying up (those of *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* are free-living and construct tubes when the mud dries up), those of *Chironomus dorsalis* left the tubes and crawled around.

The substrates' humidity was low (classes 1 and 2) in the larval trays with instars I of *Chironomus plumosus*-aggregate except in one case (class 4) (Figure 77b). In contrast with the results described for *Polypedilum tritum*, no survival of instars I occurred after 6 and 12 days of drought in the two larval trays with substrates of class 2. Instar II larvae survived up to 18 days only in trays with high water contents (classes 4 and 5). No larvae survived in two trays, which had water contents of class 2 and 3 after 30 and 24 days of drought, respectively. This stands in contrast to *Paralimnophyes hydrophilus* instars II, which always survived in trays with substrates of classes 2 and 3. In the experiments with instars III and small instars IV, survival up to 30 days occurred in substrates with water contents of classes 2 and 3. The results for the instars IV show that survival in substrates of humidity class 2 was possible until at least 30 days of drought but that survival was also strongly dependent on the duration of drought. At this level of substrate humidity (class 2), a survival of much more than 30 days is assumed to be impossible. The instars IV of the *Chironomus plumosus*-aggregate did not crawl around and were not able to develop into an adult when drying up. The results for the *Chironomus plumosus*-aggregate show that the ability to survive long periods of drought is much lower than that observed in *Polypedilum tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus*. When comparing the *Chironomus plumosus*-aggregate with *Chironomus dorsalis*, the data show evidence that (a) the drought tolerance of the instars I (and II?) is

greater in *Chironomus dorsalis*; and (b) the drought tolerance of the instars III and IV is greater in the *Chironomus plumosus*-aggregate. The more important differences were however observed with respect to (a) the larval behaviour (crawling of larger larvae of *C. dorsalis*, remaining in the tube in the *C. plumosus*-aggregate); and (b) the ability (*C. dorsalis*) or inability (*C. plumosus*-aggregate) of the instars IV to develop into an adult after the substrate had dried up.

4.4.1.6.4. The adult emergence after drying up of the substrate

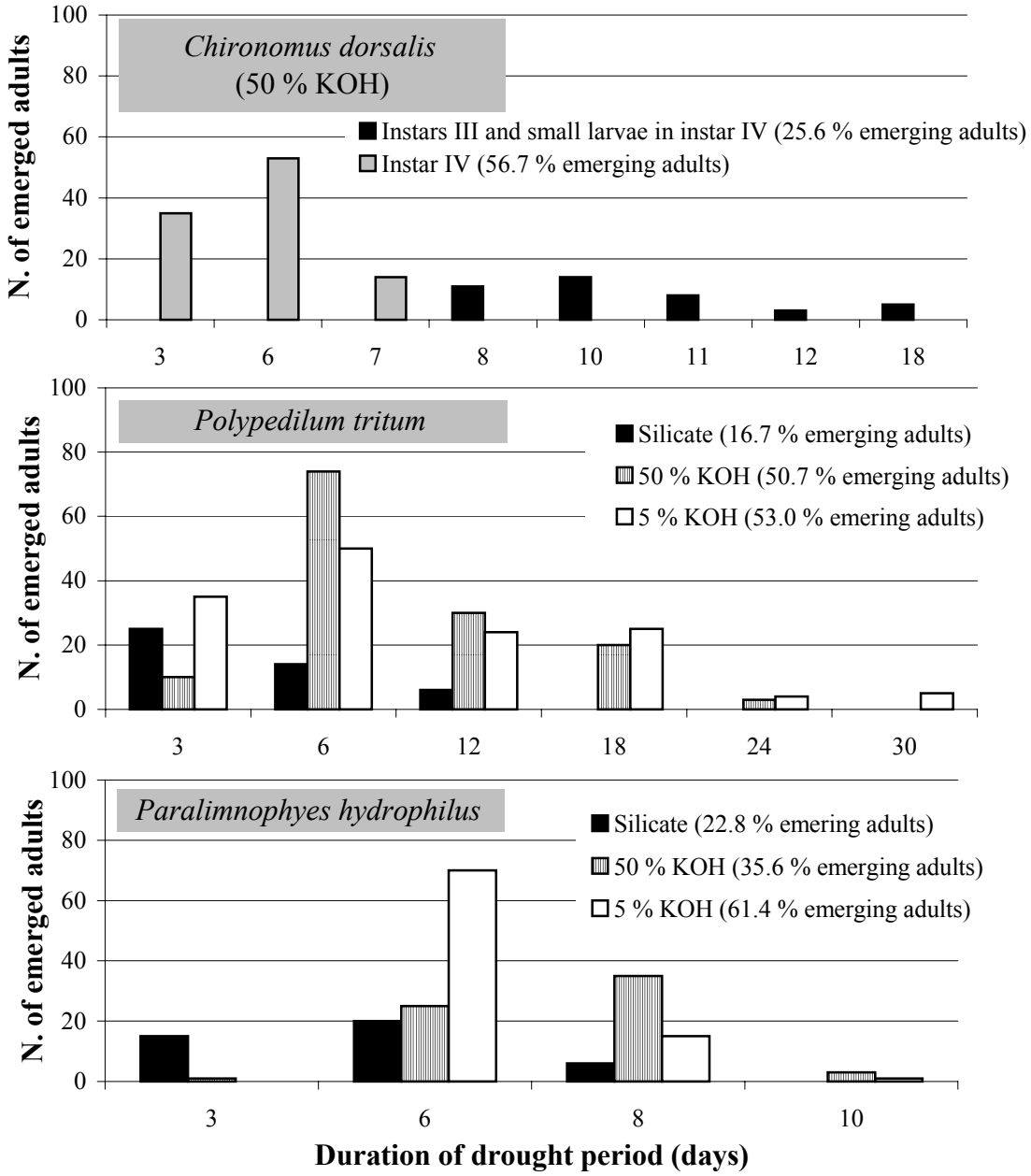

Figure 78: The emergence of adults in experiments on drought-tolerance of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*.

Three runs with different hygroscopic media were carried out in *P. tritum* and *P. hydrophilus*, whereas only one run with 50 % KOH as hygroscopic medium was done for *C. dorsalis*. *P. tritum* and *P. hydrophilus* adults only emerged in the experiments with instars IV (total number of instars IV at the beginning of the experiments: n = 3 x 270 (*P. tritum*) and 3 x 180 (*P. hydrophilus*)). *C. dorsalis* adults emerged from the run with instars III (inclusive small instars IV, n = 180 larvae) as well as from that with only instars IV (n = 180 larvae). For further explanations see text.

As mentioned above, fourth instar larvae of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* partly developed into adults after the larval trays had dried up. The process of drying up was different according to the three hygroscopic media applied: (a) 5 % potassium hydroxide caused a slow and mild drying-; (b) 50 % potassium hydroxide caused a reasonable fast but on the long run strong drying-; and (c) silicate granulate caused a very fast and intensive drying of the substrates (section 3.3.6.). The results for *Polypedilum tritum* and *Paralimnophyes hydrophilus* show that the faster the drying of the substrate the lower the proportion of larvae that were able to develop into adults (percentages are written behind the name of the hygroscopic media in Figure 78). Emergence could still occur up to 18- (*Chironomus dorsalis*), 30- (*Polypedilum tritum*) and 10 days (*Paralimnophyes hydrophilus*) after the start of the drought period depending on the speed of substrate's drying. The comparatively low percentage of 25.6 % of emerging adults in the experiment with instars III and small instars IV of *Chironomus dorsalis* probably reflects the lower proportion of instars IV rather than an ability of instars III to develop into adults.

4.4.2. Field study

In this section, the results of the emergence study of pools 1-3 (section 4.2.1.) and of the colonizing experiment (section 4.2.2.) will be analysed for *Chironomus dorsalis*, *Polypedilum tritum*, *Limnophyes asquamatus* and *Paralimnophyes hydrophilus*. The data were analysed and are presented in a synopsis with the results of section 4.4.1..

4.4.2.1. Analysis of the emergence patterns in the natural habitat

4.4.2.1.1. *Polypedilum tritum*

Polypedilum tritum was the dominating chironomid of pool 1 (Tables 22 + 23 pp 64-65) and usually rare in pool 2 (Table 24 p 66) and pool 3 (Table 25 p 67). The years 1995 (pool 3) and 1998 (pool 2) were exceptions (section 4.2.1.5.), when *Polypedilum tritum* was more abundant. The highest annual crop of emerging adults/m² in pool 1, 2 and 3 was 6,494 for pool 1/site 1b in 1999, 225 for pool 2/site 5 in 1998 and 1,600 for pool 3/site 7 in 1995. See DETTINGER-KLEMM & BOHLE (1996) and Appendix 3 for the emergence of *Polypedilum tritum* from pool 1 in 1993 and 1994. In this section, only the emergence for the years 1997-1999 (pool 1, Figure 79), 1998 (pool 2, Figure 80) and 1995 (pool 3, Figure 80) will be analysed.

Using a developmental zero of 5.2 °C (Table 41 p 143) and the daily means of water temperature (Appendix 2), it was possible to determine the periods of zero growth (set to a grey tune in Figures 79 + 80) and to calculate the degree-days available for development for any period of time.

Pool 1: In **1996**, only a few adults of *Polypedilum tritum* emerged from pool 1 (section 4.2.1.5.), the pool dried up towards the end of July and refilled on October 2 (Figure 18 p 53). Because there were no measurements of temperature available until November 25, 1996, the degree-days available for development from refilling until zero growth were estimated from the measurements taken in 1998 (about 120 degree-days). If instars I had aestivated throughout the drought period in 1996, the degree-days assumed to be available for development until the period of zero growth would have facilitated its development into instars III (Table 43 p 147). The overwintering population in the winter 1996/97 must therefore have consisted of instars IV and maybe to a lower extend of instars III as well. In **1997**, the period of zero growth ended on March 7 (Figure 79 at top). From the end of zero growth until the first emergence and the end of the emergence of the first spring generation (May 22-30, median = May 26) 56 and 230 degree-days, respectively, could have been used for development by the larvae of *Polypedilum tritum* present in pool 1 (the numbers of degree-days from the end of developmental zero until the beginning/end of the first spring generation are always provided in bold figures separated by a slash above the x-axis and are placed between the end of zero growth and the beginning of the emergence of the first spring generation). We know from section 4.4.1.2.8. (Table 43 p 147) that *Polypedilum tritum* needs about 230 degree-days to develop from the beginning of instar III until the 50 %-emergence of the adults. Therefore, from a thermal point of view, all instars IV and at least the majority of instars III present after the period of zero growth in spring 1997, were able to develop into adults until the end of the first spring emergence.

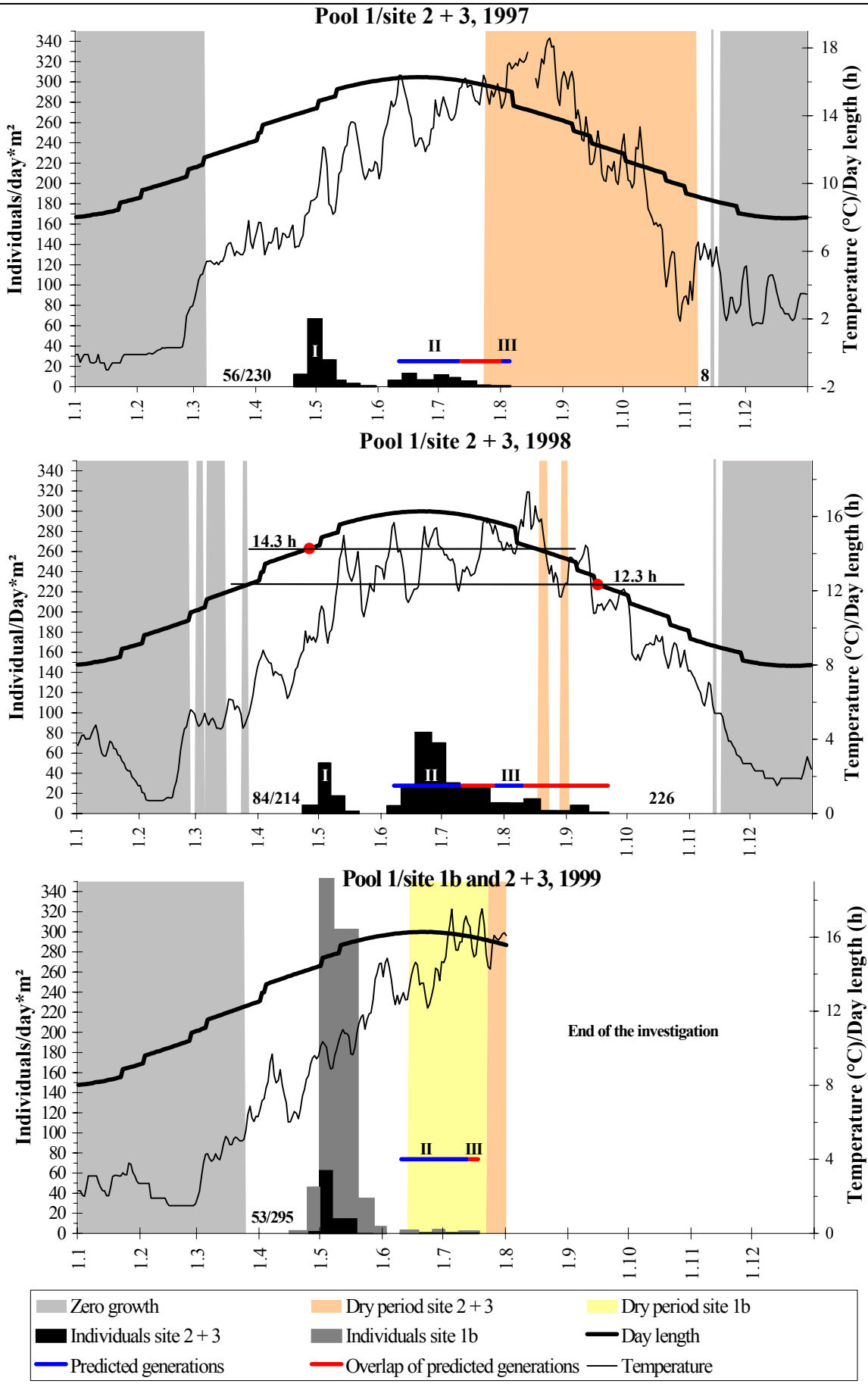

Figure 79: The emergence of *Polypedilum tritum* in pool 1 from 1997 – 1999.
For explanations see text.

It is possible to predict the time of the beginning and the end of the second generation by using the degree-days needed for total development until the first and last emergence and the water temperatures measured (at least 297 degree-days until the first- and at its maximum 592 degree-days until the last emergence, see Table 42, p 145). If the first emerging female had laid its egg mass in the evening of April 23, the first emergence of the second generation would have been on June 11. Indeed, the first emergence of the second peak was observed between June 6-12 (median = June 9), the prediction was therefore very accurate. The end of the second generation (July 31) was predicted assuming that the latest egg mass within the first spring generation was laid in the evening of May 26. According to the prediction of the second generation the first emergence of the third generation was calculated by assuming that the first egg mass of the second generation had been laid on June 9, 1997. The predicted start of the third generation was July 12. The prediction shows that there might have been an overlap of generations from July 12 (predicted start of the third generation) to July 31 (predicted end of the second generation). Because the generations 2 and 3 are not separable by the emergence data, the theoretical end of the third generation was calculated with the theoretical end of the second generation on July 31. The theoretical end of the third generation was September 29, but in fact the pool dried up at the end of July and therefore development had ceased by that date (the drought period is set to a brownish tune in the figures). The blue horizontal bars mark the predicted second and third generation in Figure 79, separated by the red horizontal bar, which indicates the overlap of predicted generations. The 1997 emergence data for *Polypedilum tritum* in pool 1 show that there was a pronounced and well-separated peak of the first spring generation and a lower second peak, which presumably consisted of members of generation 2 as well as 3. As observed in the experiment on drought tolerance (Figure 78 p 166), the emergence continued about 10 days after the start of the drought period. The emergence data for 1997 clearly indicate that larvae of all instars must have been present in the drying mud at the start of the drought period. The pool refilled late at the beginning of November 1997 and only 8 degree-days could be used for larval growth between refilling and the period of zero growth in 1997 (data on degree-days from the end of the drought period until the start of zero growth are always provided above the x-axis and are placed between the end of the drought period and the start of zero growth). The first spring peak of emergence was well separated from the second peak in **1998** (Figure 79 in the middle). The degree-days accumulated from the end of the period of zero growth until the first- and last spring emergence, were similar to those of 1997. Only instars III and IV were therefore able to develop into adults during the 1998 spring emergence and it is most likely that the instars I and II had not survived the long and intense drought period in 1997, which would apply to the results presented in section 4.4.1.6.1.. In contrast to 1997, the second peak of emergence in 1998 was higher and longer and the pool only dried up for a few days. The generations were predicted with the same methods as for 1997 (second generation: June 6. - July 26; third generation: July 11 - October 8.; fourth generation: August 11 - no end in 1998). The prediction of the start of the second generation applies exactly with the start of the second peak of emergence between June 3 and 10 (median = June 7). The predictions of generations indicate that four generations could have emerged until the end of emer-

gence on September 16 (sampling interval: 11-21.9.). The predictions also indicate that if a fourth generation had started emerging, its emergence stopped relatively early. From the end of emergence in mid September until the start of zero growth, 226 degree-days were available for larval growth. As seen in section 4.4.1.2., only short-days induced an oligopause in *Polypedilum tritum*. The stop of emergence in September 1998 must have therefore been caused by a decline in day length. The day length at the start of emergence in 1998 was 14.3 hours and 12.3 hours at the end of emergence. The photoperiodic threshold for oligopause in the instar IV therefore probably lies between these limits. Assuming an egg mass that was laid by the latest emerging female in the evening of September 16, this egg mass's larvae were able to develop into the instar III and partly into IV until the start of zero growth. Because a short-day induced delay of development is only effective in the instar IV (section 4.4.1.2.3.), the over-wintering population must have consisted mainly of instars IV. In **1999** (Figure 79 at the bottom) 53 and 295 degree-days were available for larval growth until the first and last emergence, respectively, of the first spring generation on sites 2+3 and 1b. The number of emerging adults on site 1b (very temporary part of the pool, see Table 16 p 55) was very high. The predicted start of emergence of the second generation was June 6, which again fits well with the observed start of emergence of the second generation between June 9-18 (median = June 14). The peculiarity of 1999 was the lack of a second peak of emergence on sites 2 + 3: though still aquatic only a few individuals emerged during the period of time in which the second peak was expected (see also Appendix 3).

Pool 2: In Pool 2 *Polypedilum tritum* was more abundant only in 1998, a year which was preceded by an unusually long drought period (Figure 20 p 57). Only a few adults emerged during the first spring emergence, the second peak was quite well pronounced (Figure 80 at top). The first emergence took place between May 6-13 (median = May 10) and the predicted start of the second generation was June 20. Indeed the start of the second generation was observed from June 17 to 24 (median = 21), which again shows that it is possible to accurately predict emergence times. The emergence ended between August 18-26 (median = August 22) and it is likely that a second and third generation emerged during the second peak of emergence. Because the species density was much higher in pool 1 (see above), no further conclusions can be drawn from the emergence data of pool 2 in 1998.

Pool 3: 1995 was exceptional for **pool 3**, because the drought started only at the end of June (Figure 21 p 59). Figure 80 (at the bottom) shows that, as in the years before (Appendix 3), only a few adults emerged during the period of first spring emergence. But due to the late date of drought, a second generation was able to develop, which produced a very pronounced second peak of emergence. It is also interesting that during the shrinkage of water in the end of the aquatic phase a strong peak of female emergence occurred.

The very first emergence: Table 53 provides data on the first adults caught in emergence traps from pools 1-3 in 1992-1999. Because the emergence of *Polypedilum tritum* follows an unimodal distribution, the very first emergence can be determined with certainty only when the population

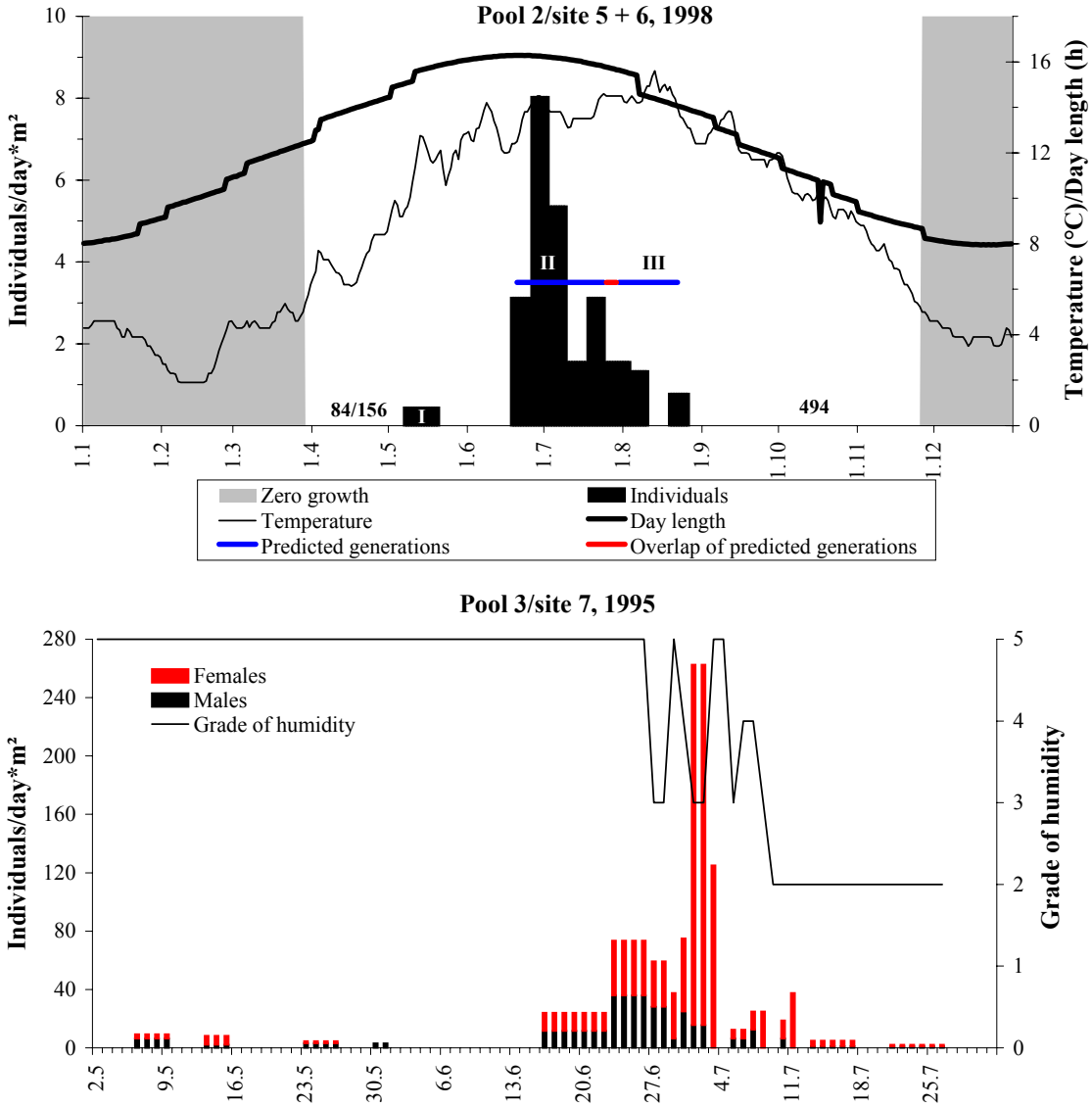

Figure 80: The emergence of *Polypedilum tritum* in pool 2, 1998 and pool 3, 1995.
Grade of humidity see Table 1 p 16; for further explanations see text.

density is high and/or when many traps are exposed. Since 'only' two or three traps per pool were used in the present investigation, only the data from pool 1 (usually high population densities) reliably provide information on the very first emergence. The first individuals emerged from pool 1 always between April 20 and May 3. The time of first emergence seems to be very fixed. The observations made in pools 2 and 3 were not likely to reflect the time of the very first emergence of the populations. The only specimens that are probably adults that emerged first are those collected in pool 3 in 1997. The available daily means of water temperatures (°C) between the sampling intervals of the very first spring emergence were 6.2-8.2; 7.0 (pool 1 1997), 5.3-7.4; 6.1 (pool 3 1997), 8.6-9.8; 9.2 (pool 1, 1998) and 6.0-9.1; 7.2 (pool 1 1999). The length of days during the very first spring emergence ranged from 14 to 15 hours.

Table 53: Time of first trapping* of *Polypedilum tritum* adults in emergence traps from 1992-1999 in pools 1-3.

Year	Pool 1	Pool 2	Pool 3
1992	30.4.-5.5. (2.5.)	-	-
1993	[14.5.-16.5. (15.5.)]	[26.-29.5. (28.5.)]	-
1994	22.-28.4. (25.4.)	6.-19.5. (13.5.)	19.-28.5. (24.5.)
1995	-	-	5.-9.5. (7.5.)
1996	1.-4.5. (3.5.)	-	-
1997	19.-26.4. (23.4.)	3.-10.5. (7.5.)	19-26.4. (23.4.)
1998	22.-30.4. (26.4.)	6.-13.5. (10.5.)	10.-17.6. (14.6.)
1999	16.-24.4. (20.4.)	-	-

Explanations:

* The sampling intervals and the median values between samplings (in parenthesis) are given as time of first trapping. If the median value was represented by two days, only the second day was given (e.g. 1.-4.5. (median value = May 2 and 3, but only May 3 is given);

- square brackets indicate that the emergence study started too late to record the very first emergence;
- sampling intervals which are shadowed indicate that fewer than 10 individuals had been caught in an emergence trap (see Tables 23-25 pp 65-67).

4.4.2.1.2. Limnophyes asquamatus

Limnophyes asquamatus was typical for the aquatic/semiaquatic chironomid community of pool 3 (Tables 22 and 25 pp 64 and 67, respectively). The species density on the sampling sites fluctuated strongly between the years and the sampling sites (Table 25 p 67). High numbers of emerging adults were caught in 1994 and 1996 and to a lower extent on site 7 in 1998. The highest annual crop of emerging adults/m² in pool 3 was 1,931 on site 7 in 1996. The emergence of the species in 1994 was already shown in DETTINGER-KLEMM & BOHLE (1996). Figure 81 illustrates the emergence for the years 1996 and 1998. It was demonstrated in section 4.3.1.1.5. (Figure 40 p 94) that the parthenogenetic ecotype '*aquaticus*' is predominantly aquatic/semiaquatic, whereas the bisexual ecotype '*asquamatus*' prefers wet soils and should be called terrestrial/semiterrestrial.

As shown in section 4.1.1.4.3. (Figure 21 p 59), pool 3 did not refill during winter 1995/96 but substrates within the drainage ditches (sampling sites 7 + 8) remained wet (grade of humidity 3) for more than two months after the beginning of emergence that occurred between April 7 and 16, **1996** (median = April 12) (Figure 81 at top). During this period the drainage ditches were somewhat inundated at the beginning of May, when small puddles (grade of humidity 4) had formed for a few days. In 1996, *Limnophyes asquamatus* emerged in two pronounced peaks. The few specimens of the parthenogenetic ecotype *Limnophyes asquamatus* forma *aquaticus* emerged only within the first peak, all other specimens belonged to the bisexual ecotype *Limnophyes asquamatus* forma *asquamatus*. Towards mid of June, the substrate continued drying up and the emergence of adults ceased when the substrate reached humidity level 2 (see Table 1 p 16).

In **1998** the flooding of pool 3 was restricted to the drainage ditches for the most part of time (section 4.1.1.4.3., Figures 14e and 21 pp 46 and 59, respectively). Specimens of *Limnophyes asquamatus* forma *aquaticus* emerged during the aquatic phase (grade of humidity 5) and while the pool was drying up (Figure 81 at the bottom). The main peak of emergence of *Limnophyes asquamatus* forma *asquamatus* took place during the semiaquatic phase (substrates with humidity of grade 3 and

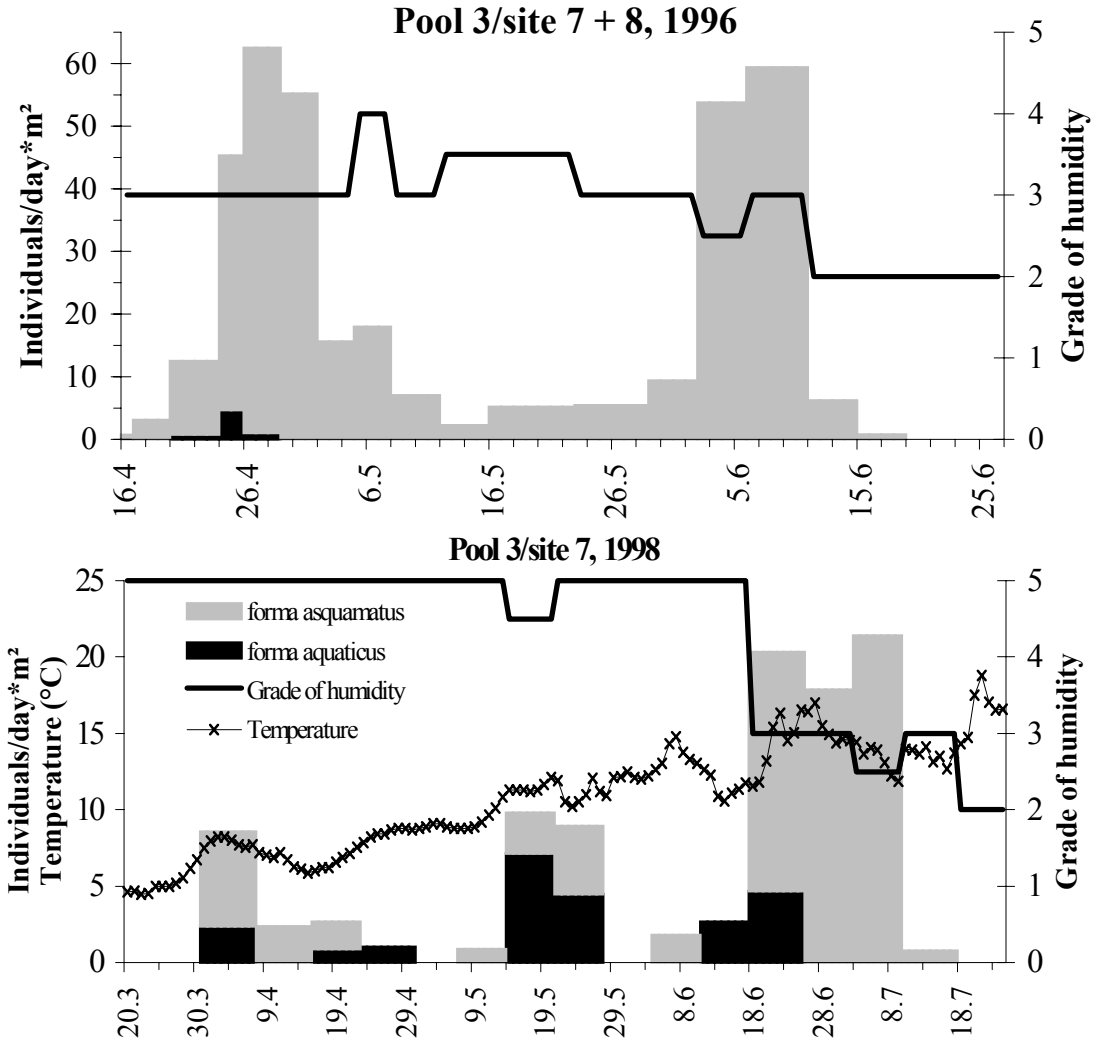

Figure 81: The emergence of *Limnophyes asquamatus* forma *asquamatus* and *Limnophyes asquamatus* forma *aquaticus* from pool 3 in 1996 and 1998.

4) and stopped when the humidity level 2 was reached. There were three emergence peaks in 1998. The parthenogenetic individuals that were lab-reared at 21.5 °C (Figure 64 p 137 and Appendix 8) needed 473 'degree-days' (cumulative daily means of temperatures above 0 °C since the developmental zero is not known) for total development until the first emergence. Assuming that the first female of *Limnophyes asquamatus* forma *aquaticus* laid its eggs on April 3 (first emergence between 30.3.-7.4.), the theoretical start of the second generation can be estimated with the daily means of water temperatures (for single values of water temperature see Appendix 2) at May 26. The data on emergence of *Limnophyes asquamatus* forma *aquaticus* show that there was a gap of emergence between the end of the first peak in April and the start of the second peak on May 17 (sampling interval: 13.-20.5.). The 'second generation' therefore started 10 days earlier than predicted with the available lab data. The 'degree-days' accumulated from the start of the first peak until the start of the second peak, were 370. According to the prediction of the 'second generation', the start of the 'third generation' was estimated following the assumption that the first egg mass of the 'second generation' was laid on May 17. The third generation was therefore expected to start on June 24. The observed start of the 'third generation' was on June 14 (sampling interval: 10-17.6.),

also 10 days earlier than expected, which applies to 340 'degree-days'. Provided three generations of *Limnophyes asquamatus* had indeed emerged from pool 3 in 1998, the 'degree-days' necessary for total development were lower in the natural habitat and the higher values obtained in the laboratory may be attributed to inadequate conditions in the culture vessels (section 3.3.1.1.). In 1998, 1115 'degree-days' had been accumulated from the first emergence on April 3 until the last emergence on July 17. Assuming that two further generations had developed after the first spring emergence, an average of 558 'degree-days' were necessary for total development in the natural habitat (the two lab experiments showed mean values of 578 and 819 'degree-days', see Appendix 8). Table 54 summarizes the above discussion on 'degree-days'.

Table 54: 'Degree-days'* necessary for total development of *Limnophyes asquamatus* calculated after data of the lab rearings and of the emergence study in pool 3, 1998.

Mean water temperatures for development	First emergence	Mean emergence
Lab culture 1 (Box 143): **21.5 °C**,	624	819
Lab culture 2 (Box 144): **21.5 °C**	473	578
First emergence 'generation 2' (April 3 - May 17): **8.3 °C**	370	-
First emergence 'generation 3' (May 18 - June 14): **12.1 °C**	340	-
Mean emergence 'generation 2 + 3' (April 3 - July 13): **10.9 °C**	-	558

* Cumulative daily means of temperatures above 0 °C, since the developmental zero is not known. For further explanations see text.

The very first and last emergence: The first spring trapping of *Limnophyes asquamatus* in an emergence funnel of pools 1-3 from 1994-1998 is listed in Table 55. For interpretations see section 4.4.2.1.1. pp 171-173. The data show that the very first spring emergence of the species occurred from March 27 to April 12. The water temperatures (daily means in °C) during the sampling intervals of the very first spring emergence were: 4.6-7.2; 5.6 (pool 1 1998), 4.6-5.7; 5.0 (pool 2 1998), 5.5-6.9; 6.3 (pool 3 1997) and 6.7-8.2; 7.7 (pool 3 1998). Low substrate humidity levels always stopped the emergence of *Limnophyes asquamatus* during the long drought period of pool 3. Only a few adults emerged from substrates that were humid (humidity level 2, see Figure 40 p 94). The 1993 flood experiment was carried out in the field (see section 4.3.1.1.1., Figures 33 and 41 pp 84 and 95, respectively). The data of this experiment indicate that, in a suitable environment, *Limnophyes asquamatus* can emerge until the end of October.

Table 55: Time of first trapping* of *Limnophyes asquamatus* adults in emergence traps of pools 1-3 from 1994-1998.

Year	Pool 1	Pool 2	Pool 3
1994	22.-28.4. (25.4.)	6.-19.5. (13.5.)	11.3.-11.4. (27.3.)
1996	-	14.-18.6. (16.6.)	7.-16.4. (12.4.)
1997	-	30.5.-5.6. (2.6.)	28.3.-5.4. (1.4.)
1998	23.-30.3. (27.3.)	23.-30.3. (27.3.)	30.3.-7.4. (3.4.)

* For comments see Table 53 p 173.

4.4.2.1.3. *Paralimnophyes hydrophilus*

Paralimnophyes hydrophilus was usually high abundant in pool 1 as well as pool 3 (Tables 23 and 25 pp 65 and 67, respectively) and low abundant in pool 2 (Table 24 p 66). The highest annual crop of emerging adults/m² in pools 1, 2 and 3 was 1,319 for pool 1/site 2 in 1994, 450 for pool 2/site 6 in 1998 and 938 for pool 3/site 8 in 1998, respectively. In pools 1 and 3, the species was only scarce in 1996 (pool 1 and 3) and 1999 (only pool 1) (see section 4.2.1.5.). Greater numbers of *Paralimnophyes hydrophilus* occurred in pool 2 only in 1998 (see section 4.2.1.5.). See DETTINGER-KLEMM & BOHLE (1996) for information on the emergence of *Paralimnophyes hydrophilus* in pool 1 in 1993 and 1994. The emergence from pool 1 in 1997 and 1998 (Figure 82 at top and in the middle), from pool 2 in 1998 (Figure 82 at the bottom) and from pool 3 in 1997 and 1998 (Figure 83) will be analysed in this section following the same method as for *Polypedilum tritum* (section 4.4.2.1.1.). For predictions of emergence dates, a developmental zero of 4.6 °C (Table 41 p 143), 263/493 degree-days for total development until the first/last emergence (Table 42 p 145), the degree-days for the different developmental stages (Table 43 p 147) and the water temperatures measured (Appendix 2) were used. The mean value for the experiments at temperatures of 14.6 -25.0 °C (except the result of box Nr. 73) was used for predictions of the degree-days for total development until the last emergence (Appendix 8).

Pool 1: The degree-days accumulated from the refilling of pool 1 on October 2, **1996** until the period of zero growth (about 200 degree-days) were estimated using the measurements taken in pool 1 in 1998. If some instars I had survived the 1996 drought period (Figure 18 p 53), they must have been able to develop into instars III and partly into instars IV before the period of zero growth. Since the majority of larvae which had survived the drought period in 1996 were likely to be later instars (section 4.4.1.6.1.), the overwintering population must have consisted predominantly of instars IV with some instars III. In **1997**, the first emerging adults were caught in pool 1 during the sampling interval of March 28 to April 5 (median = April 1) (Figure 82 at top). A second, much higher peak of emergence started on May 7 (sampling interval: 3.5.-10.5.) and ended on June 2 (sampling interval 30.5. -5.6.). According to section 4.4.2.1.1., the theoretical emergence of the generations succeeding the first spring generation up to the start of the drought period were calculated: generation 2: May 18 - June 14; generation 3: June 6 - July 16. The predicted start of the second generation was not very accurate (May 18 instead May 7). Nevertheless, the prediction shows that the second peak of emergence must be attributed to generation 2 and that no third generation emerged in 1997. The species must therefore have disappeared or the larvae fell into dormancy. After refilling at the beginning of November, only 46 degree-days were available for development until the end of the year. In **1998**, the spring peak (start: March 27 (23.3.-30.3.); end: April 26 (22.4.-30.4.)) of emergence was again clearly separated from the emergence of the subsequent generations (start on May 10, sampling interval: 6.5.-13.5.) (Figure 82 in the middle). The degree-days available for larval development from the beginning of 1998 until the start and end of the first spring emergence were 85 and 226, respectively. From the beginning of the instar III and IV 260

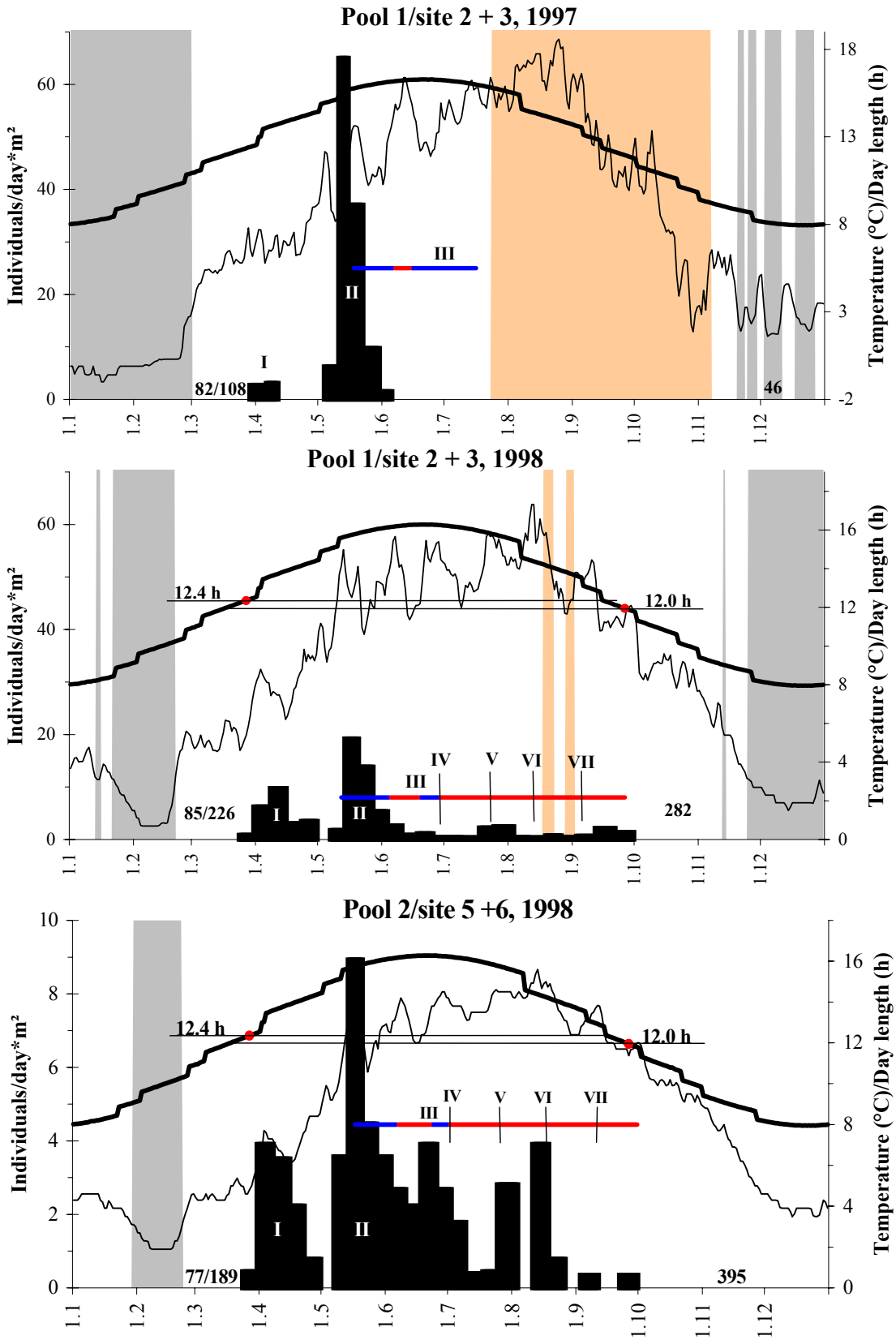

Figure 82: The emergence of *Paralimnophyes hydrophilus* from pools 1 and 2 in 1997 and 1998.
Legend see Figure 83 and explanations see text.

and 190 degree-days, respectively, are necessary until the 50 %-emergence of the adults (Table 43 p 147). The population overwintering in 1997/98 must have therefore consisted predominantly of instars IV as well as to a lower proportion of instars III. The larvae must have therefore fallen into dormancy after second 1997 generation had finished emerging and then aestivated the long and intense drought period (see Figures 18 and 19 pp 53 and 55, respectively) in the dry mud. Predictions for the generations succeeding the first spring generation in 1998 are as follow: generation 2: May 12 - June 18; generation 3: June 5 - August 1; generation 4: June 29 - September 14; generation 5: July 23 - zero growth; generation 6: August 13 - zero growth; generation 7: September 5 - zero growth; generation 8: October 5 - zero growth. The predicted start of the second generation on May 12 matches well the observed start of the second peak. The prediction shows that the second peak was formed by generation 2. In contrast to 1997, a low number of adults emerged between the predicted end of generation 2 and the last emergence on September 26 (sampling interval: 21.9.-30.9.). From a thermal point of view, it is possible that 5 subsequent generations had started to emerge until the end of the emergence in 1998. Because there was always an overlap of predicted generations from generation IV onwards, the predicted starts of the emerging generations IV-VII were indicated in Figure 82 (as well as in Figure 83) by vertical lines intersecting the red horizontal bar of overlapping emergence. After the emergence had stopped, there were still 282 degree-days available for larval growth until the period of zero growth, enough for an egg to develop into instar IV. The overwintering population was therefore likely to consist of only instars IV. The interesting observation in **1999** was, that only one female had emerged and most likely a breakdown of the population had occurred.

Pool 2: The emergence from pool 2 (Figure 82 at the bottom) in 1998 is comparable to that of pool 1 in 1998. In contrast to pool 1 there was no theoretical period of zero growth from the end of the emergence until the end of the year and 395 degree-days were available for development within this period of time. The predicted periods of emergence are as follow: generation 2: May 17 - June 22; generation 3: June 7 - August 8; generation 4: July 2 - September 20; generation 5: July 26 - end of the year; generation 6 August 17 - end of the year; generation 7: September 11 - end of the year; generation 8: October 11 - end of the year. The actual start of generation 2 (6.5.-13.5.) was earlier than predicted. As in pool 1 the thermal conditions could have allowed up to seven generations to emerge.

Pool 3: No member of the first spring generation was trapped in pool 3 in 1997 (Figure 83 at top). It is likely that the preceding drought period of 502 days (Figure 21 p 59) had caused high larval mortalities (section 4.4.1.6.1. Figure 75 p 161) and resulted in unusually low densities in spring 1997. The individuals caught emerging from pool 3 in 1997 must be attributed all to generation 2, which was immediately interrupted by the start of the drought period. It can be concluded from this observation that newly hatched instars I and instars IV were predominant in the mud at the beginning of the drought period. After refilling in the middle of November, 79 degree-days were available for development until the end of the year. About 100 degree-days are necessary for the development of

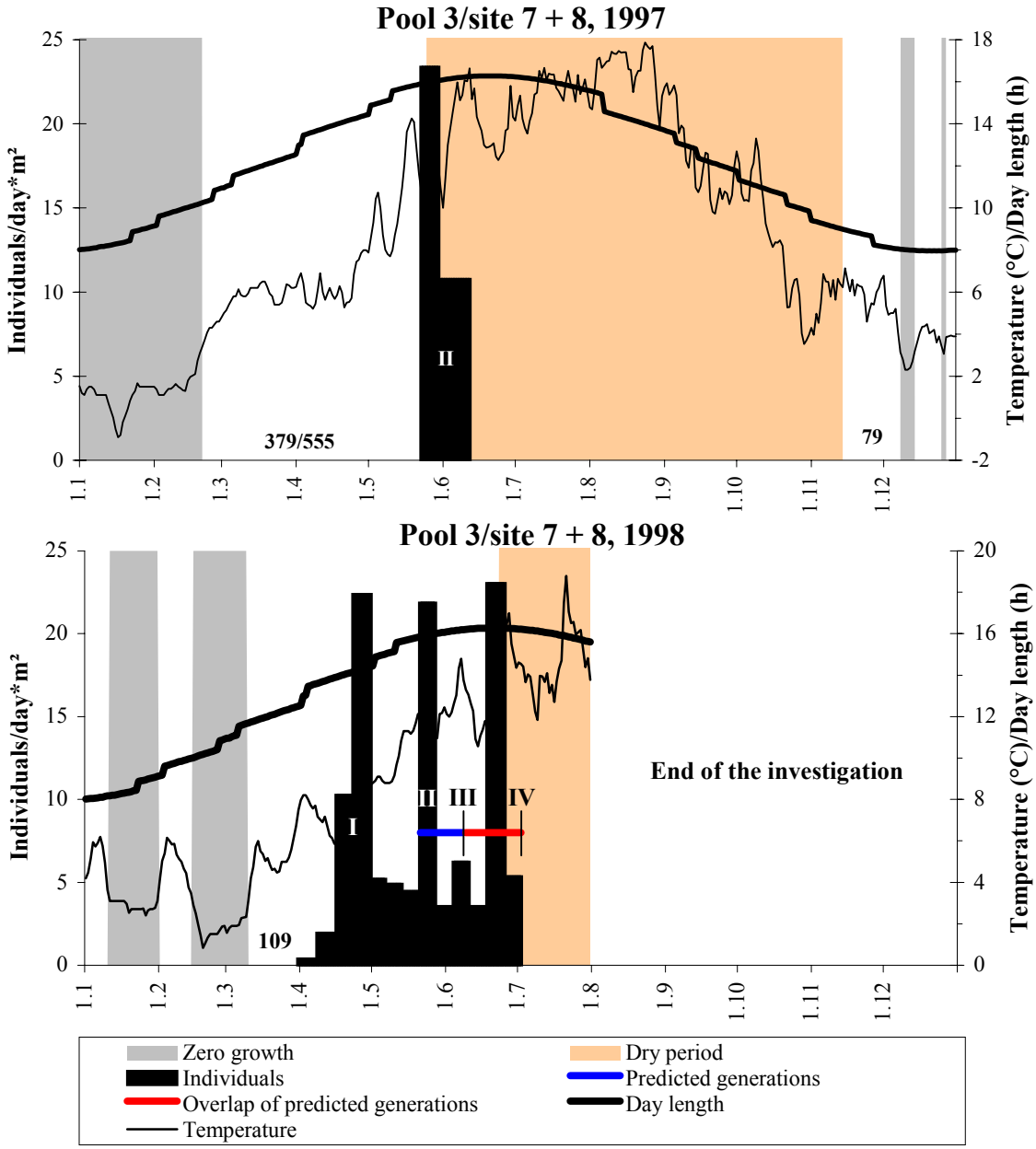

Figure 83: The emergence of *Paralimnophyes hydrophilus* from pool 3 in 1997 and 1998.
For explanations see text.

an instar I into an instar II (Table 43 p 147). The overwintering population of pool 3 in winter 1997/98 probably consisted therefore on the one hand of instars I as well as to an extent of instars II and on the other hand of large instars IV. This assumption is supported by the pattern of emergence in 1998. If early instars II were present at the beginning of the year, they would have needed about 300 degree-days to reach 50 % of their adult emergence (Tables 42 and 43 pp 145 and 147, respectively). Using the measured water temperatures of pool 3, the 50 %-emergence of overwintering instars II was predicted on May 13. The first emergence in 1998 was observed on April 3 (sampling interval 30.3.-7.4.). The start of the emergence of the second generation was predicted on May 21. There is therefore a predicted overlap in the emergence of adults originating from hibernating instars I/early instars II with the adults of the second spring generation. Indeed, and in contrast to the emergence patterns described above, the 1998 emergence patterns show a strong overlap of the first

spring peak with the emergence of the subsequent generation. The thermal conditions could have enabled a third generation to start emerging (predicted start of generation 3 is June 9). However, the emergence had ceased by the start of the drought period and all instars were probably present within the drying mud.

Low emergence following generation 2: The range and mean values of daily mean water temperatures for the periods of emergence previously described are listed in Table 56. Temperatures ≤ 20 °C are supposed to be favourable to the development of *Paralimnophyes hydrophilus* (section 4.4.1.2.8.) and therefore temperatures do not explain the low emergence observed after the end of the second spring generation.

Table 56: Mean ambient temperatures of daily means for different periods of emergence of *Paralimnophyes hydrophilus* in pools 1-3 (see Figures 82 and 83 and text).

Pool	Year	Time span	Temperature (°C)
1	1997	Generation 1 (29.3.-11.4.)	5.8-7.7; 6.8
		Generation 2 (4.5.-5.6.)	8.2-13.6; 11.3
		6.6.-23.7.	11.9-16.4; 14.4
	1998	Generation 1 (24.3.-30.4.)	4.6-9.8; 7.7
		Generation 2 (7.5.-18.6.)	9.9-15.7; 12.9
		Subsequent (19.6.-30.9.)	10.8-17.3; 13.7
2	1998	Generation 1 (24.3.-30.4.)	4.6-8.5; 6.8
		Generation 2 (7.5.-18.6.)	9.5-14.2; 12.2
		Subsequent (19.6.-30.9.)	11.4-15.6; 13.5
3	1997	Generation 2 (23.5.-12.6.)	10.0-16.6; 12.9
	1998	Generation 1 (31.3.-13.5.)	5.9-10.8; 8.0
		Generation 2 (21.5.-2.7.)	10.2-17.0; 13.0

Explanations:

- The temperature is provided in the min.-max.; mean standard of daily mean water temperatures;
- Subsequent = time span of emergence from the end of the second generation until the end of emergence.

The very first and last emergence: The dates of the very first spring emergence of *Paralimnophyes hydrophilus* from pools 1-3 during the present investigation are listed in Table 57. For interpretation of the dates see comments in section 4.4.2.1.1. pp 171-173. The data show that the first spring emergence of *Paralimnophyes hydrophilus* occurred between the end of March and the start of April (27.3.-3.4.). The water temperatures (°C) within the sampling intervals of the first spring emergence were: 5.8-7.8; 7.0 (pool 1 1997), 4.6-7.2; 5.6 (pool 1 1998), 4.6-5.7; 5.0 (pool 2 1998) and 6.7-8.2; 7.7 (pool 3 1998). The emergence was usually finished by the start of the drought period, except in pool 1 and 2 in 1998, when the last emergence was observed within the sampling interval of September 21-30 at water temperatures (°C) of 11.0-12.1; 11.6 (pool 1) and 11.4-12.0; 11.7 (pool 2) and day lengths of about 12.0 hours (Figure 82). As shown in Figure 1e in DETTINGER-KLEMM & BOHLE (1996), the emergence of *Paralimnophyes hydrophilus* from a flood experiment (see also section 4.3.1.1.1.) ended within the sampling interval of October 7-14 at day lengths of about 11.0 hours. Mean ambient temperatures of 11.0-12.0 °C did not stop larval growth (Figure 60 p 130) and the development into an adult (Figure 62 p 134). It is therefore possible that day lengths below a threshold, which may lie between 11.0 and 12.4 hours, stop development into

an adult.

Table 57: Time of first trapping* of *Paralimnophyes hydrophilus* adults in emergence traps from 1994-1999 in pools 1-3.

Year	Pool 1	Pool 2	Pool 3
1994	11.3. - 11.4. (27.3.)	11.3. - 11.4. (27.3.)	11.3. - 11.4. (27.3.)
1996	19. - 23.4. (21.4.)	5. - 10.6. (8.6.)	16. - 19.4. (18.4.)
1997	28.3. - 5.4. (1.4.)	10. - 15.5. (13.5.)	22. - 30.5. (26.5.)
1998	23. - 30.3. (27.3.)	23. - 30.3. (27.3.)	30.3. - 7.4. (3.4.)
1999	7. - 19.5. (13.5.)	-	-

* for comments see Table 53.

4.4.2.2. The adult body size in the natural habitat

4.4.2.2.1. *Polypedilum tritum*

Table 58: Overview of the material used for measurements of the adult body size of *Polypedilum tritum*.

Year	Generation 1		Generation 2		Generation 3	
	Date	♂♂,♀♀	Date	♂♂,♀♀	Date	♂♂,♀♀
1998	6.5.	10,10	10.6.	10,0	24.7.	2,2
	13.5.	7,7	17.6.	10,4	3.8.	2,2
	20.5.	4,1	25.6.	10,10	10.8.	2,2
			2.7.	9,9	18.8.	3,3
			9.7.	3,3	26.8.	2,0
			17.7.	3,3	11.9.	8,8
					21.9.	0,1
Range (mm)	♂♂: 0.889-1.087; 1.012		♂♂: 0.716-0.939; 0.834		♂♂: 0.642-0.815; 0.735	
	♀♀: 0.889-1.136; 1.032		♀♀: 0.667-0.889; 0.796		♀♀: 0.543-0.766; 0.698	
U-test	U = 159; p = 0.391		U = 413; p = 0.007		U = 113; p = 0.073	
1999	7.5.	10,10	25.6.	1,0		
	19.5.	10,10	1.7.	1,2		
	27.5.	1,2	8.7.	0,1		
			1.8.	4,0		
Range (mm)	♂♂: 0.914-1.013; 0.956		♂♂: 0.741-0.865; 0.799			
	♀♀: 0.840-1.062; 0.928		♀♀: 0.716-0.815; 0.774			
U-test	U = 196; p = 0.055		U = 7; p = 0.606			

Abbreviations:
Date = date of inspections; ♂♂,♀♀ = number of males,females measured; **Range** = min-max; mean of male and female thorax length; **U-test** = MANN-WHITNEY-U-test for differences of male and female thorax lengths.

The adult body size of *Polypedilum tritum* in the field was documented for the population of pool 1 in 1998 and 1999. Table 58 provides an overview of the material studied. The specimens were attributed to the different generations following the descriptions of section 4.4.2.1.1.. As in the lab experiments (Figure 68 p 150), there were no significant differences in the male and female thorax lengths, except in generation 2, 1998 when female thoraxes were somewhat smaller than that of males. For each generation, the mean water temperature during larval growth was usually calculated from the median value (time) of the emergence of the preceding generation until the median (time) of the generation concerned. The time spans of development and mean values of corresponding water temperatures are the following:

Generation 1, 1998: (a) predicted start of generation 3 (14.7.) until start of drought period

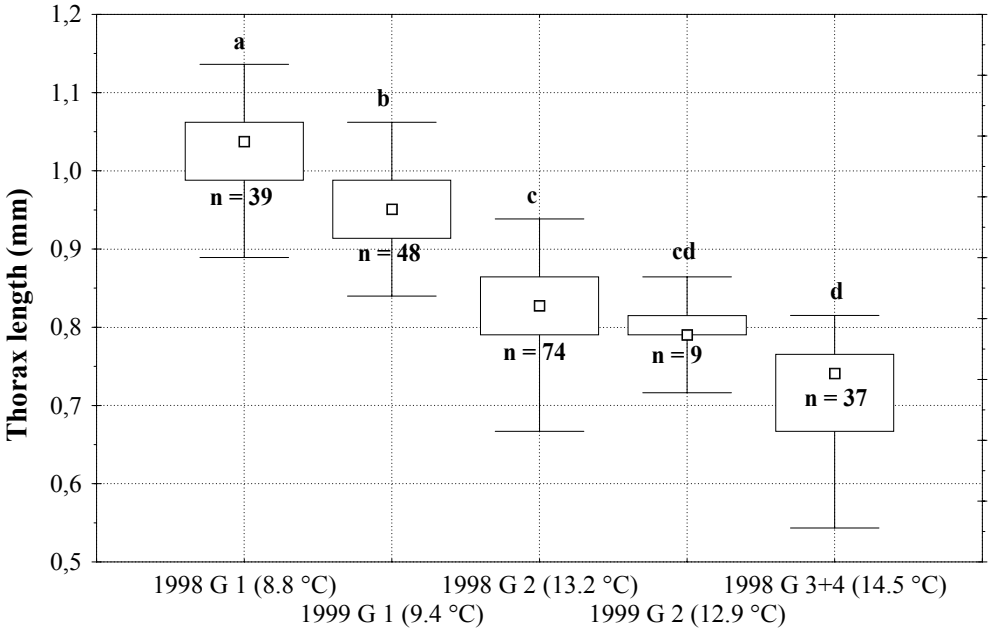

Figure 84: Size characteristics of *Polypedilum tritum* adults in pool 1 in 1998 and 1999.
Abbreviations and explanations:
G1,2,3 = generation 1, 2 and 3 in 1998 and 1999, respectively, with mean ambient temperatures for larval development in brackets (see text);
The different letters above the box-plots mark highly significant differences in size (TUKEY'S honest significant difference test for unequal N, see Table 59.

(24.7.1997); (b) refilling (7.11.) until zero growth (18.11.); (c) end of zero growth (~16.3.) until median generation 1 (7.5.1998): **8.8 °C**;

Generation 2, 1998: median generation 1 (7.5.) until median generation 2 (29.6.1998): **13.2 °C**;

Generation 3, 1998: median generation 2 (29.6.) until median generation 3 (17.8.1998): **14.5 °C**;

Generation 1, 1999: (a) median generation 3, 1998 (17.8.) until period of zero growth (17.11.); (b) end of zero growth in 1999 (25.3.) until median generation 1 (10.5.): **9.4 °C**;

Generation 2, 1999: median generation 1 (10.5.) until median generation 2 (4.7.1999): **12.9 °C**.

In Figure 84, a comparison of the adult body size of the different generations from 1998-1999 was done, a comparison with the results of the laboratory experiments can be taken from Table 59. All size differences, except those between generations 2 in 1998 and 1999, were highly significant. The first spring generation in 1998 and 1999 generated the largest specimens. In 1999 the adults of the first spring generation were smaller than in 1998. The size of specimens of the second generations lay between those of generation 1 in 1998 and 1999 and generation 3 in 1998. A correlation of the body size in relation to the mean ambient temperatures during larval development was negative and highly significant (GOODMAN-KRUSKAL'S γ: $\gamma = -0.879$, $Z = -16.3$, $p < 0.001$), which corresponds with the results obtained in the laboratory. The comparison of Table 59 shows that:

(a) the first generation in 1998 was equal in size to the specimens that had emerged from the 14.1 °C SD-experiment

Table 59: Comparison of the adult body size (thorax length) of *Polypedilum tritum* emerging in the experiments on photoperiod and temperature (section 4.4.1.2.9. Figure 68b p 150) and in pool 1 in 1998 and 1999 (Figure 84).

	14.1 °C SD	9.8 °C	14.6 °C	19.2 °C	25.0 °C	29.0 °C	30.2 °C	F 1998	F 1999	S 1998	S 1999	T 1998
14.1 °C SD	**1005 ± 42 N = 20**	0.047	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	**0.999**	0.012	< 0.001	<0 .001	< 0.001
9.8 °C		**950 ± 53 N = 20**	0.001	0.002	< 0.001	< 0.001	< 0.001	0.002	**1.000**	< 0.001	< 0.001	< 0.001
14.6 °C			**877 ± 79 N = 20**	**1.000**	< 0.001	< 0.001	0.034	< 0.001	0.006	0.030	0.030	< 0.001
19.2 °C				**879 ± 46 N = 20**	< 0.001	< 0.001	0.025	< 0.001	0.010	0.018	0.022	< 0.001
25.0 °C					**782 ± 44; N = 20**	**1.000**	**1.000**	< 0.001	< 0.001	**0.559**	**1.000**	0.007
29.0 °C						**773 ± 56 N = 16**	**1.000**	< 0.001	< 0.001	**0.408**	**1.000**	**0.113**
30.2 °C							**780 ± 24 N = 7**	< 0.001	< 0.001	**0.970**	**1.000**	**0.551**
F 1998								**1021 ± 56 N = 39**	< 0.001	< 0.001	< 0.001	< 0.001
F 1999									**943 ± 50 N = 48**	< 0.001	< 0.001	< 0.001
S 1998										**819 ± 54 N = 74**	**0.993**	< 0.001
S 1999											**790 ± 43 N = 9**	**0.137**
T 1998												**717 ± 58 N = 37**

Abbreviations and explanations:

- Abbreviations: SD = short day, F = first generation, S = second generation, T = third generation.
- The mean thorax length ± standard deviation and N are highlighted in bold black, non-significant differences in bold grey. TUKEY'S honest significant difference test for unequal N was used for the multiple comparisons.
- LEVENE'S test for homoscedasticity: F = 1.8, df = 9.32, p = 0.064.
- ANOVA result for all effects: F = 121.7, df = 9, p < 0.001.

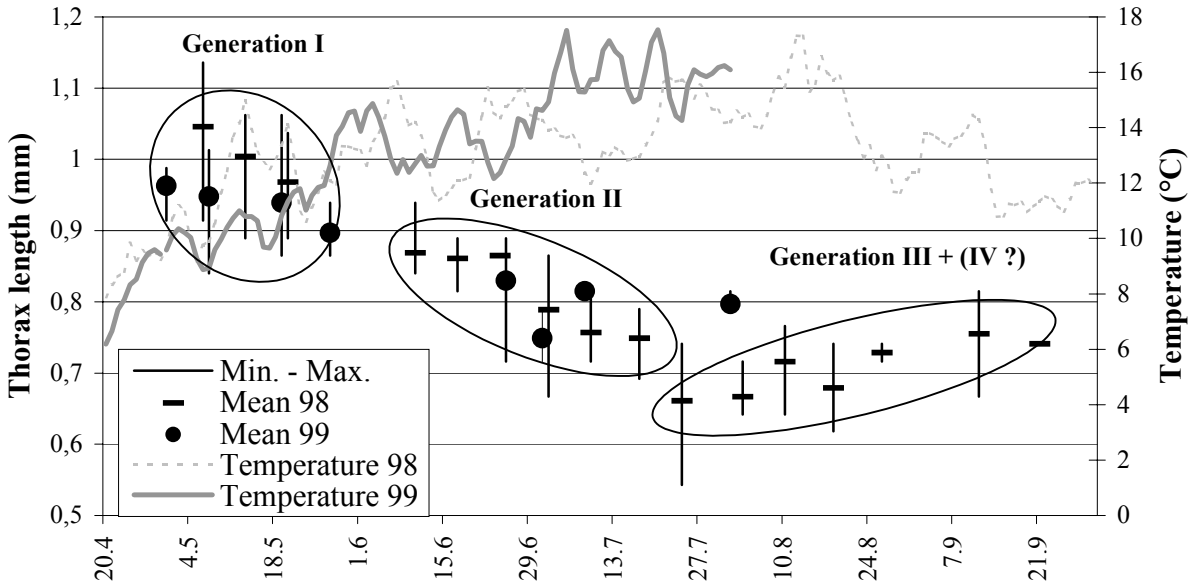

Figure 85: The adult body size of *Polypedilum tritum* at different sampling dates from pool 1 in 1998 and 1999.
For explanations see text.

(b) the specimens of the first spring generation in 1999 were equal in size to the individuals of the 9.5 °C LD-experiment;

(c) the individuals of generation 2 were smaller than those of the 14.6 °C LD- and 19.3 °C LD-experiments and equal in size to the individuals that had emerged from the 25.0 °C LD- and 30.2 °C LD-experiment; and

(d) the specimens of generation 3 were significantly smaller than the individuals from the 25.0 °C LD-experiment and no differences were found with the experiments at 29 °C LD and 30.2 °C LD.

The comparison with the results of the lab experiments clearly shows that the small size of individuals emerging from pool 1 during generations 2 and 3 was not only caused by temperature. Other, most likely temperature-dependent factors must have primarily influenced the body size of the second and especially third generation.

Figure 85 shows the minimum, maximum and mean values of body size during the different sampling intervals of the emergence study in 1998 and 1999. The body size of the first 1998 and 1999 generations and of the second 1998 generation decreased significantly as the emergence period lengthened (correlation of body size with time after the start of the emergence period (GOODMAN-KRUSKAL's-γ): generation 1, 1998: $\gamma = -0.63$, $Z = -4.17$, $p < 0.001$, $n = 39$; generation 2, 1998: $\gamma = -0.77$, $Z = -8.36$, $p < 0.001$, $n = 74$; generation 1, 1999: $\gamma = -0.29$, $Z = 2.19$, $p = 0.028$, $n = 48$). No significant correlation was obtained for the second 1999 generation ($\gamma = 0.43$, $Z = 0.13$, $p = 0.890$, $n = 9$) and the body size of generation 3 in 1998 significantly increased with time ($\gamma = 0.59$, $Z = 4.26$, $p < 0.001$, $N = 37$). From the end of April (~9.5 °C) to August 13, 1998 the daily means of water temperature showed a tendency to increase and from mid of August onwards to decrease. The data

presented by Figure 85 indicate again, that temperature and/or temperature-dependent factors (as oxygen) strongly influenced the adult body size of *Polypedilum tritum* in its natural habitat.

4.4.2.2.2. *Paralimnophyes hydrophilus*

Table 60: Overview of the material used for measurements of the adult body size of *Paralimnophyes hydrophilus*.

Year	Generation 1		Generation 2		'Generation 3 -7'	
	Date	♂♂,♀♀	**Date**	♂♂,♀♀	**Date**	♂♂,♀♀
1997	5.4.	6,1	10.5.	10,3		
	11.4.	2,4	15.5.	10,10		
			22.5.	10,10		
			30.5.	7,10		
			5.6.	1,2		
Range (mm)	♂♂: 0.766-0.889; 0.824		♂♂: 0.593-0.741; 0.662			
	♀♀: 0.790-0.865; 0.830		♀♀: 0.494-0.716; 0.608			
U-test	U = 18; p = 0.770		U = 295; p < 0.001			
1998	30.3.	1,1	13.5.	4,0	17.6.	1,1
	7.4.	7,9	20.5.	10,10	25.6.	2,1
	15.4.	10,10	27.5.	10,10	2.7.	1,0
	22.4.	2,5	3.6.	5,7	9.7.	0,1
	30.4.	2,7	10.6.	4,2	17.7.	1,0
					24.7.	4,1
					3.8.	6,2
					10.8.	1,0
					18.8.	0,1
					26.8.	1,1
					2.9.	1,0
					11.9.	2,0
					21.9.	6,1
					30.9.	2,2
Range (mm)	♂♂: 0.741-0.889; 0.835		♂♂: 0.494-0.716 0.615		♂♂: 0.519-0.692; 0.601	
	♀♀: 0.692-0.865; 0.773		♀♀: 0.494-0.642; 0.559		♀♀: 0.519-0.618; 0.559	
U-test	U = 102; p < 0.001		U = 104; p < 0.001		U = 78; p = 0.016	

Abbreviations:
Date = date of inspections; ♂♂, ♀♀ = number of males, females measured; **Range** = min-max; mean of male and female thorax length; **U-test** = MANN-WHITNEY-U-test for differences of male and female thorax lengths.

The adult body size of *Paralimnophyes hydrophilus* in pool 1 was documented in 1997 and 1998. As shown in section 4.4.2.1.3., the individuals were attributed to generation 1 and 2 or to the theoretical 'generations 3-7' (Table 60). Except in generation 1, 1997 the females' thorax lengths were significantly shorter by 7-9 % than those of males. This tendency also appeared in the lab experiments but had not been significant (Figure 68 at the bottom p 150). As in *Polypedilum tritum* (section 4.4.2.2.1.), the mean water temperatures for development were estimated for each generation and were the following:

Generation 1, 1997 (until the start of temperature recordings on November 25, 1996, the water temperatures were estimated using measurements done in 1998)**:** (a) estimated start of generation 4 (~ 13.7.) up to the start of the drought period (22.7.1996); (b) refilling (1.10.1996) up to the end of the year (except periods with zero growth); (c) end of zero growth in 1997 (1.3.) until median generation 1 (4.4.1997): **7.5 °C**;

Generation 2, 1997: median generation 1 (4.4.) until median generation 2 (20.5.1997): **8.8. °C**;

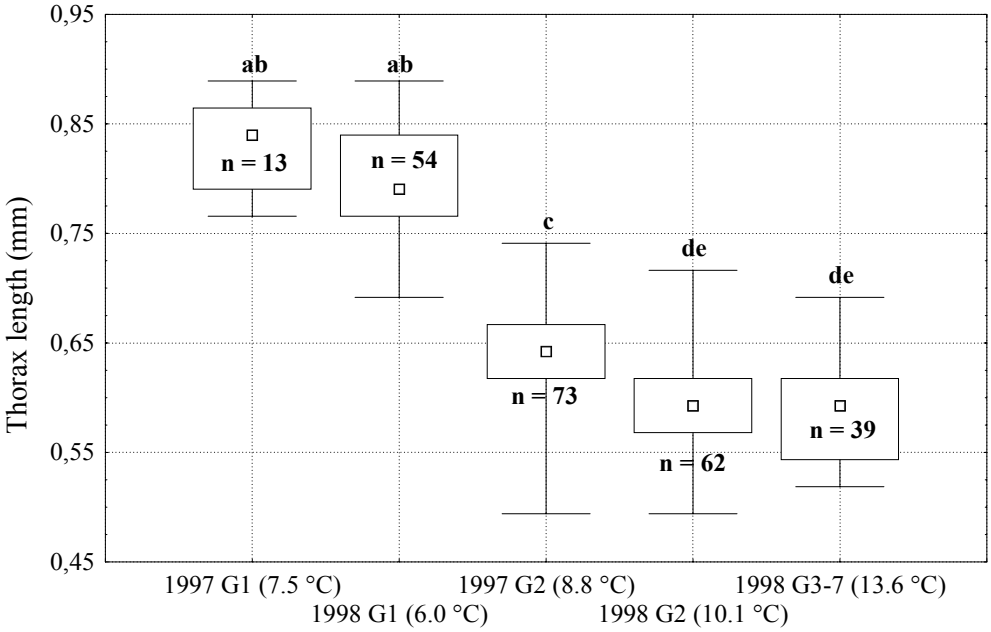

Figure 86: Size characteristics of *Paralimnophyes hydrophilus* adults in pool 1 in 1997 and 1998.
Abbreviations and explanations:
G1,2,3-7 = generation 1, 2 and '3 - 7' in 1997 and 1998, respectively, with mean ambient temperatures for larval development in brackets.
The different letters above the box-plots mark highly significant differences in size (TUKEY'S honest significant difference test for unequal N, see Table 61).

Generation 1, 1998: (a) median generation 2 (20.5.) up to the start of the drought period (11.7.1997); (b) refilling (6.11.1997) up to the end of the year (except periods with zero growth); (c) beginning of 1998 until median generation 1 (9.4.) (except periods with zero growth): **7.9 °C**;

Generation 2, 1998: median generation 1 (9.4.) until median generation 2 (24.5.): **10.1 °C**;

'Generation 3-7', 1998: median generation 2 (24.5.) until last emergence (30.9.): **13.6 °C**.

Individuals of generation 1 in 1997 and 1998 were of similar size. Individuals of generation 2, 1998 and those of 'generations 3-7', 1998 were also of similar size (Figure 86). On average, the specimens that had emerged within the first spring peak were 23-26 % larger than the individuals of the corresponding generation 2. Members of generation 2, 1997 were somewhat larger than those of generation 2, 1998. A correlation of mean ambient temperatures in relation to body size was highly significant (GOODMAN-KRUSKAL'S-γ: $\gamma = -0.75$, $Z = -14.82$, $p < 0.001$). The comparison of the adult body size in the natural habitat with the laboratory experiments (Table 61) shows that:

(a) the individuals of generations 1 in 1997 and 1998 were equal in size to the specimens reared at 4.6 °C LD;

(b) the individuals of generation 2, 1997 were significantly smaller than those reared at 4.6-14.6 °C and individuals of generation 2, 1998 were significantly smaller than those reared at 4.6-19.2 °C. The same applies to 'generation 3-7', 1998 in relation to the individuals reared at 4.6-19.2 °C; and

Table 61: Comparison of the adult body size (thorax length) of *Paralimnophyes hydrophilus* (males and females in identical proportions) emerging in the experiments on temperature (section 4.4.1.2.9. Figure 68c p 150) and in pool 1 in 1997 and 1998 (Figure 86).

	4.6 °C	9.8 °C	14.6 °C	19.2 °C	25.0 °C	F 1997	F 1998	S 1997	S 1998	T 1998
4.6 °C	**832 ± 38 N = 3**	0.021	0.038	0.002	< 0.001	**1.000**	**0.998**	< 0.001	< 0.001	< 0.001
9.8 °C		**699 ± 46 N = 21**	**0.100**	**0.934**	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
14.6 °C			**706 ± 31 N = 19**	**0.745**	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
19.2 °C				**674 ± 33 N = 14**	0.002	< 0.001	< 0.001	**0.530**	< 0.001	< 0.001
25.0 °C					**602 ± 39 N = 17**	< 0.001	< 0.001	**0.491**	**0.999**	**0.999**
F 1997						**827 ± 39 N = 13**	**0.892**	< 0.001	< 0.001	0.001
F 1998							**799 ± 51 n = 54**	< 0.001	< 0.001	< 0.001
S 1997								**636 ± 55 n = 73**	< 0.001	< 0.001
S 1998									**588 ± 49 n = 62**	**1.000**
T 1998										**589 ± 48 N = 39**

Abbreviations and explanations:

- Abbreviations: F = first generation, S = second generation, T = third – seventh (?) generation (see text).
- The mean thorax length ± standard deviation and N are highlighted in bold black, non-significant differences in bold grey. TUKEY'S honest significant difference test for unequal N was used for the multiple comparisons.
- LEVENE'S test for homoscedasticity: F = 1.4, df = 9.31, p = 0.170.
- ANOVA result for all effects: F = 107.0, df = 9, p < 0.001.

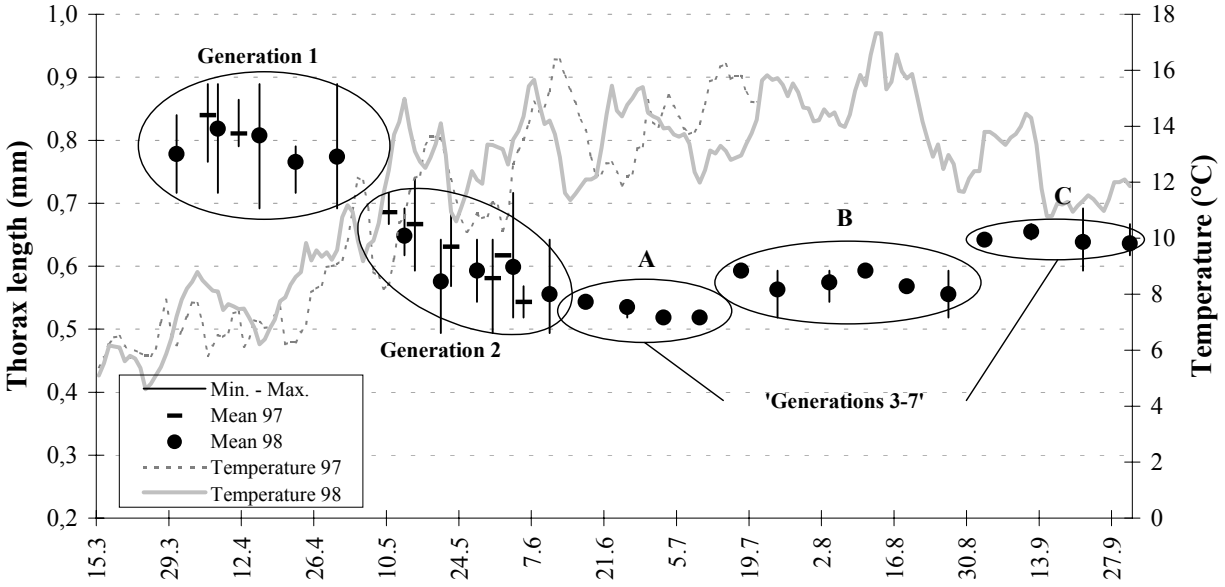

Figure 87: The adult body size of *Paralimnophyes hydrophilus* at different sampling dates from pool 1 in 1998 and 1999.
For further explanations see text and Table 62.

(c) the specimens that had emerged at 25.0 °C (suboptimal temperature for total development, see section 4.4.1.2.8) were the same size as those of generation 2, 1997, generation 2, 1998 and 'generation 3-7, 1998'.

This comparison indicates that the small size of adults belonging to generation 2 and to any of the subsequent generations, can only partly be attributed to temperature. The strong correlation between body size and temperature was probably eclipsed by at least one temperature-dependant factor.

Figure 87 shows the range and mean values of body size of individual samplings in 1997 and 1998. There was a significant decrease of the adult body size with time of emergence within the first generation of 1998 and the second generation of 1997 (GOODMAN KRUSKAL'S-γ: generation 1, 1998: $\gamma = -0.33$, $Z = -2.85$, $p = 0.004$; generation 2, 1997: $\gamma = -0.76$, $Z = -7.95$, $p < 0.001$). No significant decrease of the adult body size in correlation with time of emergence was observed in generation 1, 1997 and generation 2, 1998 (GOODMAN KRUSKAL's-γ: generation 1, 1997: $\gamma = -0.47$, $Z = -1.63$, $p = 0.104$; generation 2, 1998: $\gamma = -0.13$, $Z = -1.23$, $p = 0.220$). Within 'generations 3-7' there was a significant increase of body size with ongoing duration of emergence (GOODMAN KRUSKAL'S-γ: 'generations 3-7', 1998: $\gamma = 0.70$, $Z = 5.59$, $p < 0.001$). The increase of body size was however not continuous and showed two distinct jumps, which significantly separated three groups of different

Table 62: Multiple comparisons of the thorax lengths of groups A-C and generation 2, 1998 (see Figure 87).

	A	B	C
Generation 2, 1998	$U = 54$, $p_{new} = 0.007$	$U = 405$, $p_{new} = 0.467$	$U = 141$, $p_{new} < 0.001$
A		$U = 15$, $p_{new} = 0.022$	$U = 0$, $p_{new} = 0.002$
B			$U = 8$, $p_{new} = 0.001$

KRUSKAL-WALLIS-test: H (df = 3, N = 101) = 33.0; $p < 0.001$.
All p-values obtained by the MANN-WHITNEY-U-test were adjusted (p_{new}) according to the STANDARD-BONFERRONI-technique (k = 6).

sizes (circled groups A-C within 'generations 3-7' in Figure 87, the statistical values are provided in Table 62). Whether these three groups represent different generations is debatable.

The increase in water temperatures was strong and more or less linear from March 15 (~5 °C) to June 15 (~15 °C), 1997 and 1998 (SPEARMAN'S-ρ: 1997: $\rho = 0.912$, $t = 21.2$, $p < 0.001$; 1998: $\rho = 0.906$, $t = 20.4$, $p < 0.001$). This period of time corresponds approximately with the emergence of generations 1 and 2 (Figure 82 p 177 and Figure 87 p 188). The increase in water temperatures was then low but still significant (1997: $\rho = 0.767$, $t = 6.97$, $p < 0.001$; 1998: $\rho = 0.516$, $t = 4.6$, $p < 0.001$) from June 15 to August 15, which corresponds approximately with the emergence of groups A and B within 'generations 3-7' in 1998 (Figure 87). Finally, temperature decreased significantly from August 15 to September 30, 1998 ($\rho = -0.689$, $t = -6.3$, $p < 0.,001$), which coincides approximately with the emergence of group C. The adult body size of *Paralimnophyes hydrophilus* therefore presented a reciprocal and altered relationship with water temperatures of pool 1. The only exception was group B in 1998, which included somewhat larger adults than group A while the average temperatures were still rising until mid of August.

4.4.2.3. Analysis of the field experiments for Chironomus dorsalis

4.4.2.3.1. The emergence pattern

The experimental boxes had been exposed in the evening of May 19, 1998 (see section 3.2.). Data loggers recorded the water temperatures in box 2 and 4 (Figure 23 p 61). *Chironomus dorsalis* has a developmental zero of 4.6 °C (Table 41 p 143) and needs at least 240 degree-days for total development until the first- and on the average 400 degree-days until the last emergence (Table 42 p 145 and Figure 72 p 157). These data were used to estimate (a) the period of the first colonization of an experimental box by egg-laying females; and (b) the number of successive generations that were theoretically able to develop during the experiment.

The first emergence in box 2 occurred between June 11 and 17 (Figure 88 at top). When considering the degree-days necessary for total development until first emergence, it is likely that box 2 was first colonized by *Chironomus dorsalis* females between May 21 and 26. The shade conditions were the similar for boxes 1, 2 and 3. The first colonization of box 3 must therefore also have occurred between May 21 and 26 and between May 27 and June 4 for box 1 (Figure 88 2nd from top). The first emergence from experimental box 4 also occurred between June 11 and 17 (Figure 88 3rd from top). The box was however not shaded by the surrounding vegetation and was therefore subjected to greater daily amplitudes- and higher daily means of temperature (Figure 23 p 61). The first colonization by egg-laying females was therefore predicted later between May 26 and 30. The exposure of experimental boxes 7-10 was similar to that of box 4 (boxes 5 and 6 were not considered, see section 4.2.2.3.). The first colonization by egg-laying females of boxes 7, 9, and 10 was therefore probably between May 26 and 30 too and that of box 8 between May 31 and June 6 (Figure 88 at the bottom).

Assuming the first egg masses were laid on May 24 (Box 2) and 28 (Box 4), its first and last adult

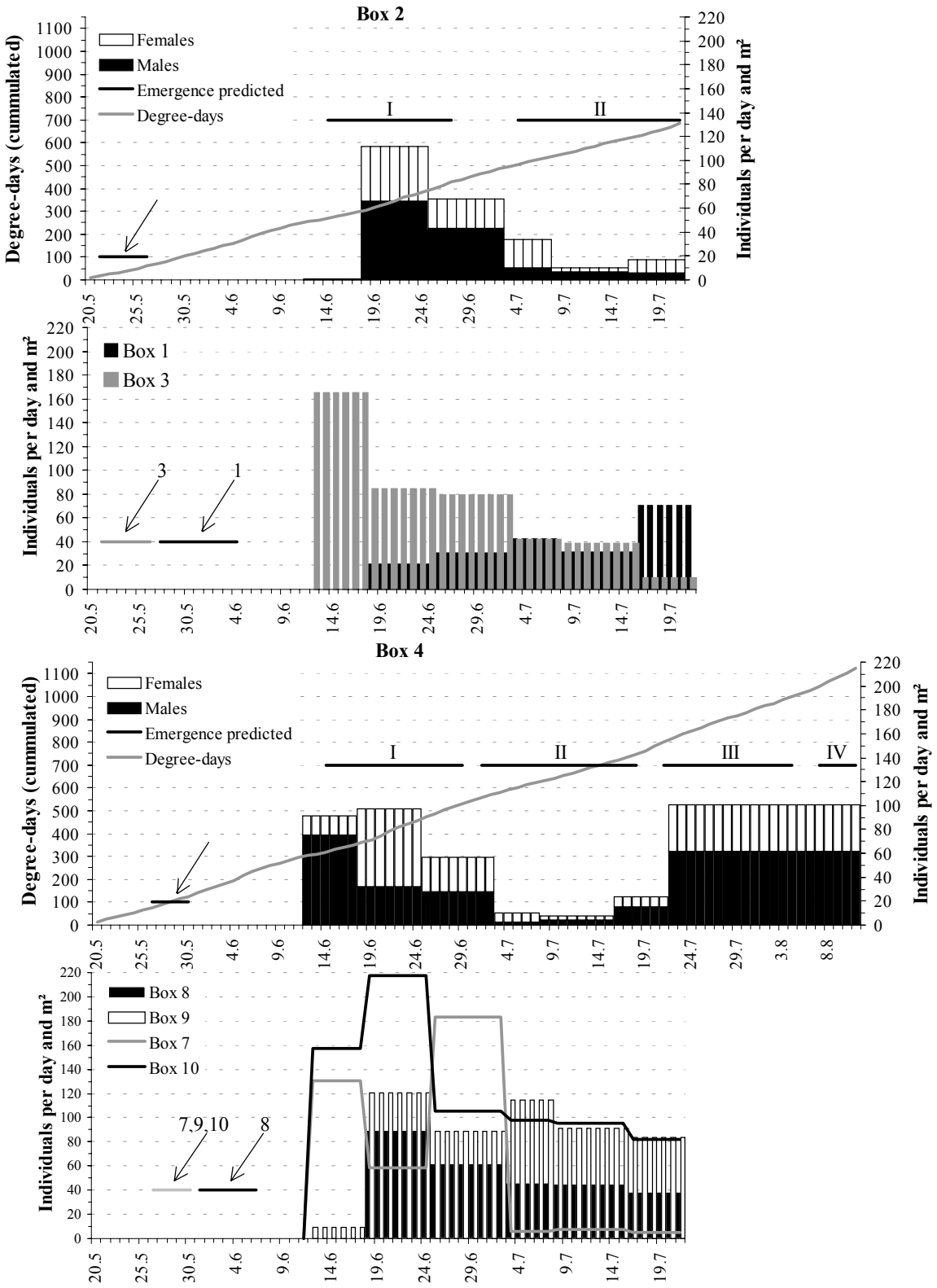

Figure 88: The emergence of *Chironomus dorsalis* from the experimental boxes of the colonizing experiment 1998.

Explanations:

degree-days = cumulative degree-days (for further information see section 4.4.1.2.8.);
emergence predicted = the theoretical periods of generations I - IV (see text);
the **arrows** point to the estimated periods of first colonization by egg-laying females (horizontal bars) of the corresponding experimental box(es) (number(s) above the arrows);
for further explanations see text.

emergences can be calculated with the water temperatures and the degree-days necessary for total development (= 'generation 1' referred to as I in Figure 88). The same prediction was done for the theoretical subsequent generations (referred to as II-IV in Figure 88), assuming an egg mass was laid on the date of the first emergence observed and on the date of the first emergence of the theoretical generations 2 and 3. Two generations were theoretically able to develop in box 2 before the end of the experiment on July 21, and three generations could have developed in box 4, which remained exposed until August 11. The predicted periods were the following:

box 2: generation 1: 14.6.-29.6.; generation 2: 4.7. - end of the experiment

box 4: generation 1: 14.6.-29.6.; generation 2: 1.7.-18.7.; generation 3: 21.7.-18.7.; generation 4: 7.8. - end of the experiment.

The predicted generations following the first peak of emergence do not fit at all with the emergence pattern observed. It is thus likely that the majority of females did not lay their egg masses in the box from which they had emerged.

4.4.2.3.2. The adult body size

MCLACHLAN (1983) showed that the female body size of *Chironomus imicola* was positively correlated with time of emergence at 'low' larval densities (10,000 eggs per m²). When larval densities

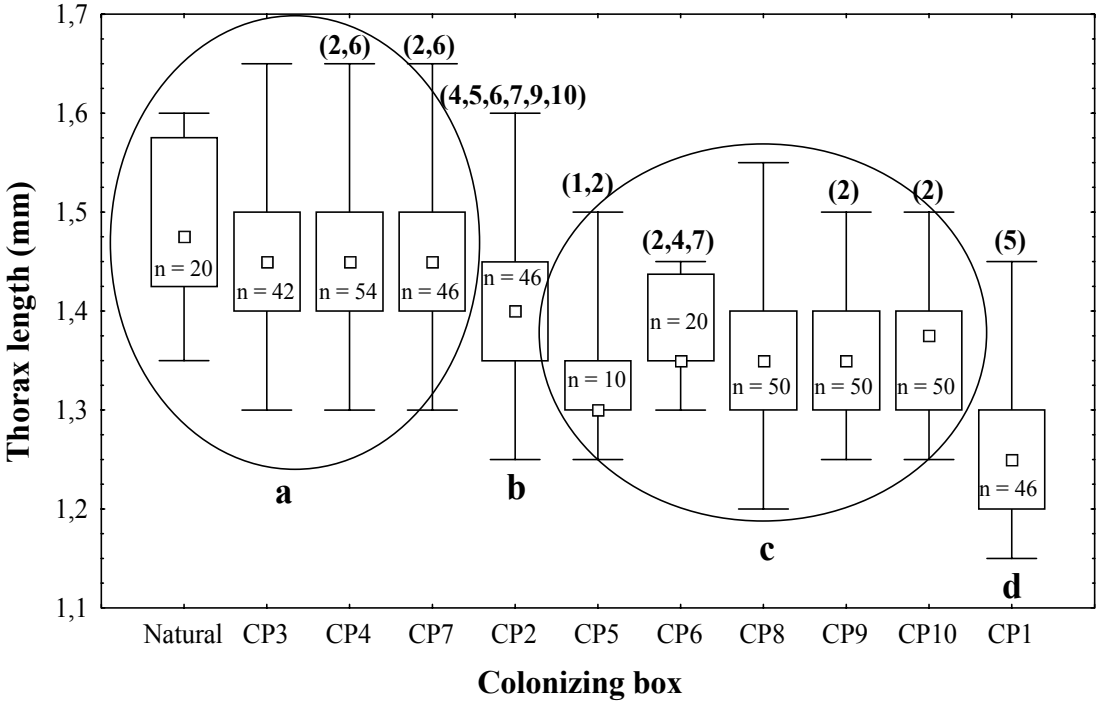

Figure 89: Comparison of the adult body size of *Chironomus dorsalis* (thorax length) between individuals emerging from the experimental boxes of the colonizing experiment 1998 and from two natural habitats (see explanations of abbreviations in Table 64).

Explanations:

The size differences were compared with an ANOVA and for multiple comparisons with the TUKEY's honest significant difference test for unequal N (see text). Within the circled box-and-whisker-plots (groups a and c) there were no significant differences ($p > 0.05$). The entries above the box-and-whisker-plots show results for colonizing boxes, which were also not significantly different but attributed to another group.

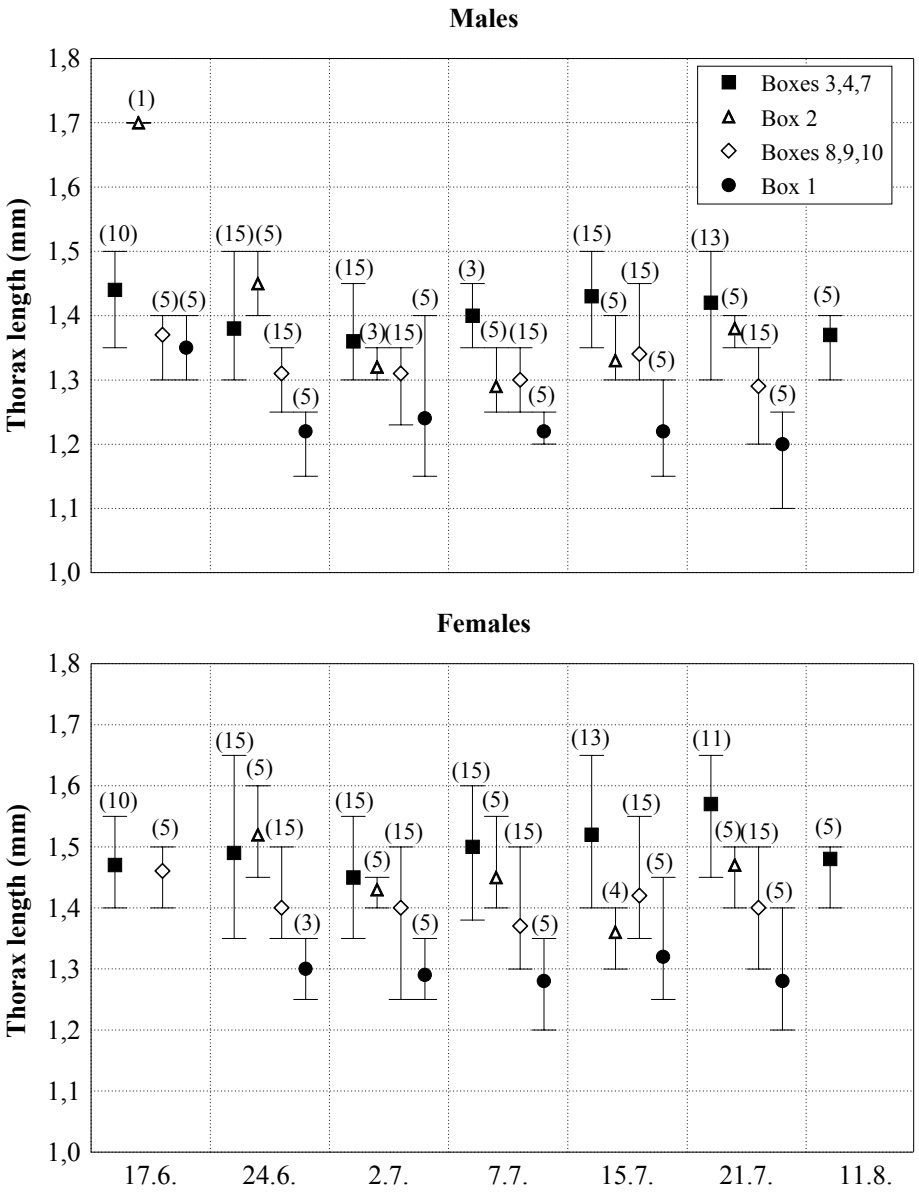

Figure 90: The adult body size of males and females during the different samplings in the colonizing experiment, 1998.

Explanations:

The boxes were combined according the results of Figure 89. The numbers of individuals measured are provided in parenthesis above the corresponding interval plots.

All size differences within the groups were compared with an ANOVA (results of the LEVENE's test for homoscedasticity in parenthesis):

a) Males of boxes 3,4,7: $F = 4.2$, $df = 6$, $p = 0.001$ (LEVENE'S test: $F = 0.3$, $df = 6.7$, $p = 0.954$);
b) Males of box 2: $F = 14.0$, $df = 4$, $p < 0.001$ (LEVENE'S test: $F = 0.6$, $df = 4.2$, $p = 0.671$);
c) Males of boxes 8,9,10: $F = 4.35$, $df = 5$, $p = 0.002$ (LEVENE's test: $F = 1.0$, $df = 5.7$, $p = 0.423$);
d) Males of box 1: $F = 4.3$, $df = 5$, $p = 0.006$ (LEVENE's test: $F = 1.1$, $df = 5.2$, $p = 0.384$);
e) Females of boxes 3,4,7: $F = 3.8$, $df = 6$, $p = 0.002$ (LEVENE'S test: $F = 1.5$, $df = 6.8$, $p = 0.188$);
f) Females of box 2: $F = 5.5$, $df = 4$, $p = 0.004$ (LEVENE's test: $F = 2.0$, $df = 4.2$, $p = 0.135$);
g) Females of boxes 8,9,10: $F = 2.1$, $df = 5$, $p = 0.071$ (LEVENE'S test: $F = 0.3$, $df = 5.7$, $p = 0.888$);
h) Females of box 1: $F = 0.4$, $df = 4$, $p = 0.841$ (LEVENE'S test: $F = 0.4$, $df = 4{,}2$, $p = 0.807$).

For multiple comparisons see Table 63 and text.

were 'high' (1 000,000 larvae per m²), adults developed into adults significantly faster and the average body size was significantly greater (but survival was only 2 % instead 44 % in the 'low' density experiment!). The author discussed the observation at 'low' densities as a way of spreading the risks of larval desiccation on the one hand and the advantages associated with large females on the other. To examine MCLACHLAN'S hypothesis for *Chironomus dorsalis* under quasi-natural conditions, the adult body size until the end of the colonizing experiment was documented separately for each experimental box (Figures 89 and 90).

As in the lab experiments, there were sexual differences in thorax length; those of females being 6 % larger on average (t-test: $t = -10.65$, $df = 419$, $p < 0.001$, N = 210 ♂♂ and 211 ♀♀). The range of male and female thorax lengths (min-max; mean) was 1.10-1.70; 1.34 and 1.20-1.65; 1.43, respectively.

The first step of the analysis was to test whether there were differences of the adult average size between the different experimental boxes and the two natural habitats (Figure 89, Table 64). Homoscedasticity was fulfilled (LEVENE's-test: $F = 1.8$, $df = 10.4$, $p = 0.065$) and an ANOVA showed a highly significant result ($F = 28.4$, $df = 10$, $p < 0.001$). For multiple comparisons, TUKEY'S honest significant difference test for unequal N was used. Four groups (labelled a-d in Figure 89) could be separated:

(a) group a contains the specimens with the greatest average size, which emerged in the two natural habitats (=Natural) and in the experimental boxes 3, 4 and 7;

(b) experimental box 2, the adults of which were not significantly larger or smaller than those emerging in most of the other experimental boxes;

(c) group c contains the relatively small specimens that had emerged in the experimental boxes 5, 6, 8, 9 and 10; and

(d) experimental box 1, which adults were the smallest.

The density of emerged adults and the adult body size of groups a-d was not coherent (Table 27 p 79).

The second step of the analysis involved testing whether there were differences in the average body size within these four groups during the different sampling occasions (Figure 90). The tests were done for each sex separately (the results of the ANOVA's are listed below Figure 90 and those of the multiple comparisons in Table 63). The first emerging males were usually the largest (except group c). After the first emergence the male body size decreased (except group c), the significant results of which are listed in Table 63. The pattern of male body size showed no further regularities. There were no differences in the female body sizes from different sampling dates within groups c and d, and no clear trends were found for groups a and b either. Any indication was therefore found that MCLACHLAN'S (1983) hypothesis of spreading the risks is also valid for *Chironomus dorsalis* under quasi-natural conditions (and densities) (see also section 4.4.1.4.).

Table 63: Results for the multiple comparisons of the average body size of *Chironomus dorsalis* from the different sampling dates in the colonizing experiment 1998.

Group	Sex	17.6.	24.6.	2.7.	7.7.	15.7.	21.7.
a (Box 3,4,7)	♂♂			< 17.6.		> 2.7	
	♀♀						> 17.6., 2.7.
b (Box 2)	♂♂			< 24.6.	< 24.6.	< 24.6.	> 7.7.
	♀♀					< 24.6., 7.7.	> 15.7.
c (Box 8,9,10)	♂♂					> 7.7.	< 15.7.
	♀♀						
d (Box 1)	♂♂		< 17.6.	< 17.6.	< 17.6.	< 17.6.	< 17.6.
	♀♀						

Abbreviations and explanations:

- If n of all samplings were equal, NEWMAN-KEYL's-test was used, otherwise a TUKEY'S honest significant difference test for unequal N was used for multiple comparisons;
- </> = specimens significantly ($\alpha = 0.05$) smaller/larger than on date xy;
- Groups a - d see text and Figure 89.

Finally, a multiple comparison of the adult body size in the colonizing experiment, in the natural habitats and in the lab experiments was performed (Table 64, see also Figures 68 and 73 pp 150 and 158, respectively). Each group compared consisted of an equal number of males and females. Whenever the original number of measured males and females was unequal, an equal number of males or females was chosen with a table of random numbers (LORENZ 1996). The mean temperatures in the experimental boxes of the colonizing experiment were 15.5 °C (shaded) and 17.4 °C (not shaded) (Table 19 p 62). The specimens which had emerged from the colonizing experiment were on average very small: (a) significantly smaller than individuals that emerged in the 13.8 °C SD-, 9.5 °C LD- and 16.0 °C LD-experiments; (b) significantly smaller than individuals emerging in the experiments on larval density (density 1 and 2 (20.5 °C)); and (c) significantly smaller than the adults that emerged from the natural habitats (in respect to single boxes see Figure 89). The specimens that emerged in the natural habitats were significantly smaller than those of the 13.8 °C SD-experiment and of the experiments with low larval densities (density 1), the level of significance was only slightly exceeded when comparing the specimens of the natural habitats with those of the 9.5 °C LD-experiment. Two important conclusions can be drawn from the multiple comparisons of the adult body size:

1. The adult body size in the lab experiments is comparable with that observed in the natural habitats (generations succeeding the first spring generation!);
2. Factors others than temperature (competition, limited food resources etc.) must have caused the small average size of adults emerging from the colonizing experiment.

Table 64: Comparison of the adult body size (thorax length) of *Chironomus dorsalis* (males and females in identical proportions) emerging in the experiments on photoperiod and temperature (section 4.4.1.2.9. Figure 68a p 150), the colonizing experiment and in two natural habitats.

	13.8 °C SD	**9.5 °C**	**16.0 °C**	**20.0 °C**	**25.0 °C**	**30.2 °C**	**Density 1**	**Density 2**	**Colo.**	**Natural**
13.8 °C SD	**1.65 ± 0.08 N = 20**	**0.914**	**0.128**	< 0.001	0.005	< 0.001	**1.000**	< 0.001	< 0.001	< 0.001
9.5 °C		**1.60 ± 0.10 N = 14**	**0.972**	0.009	**0.164**	< 0.001	**0.997**	**0.351**	< 0.001	**0.051**
16.0 °C			**1.56 ± 0.10 N = 16**	**0.190**	**0.725**	0.006	**0.452**	**0.967**	< 0.001	**0.533**
20.0 °C				**1.47 ± 0.12 N = 16**	**1.000**	**0.983**	< 0.001	**0.920**	**0.360**	**1.000**
25.0 °C					**1.47 ± 0.08 N = 8**	**0.998**	0.025	**0.995**	**0.783**	**1.000**
30.2 °C						**1.43 ± 0.09 N = 20**	< 0.001	**0.122**	**0.937**	**0.678**
Density 1							**1.63 ± 0.10 N = 70**	**< 0.001**	**0.001**	< 0.001
Density 2								**1.51 ± 0.10 N = 46**	**< 0.001**	**0.994**
Colo									**1.39 ± 0.10 N = 415**	**0.038**
Natural										**1.49 ± 0.09 n = 20**

Explanations:

- The mean thorax length ± standard deviation and N are highlighted in bold black, non-significant differences ($p \leq 0.05$) in bold grey. TUKEY'S honest significant difference test for unequal N was used for the multiple comparisons;
- LEVENE'S test for homoscedasticity: $F = 0.58$, $df = 9.64$, $p = 0.811$;
- ANOVA result for all effects: $F = 66.5$, $df = 9$, $p < 0.001$;

Abbreviations: **SD** = short day, **Density 1** = thorax length for densities of 786 – 12,575 larvae/m² (20.5 °C, see section 4.4.1.4.); **Density 2** = thorax length for densities of 25,150 – 100,602 larvae/m² (20.5 °C, see section 4.4.1.4.); **Colo.** = adults emerging from the experimental boxes of the colonizing experiment; **Natural** = adults (14.6.1992 - 24.7.1992) emerging from two puddles on contruction site (Lahnberge, Marburg, Hesse, Germany, see table 1 in DETTINGER-KLEMM & BOHLE 1996).

4.4.2.3.3. Egg deposition and first emergence

The emergence of *Chironomus dorsalis* in its hibernating habitat has not yet been studied and its first emergence is therefore not exactly known. But conclusions on the approximate time of first emergence can be drawn from the following observations:

1. During the present study, the first individuals emerged on June 12 (sampling interval: 10.-14.6.1992) from pool 1 and on June 14 (sampling interval: 11.-17.6.) from the experimental boxes of the colonizing experiment 1998 (Figure 30 p 80). The previous section showed that these adults were the offspring of colonizing females which had probably emerged in mid of May.

2. in 1996 and 1997 two plastic containers, identical to those used in the colonizing experiment, had been exposed near pool 1 to collect the egg masses of *Chironomus dorsalis* used in the lab experiments (Figure 9 p 42). Fifty-three egg masses were collected from these boxes, then individually reared into adults and finally determined to species level (Appendix 8). Out of these egg masses only three (6 %) had been laid by *Chironomus luridus* all other by *Chironomus dorsalis*. This is surprising as *Chironomus luridus* was frequent in pool 1 and *Chironomus dorsalis* was not encountered in this habitat in both 1996 and 1997 (Table 23 p 65). In 1996, the two containers were placed on April 19 and then inspected for egg masses every three or four days. The first egg mass was found on May 24, others then followed regularly from June 13 - July 10. In 1997, the containers were placed and inspected daily for newly laid egg masses from July 7 to 15 (Table 65). It seems that high atmospheric humidity facilitated the female dispersal.

Table 65: Deposition of *Chironomus dorsalis* egg masses in a plastic container near pool 1 from July 7 to 15 in 1997.

Date	7.7.	8.7.	9.7.	10.7.	11.7.	12.7.	13.7.	14.7.	15.7.
Mass	-	0	0	0	0	1	4	2	24
Precipitation*	0	0	0	0	0	7.4	0.9	3.4	4.2
Humidity*	60	61	60	51	28	85	60	85	60
Temperature*	11 - 19	12 - 18	12 - 20	11 - 22	14 - 25	14 - 25	14 - 26	11 - 22	11 - 20

Abbreviations and explanations:

Mass = number of egg masses laid; **Precipitation** is provided in mm/day; **Humidity** = relative atmospheric humidity (%) at 14:00 p.m; **Temperature** = minimum - maximum (°C).

*recorded by the meteorological station 'Am Stempel' (near Marburg, Hesse, Gemany).

These observations indicate that the first spring emergence occurs around mid of May. From section 4.4.1.2.3. we know that short-days and temperatures of 9.5 °C induce an oligopause in *Chironomus dorsalis*. The critical day-length is not known and the temperature threshold probably lies between 9.5 and 14 °C (section 4.4.1.2.8.). The ranges of daily means of water temperature (°C) from May 1 to May 15 were 8.2-12.2 (pool 1, 1997), 9.3-13.1 (pool 2, 1997), 7.7-11.0 (pool 3, 1997), 9.2-15.0 (pool 1, 1998), 9.1-12.8 (pool 2, 1998), 8.8-11.3 (pool 3, 1998) and 8.9-11.0 (pool 1, 1999) (see Appendix 2). These data show, that, depending on the habitat and climatic situation, the critical temperature threshold is likely to be reached in the first half of May. The day-lengths in the first half of May range from 14.4 to 15.7 hours.

4.4.2.3.4. Last emergence and the thresholds for oligopause

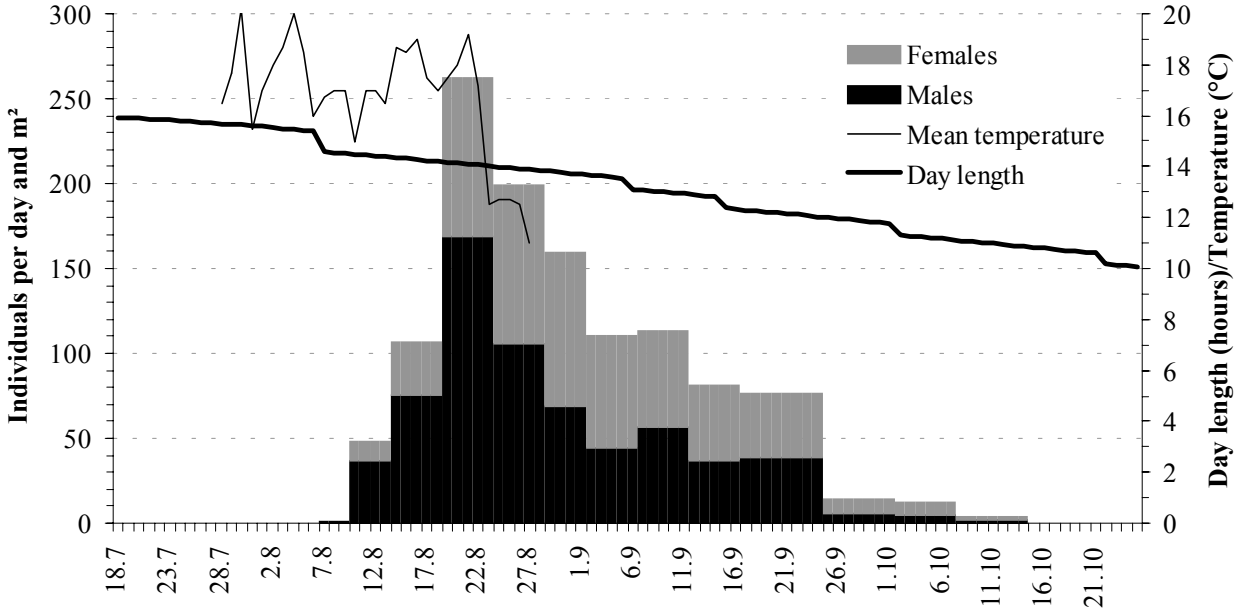

Figure 91: The emergence of *Chironomus dorsalis* from the experimental boxes 3 + 4 in the colonizing experiment 1993 (after data presented in DETTINGER-KLEMM 1995a).

The last emergence of *Chironomus dorsalis* was not observed in the present research but in my previous study in a colonizing experiment when four experimental boxes had been placed beside pool 2 on July 18, 1993 (DETTINGER-KLEMM 1995a and DETTINGER-KLEMM & BOHLE 1996). The emergence from the experimental boxes 3 and 4 is illustrated in Figure 91. The first emergence occurred between August 6 and 10 (median = 8.8.) about 21 days after the experimental boxes had been exposed in the open. Emergence first peaked abruptly and then decreased continuously until September 24 after which it dropped to almost zero. The definite end of emergence was then observed between October 7 and 14 (median = 11.10.) at day lengths of about 11 hours. From July 27 to August 27 the daily means of water temperatures ranged from 11.0 to 20.2 °C (mean: 16.7 °C). There was a strong decline of temperatures from August 21 until the end of measurements on August 27. Figure 16 p 50 showed that monthly means of water temperature start to drop in the September. The data listed in the Appendix 2 indicate that in both 1997 and 1998 temperatures started dropping continuously in the last third of August too. The daily means of temperatures recorded from September 15 to 30, 1998 ranged between 10.8-12.1 °C (pool 1) and 11.4-12.1 °C (pool 2). This indicates that in September, temperatures fall below the oligopause threshold. Up to the drop in temperatures that began in August 23, 1993, the temperatures in the experimental boxes were within the species optimum (section 4.4.1.2.8.) (Figure 91). The days were about 14 hours long when the temperatures started dropping, this day length did not stop the species' development into adults. The day length threshold for oligopause must therefore lie below 14.0 hours. In spring such day lengths only occur until mid of April. Maybe, a drop below the photoperiodic threshold for oligopause caused the abrupt decline of emergence around September 24 when days were about 12.0 hours long. If this was the case the days would only be too short for development until Mid March. The data indicate

that development into adults in August/September is first slowed down by the temperature threshold and then stopped by the day length threshold in the beginning of October and vice versa in spring. This would mean that the first spring emergence is probably very variable since the day length threshold is passed prior to the temperature threshold and water temperatures are strongly dependent on exposure and water depth.

4.4.2.4. Protandry and sex ratio

In the lab experiments, (Table 46 p 151) an unbalanced sex ratio in favour of males was significant for *Chironomus dorsalis* and *Paralimnophyes hydrophilus*. A balanced sex ratio was found for *Chironomus annularius* and *Polypedilum tritum*. In the lab experiments (Table 46 p 151), *Chironomus annularius*, *Chironomus dorsalis*, *Chironomus luridus*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* exhibited a significant tendency towards protandry.

Protandry: In this section, the tendency to protandry was tested for *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*. The following data were analysed:

(a) *Chironomus dorsalis*: all boxes of the colonizing experiment;

(b) *Polypedilum tritum*: generation 1 and 2 in pool 1, 1998 (see Figure 79 p 169);

(c) *Paralimnophyes hydrophilus*: generation 2, 1997; generation 1 and 2, 1998 (all in pool 1 see Figure 82 p 177).

1. *Chironomus dorsalis*

Table 66: Emergence characteristics of *Chironomus dorsalis* males and females in the colonizing experiment 1998.

Box	♂♂					♀♀					U	p
	First	Med	Mean	sd	N	First	Med	Mean	sd	N		
1	32.5	46.5	47.1	9.7	122	32.5	53	52.7	8.4	83	3431	< 0.001
2	26	40	38.2	7.3	153	32.5	40	39.9	8.5	116	7914	0.102
3	26	26	31.8	8.1	245	26	40	40.6	9.3	199	11381	< 0.001
4	26	32.5	34.6	10.5	166	26	32.5	36.5	8.2	145	9382	< 0.001
7	26	32.5	34.4	7.3	246	26	40	37.0	6.9	199	18749	< 0.001
8	32.5	40	42.9	9.8	194	32.5	40	43.7	9.3	117	10527	0.270
9	26	46.5	44.5	9.1	323	32.5	40	45.1	10.9	223	35239	0.662
10	26	32.5	38.7	11.5	477	26	40	41.0	10.2	332	67315	< 0.001

Abbreviations:
Box = experimental box (see Figure 2 and 3 pp 20 and 21, respectively);
First/Med/Mean/sd = First emergence/median value of emergence/arithmetic mean of emergence/standard diversity (days after start of the experiment on May 19, 1998);
N = number of emerged ♂♂ and ♀♀;
U/p = U-value and p-value of the MANN-WHITNEY-U-test.

The statistics of male and female emergence in the colonizing experiments is listed in Table 66. As it was likely that pesticides applied in the adjacent rape fields strongly affected the results of experimental boxes 5 and 6 (section 4.2.2.3.), these boxes were not considered in the analysis. In the remainder of experimental boxes, males emerged on average earlier than females and this was sta-

tistically significant for five experimental boxes. Though sampling intervals lasted one week, there was also a significant tendency to protandry in the field.

2. *Polypedilum tritum* and *Paralimnophyes hydrophilus*

Table 67: Protandry in *Polypedilum tritum* and *Paralimnophyes hydrophilus* from pool 1.

Generation	Period	Mean ♂♂	Mean ♀♀	N	U-test
Polypedilum tritum					
1, 1998	22	8.6	9.8	85 ♂♂, 75 ♀♀	U = 2649, p = 0.036
2, 1998	45	22.4	25.7	367 ♂♂, 273 ♀♀	U = 41715, p < 0.001
Paralimnophyes hydrophilus					
2, 1997	27	9.1	11.0	107 ♂♂, 122 ♀♀	U = 5436, p = 0.018
1, 1998	32	16.0	19.2	27 ♂♂, 31 ♀♀	U = 340, p = 0.193
2, 1998	22	11.2	12.8	48 ♂♂, 42 ♀♀	U = 15219, p = 0.201

Abbreviations:
Generation = generation analysed for protandry; **period** = duration of emergence from first to last emergence; **mean** = mean value of emergence within the period of emergence (days); U-test = MANN-WHITNEY-U-test.

Despite the long samplings intervals of one week, males emerged on average significantly earlier than females in *Polypedilum tritum* as well as in generation 2, 1997 in *Paralimnophyes hydrophilus* (Table 67).

Sex ratio: For each trap site and colonizing box, the sex ratios (males/females) of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* were calculated if N exceeded 10 (Tables 23-25 pp 65-67 and Table 27 p 79). The sex ratios were normally distributed, it was therefore possible to calculate the 95 % confidence lobes for the mean sex ratios (Table 68). The results confirm an unbalanced sex ratio in the field for *Chironomus dorsalis* but, contrasting with the laboratory results, not for *Paralimnophyes hydrophilus* (Table 46 p 151). As in the laboratory experiments, the sex ratio of *Polypedilum tritum* observed in the field did not significantly differ from 1:1.

Table 68: The sex ratios of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* in the field.

Species	Normality	Range	CL	N
Chironomus dorsalis	W = 0.93, p = 0.533	1.51-1.66; 1.39	1.28-1.51	8
Polypedilum tritum	W = 0.93, p = 0.207	0.38-1.75; 1.13	0.95-1.30	17
Paralimnophyes hydrophilus	W = 0.90, p = 0.060	0.42-2.13; 0.94	0.70-1.18	16

Abbreviations:
Normality = the distribution of sex ratios was tested for normality by the SHAPIRO-WILK'S-W-test; **Range** = min.-max.; mean; **CL** = 95 % confidence limits; **N** = number of sex ratios taken into account.

4.4.2.5. Infestation by water mites

Because in 1998 chironomids of pool 1 were highly infested by water mites, the rates of infestation from 1997-1999 are listed for *Polypedilum tritum* in Table 69. There were no obvious differences of infestation between the species of pool 1. Except in 1998 and 1999, infestations by water mites were observed only sporadically and only in single chironomid specimens.

Table 69: The infestation of *Polypedilum tritum* by water mites emerging from pool 1 in 1997-1999.

Site	1997		1998			1999	
	G 1	G 2	G 1	G 2	G 3	G 1	G 2
1b	-	-	-	-	-	0 %	0 %
1c	-	-	-	-	-	0 %	0 %
2	0 %	0 %	0 %	44 %	23 %	0 %	11 %
3	0 %	0 %	0 %	19 %	1 %	0 %	0 %

Abbreviations:
Site = sampling site (see Figure 9 p 42); **G 1,2,3** = generation 1, 2 and 3 (see Figure 79 p 169).

5. Discussion

5.1. The habitat

5.1.1. Pool classification

I applied the term pool to all shallow waters, which are subjected to high fluctuations of water levels and surface area (DETTINGER-KLEMM 2000b). Ponds are 'lentic waters of sufficient permanence to support submerged aquatic plants, and normally fish as well' (WIGGINS et al. 1980). Figure 92 provides a scheme of pool classification. The pools investigated in this study are all non-wetland pools that are never connected to permanent water bodies. Pool 3 is a true woodland pool and pools 1 and 2 are grassland pools on the forest edge. The low levels of dissolved oxygen in pools 1 and 3 show (Table 11 p 47, Figure 15 p 48), that both pools were highly heterotrophic. Pool 2 had a tendency to silt-up, bore large amounts of rotting plants and very little submerged vegetation, indicating that it is also heterotrophic. The situation in pools 1, 2 and 3 contrasts with that seen in pools which are more strongly influenced by photosynthesis than by respiration (authotrophic, e.g. by

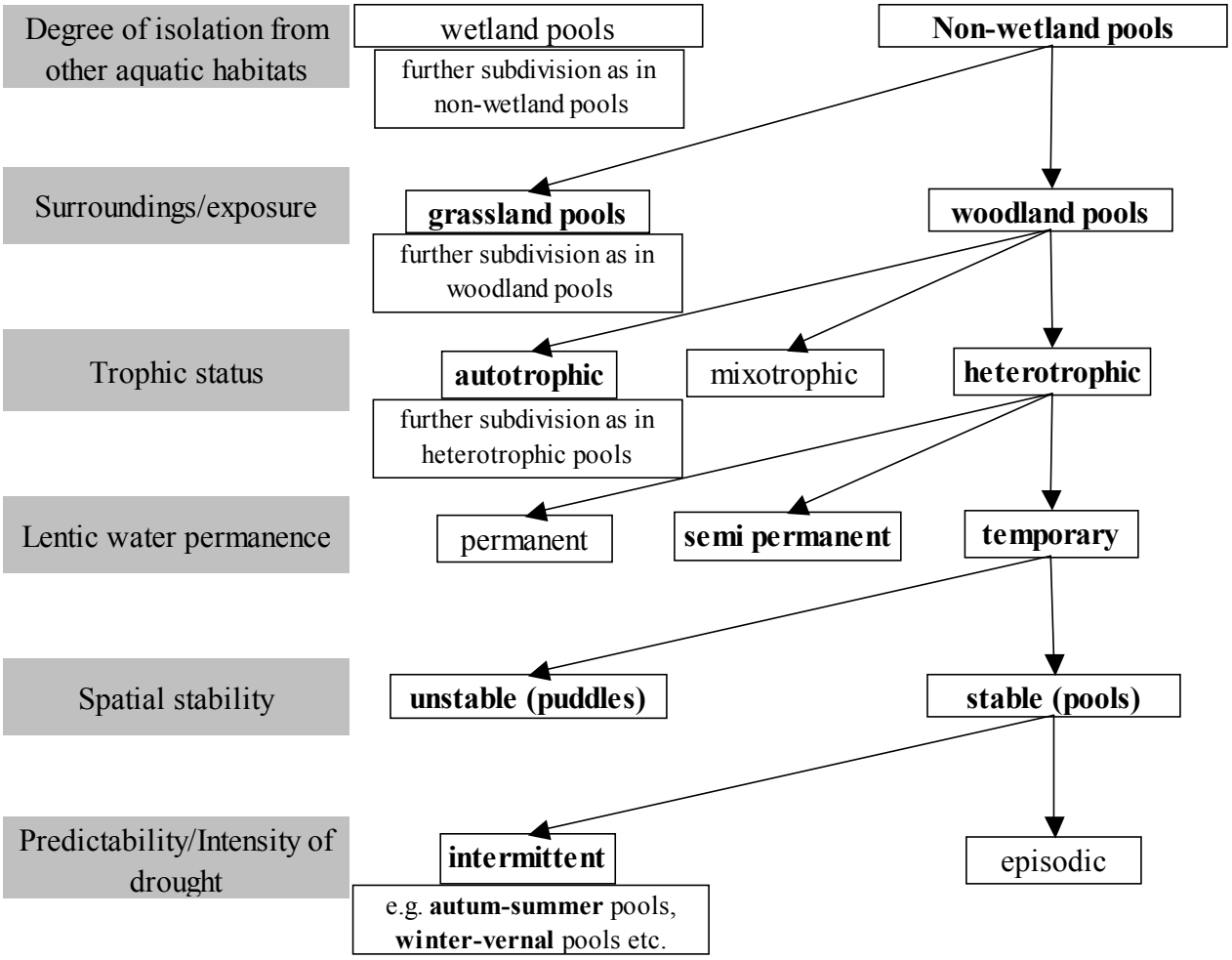

Figure 92: Scheme for subdivision of freshwater pools (compiled after WIGGINS et al., HEITKAMP 1989, WILLIAMS 1997 and DETTINGER-KLEMM 2000b).
(Features in bold were observed in the pools presently investigated)

Chara fragilis in ARLE 2002). The experimental pools of the colonizing experiment were strongly influenced by photosynthesis, which was shown by falling values of oxygen at night (minimum: 32 % of saturation) and rising during day (maximum: 79 % of saturation) (Figure 22 p 60). These pools may therefore be called authotrophic.

The factor of greatest importance when classifying pools was their hydrology. Pools 1 and 3 were truly temporary. According to WIGGINS et al. (op. cit.) I limit this term to waters that experience at least one dry period per year (WIGGINS et al. op. cit.). Water bodies that, as pool 2, dry up in some years but remain at least partly inundated in others, are called semi permanent (= perennially astatic sensu WIGGINS et al. op. cit.). The pools of the colonizing experiment were designed to mimic small temporary pools with low spatial stability, for example puddles associated with uprooted trees, paths used by game, rain-filled tires or wheel-ruts (e.g. JOGER 1981). The occurrence of such small water bodies is unpredictable as they only persist between one and a few years and are frequently subjected to short cycles of drying and refilling (JOGER 1979). Pools 1 and 3 show evidence of high spatial stability. In contrast to many permanent ponds and pools, temporary pools often appear to extremely slowly fill up with sediment and may persist over centuries or even millennia (COLLINSON et al. 1995). Reasons for these low sedimentation rates may be: (a) rapid and complete decomposition of organic materials in dry pool basins by hyphomycetes, which are able to grow because oxygen is not a limiting factor; and (b) terrestrial and emergent plants 'could serve to recycle sediment-held nutrients in temporary pool basins, incorporating them in plant tissues available for aquatic detritivores in the next wet phase' (WIGGINS et al op. cit.). The predictability and intensity of drought periods are thought to be the driving factors in the evolution of life histories specific to temporary pools and, on a synecological scale, in the determination of pool communities. According to the pattern of water disappearance, two basic types of pools can be separated: '(1) intermittent waters - which contain water in a recognizable cyclical pattern, or become dry at times of the year that are more or less predictable; and (2) episodic waters - which are water-filled on a more or less unpredictable basis' (WILLIAMS 1997). In essence, this definition corresponds to the terms periodic and non-periodic pools (HEITKAMP op. cit., DETTINGER-KLEMM op. cit.). Pools 1 and 3 are therefore both intermittent. WIGGINS et al. (op. cit.) distinguished two basic types of intermittent pools at temperate latitudes: (a) autumnal pools - which form in the autumn and dry up in summer (terrestrial phase of 3-4 months and aquatic phase of 8-9 months); and (b) vernal pools - which do not fill until spring and then dry up relatively soon (terrestrial phase 8-9 months, aquatic phase 3-4 months). The term autumnal pool corresponds exactly to the hydrology of pool 1, but pool 3 does not usually fill until winter and could neither be called vernal nor autumnal. The classification of intermittent pools as autumnal and vernal is arbitrary and reflects only two extremes within a continuum of pools with short and long aquatic phases. Whether one type is dominant over another in a given region depends on the local climate, plant cover and geology. Therefore the classification of HEITKAMP (op. cit.) is more appropriate for pool classification. This author defined pools according to their filling and drying times. Following this classification, pool 1 is (on average) an intermittent autumn-summer-pool and pool 3 an intermittent winter-vernal pool. Due to variations in the

hydrology of individual pools, (section 4.1.1.4.), temporary and semipermanent pools can hardly be classified after only one year of observation: (a) the intermittent autumn-summer pool 1 would be defined as semi permanent in 1992 and 1998 and as a winter-summer-pool in 1995; (b) the semi permanent pool 2 was permanent in 1992 and 1998 but a winter-summer-pool in 1997; and (c) the intermittent winter-vernal woodland pool 3 exhibited the most predictable drying up time but, nevertheless, did not fill up with water in winter/spring 1995/96 and the extent of inundation was highly variable. Many interpretations of pool communities and ecological implications are therefore problematic as a pool's hydrology is often only known for one year of investigation whereas the communities it harbours are mainly affected by the pools' overall hydrology and the hydrology of the preceding year (see section 5.2.).

5.1.2. Location within the habitat templet

Long-term studies are also needed in order to determine the position of a given pool within the habitat templet of lentic water permanence and drought predictability (Figure 1 p 12). The laboratory results presented in section 4.4.1.6. showed that both soil moisture content and duration of drought affected the survival of aestivating larvae. The intensity of drought may therefore be defined by the following equation:

$$\text{Average intensity of drought (DI)} = \frac{\text{average duration of drought at deepest site}}{\text{average minimum soil moisture at deepest site}} .$$

Eight years of observation were available for each of the pools used in this research (see Figure 18 p 53, Figure 20 p 57 and Figure 21 p 59). For example, the average duration of drought at pool 1's deepest site was 71 days and the average minimum soil moisture (estimated on a scale of 1 to 5, see Table 1 p 16) 1.9 (1 in 1993, 1995 and 1997; 2 in 1996; 3 in 1992 and 1998 and not known for 1994). The average intensity of drought for pool 1 was therefore 37.4. The lentic water permanence (LWP) is reciprocal to DI:

$$\text{LWP} = \frac{1}{(1 + \text{DI})} .$$

The predictability of drought (PD) may be defined as follows:

$$\text{PD} = \frac{\text{probability that the pool dries up at least once a year (\%)}}{(1 + \text{standard deviation of mean drying month})} .$$

In temporary pools, as defined above, the probability of drying is always 100 %. Pool 2 did not dry up in 2 out of eight years; its probability of drying was therefore 75 %. The drying months of pool 2 were 0 (= no drying, 1992 and 1998), 7 and 8 (1993 and 1994), 7 (1995, 1996 and 1999) and 6 and 7 (1997). The standard deviation of the mean drying month was 2.9. Thus PD of pool 2 was determined to be 25.9. These definitions of the habitat templet axis facilitate a numerical comparison between the pools (Figure 93): pool 2 shows the highest lentic water permanence and the lowest predictability of drought; the gap between pool 2 and pool 1 is much wider than that between pool 1 and 3. The colonizing pools are only placed as an example within the habitat templet (Figure 92) as

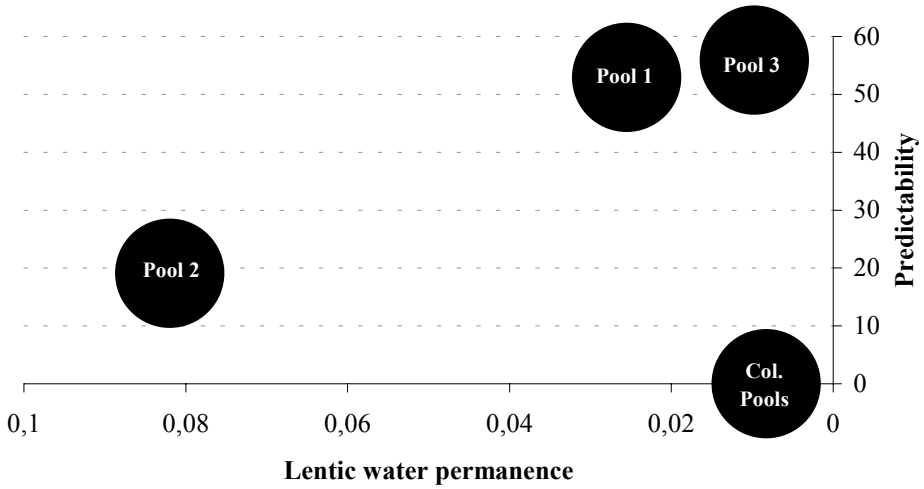

Figure 93: Position of the investigated pools within the habitat templet of lentic water permanence and predictability of favourable/unfavourable conditions (compare with Figure 1 p 12).

the appearance of such waters is unpredictable and their lentic water permanence very low (see preceding section).

5.1.3. Thermal regime

The physical and chemical characteristics of temporary pools are believed to be more variable than those of adjacent permanent pools (WILLIAMS 1997). Great variations in physicochemical characters have also been documented in the present study (Table 11 p 47), the conductivity of pool 2 (302-1620 µS/cm) was particularly variable. But as mentioned in the previous section, this pool is semi permanent and it is more likely that strong variations in physicochemical factors are typical for all pools, irrespective of whether they fully dry up or not. Temperature was the physicochemical factor that received greatest attention in the present investigation. Many authors emphasize, that temporary pools are subjected to particularly high temperatures - for example: (a)....'rapid development in spring, critically important to temporary-pool animals, may in fact be augmented by the protein-rich detritus with high temperatures' (WIGGINS et al. 1980); (b) WILLIAMS (1985) mentioned high temperatures as an important source of stress for aquatic organisms living in temporary pools; (c) 'To take an example, surface water of shallow ponds in temperate regions may, on occasion, approach 40 °C in mid-afternoon in summer. This is very near the thermal death point of most insects' (WILLIAMS 1987); (d) '...while the shallowness of temporary ponds enables them to warm up quickly in spring, encouraging growth in species which have high thermal coefficients' (COLLINSON et al. 1995).

PICHLER (1939) classified small lentic waters into 3 thermal categories:

(1) puddles: maximum depth ≤ 20 cm, their water temperatures follow more or less the daily cycle of air temperatures and there is no daily stratification of temperature;

(2) pools: maximum depth ≤ 60 cm, their thermal stratification is upset daily by a turnover and their maximum daily temperature variation is up to 15 °C at the surface and 5 °C at the bottom;

(3) ponds: maximum depth > 100 cm, their stratification is more stable but can be upset daily, their maximum daily temperature variation is up to 10 °C at the surface and up to 2 °C at the bottom.

The colonizing pools of the present study belong to thermal category 1 (puddles) (Figure 24 p 62). Organisms living in such waters might be particularly eurythermous (PICHLER op. cit.) and since the temperatures of the water in which they live can go beyond 40 °C (BREGULLA 1988) these organisms may also have higher thermal death points. We will see in section 5.3.2.1. whether this assumption applies to the results of the present study.

The maximum depths of pools 1-3 indicate that they should belong to thermal category 2 (pools). However, the daily temperature amplitudes at the bottom of these pools' were low (see Figure 17 p 51) and even the maximum daily amplitudes (Table 70) that were observed just before drought in the shallow puddles, were usually below 5 °C. According to PICHLER's (op. cit.) definition, pool 2 should belong to thermal category 3 (ponds) and pools 1 and 2 are in between thermal pools and ponds. This illustrates that such thermal categories are very arbitrary as they were based on not shaded pools and ponds. But depending on the water volume/water surface-coefficient, the exposition, the degree of overgrowth, the height of (shading) shore walls etc. (STERNBERG 1994), the thermal regimes of individual pools might vary greatly (see e.g. Table 70). Shallow waters, the littoral zone of lakes and larger lentic waters (PICHLER op. cit.) all warm up and cool down quickly, but the daily variations at the same depths are greater in waters with low water volume/water surface-coefficients (BREGULLA op. cit.). However, the mean daily values of water temperature at shallow sites seem to be the same in large and small lentic waters when insulation is identical (BREGULLA op. cit.). Daily variations of temperature in pools 1-3 were low or inexistant at water depths of ≥ 20 cm. This observation matches the data presented in STERNBERG (op. cit.). Cold air temperatures cause inverse stratifications of water temperatures, which are typical during winter (see Figure 17 p 51 and ARLE 2002), warm air temperatures result in direct stratifications of water tenperatures in the day and an upset or indirect stratification in the night (Figure 17 p 51 ARLE op. cit.). Very mobile organisms of temporary pools such as fairy shrimps (Anostraca), tadpole shrimps (Notostraca), mosquito larvae (Culicidae, Dixidae, Chaoboridae), water bugs (e.g. Corixidae, Notonectidae), water beetles (e.g. Dytiscidae, Helophoridae, Hydrophilidae, Scirtidae), damselfly larvae (Zygoptera) or dragonfly larvae (Anisoptera), may migrate between shallow and deeper sites thus benefiting from warm temperatures at shallow sites and low temperature fluctuations at deeper sites. Such movements are easily observed in tadpoles e.g. of the common frog (*Rana temporaria*): on warm days, they congregate in shallow sites and at night and on cloudy days they are well distributed throughout the pool with a predominance in deeper sites (pers. obs.). Tanypodinae larvae and some Orthocladiinae larvae (e.g. *Paralimnophyes hydrophilus* and *Limnophyes asquamatus*) are free-living and maybe also capable of such migrations. It is however unlikely that the tube-building Chironomidae larvae (e.g. *Polypedilum uncinatum* and *Chironomus dorsalis*) are able to perform such daily movements, although seasonal movements from shallow to deeper sites have been demonstrated in *Sergentia coracina* (WÜLKER 1961).

Table 70: Comparison of temperature characteristics (°C) of different temporary pools (grey shading) in the surroundings of Marburg (Hesse, Germany) and of other freshwater bodies in Hesse.

Habitat	Year	Depth	min 1	min 2	max 1	max 2	mean	Ampl.
Pool 1	96/97	59	-1.0	-1.0	18.1	16.4	5.9	4.3
	97/98		0.7	0.7	18.1	17.3	8.5	4.2
	98/99		1.5	1.5	18.4	17.5	7.4	3.5
Pool 2	98/99	35	1.9	1.9	15.6	15.6	8.7	1.5
Pool 3	96/97	55	-1.0	-0.9	11.7	11.0	4.2	1.5
	97/98		0.7	0.8	15.3	14.8	6.1	3.9
	99/2000[1]		-4.0	-2.7	17.0	15.6	5.4	5.5
	*2000	30	-	-	12.0	10.1	-	3.2
Mellnau	99/2000[1]	45	0.7	1.1	17.4	14.3	5.0	6.4
Wetter	*1999	12	-	-	15.3	13.2	-	5.0
Wolfsh.	*1999	30	-	-	20.6	17.6	-	10.4
Roth	*1999a	25	-	-	19.8	14.2	-	10.3
	*1999b	15	-	-	24.1	15.4	-	18.0
Puddles	*box 2	14	-	-	24.5	21.3	-	8.2
	*box 4	14	-	-	30.7	25.9	-	14 (18)
Borken	profundal 1993 - 1997	≤ 52.5 m	-	-	-	-	5.0 - 6.0	-
	**littoral 1997	20-30	-	-	29.8	-	-	-
Schuster	1997	40~500	1.5	4.76	27.6	21.23	12.8	9.8
Ohe	1992	50	1.0	1.5	19.4	18.5	9.2	7.6
	1993		1.0	1.0	18.4	17.5	8.9	5.7
Mardorf	2000/2001	1	-1.8	-1.7	20.6	16.7	8.2	7.5

Abbreviations and explanations:

Habitat:

Pool 1-3 and puddles: see sections 4.1.1.3.2. and 4.1.2.;

Mellnau = temporary winter-vernal grassland pool near Mellnau: with a temporary inflow and a drainage ditch, the latter of which was strongly shaded by *Juncus* spec and *Carex* spec (the temperatures were recorded in the ditch); drought period 1999 from mid May until end of November; drought period 2000 from beginning of May until beginning of December (SCHNEIDER 2000, HOOF 2001);

Wetter = in 1999 a temporary autumn-vernal floodplain pool in grassland near Wetter: temporary inflow of a helocrene spring; total drought from mid June until end of August (SCHNEIDER op. cit.);

Wolfsh. = temporary winter-vernal grassland pool near Wolfshausen: drought period 1997/98 from mid April 1997 until winter 1998; drought period 1999 from end of May until beginning of December (SCHNABEL 1999, SCHNEIDER op. cit.);

Roth = in 1999 a temporary autumn-vernal grassland pool near Roth: temporary inflow; drought period 1999 from beginning of May until September (DETTINGER KLEMM & SCHNEGELBERGER, unpbl. data);

Borken = Lake Borken (HEINMÜLLER et al 1998, HEINMÜLLER 2002);

Schuster = backwater of River Rhein (Schusterwörther Altrhein) near Leeheim (Riedstadt) (KORTE 1999);

Ohe = a 3rd order brook near Marburg (HOFFMANN 1997);

Mardorf = a helocrene spring near Mardorf (SUNDERMANN 2001).

Other columns:

Year = year of sampling; **depth** = maximum depth at sampling site (cm if not otherwise stated); **min 1** = minimum temperature, **min 2** = minimum daily mean; **max 1** = maximum temperature; **max 2** = maximum daily mean; **mean** = mean water temperatures; **Ampl.** = maximum daily amplitude of temperature.

[1] calculated from raw data collected by HOOF (op. cit.).

* temperatures only continuously recorded in the end of the hydroperiod (in all other cases the data of one year or of the whole hydroperiod (temporary pools) were considered): **pool 3**: this was site 9 (Figure 13 p 45), which was inundated from the end of January until the end of April 2000 (temperatures measured from 24.2.-20.4.2000); **puddles**: temperature measured from 8.6.-16.7. 1998 (and one day run on August 11/12); **Wetter**: temperature measured from 17.5.-26.5. 1999; **Wolfsh**.: temperature measured from 13.5.-22.5. 1999; **Roth**: temperature measured from (a) 7.4.-9.5. 1999; and (b) 7.4.-3.5. 1999.

**only spot checks from May until August 1997.

The above data suggest that: (a) there are no differences in the heat regimes of temporary and permanent pools; and (b) the differences between shallow sites whithin larger permanent lentic waters and pools are transient. The water temperature of some temporary pools (shallow, with high insulation, e.g. Wolfshausen and Roth in Table 70) varies greatly throughout the day. Other temporary pools (e.g. pools 1, 2, 3 and Wetter in Table 70) on the other hand have similar temperature regimes to that of other types of freshwater bodies.

So, in which way do the thermal regimes of temporary pools differ from that of permanent pools? The specificity of temporary pools lies in their recurrent cycle of drying and refilling. As mentioned in section 5.1.1., many pools refill in autumn until spring and dry up in spring until summer. The earlier a pool dries up, the lower the mean average temperature during the aquatic phase (see Mellnau, pool 1, pool 2 pool 3 in Table 70). In many temporary pools, the degree-days available for development are therefore comparatively low (see low average temperatures in the two winter-vernal pools Mellnau and pool 3 and compare with profundal temperatures in Lake Borken and temperatures of the helocrene spring in Mardorf (Table 70)) and species which are adapted to low temperatures (e.g. species with low developmental zeroes or low temperatures as cue to terminate dormancy) might be selected by this kind of lentic waters. Since pools exhibit greater daily temperature variations than larger lentic water bodies, high thermal coefficients seem to be also favourable to thrive in temporary pools. In permanent lentic waters five groups of organisms can be separated according to their life cycle (HEITKAMP 1989): (a) psychrophilic univoltine spring species; (b) polyvoltine eurythermous spring-summer-autumn species; (c) thermophilous summer species; (d) oligostenothermic autumn-winter species; and (e) semivoltine eurythermous species. Thus, the later a pool dries up, the more species other than psychrophilic univoltine spring dwellers are able to survive and - from a thermal point of view - communities of early drying pools might represent fragmented communities of permanent water bodies.

Low temperatures during winter are the last point to discuss. Pools that were filled with water rarely froze to the bottom but the mean daily tempertures of those that did never fell below -2.7 °C (minimum spot temperature -4.0 °C, see Table 70). In the present investigation, the temperature sensors of the data loggers were placed just above the mud's surface. It is however likely that the sensors recorded the temperatures of a 3 cm high water column (sensors were sealed in a plastic box (5.7 x 5.2 x 3.3 cm) to protect the logger against water). This assumption is supported by the data provided by DANKS (1971a) who observed that a temperate pool in northern latitudes (mean air temperatures of about -11 °C for the 3 months of midwinter!) froze solid to a depth of about 25 cm but the surface of the mud at a water depth of only 15 cm was never subjected to temperatures below −2.6 °C. In addition, temperatures of the first 5 cm of mud never fell below -1.7 °C. These data indicate that the minimum temperatures of the first 5 cm of mud at the bottom of the pools investigated are unlikely to have fallen far below 0 °C. Because incipient freezing points of most insect tissues lie between 0 °C and -3 °C (SALT 1955 cit. in DANKS op. cit.) and inoculative freezing of many chironomids starts between -1.7 and -2.8 °C (DANKS 1971c), hibernating chironomids were unlikely to

freeze when the pools were filled with water. On the other hand (compare with Figures 18 and 21 pp 53 and 59, respectively), large pool areas remained dry during parts of winter (pool 1 in 1995, pool 3 in 1994, 1999/2000) or the pool did not refill at all (pool 3 in 1995/96, see also Wolfshausen in Table 70). In such cases intense freezing would kill hibernating chironomid larvae that were not strongly freezing tolerant (DANKS 1971c). It therefore appears that temporary pools that dry up in winter are a particularly harsh environment for aestivating chironomids. The place of a given habitat within the habitat templet proposed in the previous section should therefore be completed by including the occurrence of severe freezing of the pools' bottom (not measured during the corresponding years) which is supposed to be equivalent to strong drying with grade 1 moisture levels (see section 5.3.5.3.).

5.2. The chironomid community

5.2.1. The chironomid community and the habitat templet

The chironomid communities of pools 1-3 and of the experimental puddles of the colonizing experiment were examined in sections 4.2.1. and 4.2.2. The species encountered in these pools are listed in Tables 23-25 and 27 (pp 65-67 and 79). These tables also provide some classification of the species according to larval life forms, reproduction strategies and habitat preferences which were deduced from the literature listed in Appendix 3. The purpose of this section is to analyse and discuss whether the lentic water permanence (LWP) and the predictability of drought (PD) - introduced in section 5.1.2. - provide a suitable habitat templet for temporary pools' chironomid communities.

Figure 29 (p 77) presented a cluster analysis of the annual yields of the aquatic/semiaquatic chironomid communities found in the trap sites of pools 1-3. This analysis showed that sites of pools 1 and 2 were as a rule more similar to each other than to sites of pool 3. There were however also transitions between sites of pool 1 and 3. The cluster analysis indicated a gradient of lentic water permanence that went bottom-up along the ordinate at which the trap sites were arranged. To facilitate comparisons with the habitat templet presented in Figure 93 (p 204), I now performed simpler comparisons of the total yields of aquatic/semiaquatic species of pools 1, 2, 3 and of the colonizing experiment by using similarity indices: The results of these comparisons appear in Table 71 and

Table 71: Comparison of total yields of pools 1, 2, 3 and of the colonizing experiment using similarity indices.

Index/Combination	P1⇔P2	P1⇔P3	P2⇔P3	P1⇔C	P2⇔C	P3⇔C
JACCARD's index (%) (JI)	59	31	30	36	27	21
RENKONEN's coefficient (Re)	0.405	0.274	0.179	0.045	0.044	0.008
WAINSTEIN's index (Kw)	24.1	8.5	5.3	1.6	1.2	0.2

$$JI = \frac{\text{number of species in common } (= G) * 100}{(\text{number of species in habitat A} + \text{number of species in habitat B}) - G};$$

$$Re = \sum_{i=1}^{G} \text{minimum relative abundance of a species present in habitat A + B};$$

$Kw = Re * JI$; all equations from MÜHLENBERG (1989).

confirm the similarity between the chironomid communities present in pools 1 and 2, which were clearly different from the community of pool 3. Furthermore, although there were a lot of species in common between pools of the colonizing experiment and pools 1-3, these chironomid communities differed distinctly from one another. The comparison shows that:

(1) **Pools without spatial stability** (and therefore unpredictable in their occurrence = puddles, here represented by the pools of the colonizing experiment, see Figure 92) **filter out different chironomid communities than stable pools**. But it is also evident from the data of section 4.2. that Tanytarsini were abundant in the colonizing pools but rare in pools 1-3. This is most likely to be a result of the different trophic levels in the colonizing pools (authotrophic) and in pools 1-3 (heterotrophic, see section 5.1.1.). Tanytarsini are generally thought to be more sensitive to low levels of oxygen than Chironomini (e.g. THIENEMANN 1954).

(2) **The proximity between the chironomid communities of pool 1 and 2 contrasts with the habitat templet presented in Figure 93**, which implies a closer relationship between pool 1 and 3. The main reason for this unexpected result is the early drying of pool 3 (May/June), which prevents colonizers from establishing.

Figure 94 shows some generalized features of the aquatic/semiaquatic chironomid communities found in pools 1-3, these seemed to be strongly correlated with the LWP. The proportion of Tanypodinae and the evenness of species occurrence were positively correlated with LWP and the proportion of pool species and aestivators negatively correlated with LWP. Tanypodinae are generally

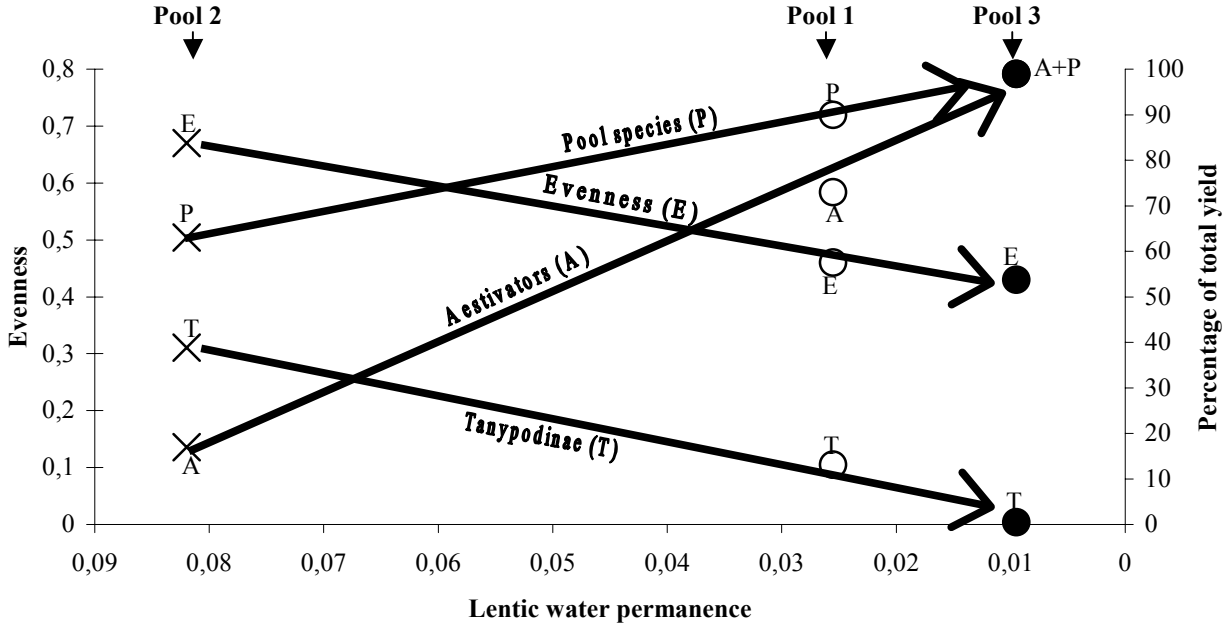

Figure 94: Four characteristics that appear to be strongly correlated with the lentic water permanence (for definition see section 5.1.2. and Figure 93 p 204).

$$\text{Evenness} = \frac{\text{Shannon diversity (= Hs)}}{\ln((\text{number of species})(= \text{H max}))}$$ (MÜHLENBERG 1989);

Percentage of total yield = relative abundance of a group in the total yield of aquatic, aquatic-semiaquatic and semiaquatic species (see column ∑ in Tables 23-25 pp 65-67);

Pool species = species typical for perman. (poo) and temporary (tp) pools and puddles (pu) (see Tab. 23-25 pp 65-67).

thought to be susceptible to drought. Many Orthocladiinae and Chironominae on the other hand, are able to endure periods of shortage in dormancy within their larval cocoons and are therefore largely preadapted to drought (see section 5.3.5.1.). The positive correlation of the evenness of the occurence of species with the LWP reflects the fact that with decreasing LWP the chironomid communities were increasingly dominated by one or two species. DRIVER (1977) observed the same phenomenon in Canadian prairie pools, which included permanent, semi permanent and temporary pools. *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* were these dominant species in the present investigation. All three species were the only drought tolerant aquatic/semiaquatic chironomids present in pools 1-3. This explains also the negative correlation between the abundance of aestivators and LWP. This negative correlation indicates that the aquatic/semiaquatic aestivators benefit from drought periods, which will be discussed in section 5.3.5. Because only three pools were investigated, it was not statistically possible to evaluate the correlations presented in Figure 94. However, Table 72 shows the results of two correlations: (a) between LWP and evenness; and (b) between LWP and proportion of aestivators (average LWP as defined in section 5.1.2., the LWP of the year of sampling and the year before sampling were calculated by taking into account the length of drought and the minimum grade of humidity of the corresponding year). The calculations were based on the annual crops of aquatic/semiaquatic chironomids found in the deepest sites of pools 1-3 (site 2, 3, 5+6, 7, 8 as clustered in Figure 29 on p 77).

Table 72: The (in)dependence of the evenness and the relative abundance of aquatic/semiaquatic aestivators occurring on deepest sites of pools 1-3 (sites 2, 3, 5+6, 7, 8, see Figure 29 p 77) on the **average** lentic water permanence (LWP), the LWP of the year of sampling (**same**) and of the year **before** sampling (for definition see section 5.1.2.).

	LWP	r/γ	F/Z	df	p
Evenness	same	r = 0.00	F = 0.0	1.16	0.999
	before	r = 0.15	F = 0.4	1.16	0.562
	average	γ = 0.29	Z = 1.4	-	0.168
Aestivators	same	r = -0.27	F = 1.3	1.16	0.276
	before	r = -0.52	F = 6.0	1.16	0.026
	average	γ = -0.96	Z = -4.69	-	<0.001

r = coefficient of determination with F-values
γ = GOODMAN-KRUSKAL'S- γ with Z-values

The proportion of aestivators on the sampling sites was significantly correlated with the LWP on the previous year and especially with the average LWP. Unsurprisingly, no correlation was found with the LWP of the year of sampling. The same trend is indicated for the correlations between LWP and evenness but was not significant in any of the three cases. **The average LWP therefore determined the average population density of chironomid aestivators, the LWP of the previous year then caused the year-by-year density fluctuations**. For example: the population density of aestivator species found in the semiaquatic pool 2 was usually low. A very intensive drought period in 1997 resulted in a clear rise of the population density in 1998, which, however, was still much lower than in most annual yields/site of pool 1 (Figure 28 p 75). I hypothesize that the aesti-

vators (whose dispersal abilities are assumed to be low) are less competitive in relation to the colonizing species and are (directly or indirectly) driven out by the latter if the pool does not dry up intensely. On the contrary, if the habitat is already mostly occupied by aestivating larvae, the settlement by colonizing species will be strongly hindered (see section 5.3.4.). In other words: the lentic water permanence seems to mediate the relative importance of physical and biological control in Chironomidae as also indicated for the invertebrate communities of seven ponds/pools of Wisconsin (USA) by SCHNEIDER & FROST (1996). However, the correlation between LWP and the proportion of aestivators may be obscured for various reasons, e.g.:

(a) Extinction of aestivators by strong drought (see also section 5.3.5.3.). Pool 1 did not refil until December 1995. It is most likely that freezing of the unprotected pool bottom killed most aestivating chironomids, colonizers were therefore predominant in 1996 (Figures 28 + 29 pp 75 and 77, respectively);

(b) Larval densities gradients between shallow and deeper sites. In 1997, pool 1 was subjected to about four months of drought, which enabled *Polypedilum tritum* to form a strong population in 1998 (Figure 79 p 169). Because in 1998, pool 1 fully dried up for a few days only, colonizers increasingly established on deepest sites but not on the shallow sites (represented by sites 1b and 1c, which were more or less dry from the mid of May onwards, see Table 16 p 55), the latter of which were occupied by high numbers of aestivating larvae. This resulted in a strong gradient of larval densities of aestivators within the pool, which was documented in 1999 by the number of emerging adults (Figure 28 p 75). LWP on sites 2 and 3 was equal, but the proportion of emerging aestivators was much higher on site 2 (located in between site 1b/1c and 3, see Figure 9 p 42) than on site 3 in 1999. It is most likely that site 2 was strongly influenced by immigrating larvae which had aestivated in the very temporary 'grass zone' of the pool where traps 1b and 1c had been placed;

(c) Time of drought. If a pool dries up early and refills late in the year, colonizers are not able to form large larval populations because colonizing is inhibited or strongly altered by low temperatures (e.g. pool 3). Because the LWP was not only defined by the duration of drought but also by the minimum water content of the mud, there are pools which severely dry up (low LWP) but relatively late (e.g. pool 1) and therefore support higher numbers of colonizers.

As a conclusion, it appears that the intensity and time of drought form the basic features of a habitat templet, which filters out colonizers or aestivators of Chironomidae in the sense of TOWNSEND et al. (op. cit.). -The habitat templet proposed for Chironomidae of pools 1-3, which consisted of lentic water permanence and predictability of drought (section 5.1.2.) has therefore to be replaced by a templet of lentic water permanence and time of drought (Figure 95), which explains well the community characteristics observed in the present study. The colonizing pools were excluded from Figure 95 since such habitats are of a particular type (spatially unstable pools (puddles), see Figure 92), which, at least in the initial phase of their existence (see section 5.3.1.), are dominated by species with high colonizing powers (which is especially true of *Chironomus dor-*

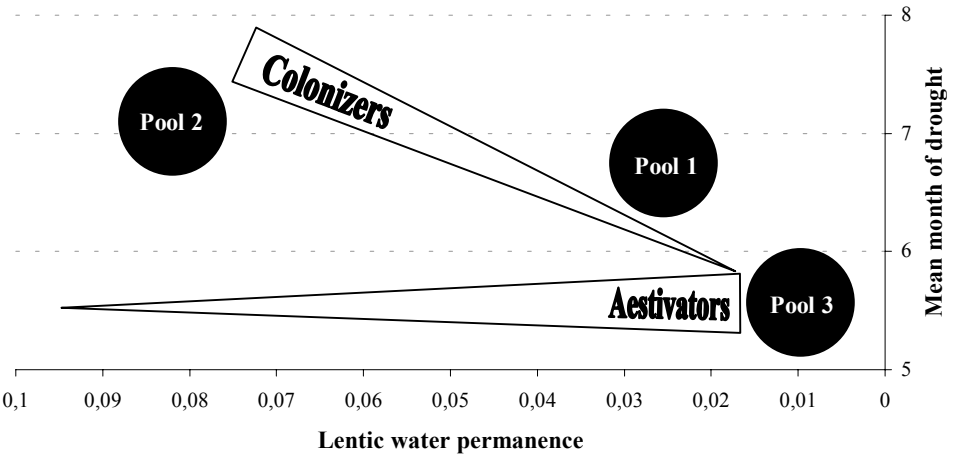

Figure 95: The proposed habitat templet of lentic water permanence and time of drought, which acts to filter out unsuccessful strategists (colonizers or aestivators) in Chironomidae.

salis). **The unimportance of drought predictability for structuring the chironomid communities investigated in the present study is due to the high flexibility of the dominant species' life histories (section 5.3.)**. There is no doubt that predictability of drought plays an important role in determining the composition of communities of other aquatic invertebrates (including that of some Chironomidae, see section 5.3.2.2.) that live in temporary pools (for examples see WIGGINS et al. 1980, WILLIAMS 1987, DETTINGER-KLEMM 2000b). This applies especially to species that exclusively rely on temporary pools and deposit their eggs on the dry pool bottom where they aestivate in eudiapause sensu MÜLLER (1992). Many mosquito species of the genus *Aedes* provide excellent examples of such life cycles which depend more or less on the occurence of a well predictable drought period (e.g. MOHRIG 1969, WIBERG-LARSEN 1978, FALLIS & SNOW 1983). It is likely that a habitat templet consisting of three axes (lentic water permanence, time of drought and predictability of drought) could explain many characteristics of invertebrate communities that occur in spatially stable temporary pool. Such a study is still to appear.

5.2.2. Chironomids of temporary pools, a review

Thirty-four investigations (including the present study) provide information on the Chironomidae of temporary pools, (taxa listed in the Appendix 11). The list does not claim to be exhaustive, as for example, information hidden in taxonomic papers (e.g. CRANSTON & NOLTE 1996 or JACOBSEN 1998 provide data on the drought tolerance of some chironomids) or articles with other purposes (e.g. MATENA & FROUZ 2000 provide data on distributional patterns in *Chironomus*) might have increased the length of the list. No data on the chironomids of temporary pools were found for the Oriental region and a dearth of information is apparent for the Neotropics (NOLTE 1989, 1995) and the Africotropics (only rock pools e.g. MCLACHLAN & LADLE 2001, MILLER 1969). The title of OGBEIBU (2001) pretends to deal with a temporary pond in Nigeria, but its lecture revealed the study site to be permanent. With the exception of the Australis (six papers), our knowledge of the Chironomidae of temporary pools is therefore very scarce for most regions where temporary pools nonetheless constitute a very typical type of lentic freshwater. Six papers were found for the Nearc-

tic- and 19 for the Palearctic, which concentrate most information on temporary pools of temperate latitudes.

5.2.2.1. Temporary wetland pools

Whenever possible, wetland and non-wetland pools were distinguished following the pool terminology introduced in section 5.1.1.. Despite the low number of papers dealing with wetland pools (8 papers), the total number of species encountered in this type of habitat (~ 160 species) is approximately the same as found in non-wetland pools (23 papers). This reflects the fact that non-wetland pools house approximately half the species (~30, e.g. DRIVER 1977 and present study) of wetland pools (60-70, e.g. LEEPER & TAYLOR 1998, STEINHART 1999a, SCHNABEL & DETTINGER-KLEMM 2000a). Wetland pools communities consist largely of species that reach the pool via floods of nearby running waters (SCHNABEL & DETTINGER-KLEMM 2000b). Species typical of running waters were therefore collected in temporary wetland pools (e.g. members of the genera *Cryptochironomus*, *Nanocladius*, *Orthocladius*, *Rheocricotopus*, *Rheotanytarsus* and *Virgatanytarsus*). Most species present in wetland pools are euryoecious and do not specifically live in this type of habitat (SCHNABEL & DETTINGER-KLEMM 2000b); the genera *Ablabesmyia* (e.g. *Ablabesmyia monilis*), *Acricotopus* (e.g. *Acricotopus lucens*), *Chironomus* (e.g. *Chironomus riparius*), *Corynoneura* (e.g. *Corynoneura scutellata*), *Cricotopus* (e.g. *Cricotopus sylvestris*), *Limnophyes* (e.g. *Limnophyes pentaplastus*), *Paratendipes* (e.g. *Paratendipes albimanus/plebejus*), *Phaenopsectra* (e.g. *Phaenopsectra flavipes*) *Polypedilum* (e.g. *Polypedilum nubeculosum*), *Procladius* (e.g. *Procladius choreus*) or *Tanytarsus* (e.g. *Tanytarsus palidicornis*) are typical representatives of these euryoecious species. Characteristically, these species also occur in non-wetland pools. However, some aquatic/semiaquatic species known to be typical of temporary pools (high power colonizers and drought tolerant/resistant aestivators) are a characteristic feature of temporary wetland pools as well, such as *Chironomus tepperi* (Australis, colonizer, STEVENS 1995), *Hydrobaenus lugubris* (Palaearctic, drought resistant, ASHE & CRANSTON 1990, STEINHART 1999), *Kiefferulus* spp. (unclear, genus of worldwide distribution, CRANSTON et al. 1989b), *Limnophyes asquamatus* (Holarctic, drought tolerant, SÆTHER 1990, present study), *Paraborniella* (Australis, drought resistent, JONES 1975, HILLMAN & NIELSEN 1995) and *Polypedilum tritum* (Holarctic, drought tolerant, ASHE & CRANSTON 1990, present study). Of these, *Hydrobaenus lugubris* may be a typical floodplain chironomid whilst the other species are also known from non-wetland pools.

5.2.2.2. Temporary non-wetland pools

THIENEMANN (1954) wrote (loosely translated): 'Since the natural distribution and ecology of chironomids is still poorly known, we do not know with certainty if there are indigenous chironomids of temporary pools although there are some species hitherto only encountered in such habitats (e.g. *Lapposmittia parvibarba*)'. This sentence still applies in 2003! JACKSON & MCLACHLAN (1991) listed 6 species (*Allotrissocladius amphibius*, *Chironomus imicola*, *Chironomus pulcher*, *Harrisonia petricola*, *Paraborniella tonnoiri*, *Polypedilum vanderplanki*) thought to be indigenous to

rain-pools on rock and 1 species (*Chironomus tepperi*) that may be indigenous to rain pools on mud. But at least two of the Australian species (*Paraborniella tonnoiri*, *Chironomus tepperi*) were also recorded in permanent waters (HILLMAN & NIELSEN 1995, SUTER et al. 1995), as is the case for probably all European species (e.g. MOLLER PILLOT & BUSKENS 1990). Considering the little knowledge on temporary pool chironomids of Africa and even Australia it is currently impossible to confirm a species as indigenous or not. There are however typical species of temporary non-wetland pools all over the world, with life histories best suited to this kind of habitat. I presented in section 5.2.1. the two main strategies that determine the communities of temporary pools - colonizing and aestivating. In the following paragraph I discuss the relation of these two groups to temporary non-wetland pools.

The group of **colonizers** comprises (a) ubiquists representing stranded faunas of different permanent freshwater habitats (e.g. *Chironomus riparius, Acricotopus lucens, Corynoneura scutellata, Cricotopus sylvestris, Procladius choreus* in the present study), (b) species typical of permanent pool (e.g. *Xenopelopia falcigera, Xenopelopia nigricans, Psectrotanypus varius* in the present study), (c) eurytopic more specialised colonizers (e.g. *Tanytarsus brundini, Micropsectra lindrothi, Zavrelimyia barbatipes/nubila* in the present study) and (d) highly specialized colonizing species (e.g. *Apedilum elachistus* (NOLTE 1995)*, Chironomus dorsalis* (present study)*, Chironomus imicola* (e.g. MCLACHLAN 1986)*, Chironomus tepperi* (e.g. STEVENS 1995). The dominant subgroup in a given temporary pool community will probably be determined by the species' traits and the potential pool of species present in the surrounding freshwater habitats (e.g. THIENEMANN 1948). However, unless they are already occupied by aestivating species, temporary non-wetland pools should favor the polyvoltine, euryplastic species with high powers of dispersal, the ovipositing females of the larger species might more specifically select the small lentic water bodies. Such a situation was observed during the present investigation and there are unfortunately no other studies to be consulted on that matter. Of the most dominating colonizers reproducing in pools 1-3, *Chironomus luridus*, *Chironomus pseudothummi/uliginosus*, *Psectrotanypus varius*, *Xenopelopia falcigera* and *Xenopelopia nigricans* were typical pool species and only *Corynoneura scutellata* an ubiquist of lentic waters.

Aestivators are the most typical element of chironomid assemblages found in temporary non-wetland pools. These are usually represented by only a few species, which nevertheless - depending on the intensity of drought (section 5.2.1.) - dominate the temporary pool communities at least in terms of abundance. Unfortunately, most European studies on temporary pool chironomids have not collected larvae during the drought period (such collections were only done by DETTINGER-KLEMM & BOHLE 1996, SCHNABEL 1999 and STEINHART 1999). Our knowledge of European aquatic/semiaquatic aestivators is therefore apparently poor. Until now, the only proofs of drought tolerance (for definition see section 5.3.5.3.) were made for *Hydrobaenus lugubris*, *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* (Palaearctic, SÆTHER et al. 2000) and *Polypedilum tritum*. It is likely that *Lapposmittia parvibarba*, *Lasiodiamesa gracilis* (THIENEMANN 1941), *Natarsia*

punctata (FROUZ & MATENA 2000), *Telmatopelopia nemorum* (KREUZER 1940, RAPP 1983, MOLLER PILLOT & BUSKENS op. cit.), *Trissocladius brevipalpis* and *Zalutschia humphriesiae* (MOLLER PILLOT pers. comm.) are also drought tolerant aestivators. It is likely that there are more European aestivator species e.g. *Metriocnemus corticalis* (highly abundant in a temporary pool near Roth (Marburg, Hesse, Germany, see Table 70 p 206 and Appendix 11) or *Propsilocerus lacustris* (= *P. lusatiensis* in BARTHELMES 1964, revised in SÆTHER & WANG 1996). WIGGINS et al. (1980) and GRODHAUS (1976, 1980, 1987b) found *Chironomus*, *Guttipelopia*, *Hydrobaenus*, *Paratanytarsus*, *Phaenopsectra*, *Polypedilum*, *Prodiamesa*, *Tanytarsus*, *Tribelos* and *Wirthiella* on the dry pool bottom of Nearctic temporary pools after long periods of drought. Aestivators therefore occur in all these genera. Do these genera also include aestivator species in the Palaearctic, especially in Germany?

All over the world, *Chironomus* is a typical component of the fauna found in most temporary pool (see Appendix 11). In Central Europe, *Chironomus dorsalis*, *Chironomus lacunarius*, *Chironomus luridus*, *Chironomus piger*, *Chironomus pseudothummi*, *Chironomus riparius* and *Chironomus uliginosus* have also been frequently encountered in temporary pools (e.g. KRIEGER-WOLFF & WÜLKER 1971, WÜLKER & KLÖTZLI 1973, RYSER et al 1978, MATĚNA 1986 & 1990, MATĚNA & FROUZ 2000, present study). These species should be all considered (*Chironomus lacunarius*?) to be colonizers, the most specific of which being *Chironomus dorsalis* (see section 5.3.1.). It is unlikely that *Chironomus* species present in Germany (SAMIETZ 1999) include aestivators as they are defined in this study (section 5.3.5.3.).

There are only two Holarctic species within the genus *Guttipelopia*, *Guttipelopa guttipennis* (Palaearctic) and *Guttipelopia multipunctata* (Nearctic). FITTKAU (1962) notes that *Guttipelopia guttipennis* is typically found in temporary pools and may represent another aestivator species within the Tanypodinae.

There are 17 known Palaearctic species of *Hydrobaenus* (SÆTHER et al op. cit.), three of which (*H. distylus, H. lugubris and H. pilipes*) occur in Germany (SAMIETZ op. cit.). *Hydrobaenus lububris* was previously mentioned as being drought tolerant and it is most likely to be also the case of the two other species.

Many Palaearctic species of *Paratanytarsus* inhabit shallow stagnant waters (REISS & SÄWEDAL 1981) and the genus is also recorded in Australian temporary pools (Appendix 11). Our current knowledge of the ecology of Central European species does not enable us to assume that any German (SAMIETZ op. cit.) *Paratanytarsus* are aestivators.

Only two species of *Phaenopsectra* are known for Germany (SAMIETZ op. cit.). Both species are widespread (*P. flavipes* in the Holarctic and Afrotropical region, *P. punctipes* only in the Holarctic region (SÆTHER et al op. cit.)). There are also no reasons to believe that either of these species are aestivators (GRODHAUS 1987b).

Polypedilum has been encountered in temporary pools all over the world (Appendix 11) and, along

with *Polypedilum vanderplanki*, represents one of the most spectacular example of an aestivator species (section 5.3.5.1.). It is highly likely that this genus comprises a lot more aestivator species as yet unknown. It would therefore be valuable to investigate temporary pool *Polypedilum* species from all over the world.

Until now, there are seven species of *Prodiamesa* known for the Palaearctic (SÆTHER et al. op. cit.), three of which (*P. delphinensis*, *P. olivacea* and *O. rufovittata*) occur in Germany (SAMIETZ op. cit.). There is no reason to consider any of these species as aestivators (e.g. BRUNDIN 1956), though the type locality of *P. delphinensis* is a large but shallow pool, which completely dried up in some years (SERRA-TOSIO 1964).

Many *Tanytarsus* species were collected from autotrophic/mixotrophic temporary and permanent pools all over the world (THIENEMANN 1954, Appendix 11). It is likely that they are predominantly colonizers and there are no indications that any Central European species are aestivators.

There are two Palaearctic species of *Tribelos* (SÆTHER et al. op. cit.) one of which occurs in Germany (*Tribelos intextus* (SAMIETZ op. cit.)). This species is unlikely to be an aestivator (MOLLER PILLOT 1984a, MOLLER PILLOT & BUSKENS op. cit.).

Wirthiella is not known from the Palaearctic (SÆTHER et al op. cit.).

To summarize this section, it appears that temporary pools potentially house a large number of species (Appendix 11) most of which are indeed stranded faunas from other permanent lentic waters. As a rule, only a few aestivator species should be assumed to predominate in the chironomid communities of temporary pools. Although not restricted to temporary pools, these aestivator species are thought to strongly rely upon this habitat in which they achieve high reproductive success. The reasons of this success will be discussed in the following section.

5.3. Autecology

The following sentence written by DANKS (1971c) also applies to the present study: 'This has been a wide-ranging study of chironomid (....) biology, and therefore takes the form of a general exploration of the subject, rather than presenting a detailed analysis of any single aspect'. It is not the scope of this section to discuss every detail of the presented results, but to focus on the question of whether a species' trait can be seen as a specific adaptation to the habitat or not.

5.3.1. *Adult dispersal - the case of Chironomus dorsalis*

5.3.1.1. Introduction

Most dispersal in Chironomidae is thought to be passive (ARMITAGE 1995) and the adult midge 'generally exhibits poor powers of flight and oviposition site selection' (DAVIES 1976). This view is almost certainly simplified and the wish is probably father to the thought. STRENZKE (1960b) hypothesized that, in *Chironomus,* active habitat selection by ovipositing females ('aktive Verteilungs-

regulation') is likely to be more important than passive oviposition in any given body of water ('passive Verteilungsregulation'). In african rock pools, MCLACHLAN (1993) demonstrated that sun exposure was the key factor that determined whether *Chironomus imicola* (sunny pools) or *Chironomus pulcher* (shady pools) laid their eggs in a pool. In the present study (section 4.4.2.3.3.), it appears likely that *Chironomus dorsalis* actively selects puddles as oviposition sites whereas *Chironomus luridus* usually avoids these habitats. High numbers of *Chironomus dorsalis* occured in all ten experimental puddles and was therefore the most characteristic midge of the colonizing experiment (section 4.2.2.). This could be explained (a) by *Chironomus dorsalis* being a specialist invader and thus the first species to arrive; or (b) simply the result of oviposition site selection excluding many species that nonetheless exhibit comparable powers of dispersal. It is likely that both of these aspects were involved in the success of *Chironomus dorsalis*, which fits with MCLACHLAN & CANTRELL'S (1980) definition of an invader as the species''aptitude for finding new pools' (which includes both good dispersal abilities and the aptitude to detect a habitat). This author and coworkers investigated African rock pools most of which were inhabited by a single species - the non-drought tolerant colonizers *Chironomus imicola* or *Chironomus pulcher*, the cryptobiotic *Polypedilum vanderplanki* and the drought resistant Ceratopogonidae *Dasyhelea thompsoni*. *Polypedilum vanderplanki* and *Dasyhelea thompsoni* were restricted to the most transient pools with inundation periods of 1-11 days, while the colonizers formed monocultures in the largest pools with a habitat lasting up to 37 days (MCLACHLAN & CANTRELL op. cit., MCLACHLAN 1988). Because they always harboured several species (see Figure 30 p 80), the puddles of the colonizing experiment were more complex habitats than that of the African rock pools. Furthermore, according to the terminology in section 5.1.1. (Figure 92 p 201) the African rock pools are temporary pools with high spatial stability (and thus offer shelter to aestivators), while the experimental puddles of the colonizing experiment mimic puddles that characteristically exhibit low spatial stability (and thus harbour no or few aestivators). The above terminology was however created with habitat and community characteristics in mind. From a species' point of view, the perspective is different: a habitat is perceived as permanent when a population is able to persist for a long time in the same place or as temporary when the population frequently becomes extinct (HARRISON 1980). From this point of view, *Chironomus imicola* and *Chironomus pulcher* 'perceive' the rock pools as highly temporary dependent on refuges from which they recolonize the rock pools each rainy season (MCLACHLAN 1988). *Chironomus dorsalis* might therefore be considered as the European counterpart of *Chironomus imicola* and *Chironomus piger/riparius* (the second typical species of the colonizing experiment) possibly of *Chironomus pulcher*. *Chironomus imicola* is the better invader (higher abilities of dispersal, shorter generation time) (MCLACHLAN 1988) and *Chironomus pulcher* the better competitor (MCLACHLAN 1993). 'An efficient invader is the first species to arrive and competition with other species for resources, probably for space rather than food, is consequently often not involved initially' (MCLACHLAN & CANTRELL op. cit.). The ability to escape from competition and predation might therefore be the most important factors dictating the evolution of an expert invader, which in turn implies low competitive abilities or predation vulnerability of such invader species (see section

5.3.4. for discussion).

The question that logically arises is whether the present study combined with published data give indications to the effect that *Chironomus dorsalis* and - to a lower extent - *Chironomus piger/riparius* are expert invaders.

5.3.1.2. How specific?

Chironomus dorsalis has been numerously encountered from rain puddles as for example wheel ruts (KEYL 1962, KRIEGER-WOLFF & WÜLKER 1971, RYSER et al. 1978, MATĚNA 1986, DETTINGER-KLEMM & BOHLE 1996, WÜLKER 1999, MATĚNA & FROUZ 2000). The species was also shown to occur in other types of habitat, such as lakes and rivers (WÜLKER op. cit.), and especially ponds (RYSER et al. op. cit., DETTINGER-KLEMM 1995b, MATĚNA & FROUZ op. cit.), where the species was usually rare (except when the habitat had been newly created). These permanent habitats may represent low-density refuges as already discussed for the great African lakes in the case of *Chironomus imicola* (MCLACHLAN 1988).

Chironomus riparius is a euryoecious species (ubiquist in lentic and lotic waters) that is highly tolerant to environmental pollution (for some references see Appendix 3). Nevertheless, it also typically occurs in temporary waters (MATĚNA & FROUZ op. cit.) and is also able to numerously colonize newly created habitats (RYSER et al. op. cit., present study). Following the previous definition, the species is therefore likely to be an invader.

5.3.1.3. How remote?

One scope of the colonizing experiment was to reveal differences in colonization patterns in relation to the distance of puddles from the closest potential colonization source. The experiment failed to meet that aim (section 4.2.2.3.) since the distances to the closest aquatic habitat did not exceed 700 metres (Table 4 p 20) and the dispersal ability of the Chironomidae had been greatly underestimated (pilot study). Thus, the midge communities of the experimental puddles were very similar (Figure 32 p 83). Using radio-tagged individuals of *Chironomus imicola*, MCLACHLAN (1983a) calculated an average dispersal distance of 442 m (0-847 m) during the rainy season. In another study MCLACHLAN (1988) showed that the average distance of 'imicola-pools' to the closest potential refuge was 920 m. However, these data rather reflect the limitations of the methods applied than the species real dispersal ability, since MCLACHLAN & CANTRELL (1980) showed that *Chironomus imicola* was able to colonize artificial pools from natural pools the nearest of which was several kilometres distant. A scale of several kilometres would therefore be necessary for a colonizing experiment as conducted during the present study to directly reveal differences in the species dispersal abilities.

5.3.1.4. How fast?

The time until first emergence was used as an indicator of colonization velocity. These measure-

ments encompass the time until the first oviposition and the duration of total development. The data indicate (differences not significant for each species, see Figure 31 p 81) that amongst the four typical chironomid invaders (*Chironomus dorsalis*, *Chironomus piger/riparius*, *Corynoneura scutellata* and *Tanytarsus buchonius*), *Chironomus dorsalis* was the first to emerge on average. Development times were supposed to be comparable (section 5.3.2.3.). These data therefore support the hypothesis that *Chironomus dorsalis* is the better invader. Daily inspections and counts of egg masses would have been much more appropriate (and accurate!) in order to answer the question of whether *Chironomus dorsalis* is the fastest invader. This method would unfortunately also be very laborious (as attributing an egg mass to a given species would have involved time-consuming lab rearings). Since the colonizing experiment was conceived as a pilot study, such time-consuming design was not chosen. It was however possible to estimate the time of first colonization by ovipositing females of *Chironomus dorsalis* by taking into account the temperature characteristic of the species' developement and the ambient water temperatures measured (section 4.4.2.3.1.). The results revealed that the first *Chironomus dorsalis* females arrived 2-7 days after the experimental pools were exposed. This is also the case of *Chironomus imicola* who also requires several days to appear in a newly flooded pool (MCLACHLAN & CANTREL 1980).

5.3.1.5. Are there morphological indicators of flight ability?

Permanent habitats select for non-dispersers and temporary habitats for dispersers (from the species point of view as previously mentioned, HARRISON (1980)). If wings are vestigal (e.g. *Tethymyia*, a species of intertital rocks (CRANSTON et al. 1989a)), strap-lake (e.g. the terrestrial *Eretmoptera* (CRANSTON et al. op. cit.)) or short-winged (e.g. the terrestrial *Smittia brevipennis* (GOETGHEBUER 1934) or *Clunio* (CRANSTON et al. op. cit.)), limitations in flight are evident. This, accordingly, also applies to species with reduced flight ability ('skaters', e.g. *Hydrobaenus lugubris*, *Fleuria lacustris* and *Propsilocerus lacustris* (BARTHELMES 1964, STEINHART 2000b). A switch of morphs within a species (e.g. alate and apterous morphs in aphids (HARRISON op. cit.)) is not yet known to occur in the Chironomidae (ARMITAGE 1995). However, DELETTRE (1988) observed in the immigrant species *Limnophyes minimus* clear differences of the average wing length between individuals present in the aerial flow (long wings) and the resident emerging population (short wings). This result indicates that there might be 'flyers' and 'non-flyers' within the same species of a chironomid midge.

MCLACHLAN (1986) showed that flight requirements are very different for males and females of the expert invader *Chironomus imicola*: males are primarily selected for the aerobatic ability necessary in swarms (small body size, narrow, fast-beating wings with short stroke and lower ability to perform sustained flights), while females primarily fly in order to disperse and lay eggs (larger body size, longer and broader wings to carry the load of eggs, slower wing beat with greater amplitude and a much higher ability (about 40 %) to perform sustained flights). Most male Chironomidae do form mating swarms into which females enter to gain a mate. Though there are differences in swarming behaviour (for review see ARMITAGE op. cit.), the selection for aerobatic ability in males seems to be most important (MCLACHLAN & CANT 1995, MCLACHLAN 1997, MCLACHLAN 1999).

Therefore - at least for closely related species - the necessities for male flight might not much differ between the species, irrespective of whether species is a colonizer or not. This seemed to be the case in the present study as the wing length/wing width ratio (= aspect ratio) of the males in all four species (*Chironomus dorsalis*, *Chironomus luridus*, *Chironomus piger/riparius* and *Chironomus pseudothummi/uliginosus*) was identical (Figure 56 p 122):

Since females fly primarily in order to disperse and lay eggs (MCLACHLAN 1986), there should be morphological differences between colonizers and non-colonizers whenever active flying is of importance. To date three hypotheses have been investigated:

(1) The females of larger chironomid species are the better dispersers (MCLACHLAN 1985b). This does not seem to be the case (e.g. DELETTRE op. cit.). The present study revealed that very small species such as *Corynoneura scutellata*, small species such as *Tanytarsus buchonius* and medium-sized species such as *Chironomus dorsalis* and *Chironomus piger/riparius* were all good colonizers. Within the genus *Chironomus* (a genus with comparatively large species), the larger species (*Chironomus plumosus* being one extreme) live in the permanent habitats and the smaller species (*Chironomus dorsalis* being one of them) live in temporary habitats. MCLACHLAN (1985b) found this to be the case but disregarded it in favour to his a priori hypothesis of larger species being the better invaders.

(2) Larger females within a species are the better invaders (MCLACHLAN 1983b, 1986). Even this remains questionable, since wing load (body weight/wing area) increases with size (DELETTRE op. cit.). The aspect ratio of the female 'imicola' wing remains constant in individuals of any size. Consequently - for simple allometric reasons (wing length increases with an exponent of 2 and the body volume with an exponent of 3) - the wing load increases in larger females of *Chironomus imicola* too and MCLACHLAN never showed that larger females were able to carry a higher load for longer.

(3) Because they have different flight requirements, males are smaller than females (MCLACHLAN 1986). This cannot be maintained in such a universal sense. For example, in *Smittia* spec. 1 and *Smittia pratorum* the weight of both sexes were similar (DELETTRE op. cit.), wing lengths (a commonly used correlate of body length) indicate that males of *Paratrichocladius rufiventris* might be larger than females (MCLACHLAN 1999).

Chironomidae are very small and 'flying in a universe approaching the consistency of treacle' (MCLACHLAN & NEMMS 1996). *Chironomus imicola* and *Chironomus pulcher* both select their oviposition sites and both exhibit wide-range dispersal - active dispersal (at least directed movements from and to a habitat) must therefore be involved. Insects seem able to control their flight, within a layer of air near the ground ('boundary layer', DELETTRE op. cit.). Some species avoid downwind transport and try to remain within the 'boundary layer' (residents, DELETTRE op. cit.). In the present study, the aestivator *Polypedilum tritum* usually behaved in such a way by flying near the ground. In contrast (as evidenced by the very small *Limnophyes minimus* in DELETTRE op. cit.), colonizers

may tend to free themselves from the 'boundary layer' by actively searching downwind transport and the wide-range dispersal that would stem from it. Once eclosed from the pupa, *Chironomus dorsalis* rises up into the air until the observer looses sight of it (pers. obs.). This behaviour contrasts with that of *Polypedilum tritum*. It is likely that *Chironomus dorsalis* is actively trying for achieve downwind transport as previously described. Behaviour rather than body size therefore seems to determine whether a species is a disperser or resident and even very small species are capable of wide-range dispersal. It is questionable whether small Chironomids with wide-range dispersal are also able to actively search for a very distinct type of habitat (as observed in *Chironomus imicola* and as very likely in *Chironomus dorsalis*). For example, the very small *Corynoneura scutellata* is an ubiquist of lentic waters and the small *Tanytarsus buchonius* - once thought to be crenophilic - encounters very different types of habitats (for quotations see Appendix 3). Possibly only the larger species amongst Chironomidae are capable of actively selecting their habitat. I suggest that in these **passive downwind transport is the most important for wide-range dispersal whereas directed flights are finally undertaken by females selecting the habitat for oviposition**. Distinct differences of the morphological flight parameters between long-winged dispersers and non-dispersers might therefore be particularly obvious in the larger species. In the present study, I assumed that the better invaders had relatively broader wings (lower aspect ratio), relatively more muscles (lower thorax ratio) and more marked sexual dimorphism. All these assumptions were confirmed in the present study (section 4.3.3.): (a) females of *Chironomus dorsalis* (and to a lower extent those of *Chironomus piger/riparius*) had relatively broader wings and relatively longer thoraxes than *Chironomus luridus* and *Chironomus pseudothummi/uliginosus*; (b) sexual dimorphism was strongest in *Chironomus dorsalis*, intermediate in *Chironomus piger/riparius* and lowest in *Chironomus luridus* and *Chironomus pseudothummi/uliginosus*. **The aspect ratio and the thorax ratio may therefore act as a true indicator of a species' dispersal ability**.

All data available indicated that *Chironomus dorsalis* is an expert invader and that the species is largely comparable with *Chironomus imicola* that occurs in African rock-pools.

5.3.2. Characteristics of growth and development

5.3.2.1. Low developmental zero? High thermal coefficients? Higher upper lethal limits?

High thermal coefficients and a low developmental zero (early resumption of growth in winter/spring and an early spring emergence) are advantageous to species dwelling in temporary pools that usually dry up in spring (section 5.1.3.). The temporary woodland pool 3 was a good example of the type of pool that dries up in spring. *Paralimnophyes hydrophilus* - a typical inhabitant of woodland pools - presents some of the characteristics thought to advantage species of these pools. But when comparing with the literature (see Appendix 12), **there is no reason to assume the developmental zero of 3 °C and an early spring emergence to be a specific character of temporary pool species** (TOKESHI 1995a). The eurytopic species *Acricotopus lucens* (Figure 26 p 70) and

Tanytarsus sylvaticus (GODDEERIS 1987), for example, are early spring species and the two eurytopic species *Paratendipes albimanus* and *Phaenopsectra flavipes* have developmental zeroes of 4°C (WARD & CUMMINS 1979) and 2.4 °C (MACKEY 1977), respectively. An impressing example of hibernal growth and emergence is *Hydrobaenus kondoi* living in Kiso River (Japan), which exhibits two distinct emergence peaks in December and February with a theoretical zero growth of -2 °C (KONDO 1996). Hibernal emergence is not rare in Chironomidae (FERRINGTON 2000). Since cool headwaters may represent an ancestral habitat of chironomids (DANKS 1971c, ROSSARO 1991) adaptations to coldness should be considered a widespread characteristic of Chironomidae.**The high thermal coefficients of total development (Q_{10} = 4.2-5.7, see Table 44 p 148) over a relatively wide range of temperatures (5-15 °C) in *Paralimnophyes hydrophilus* might however be the result of a specific adaptation**, because the daily temperature of temporary pools can strongly fluctuate (section 5.1.3.). Investigations of the developmental period over a wide range of temperatures are rare (Appendix 13) and species with relatively high developmental zeroes and/or cue temperatures for dormancy (see below) can be excluded from the present considerations. *Eukiefferiella ilkleyensis* is an epiphytic species living in rivers and brooks (LEHMANN 1972, STOREY 1987), which are habitats with comparatively mild temperatures (see e.g. Table 70 p 206). From the data presented in STOREY (op. cit.), I calculated the theoretical developmental zero (T_0) and the Q_{10}-values for total development, which gave the following figures: T_0 (larval growth) = 1 °C (by exclusion of mean growth rate at 18 °C when fed with 'winter diet'), Q_{10} (total development at 9-14 °C) = 2.6 (no emergence at 5 °C). This species has a comparatively high temperature threshold for pupation and adult emergence (between 5 and 9 °C) and Q_{10}-values of the most relevant temperature range can be interpreted as normal. *Hydrobaenus kondoi* represents a cold stenothermous chironomid (T_0 see above) which forms larval cocoons when temperatures are ≥ 10 °C (summer-dormant). Again Q_{10}-values were calculated from data on total development provided (KONDO op. cit.): Q_{10} (3.5-6.0 °C) = 4.1, Q_{10} (6-8 °C) = 3.2. These Q_{10} values are comparatively high, but the temperature range which can be used for growth and development is quite narrow. *Hydrobaenus lugubris* is the third species for which data that can be used for comparison are available. This species is typical of temporary pools in flood plains, it usually enters Parapause sensu MÜLLER (1992) on reaching instar II in spring (summer-dormant) and when temperatures are around 5 °C this species comes out of dormancy in autumn (STEINHART 1999). Again T_0 and Q_{10}-values for total development were calculated from the original data: T_0 = 3.7; Q_{10} (5-10 °C) = 8.8; Q_{10} (10-15 °C) = 4.8; Q_{10} (15-20 °C) = 0.9. These data indicate that *Hydrobaenus lugubris* is psychrophilic with upper suboptimal temperatures lying between 15 and 20 °C. Development into adults is at least possible from 5 °C upwards and high Q_{10} values are reported for 5-15 °C as in *Paralimnophyes hydrophilus*. **Again, the temporary pool species presents high thermal coefficient over a wide range of temperatures**. This, indeed, can be a result of specific adaptations to the temporary habitat. More data on other species are still to appear before this assumption can become more than speculation. In contrast to *Hydrobaenus lugubris*, *Paralimnophyes hydrophilus* is not clearly psychrophilic and the laboratory data compelled me to designating the species as psychrophilic-eurythermous.

Because of a lack of data, *Limnophyes asquamatus* must be excluded from the present considerations. *Polypedilum tritum* (eurythermous-thermophilous) and especially *Chironomus dorsalis* (thermophilous) are warm-water species with late spring emergence. These species both have developmental zeros around 5°C, high upper and lower lethal limits for total development. *Chironomus dorsalis* also has a high cue temperature for oligopause. These characteristics are hardly suited to temporary pools with an early drought. This was observed for the population of *Polypedilum tritum* in the woodland pool (section 4.4.2.1.1.). As there is unsufficient information available, it is not known whether the relatively high upper lethal limit for total development in *Chironomus dorsalis* (between 31.1 and 33.5 °C) is a specific adaptation to the strong daily fluctuations of temperatures in puddles (section 5.1.3.) or whether congeners living in other lentic waters exhibit the same values. In the present study however, the permanent pond species *Chironomus annularius* and *Chironomus* cf. *nuditarsis* were successfully raised to the imago stage at 30.2 °C. **It is therefore likely that the upper lethal limit determined for *Chironomus dorsalis* is not unusual within lentic water *Chironomus***.

5.3.2.2. Timing of the life cycle, dormancies

5.3.2.2.1. Overview

In most aquatic insects, the larval stage of development is highly susceptible to drought and the egg is the potential 'blank' on which many mechanisms of life cycle timing and resistance evolved. This is not the case in Chironomidae. In this dipteran family the larva is the most resistant developmental stage which allows for a more flexible timing and fine-tuning of the life cycle. Though investigations are scarce, a discrete arrest of development (dormancy) has been documented for all larval instars: instar I e.g. *Paratendipes albimanus*, (WARD & CUMMINS 1978); instar II e.g. *Polypedilum 'uncinatum'* (BEATTIE 1978b), *Tanytarsus lestagei*-agg. (GODDEERIS 1987), *Hydrobaenus kondoi* (KONDO 1996) and *Hydrobaenus lugubris* (STEINHART 2000b)); instar III e.g. *Tanytarsus debilis*, *Tanytarsus sylvaticus* (GODDEERIS 1987), *Stempellina* spec. (SUNDERMANN & DETTINGER-KLEMM 2002) and *Parametriocnemus stylatus* (see Table 40 p 139); instar IV e.g. *Chironomus plumosus*, *Chironomus nuditarsis* (FISCHER 1974) and *Pseudodiamesa branickii* (NOLTE & HOFFMANN 1992). Most growth occurs in the instar IV (e.g. 40-45 % growth in length in *C. dorsalis, P tritum and P. hydrophilus*), which, looking at the imaginal discs, can be subdivided into 9 subphases (WÜLKER & GÖTZ 1968) and a 'fine-tuning' of the life cycle can be even achieved by developmental pauses within these subphases (BUTLER 1982, 1987). Despite the assumptions of some authors, (WILLIAMS & HYNES 1976a,b, GODDEERIS 1987), it is still unclear whether there is egg dormancy or delayed hatching in Chironomidae (TOKESHI 1995a). Normally, the eggs and pupae should be considered the most vulnerable aquatic stages in Chironomidae.

The most frequent cues for dormancy are temperature and/or day lengths below a specific threshold (e.g. DANKS 1971c, FISCHER op. cit., STEINHART 1999, 2000a,b, GODDEERIS et al. 2001, SUNDERMANN & DETTINGER-KLEMM op. cit.). But low food quality/availability (BEATTIE op. cit.,

WARD & CUMMINS 1978, 1979) or low oxygen concentrations (HAMBURGER et al. 1994) can also induce dormancy. Quiescences and oligopauses sensu MÜLLER (1992) are the most common types of dormancies. *Hydrobaenus lugubris* actually offers the only well-studied example of a parapause sensu MÜLLER (op. cit.). Many summer-dormant species, such as *Parametriocnemus stylatus* (see Table 40 p 139), *Stempellina* spec. (SUNDERMANN & DETTINGER-KLEMM op. cit.) and all the species of the genera *Hydrobaenus*, *Trissocladius* and *Zalutschia* (MOLLER PILLOT pers. comm.) might follow a similar pattern. To date no eudiapause sensu MÜLLER (op. cit.) is known for Chironomidae.

5.3.2.2.2. Quiescences induced by factors other than temperature and photoperiod

Under laboratory conditions, *Polypedilum tritum* showed a **nutritive quiescence**, which was also observed in *Chironomus plumosus* (REIST & FISCHER 1987). When food supply was discontinued, the larvae suspended their development into adults and did not resume their growth until new food was added. The larvae were kept in nutritive quiescence for more than one year (pers. obs.).

In the field (section 4.4.2.1.1.) the second generation of *Polypedilum tritum* occurring in pool 1 in 1997 was not very abundant and there appeared to be no emerging second generation for pool 1 in 1999, although water was still present (Figure 79 p 169). A similar situation was observed for the third generation of *Paralimnophyes hydrophilus*, which almost failed to emerge, especially in 1997 when no single specimen emerged during the time when individuals of the third generation were expected (section 4.4.2.1.3. Figure 82 p 177). The data indicated that larvae of both species fall into dormancy, maybe in reaction to **low oxygen** levels or other environmental **stressors**.

All larval stages of *Polypedilum tritum* and *Paralimnophyes hydrophilus* were drought tolerant (section 5.3.5.3.). The species' life cycles are therefore not tightly linked to the drying cycle and their response to **drought** is also a quiescence.

The ability to fall into quiescence when the environment's harshness goes beyond an unknown threshold is probably an adaptation to adverse habitats/conditions in general (A-selection). *Polypedilum tritum*, for example, is not restricted to temporary pools (for references see Appendix 3) and, in The Netherlands, was also abundant in acidified waters (BUSKENS 1987, BUSKENS & VERMIJMEREN 1989). Such A-selected species are probably largely preadapted to life in temporary pools and even minor changes in their physiology are likely to enhance their ability to withstand long periods of drought (section 5.3.5.).

5.3.2.2.3. Annual timing of the life cycle

The oligopauses observed in the instar IV of both *Chironomus dorsalis* and *Polypedilum tritum* (section 4.4.1.2.3.) are widespread amongst Chironomidae (DANKS 1971b, 1978, TOKESHI 1995a). These oligopauses synchronize the emergence of the first spring generation. Synchronized emergence ensures that individuals are able to find a mate (see section 4.4.2.1.) which is probably of particular importance in populations with few individuals (e.g. *P. tritum* and *P. hydrophilus* in pool 2) or after the breakdown of a population (e.g. *Polypedilum tritum* in pool 1, 1996 or *Paralimnophyes hydrophilus* in pool 1, 1996/1999 and pool 3, 1997). The oligopauses of *Chironomus dor-*

salis, Chironomus nuditarsis, a large permanent water species (FISCHER 1974), the eurytopic *Chironomus riparius* (SCHARFF 1973, GODEERIS et al. 2001) and probably also the pool dweller *Chironomus luridus* (section 4.4.1.2.7.) are all induced by low temperatures and short-days. The oligopause in *Chironomus dorsalis* is therefore not the result of an adaptation to temporary pools as this phenomenon is widespread within the genus. The same applies to the daylength induced oligopause in *Polypedilum tritum* (the threshold of daylength is assumed to lie between 12.3 and 14.3 h), which is very close to the situation described for *Chironomus plumosus* (threshold of day length 13.5 h, FISCHER op. cit., RYCHEN-BANGERTER & FISCHER 1989). *Chironomus dorsalis* has a relatively high thermal threshold for oligopause and is therefore clearly thermophilous. *Polypedilum tritum* however does not present such a threshold why I definded it as eurythermous-thermophilous. Nevertheless, both species emerge relatively late and their life histories are largely unsuited to temporary pools (like pool 3) that usually dry up in May. *Polypedilum tritum* nonetheless occured even in pool 3, its numbers being low in all years but 1995 when it thrived following an unusually late drought which allowed a second generation to emerge.

The impact of the photoperiod on larval development for *Paralimnophyes hydrophilus* and *Limnophyes asquamatus* was not investigated in the laboratory. Both species start to emerge at the end of March and stop in October. The field observations (section 4.4.2.1.3.) indicated that days shorter than 11.0-12.4 h block the developement of *Paralimnophyes hydrophilus* into adults. On the other hand, temperatures above the developmental zero did not induce a dormancy of *Paralimnophyes hydrophilus* larvae in the laboratory experiments. The annual timing of the life cycle therefore seems as straightforward as that of *Polypedilum tritum*, with the difference that the threshold of day length seems lower in *Paralimnophyes hydrophilus.* The same may apply for *Limnophyes asquamatus* although this species may only exhibit a thermal quiescence as postulated by DELETTRE & TREHEN (1977) for *Limnophyes minimus*.

As a conclusion, the **annual timing of the life cycles of all four species typical of temporary pools is not at all linked to the drying cycle and multiple generations are able to develop whenever conditions are suitable**. Additionally, there is great evidence (section 4.4.2.1.3., Figure 83 p 179) that the drought of the previous year can desynchronise the spring emergence.

At first sight, the annual timing of the life cycle of *Hydrobaenus lugubris*, a typical species of temporary floodplain pools (section 5.2.2.1.), seems to be strongly linked to the pool's drying cycle. After the early emergence of adults in spring, the majority of larvae develop only into instar II then stop growth and development and build a cocoon from which they do not emerge until the temperatures fall below a threshold of about 5°C (STEINHART 1999, 2000a, 2000b). Similar summer dormancies appear however widespread amongst Chironomidae, regardless of the habitat permanence (see section 5.3.2.2.1.). Summer-dormant species are largely preadapted to life in temporary pools that dry up in early spring. **This chapter and the previous therefore indicate that there are two strains of Chironomidae which are preadapted to life in temporary pools: (a) the stress-tolerant species; and (b) the summer-dormant species**. Only a few further adaptations to drought (section 5.3.5.) or dispersal (see section 5.3.1.) are considered necessary for a well-adapted tempo-

rary pool species.

The induction of dormancy by long-days in *Chironomus annularius* was not yet known in Chironomidae. The data presented in SMITH & YOUNG (1973) suggested the species to be bivoltine, exhibiting a spring peak of emergence in April/May and a lower autumn peak in the August. *Chironomus annularius* is typical of larger permanent water bodies and even tends to dominate newly created and polluted habitats (KRIEGER-WOLFF & WÜLKER 1771, RYSER et al. 1978, MATĚNA 1990, DETTINGER-KLEMM 1995b). Low oxygen levels in summer may be the key factor in the life history of species living in such habitats (HAMBURGER et al. 1994, 2000). Dormancies induced by long days has possibly evolved to adjust the life cycle of *Chironomus annularius* to periods when oxygen levels are low or absent and may therefore be a specific adaptation to habitats with cyclically depleted oxygen levels. Further investigations are however needed before confirming this assumption.

5.3.2.3. Exclusively fast development?

Short generation times are often thought to be an adaptation that enables species to successfully colonize temporary pools (e.g. MCLACHLAN & CANTRELL 1980, NOLTE 1995, DETTINGER-KLEMM & BOHLE 1996). But this assumption does not rule out the possibility that short life cycles are a widespread preadaptation among Chironomidae. I have gathered much data on development times of Chironomidae (see Appendix 13). To this date, most information is concerned with the genus *Chironomus* whereas only little is known about Tanypodinae and Diamesinae.

I will now discuss with particular attention the results obtained for *Chironomus dorsalis.* I concentrate on this species as its larvae are not drought tolerant and must therefore really comply with a temporary habitat (puddles). This species might accordingly exhibit short generation times in order to successfully exploit its highly temporary habitat and to escape from desiccation. The fastest development time (only 11 days) was observed for temperatures of above 27 °C. This development is indeed very fast and comparable with that of some tropical species of the genus. The fastest generation time known so far for Chironomidae is of 7 days for the neotropical *Apedilum elachistus* (NOLTE op. cit.). MACKEY's (1977) data are questionable, particularly the larval growth periods (15 °C!?) of 5 d (*Corynoneura coronata*), 6 d (*Microcricotopus bicolor*), 7 d (*Parachironomus biannulatus*), 8 d (*Dicrotendipes modestus*, *Rheotanytarsus photophilus*), 9 d (*Synorthocladius semivirens*) and 10 d (*Cladotanytarsus atridorsum*) appear highly unreliable and are thus excluded from this discussion. There is almost a total absence of information for the development of European species at temperatures above 27 °C but the permanent water species *Chironomus annularius* showed the same minimum generation time as *Chironomus dorsalis*. The most relevant temperatures for temperate species are that below 25 °C and the data presented in the Appendix 13 and analysed in the section 4.4.1.2.6. give no evidence that *Chironomus dorsalis* has the exclusivity of a fast generation time. Furthermore, the generalized view that the smaller species develop faster than the larger ones (e.g. WOTTON et al 1992, TOKESHI 1995a) does not seem to hold for Chironomidae. **I conclude that short generation times are a prerequisite common in lotic and lentic Chironomidae**.

5.3.3. Determinants of the adult body size

The present study showed that thorax length and wing length were strongly correlated with body size in *Limnophyes asquamatus*, *Paralimnophyes hydrophilus*, *Chironomus dorsalis* and *Polypedilum tritum*. The correlation between body size and wing length on the one hand and body size and fecundity on the other is a well-documented phenomenon in Chironomidae (e.g. MCLACHLAN 1983b, MCLACHLAN 1985b, XUE & ALI 1994a,b, SURAKARN & Yano 1995). **Body size, wing length and thorax length can therefore be used as good indicators of fecundity**. Generally, large species carry more eggs than smaller ones, the latter having the relative larger eggs (NOLTE 1993, section 4.4.1.1.). An interspecies comparison of fecundity is not possible before a reliable correlation of species fecundity and body size is available. Such a correlation would enable the definition of a species' average fecundity in relation its size. To complicate matters in addition, there are species that always lay one egg mass (semelparous e.g. XUE et al. 1994, MCLACHLAN & YONOW 1989) and other capable of laying up to six masses of increasingly small size (iteroparous e.g. FISCHER 1969, DANKS 1971b, MARTIN & PORTER 1977, MCLACHLAN & YONOW 1989, XUE & ALI 1994b). It is also known that at least some adult Chironomidae feed and produce more eggs and/or egg masses when they have taken food (e.g. MARTIN & PORTER op. cit., MCLACHLAN & YONOW op. cit.). It is likely that *Chironomus dorsalis* is potentially iteroparous as are many other species of the genus. *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* are semelparous, which probably also applies to *Polypedilum tritum*. I could demonstrate that *Limnophyes asquamatus* females live longer when food is available (section 4.4.1.1.). The question of whether feeding enhances the fecundity of this species however requires further testing.

5.3.3.1. Temperature and dormancy

The laboratory experiments revealed that body size was strongly dependent of temperature and the occurence or not of dormancy (section 4.4.1.2.9.). Not surprisingly, the largest individuals that emerged in this study's natural habitats did so in spring (section 4.4.2.2.) as also described in literature (e.g. REIST & FISCHER 1987, OKAZAKI & YANO 1990, SURAKARN & YANO 1995, GODDEERIS 2001). The decrease of body size with increasing temperatures is mainly due to a faster development rate in relation to growth rates so that larvae pupate at progressively shorter lengths (OSTROVSKY 1995). The increase in adult body size when dormancy interrupted development is also easily explained: oligopausing larvae continue feeding and growing when temperatures are above the developmental zero and thus become larger (INEICHEN et al. 1979). This is not the case in species that build cocoons in which they remain inactive throughout dormancy (see section 5.3.2.2.1.).

5.3.3.2. Larval densities and the adult body size in *Chironomus dorsalis*

In the lab experiments, high larval densities and the presence of a competitor led to smaller adults of *Chironomus dorsalis*. This confirms the results of other studies (e.g. RASMUSSEN 1985, REIST &

FISCHER 1987 and OKAZAKI & YANO 1990). Food quantity, food quality and predation are also known to alter the growth and final size of larvae and adults (BIEVER 1971, WARD & CUMMINS 1979, BALL & BAKER 1995, GRESENS 1997, VOS et al. 2000). MCLACHLAN (1983a) proposed two size dependant strategies in *Chironomus imicola* at 'low' (10^4 larvae/m², supposed to mimic the initial phase of the drying cycle) and 'high' larval densities (10^6 larvae/m², supposed to mimic situations before habitat extinction). At 'low' densities there was a positive correlation of female body size and time to emergence and MCLACHLAN (op. cit.) assumed a mode of spreading the risks: (a) the first adults emerge relatively safely but are small whereas the late emergers are the most fecund and better invaders but have a higher risk of being subjected to drought; (b) at 'high' densities, larvae grew asynchronous, their majority remained small with a few that grew fast and emerged early as large 'super' females. Survival at 'high' densities was extremely low and probably dead larvae were recycled as protein rich food source by the few larvae that had not stopped growing. This 'high density strategy' sacrificed survival of large numbers in favour of the development of a few large adults. MCLACHLAN's hypothesis of 'spreading the risks at 'low'-and 'super females' at 'high' densities was not confirmed for *Chironomus dorsalis* (section 4.4.2.3.2.). But my results are in accordance with those presented by WOTTON & ARMITAGE (1995). These authors investigated the colonization of slow sand filter beds by *Cricotopus sylvestris*, *Psectrocladius limbatellus* and *Tanytarsus fimbriatus* in Great Britain. Despite the authors' expectations, the largest adults of these three species emerged first from the slow sand filter beds and the size of emerging adults then diminished markedly. This decline of the adult body size after the initial emergence from the slow sand filter beds was then followed by an intermediate increase and then by a further decrease of the adult body size during the course of emergence. The adult body size of *Chironomus dorsalis* in the colonizing experiment generally followed a similar although much less pronounced pattern (Figure 90 p 192). Which are the factors causing these fluctuations of adult body size?

Comparisons between the adult body size of *Chironomus dorsalis* in two natural habitats and in the laboratory rearings (Table 64 p 195) showed that the adults of the colonizing experiment were extremely small. WESTPHAL (1982, 1984) exposed exactly the same experimental boxes within the open-air area of the department of Biology of the Philipps-University of Marburg (see Figure 8 p 41). Accordingly the most dominant benthic invertebrate species was *Chironomus dorsalis*. The larval densities reached 17 300-40 800 larvae/m². He used a mesh size of 0.25 mm in which only instars III and IV were likely to remain so the overall larval densities of *Chironomus dorsalis* were probably much higher. These densities can be compared with the present study. The density experiment (section 4.4.1.4.) indicated that the adult body size and survival were dependent on a density threshold that lay between 25 000 and 50 000 larvae/m². These results are comparable to those of KAJAK & PRUS (2001) who found that densities above 20 000 to 40 000 larvae per square metre were detrimental to the development of *Chironomus plumosus*. With regard to larval densities provided by WESTPHAL (op. cit.), **there is great evidence that high larval densities of the conspecifics were at least partly responsible for the small size of adults that emerged from the experimental boxes of the colonizing experiment.** IKESHOJI (1973, 1974) identified calcium nitrite

as an overcrowding factor in a *Chironomus* species which larger larvae impeded development of the younger larvae at high densities. **Furthermore there is great evidence that high larval densities can induce dormancy and consequently alterations in voltism** (MCLACHLAN op. cit., RASMUSSEN op. cit., IWAKUMA et al. 2000). Accordingly, I explain the emergence- and body size pattern of *Chironomus dorsalis* in the colonizing experiment (Figures 88 and 90 pp 190 and 192, respectively) by the following reasoning:

(1) During the initial phase of colonization there is a strong increase in larval densities. For example, the initial densities increased from 350 to 10 850 larvae/m² (Table 65 p 196, a mean egg number of 371 was used for calculation (see section 4.4.1.1.)) within four days. Larvae hatching from the first mass(es) are likely to grow better than the later ones, which consequently resulted in the first emergers being relatively large and a subsequent decline of the adult body size.

(2) A critical density of the larger larvae induces dormancy in the smaller ones. This dormancy does not end until the first cohort of larger non-dormant larvae has emerged. A density-induced dormancy in the younger larvae would explain the emergence trough after the initial peak of emergence in the colonizing experiment (Figure 88 p 190).

(3) Towards the end of the first emergence peak, dormant larvae continue to grow and, again, the larger larvae do better than the smaller ones. This would account for the intermediate increase and subsequent decrease of the adult body size following the first emergence peak, which was only suggested in the present study (Figure 90 p 192) but clearly shown by WOTTON & ARMITAGE (op. cit.).

Further research is however necessary before these thoughts can become anything more than speculation. Aditionally, the adults that emerged in the colonization experiment were even smaller than those of the high-density lab experiments (Density 2 in Table 64 p 195). **Interspecific competition and/or low food levels may therefore also have had a negative influence on the adult body size of *Chironomus dorsalis* in the colonizing experiment**. Oxygen levels within the experimental pools did not seem to be critical (see Figure 22 p 60 and the following section). Fast colonizing and growth, combined with a density-dependant dormancy (that only takes place at very high densities) may be key factors in achieving an efficient exploitation of resources (space and food) available in a new but transient waterbody.

5.3.3.3. Oxygen

Day-runs done in spring indicated that **oxygen levels in pools 1 and 3 did not exceed 2 mg/l** and averaged 0.1-1.0 mg/l (section 4.1.1.3.1.). A comparison of the adult body size of *Polypedilum tritum* and *Paralimnophyes hydrophilus* in their natural habitat with the lab data indicated that temperatures were only partly responsible for small size in individuals of generation 2 and succeeding generations (section 4.4.2.2.). The adult body size in the natural habitat was nevertheless strongly correlated with the water temperatures. Since oxygen levels in the natural habitat were very low and

oxygen varies strongly with temperature **I think that low oxygen levels are primarily responsible for the small adults, especially those of *Paralimnophyes hydrophilus,* emerging after the first spring generation.**

Oxygen is certainly an important determinant of the chironomid communities in lentic waters as all Chironominae, most Tanypodinae, but only very few Orthocladiinae larvae have haemoglobin (INT PANIS et al. 1996a,b). *Paralimnophyes hydrophilus* larvae have long lateral hairs (Figure 51d p 115), which may help them to remain at the water's surface thus enhancing respiration. The laboratory experiments revealed that, provided conditions are suitable, ***Paralimnophyes hydrophilus*** is polyvoltine. This species emergence pattern in the field was however **virtually bivoltine** (section 4.4.2.1.3.). **The pattern of voltism observed in the field was probably a result of dormancy induced by low levels of oxygen**. After the end of the second spring emergence a few larvae probably did not became dormant and therefore emerged as low-fertile small adults. HAMBURGER et al. (1994, 1995) showed that, when oxygen levels were very low, *Chironomus anthracinus* larvae lose large amounts of body reserves because of an anaerobic degradation of glycogen. During long phases of summer stagnation *Chironomus anthracinus* larvae fell into dormancy but, nevertheless, were dependent on minute oxygen supplies, the critical level of which was 2-3 mg/l (HAMBURGER et al. 2000). These results indicate that, unless larvae have entered dormancy, critically low oxygen levels reduce growth rates and consequently adult size. The lack of a well-defined third generation, the emergence of very small individuals in summer and a sometimes low or absent second generation **indicates that there is also an oxygen-induced dormancy in *Polypedilum tritum***. It is possible that the species is selected for drought tolerance rather than for its ability to utilize extremely low oxygen levels for respiration. The oxygen-induced dormancy mechanism might prevent temporary pool species from becoming extinct when the pool dries up relatively late. Small individuals with low fertility are likely to be outcompeted by species better adapted to low oxygen levels (e.g. *Chironomus riparius*, see HAMBURGER et al. 1998) and are therefore likely to be replaced or strongly reduced before the onset of drought. **Oxygen-induced dormancy is thought to be the mechanism to maintain high larval densities of more or less inactive larvae within the mud until the competitors are removed by desiccation.** These assumptions however still require further research.

5.3.4. Poor competitors or specifically vulnerable to predation?

5.3.4.1. Competition

The results of the pilot experiments on competition (section 4.4.1.3.) indicated that 'competitive ability' was strongest in the pond species *Chironomus annularius*, intermediate in the colonizer *Chironomus dorsalis* and lowest in the aestivator *Polypedilum tritum*. Newly hatched larvae did not negatively influence the development and survival of large larvae of any species but the opposite was true for the larval combinations 'large *Chironomus annularius*/small *Chironomus dorsalis* or *Polypedilum tritum*' and 'large *Chironomus dorsalis*/small *Polypedilum tritum*'. This might have

been at least partly the result of the larger larvae preying on the smaller ones (e.g. JONES 1974, BERG 1995). Hatchling survival in the permanent water species *Chironomus plumosus* did not seem negatively affected by the presence of large larvae of either *Chironomus dorsalis* or *Polypedilum tritum*. This result was however highly preliminary. The presence of antagonistic hatchlings (*Chironomus annularius* or *Chironomus dorsalis*) strongly reduced survival of *Polypedilum tritum* hatchlings. This might have been, for example, the result of competition for space (e.g. MCLACHLAN 1977) or of a chemical interaction with the metabolites of one species that negatively influenced the growth and survival of the other (MCLACHLAN 1985a). Whatever the proximate factors are, the larvae of the **first species to arrive have the decisive advantage of being larger**.

African rock pools are inhabited by monocultures of three chironomid species - the colonizers *Chironomus pulcher* and *Chironomus imicola* and the aestivator *Polypedilum vanderplanki*. Competitive ability was strongest in the first-, intermediate in the second- and smallest in the latter species (CANTRELL & MCLACHLAN 1982, MCLACHLAN 1985a, 1988, 1993). Consequently *Polypedilum vanderplanki* was restricted to the most transient pools (pools' life span < 1 wk), which were frequently cleared off from potential competitors. However, once established *Polypedilum vanderplanki* was able to maintain its own monoculture for a while against potential invaders (CANTRELL & MCLACHLAN op. cit., MCLACHLAN 1985a). The life history of *Chironomus imicola* was better suited than that of *Chironomus pulcher* to short-lived puddles, particularly as the first species is the better invader. *Chironomus imicola* is therefore exclusively dominant in pools that are remote from rivers, (rivers serve as potential refuges for both species) and which drying cycles are long enough to enable the developmlent of at least one generation (> 10 days). *Chironomus pulcher*, finally, maintains its own monocultures in shady pools, which are not so distant from the potential refuge (MCLACHLAN 1988, 1993). Different cues for the selection of oviposition site have evolved in *Chironomus imicola* and *Chironomus pulcher* to avoiding competition. 'The ghosts of competition past' could accordingly be the reason why competition was so difficult to demonstrate in MCLACHLAN's study (1993). Field data gathered in the present study revealed that the typical temporary pool aestivator species did not exhibit competitive exclusion and did not maintain high population densities when aquatic phases were long enough to facilitate the establishment of invaders thus resulting in their negative dependence on lentic water permanence (see section 5.2. for discussion). **In the long run the initial size advantage of the invader- and especially aestivator species present in a temporary pool after its formation is not great enough to prevent permanent pool species from invading. The latter are generally supposed to be the better competitors and thus would replace the temporary pool species unless the pool does not dry up.** This assumption was supported by the pilot experiments on competition and requires further research.

5.3.4.2. Predation

The importance of predation in pool communities is negatively correlated with the mean pool duration (averaged for several years of investigation) and drought periods significantly reduce predation rates after refilling (SCHNEIDER & FROST 1996, SCHNEIDER 1997). Furthermore, the importance of

predation is negatively correlated with pool size (ROTH & JACKSON 1987) and habitat: woodland pools harbor relatively few and grassland pools relatively many predators (BATZER & WISSINGER 1996). Thus **exposition, pool size and habitat duration mediate the importance of predation within the pool communities**. A reduced risk of predation might have driven species to develop specific adaptions to temporary pools in order 'to find a haven from predation' (BATZER & WISSINGER op. cit.). There is for example great evidence that the reduction of predation in amphibians or mosquitoes was a major selective pressure in the evolution of their life histories and one way of escaping from predation being the adaptation to life in temporary pools (e.g. KÖGEL 1984, ROTH & JACKSON op. cit.). As a group, Chironomidae constitute a vital nexus in the overall trophic structures of many freshwater ecosystems, they fall prey to virtually all types of predators, both invertebrates and vertebrates (TOKESHI 1995c). The importance of body size as a determinant of vulnerability to predation depends on the size of the main predators present. Large predators such as fish select larger larvae (e.g. ROBINSON 2000) whereas small invertebrate predators such as oligochaetes and other chironomids may only feed on first instars (TOKESHI op. cit.). Mortality of *Tokunagayusurika akamusi* instars I was 98 %, the reasons for this high rate remain unknown (IWAKUMA 1986 cit in TOKESHI 1995a). **Predation should therefore be considered as an important selection pressure in Chironomidae as well**. **Free-ranging** species such as *Paralimnophyes hydrophilus* seem to be most susceptible to predation, whilst the vulnerability of **tube-dwelling** species such as *Polypedilum tritum* and *Chironomus dorsalis* depends on the amount of time they spend outside their tubes (TOKESHI op. cit.). Building tubes involves e.g. construction costs and a decreased mobility which may reduce the availability of food. These (dis)advantages should therefore play an important role in determining whether tube-dwelling or free-ranging is the favored strategy in a given habitat. Interestingly some species (e.g. *Cricotopus sylvestris*) are able to switch between free-ranging and tube-building (facultative tube-builders sensu CHALONER & WOTTON 1996). In the case of free-rangers, long body hairs, as seen in *Paralimnophyes hydrophilus*, might have evolved to impede ingestion by predators. *Cricotopus* species, for example, are characterized by the presence of setal tufts on the abdomen, which grow stronger in presence of predators and which were shown to reduce predation risk (HERSHEY & DODSON 1987). Burrowing (BUND & GROENENDIJK 1994) or a reduced filtering activity and activity outside mines (KOPERSKI 1998) are direct antipredator responses that do not only reduce predation risk but also fecundity (BALL & BAKER 1995). The evolution of different larval tubes, e.g. transportable larval cases in *Stempellina* (THIENEMANN 1954), larval tubes many times the body length e.g. in some *Paratanytarsus* and *Tanytarsus* species (LANGTON et al. 1988, ROBINSON op. cit.), flimsy silk galleries in *Fissimentum desiccatum* (CRANSTON & NOLTE 1996), the formation of several tubes per larva (CHALONER & WOTTON op. cit.), the *Lithotanytarsus* tuft (THIENEMANN op. cit.) and J- or U-shaped tubes that, in *Chironomus*, are buried into the bottom sediment (MCLACHLAN & CANTRELL 1976), might have been partly encouraged by improving the ability to escape predation. However, considering their likely influence on fundamental processes of aquatic systems, the biological function or ecological role of larval tubes has not been sufficiently studied (CHALONER & WOTTON op. cit.). In contrast to *Chironomus*

plumosus, *Chironomus piger/riparius*, *Chironomus luridus* and *Polypedilum tritum* that dig their tubes vertically into the mud of laboratory soil cores, *Chironomus dorsalis* constructed horizontal tubes on the mud's surface, probably as it is more susceptibible to low oxygen levels (KAJAN 1997, KAJAN & FRENZEL 1999). Digging into organically enriched sediments therefore requires the extra ability to cope with hypoxia. The horizontal tubes of *Chironomus dorsalis* probably expose the species to a higher predation risk.

Usually only a few adults of the free-ranging *Paralimnophyes hydrophilus* emerged from the semi permanent pool 2 (usually occupied by high numbers of predatory species), excep in 1998 when the aquatic phase was preceded in 1997 by a severe drought. The opposite was observed in the temporary pool 1 where *Paralimnophyes hydrophilus* was usually frequent but had almost totally disappeared from the emergence funnels in 1999 which was preceded by a year with only a few days of drought (see Figures 18 and 20 pp 53 and 57, respectively, Tables 23 and 24 pp 65-66; for 1996 when *Paralimnophyes hydrophilus* was also rare in pool 1 and pool 3 see section 5.3.5.3.). **I attribute this virtual dependence of *Paralimnophyes hydrophilus* on a habitat that regularly dries up to the species' susceptibility to predation rather than to other biotic or abiotic interactions**. The quasi lack of a drought period in 1998 enabled large numbers of the omnivorous/predacious tanypods and the predaceous dytiscid- and newt larvae to establish in pool 1 (unpl. data.), which coincided with the disappearance of *Paralimnophyes hydrophilus*.

Table 73: The aquatic Chironomidae of the semi aquatic pool 2: proportion of subfamilies in net samplings and emergence traps in 1993 and a comparison of the total yields of Chironomidae before (1992-1997) and after (1998) a severe drought period that occurred in 1997.

Subfamily	Emergence 1993	Net 1993	Emergence 1992 - 1997	Emergence 1998
Tanypodinae	91 % (n = 389)	26 % (n = 75)	68 % (n = 449)	16 % (n = 125)
Orthocladiinae	3 % (n = 12)	1 % (n = 2)	16 % (n = 105)	64 % (n = 514)
Chironominae	6 % (n = 28)	73 % (211)	16 % (n = 105)	20 % (n = 159)

Table 73 summarizes some faunistical characteristics observed in pool 2. These characteristics indicate a strong predator pressure on and within the pools' chironomid community. The results can be summarized as follows:

(1) The overall number of emerging chironomids before the severe drought of 1997 was extremely low and the omnivorous/predaceous Tanypodinae (TOKESHI op. cit.) were predominant (68 %);

(2) Comparison between the composition of larval populations (net samplings) and the emerging adult population in 1993 revealed strong differences and nearby reversed proportions of Chironominae/Tanypodinae in the net samplings (73 %/26 %) and the emergence funnels (6 %/91 %);

(3) The total yield of emerging aquatic chironomids in 1998 (n = 798) was higher than the total number of aquatic chironomids caught by emergence funnels from 1992 to 1997 (n = 659). The share of emerging Tanypodinae (16 %) was relatively low and the share of Orthocladiinae (mainly consisting of two free-rangers, the tiny *Corynoneura scutellata* (n = 381) and

Paralimnophyes hydrophilus (n = 129)) high (64 %).

These results indicate a strong predatory influence of the Tanypodinae on the larvae of Orthocladiinae and Chironominae. Since the share of Tanypodinae declines with habitat duration (section 5.2.1.), non-predatory chironomids living in temporary pools (as pool 1, 3 and the boxes of the colonizing experiment) would benefit from lower predation risks. In addition, the largest numbers of predatory species other than Tanypodinae occurred in the semi permanent pool 2, followed by the temporary autumn-summer pool 1 and lower numbers of predators occurred in the winter-vernal pool 3 and the boxes of the colonizing experiment (DETTINGER-KLEMM 1995a and unpl. data). Damselfly and dragonfly larvae, adults and larvae of water newts (*Triturus alpestris*, *Triturus vulgaris*) and back-swimmers (*Notonecta* spec.), were the greatest predators of mosquito larvae in pool 2 (DETTINGER-KLEMM op. cit.). *Notonecta* larvae 'strongly reduces or even eliminates large pelagic or neustonic species, but does not affect densities of small or benthic species' (BLAUSTEIN 1998). Newts (SCHABETSBERGER & JERSABEK 1995), damselfly- (KOPERSKI 1998) and anisopteran larvae (ARENA & CALVER 1996) feed effectively on tube-building chironomids. The most dominant predators in pool 2 throughout the years were geophilous anisopterans, predominantly *Sympetrum* spec. (unpl. data). Geophilous anisopterans that burrow into the sediment and detect their prey mechanically as well as visually, seemed to be the most effective predators of sediment-living and tube-building chironomids. A preliminary experiment was therefore conducted with *Libellula depressa* larvae that also occur in temporary pools. The dragonfly larvae effectively fed on those of the temporary pool dwellers *Chironomus dorsalis* and *Polypedilum tritum* as well as on those of the pond dweller *Chironomus plumosus*-aggregate (section 4.4.1.5.). It therefore appears likely that **tanypods, geophilous anisopterans and newts were chiefly responsible for low numbers of Chironominae and Orthocladiinae emerging from the semi permanent pool 2** before the drought of 1997.

Although predation was only a minor aspect of the present investigation, the above discussion indicates that temporary pools do indeed provide a 'haven from predation'. Whether pond species are more successful in avoiding predation requires further research and food-web analyses between ponds of different lentic water permanence (e.g. SCHNEIDER op. cit.) would appear a worthwhile study.

5.3.5. Reactions to drought

5.3.5.1. Is soil moisture an appropriate measure for interspecific comparisons of drought tolerance?

In chapter 5.2.2.2., I provided an overview of chironomids hitherto known to be drought tolerant. Chapter 5.3.2.2.3. presented two strains of chironomids that could be considered preadapted to life in temporary pools - the stress-tolerant- and the summer-dormant species. The species shown to be drought-tolerant in the present study - *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* - all belong to the stress-tolerant species and show a consecutive response to

drought which is not confined to a single developmental stage as is the case with the summer-dormant species (see section 5.3.2.2.1.). 'The wide tolerance of many individual species and the variety of species which exploit even temporary, semi-terrestrial, winter-frozen and other habitats, leads us to expect some common features of chironomid larvae which impart resistance and adaptability to a wide range of rigorous conditions' (DANKS 1971c). I suggest that these common features are:

(a) The ability of many chironomids to fall into dormancy in response to a great variety of environmental stimuli (see sections 5.3.2.2., 5.3.3.2. and 5.3.3.3.) - I would call this **the quiescence strategy of the Chironomidae**, the physiology of which is hardly understood;

(b) The widespread ability (except for Tanypodinae) to form a **larval cocoon** when aestivating (DANKS op. cit.).

JONES (1975), GRODHAUS (1980) and STEINHART (1999a) demonstrated the importance of larval cocoons for the ability to withstand desiccation. 'The larvae are tightly sealed in a firm cocoon and with the body folded to pack out the cocoon so that there is no liquid film between the larva and its cocoon' (DANKS op. cit.). Chironomidae larvae build their tubes out of silk-like salivary secretions; these can be used to cement together particles of various types and sizes (CHALONER & WOTTON 1996). STEINHART (1999 op. cit.) described and illustrated the cocoon formation in *Hydrobaenus lububris*. Cocoon formation in this species lasted about 2.25 h and was performed by building a new structure with smooth, transparent walls in the interior of the existing larval tube (STEINHART 2000b). The apneustic larvae of the Chironomidae are incapable of preventing water losses as they do not have a water-proofed cuticle simply for their respiratory requirements (HINTON 1951). Furthermore there are no indications that Chironomidae are able to reduce water loss through manipulations of osmosis (JONES op. cit.). Without a cocoon, drought resistant-, terrestrial- and aquatic larvae do not seem to survive much different degrees of water loss from their body tissues, the maximum of which is approximately 60 % (BUCK 1965, JONES op. cit., DELETTRE 1988). Cocoons may reduce but do not prevent the loss of body water in the aestivating larva (STEINHART op. cit.). To this date there are however no figures that could support the first assumption. The cryptobiotic (cryptobiosis is the state of an organism when it shows no visible signs of life and when its metabolic activity comes to a reversible standstill (HINTON 1960b)) larva of *Polypedilum vanderplanki* also folds up in a cocoon during desiccation and was shown two survive two decades of storage over silica gel (that means nearly complete dehydration (HINTON 1960b, ADAMS 1984)). However, mortality of unprotected (no cocoon) and finally completely dehydrated larvae decreased with increasing rate of drying (water loss/time) (LEADER 1962). In addition, the larvae are highly susceptible to mechanical damage (HINTON 1968). **The cocoon probably prevents larvae from loosing water too fast, protects them from mechanical damage and maintains the larvae's morphological integrity when dehydrated**. However, the physiological processes of drought tolerance in Chironomidae and the role of their cocoon are still hardly understood.

The scope of the present study was not physiological, but ecological. The survival of an aestivating

larva strongly depends on a combination of three factors:

(a) the larva's ability to endure water losses;

(b) the construction of a cocoon; and

(c) the water content of the mud in which the cocoon is concealed.

The drought-resistant species *Hydrobaenus lugubris*, for example, was only capable of surviving long periods of desiccation when the cocoons were exposed to a relative air humidity of over 95 %. If the cocoon does not prevent larvae from loosing body water, the minimum moisture content of dry *Hydrobaenus lugubris* larvae should not be expected to fall below 30 % (HINTON 1960b). This example shows that even drought resistant larvae of Chironomidae require saturated air humidities to survive desiccation. This also applies to terrestrial chironomids (e.g. DELETTRE & BAILLIOT 1977, DELETTRE 1988). The humidity of the air between particles of the earth a few centimeters down may be more or less permanently maintained at a high level (HINTON 1968). **I expect that the water content of soil substrates that conceal larvae and cocoons are an adequate measure for ecological comparisons**. I therefore designed the present study's experiments to mimic the natural processes of drought and provided each species with natural substrates (section 3.3.6.).

5.3.5.2. Initial responses to desiccation

The initial response of larvae to desiccation may be subdivided into one of three categories:

(a) the larvae perform horizontal movements to escape from desiccation;

(b) the larvae burrow into the mud; and

(c) the larvae dry in situ.

To escape desiccation, the non-drought tolerant larvae of *Chironomus dorsalis* crawled at the surface of the mud, as also observed for *Chironomus imicola* (MCLACHLAN 1983a). Another kind of migration was described for *Pseudosmittia nanseni* (STEINHART 1999a): the larvae performed 3-4 cm wide jumps by writhing and quickly straightening their bodies. The *Chironomus plumosus*-agg. larvae investigated in the present study did not perform horizontal migrations by leaving their tubes. HILSENHOFF (1966) showed that non-feeding overwintering larvae of *Chironomus plumosus* could burrow up to 51 cm deep into the mud of Lake Winnebago, USA. Thus the species is probably able to burrow into the mud before a pond dries up. The permanent water species *Chironomus plumosus* has only occasionally to deal with desiccation, e.g. when living in carp ponds that are artificially dried up once a year (BAKHTINA 1980). Larvae of *Polypedilum tritum* also did not undertake horizontal migrations. The other possible reactions to drought (cocoon formation, burrowing or in situ drying) were not observed since it was not possible to observe the larvae in the experiment on drought tolerance as the mud concealed them. The conspecifics *Polypedilum halterale* (= *Polypedilum simulans* in DANKS op. cit.) and *Polypedilum vanderplanki* (MCLACHLAN (op. cit.) did not however migrate vertically or horizontally. While planning the drought tolerance experi-

ment, I transferred some free ranging larvae of *Limnophyes asquamatus* and *Paralimnophyes hydrophilus* into Petri dishes filled with water and sterilized mud, the latter of which formed a water-land transition zone. The water was allowed to dry up and the reaction of the larvae observed. When the substrate humidity diminished to an extent that prevented the larvae to continue with their normal activities, they burrowed into the substrate and constructed silk-lined tubes around themselves.

Regardless of whether a larva dries in situ or burrows into the mud, **cocoon formation seems to be a specific initial reaction to drought that is probably in common to all aestivator species**.

5.3.5.3. The ability to survive desiccation

Table 74: Definition of four levels of drought susceptibility.

	Cryptobiosis	Drought resistance	Drought tolerance	Non-tolerance
Survival of at least several months...	total loss of body water	concealed by substrates with water contents of 0-19.9 %	concealed by substrates with water contents of 20-39.9 %	concealed by substrates with very high water contents of > 60 %
Survival of ± one month...				concealed by substrates with water contents of 20-59.9 %
Group	**Aestivators**			**Colonizers**
Examples	*Po. vanderplanki*[1]	*H. lugubris* [2] *Pa. tonnoiri* [3] *Po. dewulfi* [4]	*L. asquamatus*[5] *Paral. hydrophilus*[5] *Po. tritum*[5] *Stempellina* spec.[6]	*C. plumosus*[5, 7] *C. dorsalis*[5, 8]

[1] e.g. ADAMS 1984; [2] SCHNABEL 1999; [3] JONES 1975; [4] MILLER 1969; [5] present study; [6] SUNDERMANN 2001; [7] BAKHTINA 1980; [8] BUCK 1965.

The term temporary pool implies that drought is detrimental to an aquatic organism. The drought is often simply defined as the absence of surface water. But provided that substrate humidities are high enough, many aquatic animals (e.g. Odonata, Plecoptera, Trichoptera) are able to endure periods when surface water is totally absent. This is also the case in Chironomidae. The present study showed that permanent water species as *Chironomus plumosus* agg. and non-drought tolerant colonizers as *Chironomus dorsalis* could survive at least four weeks of drought (section 4.4.1.6.3.). In particular, investigations on Chironomidae of fish ponds that are artificially dried once a year, revealed that some form of drought tolerance is common in Orthocladiinae and Chironominae (e.g. MAYENNE 1932, BORODIČOVÁ 1958, BARTHELMES 1964, SZITÓ 1970, BAKHTINA op. cit.). BAKHTINA (op. cit.) mentioned that prolonged drying of the pond bed in the autumn and winter caused the death of chironomid larvae (*Chironomus plumosus* was one of the most dominant species) within 1-1.5 months. A given species' drought tolerance must therefore be defined in terms of the value and length of exposure to dry conditions**. I suggest that four levels of drought tolerance can be applied in Chironomidae** (Table 74). These levels might be useful for ecological classifications, but, nevertheless, in nature the range from cryptobiosis to non-drought tolerance is more likely to be continuous. **Cryptobiotic-, drought resistant- and drought tolerant species were combined as aestivator species since they seem to be specifically adapted to coping with drought periods**. Intensive periods of drought are detrimental to non-aestivators, which recolonize the habitat on the wing and may therefore all be called colonizers. **A pool is only perceived as**

temporary when its drought periods are long and intensive enough to be detrimental to non-aestivator species!

The aestivator species investigated in the present study were only drought tolerant and therefore required substrate humidities above 20 % to survive long periods of drought. In addition, mortality in the drought tolerant species is not only dependent on soil moisture but also on the duration of drought and the instar concerned (sections 4.4.1.6.1. and 4.4.1.6.2.). The smaller larvae were more susceptible to strong reductions of soil water contents, probably because the cutaneous transpiration does not change with body size (BUCK op. cit.) and water loss is consequently faster in the smaller larvae (higher ratio of body surface/body volume). The field data clearly indicated that long and/or severe periods of drought cause high mortalities of drought tolerant species in their natural habitat. Pool 1, for example, underwent an unusually long drought in 1995 that did not end until the end of December (Figure 18 p 53). It is likely that soil freezing increased the mortality of aestivating larvae (see section 5.1.3.). As a consequence, the number of emerging aestivators in 1996 was extremely low (Table 23 p 65). Another good example is the long drought period of more than sixteen months to which pool 3 was subjected in 1995/96 (Figure 21 p 59). Despite a good recruitment of both species before the drought of 1995/96, only very few adults of *Polypedilum tritum* and *Paralimnophyes hydrophilus* emerged during the first emergence of spring 1997 (e.g. *Paralimnophyes hydrophilus* Figure 83 p 179, Table 25 p 67). In such situations, a second generation is needed to replete the initial stock of larvae present at the start of drought. Because drought intensities fluctuate between the years, which results in varying mortalities amongst the aestivating larval populations, **drought tolerant aestivator species are only able to maintain high population densities in pools that normally enable a second generation to emerge**. *Polypedilum tritum* in pool 3 is a typical example of such a situation (section 4.4.2.1.1.). Variations in sensitivity to desiccation amongst the instars were also underlined by the analysis of the emergence patterns in the field (section 4.4.2.1.). It is likely that only instars III and IV survived the intense drought of pool 1 in 1997. On the other hand, survival of all instars is likely to be a rule in pool 3 since soils always remain humid. Survival of all instars and refilling in winter resulted in a desynchronisation of the spring emergence of *Paralimnophyes hydrophilus* in 1998 (Figure 83 p 179).

Although STEINHART (1999a) demonstrated that survival of the summer-dormant *Hydrobaenus lugubris* depended on high air humidities (section 5.3.5.1.), I classified the species as drought resistant. SCHNABEL (1999) found that the substrate humidity of the natural habitat fell below 10 % and high numbers of adults emerged from these substrates when flooded in the laboratory. In addition, this habitat was sometimes subjected to drought periods of about two years (see Table 70 p 206 Wolfsh.). The drought tolerant larvae of *Limnophyes asquamatus*, *Paralimnophyes hydrohilus* and *Polypedilum tritum* do not survive such degrees of desiccation and are consequently virtually absent from such habitats. I therefore consider that **soil moisture content is a good measure for ecological comparisons**. *Hydrobaenus lububris* is the only European species known to be drought resistant and it is possible that summer-dormant species generally have higher abilities to withstand severe

drought periods (GRODHAUS 1980, MOLLER PILLOT pers. comm.). On the other hand, summer-dormant species are less flexible in exploiting aquatic phases of varying lengths, than the species with a consecutive response to drought. For Europe, it is yet unknown whether the communities of pools which soil water contents remain below 10 % for longer periods are generally predominated by drought resistant species or by colonizers. Colonizers should predominate these communities when drought resistant species are as rare as suggested by our current knowledge (*Hydrobaenus lugubris* seems to be restricted to marshes). But with regard to the results of GRODHAUS (1976, 1980, 1987b) for the Nearctic it is more likely that aestivators also predominate these pools' chironomid communities in Europe and that many drought resistant species have been so far overlooked.

5.3.5.4. Other responses to desiccation

Two further strategies that may enable a species to escape desiccation remain to be discussed:

(a) the acceleration of larval development resulting from an accumulation of individuals/metabolites caused by the progressive reduction of the water body;

(b) the ability to emerge into adults on dry land (terrestrial eclosion) after the surface water has disappeared.

5.3.5.4.1. Acceleration of development

If a species' larvae follow the shrinkage of their habitat by horizontal migrations (as observed in *Chironomus dorsalis* see section 5.3.5.2.), such larvae and consequently their metabolites would accumulate as the pool diminishes. Normally, increased densities of larvae reduce growth rates and prolong the overall development times (e.g. BIEVER 1971, IKESHOJI 1974, REIST & FISCHER 1987, OKAZAKI & YANO 1990, YANO et al. 1991). This common pattern was also observed in *Chironomus dorsalis* (section 4.4.1.4.) and is counterproductive when a habitat is going to disappear. The length of development of *Polypedilum tritum* decreased with larval density, which is, as far as I am aware, the first record of such behavior in Chironomidae although it is known in, for example, some mosquito species (CHODOROWSKI 1969). The average time that *Polypedilum tritum* needed to emerge at the highest densities was about five days less than when densities were at their lowest. Interestingly, the different density levels did not significantly affect the adult body size. This is difficult to explain and did not appear correlated to variations in mortalities within the experiments and therefore to different numbers of dead larvae which may provide surviving larvae an additional protein-rich food (compare with Table 50 p 156, Figure 72 p 157). The laboratory experiments on the impact of larval density on development in *Chironomus dorsalis* and *Polypedilum tritum* were only conducted as pilot experiments so the correct interpretation of their results still requires further research. **The unusual decrease of development time with increasing larval densities in *Polypedilum tritum* is probably an adaptation to temporary pools**: larger larvae hasten their development when a pool is going drying up and lay their eggs in the remaining puddles where the larvae hatch quickly and join the stock of aestivating larvae at the deepest and therefore safer sites (highest minimum soil

moisture contents within a pool). Such an emergence pattern was observed in 1995 for *Polypedilum tritum* in the woodland pool (pool 3) when there was a strong surplus of emerging females (Figure 80 p 172).

5.3.5.4.2. Terrestrial eclosion

In the present investigation, instar IV larvae of *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus* partly pupated and then emerged as adults under terrestrial conditions (up to 61 % of the aestivating population) (Figure 78 p 166). Instars I-III were however unable to develop into adults under such conditions. Terrestrial eclosions of these species were also observed in their natural habitats (*Polypedilum tritum* section 4.4.2.1.1., *Paralimnophyes hydrophilus* section 4.4.2.1.3. and *Chironomus dorsalis* Figure 58 in DETTINGER-KLEMM 1995a). I found no mention of terrestrial eclosion of other aquatic Chironomidae in the literature available so the question of whether this ability is an actual adaptation requires further investigations. *Chironomus plumosus* agg. instars IV were however inable to develop into adults unter terrestrial conditions (section 4.4.1.6.3.). This indicates that **terrestrial eclosion of aquatic species may be considered a specific adaptation to temporary pools**. Further not yet mentioned personal observations during the experiments on drought tolerance indicated that development into adults is directly accelerated by the disappearance of the surface water and that the adults were then often fairly small. These observations should provide interesting directions for future investigations! The **advantage of terrestrial eclosion** in the non-drought tolerant colonizer *Chironomus dorsalis* is evident: it **escapes from desiccation by flying**. It is unlikely that *Paralimnophyes hydrophilus* and especially *Polypedilum tritum* lay their eggs on quasi-terrestrial soils. Thus the 'bet-hedging' portion of 'terrestrial eclosers' has only two possibilities to contribute to the overall maintenance of populations/metapopulations:

(a) by flying to remaining puddles on other sites of the pool where they lay their eggs, the larvae of which hatch quickly and fill up the stock of aestivating larvae at deeper and thus safer sites (higher minimum soil moisture contents within the pool);

(b) by searching upwind transport for wide-range dispersal and thus colonizing new water bodies.

The first possibility strikes me as more plausible and would result in a spreading of the risks in space: some fourth instars aestivate in situ, others effectively disperse as adults to deeper sites where they produce many but more vulnerable first instar larvae. The success of the second strategy depends on the moisture contents at deeper sites or on how long the puddles at deepest sites last thus enabling larval growth and development. The present study revealed that the level of filling (especially of the woodland pool) was very variable within and between the years (section 4.1.1.4.3.). **I consider that the risk spreading strategy of 'terrestrial emergers' and 'in situ aestivators' is an ideal answer to coping with these habitat vagaries**.

5.3.6. Parthenogenesis

Although not considered particularly common, parthenogenesis in Chironomidae occurs mostly in Orthocladiinae and Tanytarsini (ARMITAGE 1995, LANGTON 1995). In the present study, seven species without males or presenting strongly biased sex ratios occurred in the two temporary pools, the semi permanent pool and the colonizing boxes. These species were *Corynoneura scutellata* (1 ♂ 1066 ♀♀), *Limnophyes asquamatus* (393 ♂♂ 738 ♀♀), the *Limnophyes minimus*-complex (1477 ♂♂ 5983 ♀♀, for taxonomic remarks see section 4.3.1.2.), *Pseudosmittia* spec. A (17507♀♀), *Pseudosmittia conjuncta* (551♀♀), *Smittia* spec. A (826♀♀) and *Paratanytarsus grimmii* (309♀♀). With the exception of *Corynoneura scutellata* (aquatic), *Limnophyes asquamatus* (semiaquatic) and *Paratanytarsus grimmii* (aquatic), these were terrestrial orthocladine species in which parthenogenesis seems quite common (cf. CRANSTON et al. 1989a). Until now, only **thelytokous parthenogenesis** (in which females are produced from unfertilised eggs) is known for Chironomidae, which was also the case in the present study. The cytological mechanisms of thelytokous parthenogenesis in Chironomidae have not so far been investigated and it is unknown whether it is automictic (oogenesis with normal meiosis and haploid eggs that are restored to a diploid state by some cytological mechanisms) or apomictic (oogenesis with suppressed meiosis and diploid eggs that form mitotically). **Facultative parthenogenesis** (the eggs develop irrespective of whether they are fertilized or not) has **often been claimed** (e.g. THIENEMANN & STRENZKE 1940, LINDEBERG 1971) **but never proven** in Chironomidae or within any other group of aquatic insects (BUTLER 1984). *Paratanytarsus grimmii* is obviously an **obligatory parthenogenetic** species (no males known), which often is a 'weed' of the drinking water supply systems (LANGTON et al. 1988). In *Corynoneura scutellata*, as in *Limnophyes asquamatus*, bisexual and parthenogenetic reproduction is known to occur: 'The reasons for the occasional occurrence of facultative parthenogenesis (note: in *Corynoneura scutellata*) are not known yet. 'Geographical parthenogenesis' as assumed by VANDEL (1931 p 198) has surely to be discarded and it is also unlikely that there are two distinct races of which one is obligatory parthenogenetic and the other obligatory bisexual' (THIENEMANN 1954 p 283, translated). This is a good example of the speculative character of most statements published to date on parthenogenesis in Chironomidae. In contrast to THIENEMANN'S assumption ***Limnophyes asquamatus* turned out to have an obligatory bisexual ecotype** (forma *asquamatus*). In addition, there are **at least two parthenogenetic strains,** one of which can be separated from the bisexual ecotype (forma *aquaticus*), the other not (forma *limosus*). **Whether these ecotypes are obligatorily or facultatively parthenogenetic still requires further investigations** and genetical, cytological and karyological methods are needed to tackle that problem. The presence of two parthenogenetic ecotypes in *Limnophyes asquamatus* complies with LINDEBERG'S (1971) speculations on *Tanytarsus gregarius* and *Tanytarsus norvegicus* in which the author also assumed two parthenogenetic strains. It would be of great interest to determine how often parthenogenetic clones arise from bisexual species. If this is not rare, then many habitats are likely to have their own ecotypes, some of which **occupying new niches than the parental bisexual race** (as shown for forma

aquaticus in section 4.3.1.1.5.). In this case, the definition of discrete ecotypes (or parthenogenetic 'species') would not make sense, irrespectively of whether they exhibit obligatory or facultative parthenogenesis. This is exactly what I would expect (see for example sporadic parthenogenesis in *Chironomus* (GRODHAUS 1971)) - but the **ecotypes defined here in the sense of a working hypothesis** (section 4.3.1.1.6.) will hold until future research shows either that these ecotypes are facultatively parthenogenetic, or that clones continuously arise from the bisexual race. With future research in mind, the STRENZKE's observations (1960a) on *Pseudosmittia angusta* (possibly identical with the parthenogenetic *Pseudosmittia* spec. A of the present study, see comments in the Appendix 3) are of great interest. In contrast to what I found for *Limnophyes asquamatus*, STRENZKE was able to easily entice the males to mate with 'bisexual' females. Interestingly, *Pseudosmittia angusta* has also at least one parthenogenetic strain which is identical to the bisexual females. However, STRENZKE was not able to encourage the males to mate with females from his parthenogenetic cultures. This observation suggests that **facultative parthenogenesis is unlikely to occur in *Pseudosmittia angusta*, which would be an ideal test species for future research**. Since the mode of parthenogenesis is presently hardly understood, the **descriptions of parthenogenetic species are highly problematic** (cf. MAYR 1996). I agree with LINDEBERG (1974) who assumed that 'it would not be surprising to find that most or even all parthenogenetic forms hitherto known or yet to be detected had their corresponding normally reproducing populations in the recent fauna.' It is thus only advisable to accept a parthenogenetic species that presents clear differences to any other described species of a genus and then to consider similar males (with respect to the specific larval and especially pupal characters), that may be discovered later, as their bisexual conspecifics. All parthenogenetic species that are not distinctly different to a bisexual congener should be treated as the parthenogenetic strains within the same species. This system therefore requires synonymization, which is also the view expressed by LANGTON et al. (op. cit.). The parthenogenetic *Limnophyes punctipennis* Goetghebuer, 1919 may therefore be a parthenogenetic race of *Limnophyes minimus* (Meigen, 1818), but the troublesome taxonomic situation still prevents the two species from being synonymized (see section 4.3.1.2.).

The occurrence of **populations consisting of only parthenogenetic species** is easy to be understood: they were founded by one or a few thelytokous females (see for example the presence of only parthenogenetic specimens of *Corynoneura scutellata* and *Limnophyes asquamatus* in the colonizing experiment (Table 27 p 79)). Because parthenogenetic females are independent of swarming, they are particularly **preadapted to colonizing transient habitats** (LINDEBERG 1971). This explains the high frequency of parthenogenesis within the habitats presently investigated.

5.4. Why do chironomids thrive in temporary pools? - the outcome

Contrasting with what is known for many other inhabitants of temporary pools (e.g. mosquitoes or water beetles), the temporary pool chironomids presently investigated showed **only one programmed life history trait** - the way of **the annual timing** - which is widespread amongst Chironomidae. All **other life history traits were highly flexible** and consecutively followed the actual situation within the habitat. The life histories of *Limnophyes asquamatus*, *Paralimnophyes hydrophilus*, *Chironomus dorsalis* and *Polypedilum tritum* are therefore rather opportunistic. A **mixture of r- and A-selected traits** achieves this enormous flexibility of the life histories, which also seems to be widespread amongst Chironomidae. The ability to enter dormancy when environmental factors go below/beyond a given limit is the central element of the species' life histories. I call this capacity the **quiescence strategy of Chironomidae**, the knowledge of which is still fragmentary. The ability to facultatively fall into dormancy, a high physiological tolerance of the larvae and many r-selected traits, lead to a **high plasticity of life histories** (Figure 96). The fine-tuning to the temporary habitat has been mainly achieved by **an adaptive improvement of a few preadaptive properties** present in Chironomidae:

(a) The effective colonization of spatially unstable temporary pools was mainly achieved by the improvement of the **dispersal abilities** in *Chironomus dorsalis*;

(b) The improvement **of larval drought tolerance and its related features** (such as acceleration of

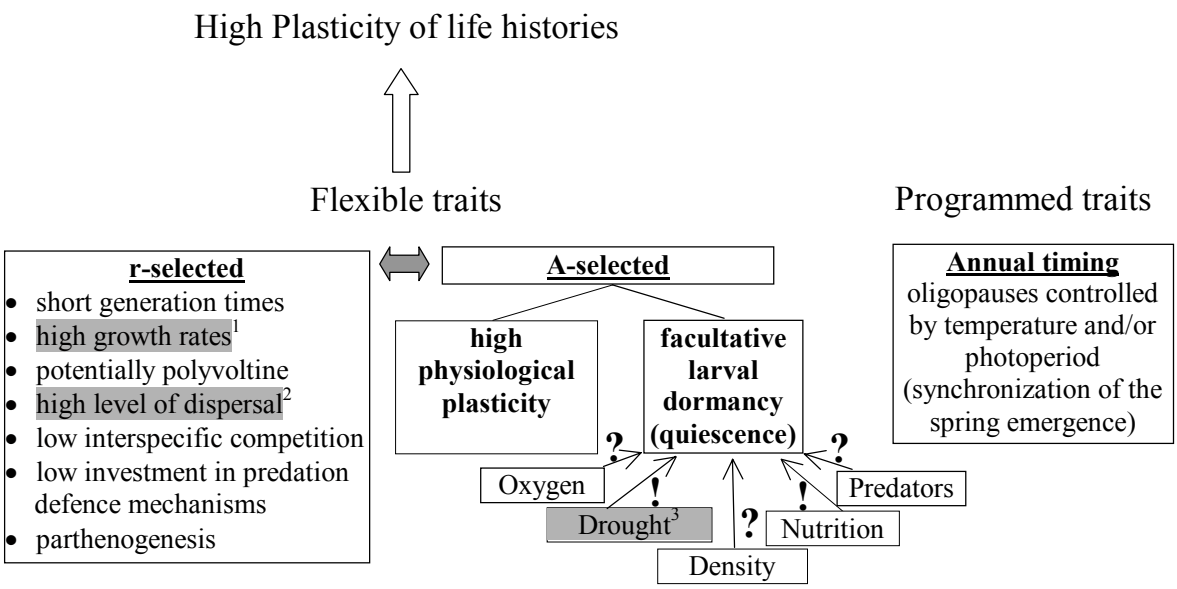

Figure 96: Important life history parameters in temporary pool species with consecutive responses to drought.

Comments:

features which are specific adaptations to temporary pools are **shaded in gray**: [1] high thermal coefficients over a wide range of temperatures were observed in *Paralimnophyes hydrophilus* (section 5.3.2.1.); [2] *Chironomus dorsalis* was shown an expert invader (section 5.3.1.); [3] (a) drought tolerant: *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum*; (b) accelerated development at high larval densities: *Polypedilum tritum*; (c) terrestrial eclosion: *Paralimnophyes hydrophilus, Chironomus dorsalis, Polypedilum tritum* (section 5.3.5.).

? = an induction of dormancy at critical levels is likely/possible; **!** = the induction of dormancy was clearly shown by the present study.

development at high larval densities and the capacity for terrestrial eclosion) enabled *Limnophyes asquamatus*, *Paralimnophyes hydrophilus* and *Polypedilum tritum* to effectively colonize spatially stable temporary pools.

The evolution of an expert invader as well as of drought tolerance can be regarded as a **strategy of being the first**: the first species present after pool formation has the decisive advantages of (a) larger larval size in relation to other potential competitors and; (b) low numbers of predators. Many other insects of temporary waters were forced to evolve life cycles specifically linked to drought because they are able to survive drought only in a species-specific development stage (e.g. the egg stage in mosquitoes). This was quite different in the drought tolerant species investigated in the present study: **all instars proved to be drought tolerant and resumed development without any risk whenever water was present**. Whether the **high thermal coefficients** over a wide range of temperatures that was observed in *Paralimnophyes hydrophilus* are really an adaptive feature still remains questionable.

6. Summary/Zusammenfassung

6.1. Summary

The main aim of the present study was to determine how Chironomidae cope with the environmental changes to which temporary pools are exposed. Are the species specifically adapted to the habitat or opportunistic? The problem was approached by:

(a) an emergence study done in the Lahnberge mountain range (Marburg, Hesse, Germany) on three pools that were subjected to different lengths of drought (two of which were really temporary and one semipermanent);

(b) an emergence study done in order to investigate the dispersal ability of *Chironomus dorsalis* (colonizing experiment) in ten experimental pools that had been exposed in the field in 1998 and that mimicked spatially unstable pools;

(c) laboratory investigations of some fundamental biological characteristics (role of temperature, photoperiod and density in growth and development, drought tolerance and parthenogenesis) of the four principal temporary pool dwellers *Limnophyes asquamatus*, *Paralimnophyes hydrophilus*, *C. dorsalis* and *Polypedilum tritum*.

The **natural habitats** investigated in this study were numbered pool 1, 2 and 3 and can be characterized as:

- pool 1, an autumn-summer pool on the forest's edge (variation of drought period: 7-157; 71 d (n = 8 years); onset of drought between end of May to end of August, usually in July);
- pool 2, a semi permanent pool on the forest's edge (variation of drought period 0-130; 34 d (n = 8 years); onset of drought in July); and
- pool 3, a temporary winter-vernal woodland pool (variation of drought period 109-502; 221 d (n = 8 years); onset of drought between mid-May and end of June, usually in the second half of May/first half of June).

Since the temporary pools investigated were dry during the warmest period of the year, temperatures (recorded by data loggers) available for development of aquatic animals are relatively low compared to other permanent shallow lentic water bodies.

Chironomid communities of pools 1, 2 and 3 were counted 33 (n = 8250 individuals), 33 (n = 3543 individuals) and 23 species (n = 26376 individuals), respectively. The proportions of semiaquatic-terrestrial and truly terrestrial individuals within an annual crop ranged between 27-58 % (pool 1), 39-69 % (pool 2) and 79-96 % (pool 3). The pool communities of aquatic/semiaquatic chironomids were mainly determined by the average lentic water permanence

$\left(LWP_{av} = \frac{1}{\left(1 + \frac{\text{average duration of drought at deepest site}}{\text{average min imum soil moisture at deepest site}}\right)} \right)$, LWP_{prev} of the previous year and by the month in which drought occurred. The proportion of individuals that could be defined as aestivators (= species surviving at least several months of drought concealed by substrates with water contents of 20-40 % of total soil weight) was negatively correlated with the LWP_{av} and LWP_{prev}. The proportion of colonizers strongly depended on the month in which drought occurred. The temporary pools 1 and 3 were usually predominated by one to three aquatic/semiaquatic aestivator species (65.5 % of the community in pool 1 and 100 % in pool 3 on average). These were *L. asquamatus*, *P. hydrophilus* and *P. tritum*. The average proportion of aquatic/semiaquatic aestivator species emerging from the semi permanent pool 2 was comparatively low (17.4 %).

Twenty one species of chironomid (n = 7482 individuals) and 2 mosquito species (n = 2771 individuals) were encountered in the experimental boxes of the **colonizing experiment**. The midge communities of the experimental pools were very similar, and distance to the closest aquatic habitat (up to 700 m) did not result in regular colonization patterns. The dispersal abilities of all species were therefore quite high and only distances up to several kilometres would produce regular colonization patterns in such an experiment. The most dominant colonizers were *Chironomus dorsalis* (40.0 %), *Culex torrentium* (20.4 %), *Chironomus piger/riparius* (16.7 %), *Tanytarsus buchonius* (9.8 %) and *Culex pipiens* (9.6 %). Colonizing efficiency (measured as time from exposure until first emergence, presence (number of boxes from which a species had emerged) and abundance) was highest in *C. dorsalis* and consecutively lower in *Chironomus piger/riparius*, *Tanytarsus buchonius* and *Corynoneura scutellata*. The dispersing strategy used by *C. dorsalis* is probably a combination of actively searched passive downwind transport (for wide-range dispersal) and of the active selection of oviposition sites. The first ovipositing females arrived between 2-7 days after exposure of the experimental puddles. Low values of the aspect ratio (wing length/wing width) and the thorax ratio (wing length/thorax length) seem to be good morphological surrogates for a chironomids' ability for active dispersal. These morphological parameters also confirmed that *C. dorsalis* was an expert invader.

Morphological features of the egg masses, larvae, pupae and adults of the four principal temporary pool species' were presented and partly illustrated. Taking into account the separation characters currently available, it was not possible to separate *P. tritum* from *P. uncinatum*. It is therefore likely that *P. uncinatum* is a junior synonym of *P. tritum*; this conclusion however awaits investigation of the type material. Nevertheless, the present study used *P. tritum* instead of the more accurate term *P. uncinatum/tritum*.

An extensive morphological-taxonomical analysis of the larva, pupa and the adult female of the **parthenogenetic and bisexual ecotypes of *L. asquamatus*** was carried out. The distinction into two species was not morphologically backed up. Using two morphological characteristics (presence of lanceolate prescutellars, number of preepisternals) most individuals of the obligatory bisexual

reproducing females (*L. asquamatus* forma *asquamatus*) could be separated from the parthenogenetic ecotype *L. asquamatus* forma *aquaticus*. It turned out that the bisexual forma *asquamatus* clearly prefers wet soils and should be called terrestrial/semiterrestrial whereas the parthenogenetic ecotype *aquaticus* was predominantly aquatic/semiaquatic. However, during a wide range comparison of parthenogenetic females, including material from The Netherlands and Eastern Germany, a second parthenogenetic ecotype (*L. asquamatus* forma *limosus*) was discovered which is not separable from the obligatory bisexual females and probably occupies a similar (terrestrial) microhabitat. It still remains unclear whether males actually mate with parthenogenetic females and how often parthenogenetic clones arise from the obligatory bisexual parental ecotype. The ecological significance of parthenogenesis in the Chironomidae seems to be the occupation of new niches combined with the advantage of asexual reproduction in colonizing transient habitats. The **larva of *L. asquamatus* was described for the first time**. While searching for characteristics that separate larvae of *L. asquamatus* from other species of the genus, a comparison with larvae of the *L. minimus*-complex and *L. natalensis* was undertaken. It turned out that SÆTHER (1990) had not described the larva of *L. natalensis* but of another species and thus the **larva of *L. natalensis* was also described for the first time**. **The larval and pupal keys in SÆTHER (1990) were accordingly amended**.

The **temperature dependence of development** from oviposition to adulthood was studied intensively for *P. hydrophilus*, *C. dorsalis* and *P. tritum*. The development of these species was influenced as follows by temperature:

- lower/upper lethal limit for development from oviposition to adulthood: <4.5 °C/between 25.0 and 29.1 °C (*P. hydrophilus*), between 4.5 and 9.5 °C/between 31.1 and 33.5 °C (*C. dorsalis*), between 4.5 and 9.5 °C/± 30.2 °C (*P. tritum*);
- developmental zero: 3.1 °C (*P. hydrophilus*), 4.6 °C (*C. dorsalis*), 5.2 °C (*P. tritum*);
- cue temperature of oligopause: only in *C. dorsalis* an developmental stop in the instar IV at temperatures ≤ 9.5 and 13.8 °C (→ cue ~ 12 °C);
- favourable temperatures for total development: 9-19 °C (psycrophilic-eurythermous, *P. hydrophilus*), ~12-27 °C (thermophilous, *C. dorsalis*), 10-25 °C (eurythermous-thermophilous, *P. tritum*);
- thermal constants (cumulated degree-days above the developmental zero) for development from oviposition until first-/50 %-/last emergence: 347/443/560 (*P. hydrophilus*), 308/344/406 (*C. dorsalis*), 339/416/503 (*P. tritum*). Thermal constants necessary to complete each developmental stage (egg, instar I, II, III, IV, pupa) were accordingly provided;
- *P. hydrophilus* presents high thermal coefficients (Q_{10}-values between 4 and 6) over a wide range of temperatures (5-15 °C), which might be an adaptation to daily fluctuations of temperatures in shallow waters;
- the adult body size is negatively correlated with temperature;

- males emerge before females.

The laboratory study showed that the temperature characteristics of the temporary pool species did not differ to those of many other permanent water Chironomidae. These attributes are therefore of preadaptive nature (with the possible exception of thermal coefficients in *P. hydrophilus*). For comparative reasons, the following species were also included in the investigation program: *Acricotopus lucens*, *L. asquamatus*, *Limnophyes minimus* s. str., *Parametriocnemus stylatus*, *Chironomus annularius*, *Chironomus luridus*, *Chironomus* cf. *nuditarsis*, *Chironomus plumosus*-agg., *Dicrotendipes notatus*, *Glyptotendipes foliicola*, *Glyptotendipes pallens* and *Paratanytarsus grimmii*. An intensive literature research was additionally carried out.

The impact of the **photoperiod** on the development of *C. dorsalis*, *P. tritum* and of the permanent water species *Chironomus annularius* was studied. Short-days (8h/16h) induced an oligopause in the instar IV of the first two species. Field data imply that this is also the case for *P. hydrophilus*. If possible, the critical thresholds of day length were estimated from the field data; these lay between 12.3 and 14.3 h (*P. tritum*) and 11.0 and 12.4 h (*P. hydrophilus*). Larvae that had been undertaken an oligopause produced the largest adults (feeding and growth during oligopause). Oligopauses induced by short-days are widespread amongst the Chironomidae. Long days delayed the development of *Chironomus annularius*, which is the first such record for Chironomidae.

Food shortage induced a **nutritive quiescence** in *P. tritum*.

Preliminary results of a pilot experiment on **interspecific competition** indicated that large larvae were the better competitors. The competitive ability of the permanent water species (*C. plumosus*-agg. and *C. annularius*) was higher than in the temporary pool species (*C. dorsalis* and *P. tritum*).

Increasing **larval densities** prolonged the total development time of *C. dorsalis* and accelerated development in *P. tritum*. Acceleration of development is probably an adaptation to temporary pools as larvae are likely to accumulate when the water body shrinks.

A pilot experiment showed that geophilous dragonfly larvae preyed effectively upon the tube- and mud-dwelling larvae of *C. dorsalis* and *P. tritum*. Analysis of the field data also indicated that **predation** was an important factor in determining the species communities and that temporary pools provide a haven from predation.

Experiments revealed that larvae of *L. asquamatus*, *P. hydrophilus* and *P. tritum* were **drought tolerant**. Drought tolerance was defined as the ability to survive at least several months of drought concealed by substrates with water contents (% water of total soil weight) of 20-40 %. Larvae normally did not survive a reduction of the soil moisture below 20 %, in some cases some larvae survived these low soil moisture contents for a few days. The laboratory experiments showed that all instars were drought tolerant but that the degree of tolerance increased with larval size. Survival of the larvae depended strongly on soil moisture and on the duration of drought. Field data showed that all three species survived the 502 days of drought to which the temporary woodland pool 3 was subjected in 1995/96. However, emergence data obtained after this unusual long period of drought

indicated very high mortalities. *C. dorsalis* and *C. plumosus*-agg. were included into the investigation for comparative reasons. These larvae were not drought tolerant. Such species, however, survive about one month concealed in substrates with soil moisture contents of 20-60 % or up to several months in substrates with moisture contents exceeding 60 %. Such an ability to survive 'desiccation' seems to be quite common in permanent water Chironomidae. The experiments showed that *L. asquamatus*, *P. hydrophilus* and *Polypedilum tritum* were particularly adapted to surviving periods of drought. It is likely that the ability of instars IV to moult into the pupa and then to emerge as adults after desiccation (**terrestrial eclosion**) is also an adaptation to temporary pools. Terrestrial eclosion (up to 61 % of instars IV) was observed in *P. hydrophilus*, *P. tritum* and *C. dorsalis*.

The most important results of the **autecological analysis of the field data** were the following:

- first date- /last date of emergence/number of possible generations: 27.3./end of October/up to seven (*L. asquamatus*); 27.3./begin of October/up to seven (*P. hydrophilus*), begin of May/begin of October/~five (*C. dorsalis*); 20.4./16.9./three (up to four?) (*P. tritum*);
- in accordance with the laboratory data, individuals of the first spring generation were the largest;
- predicted generations using the laboratory data of temperature dependence of development and the water temperatures in the natural habitats corresponded very well with the observed emergence patterns of *P. hydrophilus* and *P. tritum* in the field;
- laboratory data of temperature dependence of development in *L. asquamatus* were only fragmentary and did not fit very well with the field data. 'Degree-days' (cumulated daily means above 0°C since the developmental zero is not known) necessary from oviposition until the first- (~350 'degree-days'), mean- (~450 'degree-days') and last emergence (~550 'degree-days') were therefore determined from the field data;
- *P. hydrophilus* and to a lesser extent *P. tritum* were virtually bivoltine. The number of adults emerging after generation two was quite small. In addition, individuals that emerged after generation two were all very small (dwarfs). Although the adult body size in the field was strongly correlated with temperature, comparison with the laboratory data indicated that temperature was not responsible for these dwarfs. Oxygen is a strong correlate of temperature and is of high physiological significance. Measurements showed that oxygen was an important stressor for the chironomid larvae since during day runs its values did not exceed 2 mg/l and averaged (daily means) from 0.1-1.0 mg/l. Oxygen contents were therefore likely to impede growth and development and subsequently produce small adults;
- in some years, larvae of *P. hydrophilus* and *P. tritum* fell into dormancy after the eclosion of generation 1 or 2. It is discussed that low oxygen levels induced these dormancies;
- intense drought periods (very long and/or strong reduction of soil moisture content) can strongly reduce the populations of aestivating drought-tolerant larvae. The populations of aestivator spe-

cies therefore often depend on the recruitment of a second generation that fills up the stock of the aestivating larvae and ensures high population levels in the following year;

- populations of *Chironomus dorsalis* 'overshoot' after the initial colonization, which probably caused the observed decrease in the adult body size with time. The presence of a density induced dormancy is discussed.

The present study showed that the responses of temporary pool species to environmental changes in their habitats are opportunistic. Beside physiological plasticity, it is facultative dormancy induced by various cues (drought, day length, nutrition, density (?), oxygen (?)) that leads to the high plasticity in the species' life histories. Specific adaptations to drought (such as drought tolerance, terrestrial eclosion, acceleration of development) evolved. In the case of *C. dorsalis*, these adaptations also include dispersal. Temporary pools that are spatially stable are more suited for aestivators, (here *L. asquamatus, P. hydrophilus and P. tritum*) whereas spatially unstable pools (puddles) are colonized by expert invaders (here *C. dorsalis*).

6.2. Zusammenfassung

Die Überlebensstrategien von Chironomiden temporärer Tümpel standen im Zentrum der vorliegenden ökologischen Fallstudie. Welche Eigenschaften sind als spezifische Anpassungen- und welche sind als Präadaption zu werten? Ist der Lebenszyklus spezifisch oder opportunistisch auf die Wechsel zwischen aquatischer- und terrestrischer Ökophase eingepasst? Untersuchungen auf drei verschiedenen Ebenen sollten diese Fragen beantworten helfen:

(a) Drei Tümpel auf den Lahnbergen (Marburg, Hessen, Deutschland) mit unterschiedlich langen Austrocknungsperioden wurden in einer mehrjährigen Emergenzstudie untersucht. Zwei der Tümpel waren temporär, der dritte war semipermanent;

(b) In einem Freilandexperiment wurde das Besiedlungsvermögen von *Chironomus dorsalis* untersucht (Besiedlungsversuch). Mit der Absicht räumlich instabile Lachen, wie z.B. Wagenspuren, zu imitieren, wurden 1998 zehn künstliche Besiedlungsbehälter in unterschiedlichen Abständen zueinander und zu potentiellen Besiedlungsquellen aufgestellt. Emergenzfallen erfassten die aus diesen Behältern schlüpfenden Insekten;

(c) In Laboruntersuchungen wurden vor allem Grundlagendaten zum Einfluss von Temperatur, Photoperiode und Dichte auf das Wachstum und die Entwicklung, zur Austrocknungstoleranz und zur Parthenogenese erhoben. Im Zentrum des Interesses standen die vier typischen Arten temporärer Tümpel, *Limnophyes asquamatus*, *Paralimnophyes hydrophilus C. dorsalis* und *Polypedilum tritum*.

Die drei untersuchten **natürlichen Tümpel** lassen sich wie folgt charakterisieren:

(1) Tümpel 1: temporärer Herbst-Sommertümpel am Waldrand mit einer Austrocknungsdauer von 7-157 Tagen (Mittel 71 Tage, n = 8 Jahre) und einem möglichen Austrocknungsbeginn von Ende Mai bis Ende August (normalerweise im Juli);

(2) Tümpel 2: semipermanenter Tümpel am Waldrand mit einer Austrocknungsdauer von 0-130 Tagen (Mittel 34 Tage, n = 8 Jahre) und einem möglichen Austrocknungsbeginn im Juli;

(3) Tümpel 3: temporärer Winter-Frühjahrstümpel im Wald mit einer Austrocknungsdauer von 109-502 Tagen (Mittel 221 Tage, n = 8 Jahre) und einem möglichen Austrocknungsbeginn von Mitte Mai bis Ende Juni (normalerweise Ende Mai/Anfang Juni).

Da viele temporäre Tümpel während der wärmsten Jahreszeit kein Wasser führen, sind die für eine Entwicklung aquatischer Organismen zur Verfügung stehenden Wassertemperaturen im Vergleich zu anderen flachen Stillgewässern vergleichsweise niedrig. Die Wassertemperaturen wurden kontinuierlich durch Datalogger aufgezeichnet.

In den Tümpeln 1, 2 und 3 wurden 33- (n = 8.250 Individuen), 33- (n = 3.543 Individuen) und 23 Arten (n = 26.376 Individuen) festgestellt. Die Anteile semiaquatischer-terrestrischer und wirklich terrestrischer Individuen an der Jahresgesamtemergenz betrugen 27-58 % (Tümpel 1), 39-69 %

(Tümpel 2) und 79-96 % (Tümpel 3). Die Zusammensetzung der aquatischen/semiaquatischen **Chironomidengemeinschaften** wurde vor allem durch die folgenden drei Faktoren bestimmt:

(a) die durchschnittliche Stillgewässerpermanenz eines Tümpels (LWP = lentic water permanence);

$$\left(LWP_{Mittel} = \frac{1}{\left(1 + \frac{\text{durchschnittliche Austrocknungsdauer an der tiefsten Stelle}}{\text{durchschnittlich niedrigsten Bodenwassergehalt an der tiefsten Stelle}}\right)} \right);$$

(b) die Stillgewässerpermanenz des Vorjahres ($LWP_{Vorjahr}$); und

(c) der Monat der vollständigen Austrocknung.

Der Individuenanteil an Überdauerern (= Arten die zumindest mehrere Austrocknungsmonate in Substraten mit Restwassergehalten von 20-40 % überleben) war negativ mit der $LWP_{Vorjahr}$ und der LWP_{Mittel} korreliert. Der Individuenanteil der Neubesiedler hing stark vom Zeitpunkt der Austrocknung ab. Ein bis drei Überdauerer-Arten dominierten in den meisten Jahren die Chironomidengemeinschaften der temporären Tümpel 1 und 3; die durchschnittlichen Individuenanteile der Überdauerer betrugen 65,5 % (Tümpel 1) und 100 % (Tümpel 3). Die Überdauererarten waren *L. asquamatus*, *P. hydrophilus* und *P. tritum*. Der durchschnittliche Individuenanteil der aquatischen/semiaquatischen Überdauerer in dem semipermanenten Tümpel 2 betrug lediglich 17,4 %.

In dem **Besiedlungsversuch** wurden 21 Chironomiden- (n = 7.482 Individuen) und zwei Stechmückenarten (n = 2.771 Individuen) nachgewiesen. Die Mückengemeinschaften der einzelnen Becken waren sich sehr ähnlich und die unterschiedlichen Abstände zur nächsten aquatischen Besiedlungsquelle (Abstand bis zu 700 m) verursachten keine deutbaren Besiedlungsmuster. Die gewählte Distanzmatrix war zu klein im Verhältnis zum Besiedlungsvermögen der nachgewiesenen Arten. Regelmäßige Besiedlungsmuster in Abhängigkeit von den Abständen zu potentiellen Besiedlungsquellen sind vermutlich erst bei sehr weiten Abständen von bis zu mehreren Kilometern zu erwarten. Die hinsichtlich ihrer Individuenanteile wichtigsten Arten des Besiedlungsversuches waren *C. dorsalis* (40,0 %), *Culex torrentium* (20,4 %), *Chironomus piger/riparius* (16,7 %), *Tanytarsus buchonius* (9,8 %) und *Culex pipiens* (9,6 %). Das höchste Besiedlungsvermögen (gemessen anhand der Parameter (a) Expositionszeit bis zum ersten Erscheinen einer Art in der Emergenz, (b) Stetigkeit (Anteil besiedelter Behälter) und (c) Abundanz) innerhalb der Chironomiden hatte *Chironomus dorsalis* gefolgt in fallender Reihenfolge von *Chironomus piger/riparius*, *Tanytarsus buchonius* und *Corynoneura scutellata*. Nach dem Schlupf schrauben sich die Imagines von *Chironomus dorsalis* in die Höhe, was vermutlich eine Langstreckenverbreitung mittels Wind ermöglicht. Da eine aktive Habitatwahl durch eierlegende Weibchen wahrscheinlich gemacht werden konnte, ist anzunehmen, dass die Weibchen, zumindest in der terminalen Phase des Ausbreitungsfluges, gerichtete Flugbewegungen durchführen. Die Besiedlungsbehälter wurden bereits nach 2-7 Tagen von eierlegenden Weibchen aufgesucht. Niedrige Werte des Flügelverhältnisses (Flügellänge/Flügelbreite) und des Thoraxverhältnisses (Flügellänge/Thoraxlänge) scheinen gute Indikatoren für das aktive Ausbreitungsvermögen einer Chironomidenart zu sein. Auch diese morphologi-

schen Kennwerte weisen *Chironomus dorsalis* als einen Besiedlungsspezialisten aus.

In einem **morphologischen Teil** wurden morphologische Merkmale/Kennwerte der Gelege, Larven, Puppen und Imagines der im Zentrum der Arbeit stehenden Arten erhoben und dargestellt. *P. tritum* konnte nach den derzeitig verwendeten Merkmalen nicht von *P. uncinatum* unterschieden werden. Beide Arten sind wahrscheinlich synonym. Dies muss allerdings noch durch eine Untersuchung des Typusmaterials abgeklärt werden. Trotz dieser Einschränkung wurde in der vorliegenden Arbeit nur das mutmaßlich ältere Synonym *Polypedilum tritum* verwendet.

Da sich gleich zu Beginn der Arbeit herausstellte, dass es innerhalb von ***L. asquamatus*** **eine obligatorisch bisexuelle und eine parthenogenetische Ökoform** gibt, wurde eine umfangreiche morphologisch-taxonomische Analyse durchgeführt. Das Vorliegen von zwei diskreten Arten konnte zumindest aus morphologischer Sicht abgelehnt werden. Es war jedoch möglich, mit Hilfe zweier Merkmale (Vorhandensein von lanzettförmigen Präskutellarborsten, Anzahl der Präepisternalborsten) in der überwiegenden Mehrzahl der Fälle die obligatorisch bisexuellen Weibchen (*L. asquamatus* forma *asquamatus*) von den parthenogenetischen Weibchen (*L. asquamatus* forma *aquaticus*) zu unterscheiden. Es zeigte sich sehr deutlich, dass sich die bisexuelle Form *asquamatus* schwerpunktmäßig in nassen Böden entwickelte (terrestrisch/semiterrestrisch), während die parthenogenetische Form *aquaticus* eine aquatische/semiaquatische Lebensweise hatte. Das Bild verkomplizierte sich aber durch den Vergleich mit parthenogenetischen Weibchen aus verschiedenen Populationen, darunter auch solchen aus Ostdeutschland und den Niederlanden. Es zeigte sich, dass es parthenogenetische Weibchen gibt (*L asquamatus* forma *limosus*), die sich absolut nicht von der obligatorisch bisexuellen Form unterscheiden lassen und offensichtlich auch dasselbe terrestrische/semiterrestrische Mikrohabitat bewohnen. Es ist noch immer unklar, ob sich die Männchen mit den parthenogenetischen Weibchen verpaaren können und wie oft parthenogenetische Klone aus der obligatorisch bisexuellen Elternform entstehen. Die ökologische Bedeutung der Parthenogenese bei den Chironomiden scheint darin zu bestehen, dass die Klone neue Nischen erobern und temporäre Habitate effizienter neu besiedeln. **Die Larve von *L. asquamatus* wurde das erste mal beschrieben**. Während der Suche nach Merkmalen, die die Larve von *L. asquamatus* von jenen ander Arten der Gattung unterscheiden, wurde ein morphologischer Vergleich mit Larven des *Limnophyes minimus*-Komplexes und *Limnophyes natalensis* durchgeführt. Es zeigte sich, dass SÆTHER (1990) nicht die Larve von *L. natalensis*, sondern einer vermutlich neuen Art beschrieb. Daher wurde die **Larve von *L. natalensis* in der vorliegenden Arbeit ebenfalls neu beschrieben**. Ergänzungen zu den Larven- und Puppenschlüsseln von SÆTHER (1990) wurden vorgenommen.

Die **Temperaturabhängigkeit der Gesamtentwicklung** vom Ei bis zur Imago wurde für *P. hydrophilus*, *C. dorsalis* und *P. tritum* ausführlich untersucht. Diese Arten zeigten die folgenden Temperaturcharakteristika:

- Untere/obere Letaltemperatur für die Gesamtentwicklung: <4,5 °C/zwischen 25,0 und 29,1 °C (*P. hydrophilus*), zwischen 4,5 und 9,5 °C/ zwischen 31,1 und 33,5 °C (*C. dorsalis*), zwischen 4,5 und 9,5 °C/± 30,2 °C (*P. tritum*);

- Entwicklungsnullpunkt: 3,1 °C (*P. hydrophilus*), 4,6 °C (*C. dorsalis*), 5,2 °C (*P. tritum*);
- Eine Schwellentemperatur zur Oligopause war nur bei *C. dorsalis* vorhanden. Die Temperaturschwelle liegt zwischen 9,5 und 13,8 °C (→ Schwelle ~12 °C) und stoppt die Entwicklung während des vierten Larvenstadiums;
- Günstige Temperaturbereiche für die Gesamtentwicklung: 9-19 °C (psychrophil-eurytherm, *P. hydrophilus*), ~12-27 °C (thermophil, *Chironomus dorsalis*), 10-25 °C (eurytherm-thermophil, *P. tritum*);
- Thermalkonstanten (kumulierte Tag Grade über dem Entwicklungsnullpunkt) für die Gesamtentwicklung bis zum Erst-, 50 %- und Letztschlupf: 347/443/560 (*P. hydrophilus*), 308/344/406 (*C. dorsalis*), 339/416/503 (*P. tritum*). Die Thermalkonstanten dieser drei Arten wurden auch separat für die verschiedenen Entwicklungsstadien (Embryonalstadium, Larvenstadium I, II, III und IV, Puppenstadium) ermittelt;
- *P. hydrophilus* zeigte hohe Q_{10}-Werte (zwischen 4 und 6) über einen weiten Temperaturbereich von ungefähr 5-15 °C. Dies könnte man als Anpassung an die oftmals hohen täglichen Temperaturamplituden in flachen Stillgewässern werten. Vergleichdaten, die diese Vermutung stützen fehlen allerdings;
- Die Imaginalgröße ist negativ mit der Temperatur korreliert;
- Männchen schlüpfen vor den Weibchen;

Die Temperaturcharakteristika der untersuchten Arten temporärer Tümpel unterscheiden sich nicht von jenen vieler Arten permanenter Gewässer (mögliche Ausnahme Q_{10}-Werte bei *P. hydrophilus*) und sind daher präadaptiv. Zu Vergleichszwecken wurden folgende Arten mit in das Untersuchungsprogramm einbezogen: *Acricotopus lucens*, *L. asquamatus*, *Limnophyes minimus* s. str. *Parametriocnemus stylatus*, *Chironomus annularius*, *Chironomus luridus*, *Chironomus* cf. *nuditarsis*, *Chironomus plumosus*-agg., *Dicrotendipes notatus*, *Glyptotendipes foliicola*, *Glyptotendipes pallens* und *Paratanytarsus grimmii*. Ein umfangreicher Literaturvergleich wurde vorgenommen.

Die Auswirkung der **Photoperiode** auf die Entwicklung wurde für *C. dorsalis* und *P. tritum* untersucht. Eine Art permanenter Stillgewässer, *C. annularius*, wurde zu Vergleichszwecken ebenfalls mit in das Untersuchungsprogramm aufgenommen. Kurztage (8h/16h) induzierten eine Oligopause im vierten Larvenstadium von *C. dorsalis* und *P. tritum*. Die Analyse der Freilanddaten machte es wahrscheinlich, dass eine Kurztagshemmung der Larvalentwicklung auch bei *P. hydrophilus* vorliegt. Durch die Analyse der Freilanddaten ließen sich auch die Schwellen für die kritischen Tageslängen bei *P. hydrophilus* und *P. tritum* abschätzen. Diese lagen zwischen 11,0 und 12,4 h (*P. hydrophilus*) und 12,3 und 14,3 h (*P. tritum*). Larven die für eine Weile in Oligopause verharrten, entwickelten sich später zu den größten Imagines (→Fortsetzung der Nahrungsaufnahme und des Wachstums während der Oligopause). Kurztaginduzierte Oligopausen sind innerhalb der Chironomiden weit verbreitet. *Chironomus annularius* zeigte eine Langtagshemmung der Larvalent-

wicklung, die bei Chironomiden bisher nicht bekannt war.

Nahrungsmangel induzierte eine **nutritive Quieszenz** bei *P. tritum*.

Ein Pilotexperiment zur **interspezifischen Konkurrenz** zeigte, dass große Larven einen Wettbewerbsvorteil gegenüber frisch geschlüpften Larven haben. Die Ergebnisse wiesen auch darauf hin, dass die Konkurrenzfähigkeit der beiden permanenten Stillgewässerarten (*C. plumosus*.-agg. und *C. annularius*) höher war als jene der beiden Arten temporärer Tümpel (*C. dorsalis* und *P. tritum*).

Steigende **Larvaldichten** führten bei *C. dorsalis* zu einer Entwicklungsverlängerung und bei *P. tritum* zu einer Entwicklungsverkürzung. Letzteres kann als Adaption an temporäre Tümpel gewertet werden: bei fortschreitender Austrocknung ist eine Konzentration der Larven in dem (den) noch verbleibenden Wasserkörper(n) wahrscheinlich. Die beschleunigte Entwicklung mit zunehmender Larvendichte bewirkt auf diese Weise, dass viele Tiere vor der Austrocknung entweichen und in anderen Tümpelarealen/Gewässern zur Eiablage schreiten können.

In einem Pilotexperiment zur **Prädation** erbeuteten geophile Großlibellenlarven effizient die schlammbewohnenden und röhrenbauenden Larven von *C. dorsalis* und *P. tritum*. Die Analyse der Freilanddaten wies darauf hin, dass Prädation ein wesentlicher Faktor hinsichtlich der Artenzusammensetzung ist und dass die untersuchten temporären Tümpel in der Tat einen feindarmen Lebensraum darstellen.

In Laborexperimenten erwiesen sich die Larven von *L. asquamatus*, *P. hydrophilus* und *P. tritum* als austrocknungstolerant. **Austrocknungstoleranz** wurde als die Fähigkeit definiert zumindest mehrere Monate in Substraten überdauern zu können, die Restwassergehalte (Gewichtsprozente des Wassers am Substratgesamtgewicht) von 20-40 % aufweisen. Eine Austrocknung, die zu Restwassergehalten unter 20 % führte, wurde nicht oder nur für wenige Tage überlebt. Alle Larvenstadien waren austrocknungstolerant, allerdings nahm die Toleranz mit zunehmender Larvalgröße zu. Die Überlebensrate der überdauernden Larven war stark abhängig von den Restwassergehalten im Boden und der Expositionsdauer. Die Freilanddaten zeigten, dass Trockenperioden einer Länge von bis zu 502 Tagen (Tümpel 3 1995/96) von allen drei Arten überlebt wurden. Die Emergenzdaten ließen allerdings bei derart langen Austrocknungsereignissen auf sehr hohe Mortalitäten schließen. Die Larven von *C. dorsalis* und *C. plumosus*-agg. wurden in das Untersuchungsprogramm zum Vergleich mit einbezogen. Beide Arten haben innerhalb der Chironomiden keine erhöhte Austrocknungstoleranz. Trotzdem sind sie in der Lage bis zu ungefähr einem Monat in Substraten zu überleben, die noch Restwassergehalte zwischen 20 und 60 % aufweisen. In Substraten mit Restwassergehalten von >60 % ist ein Überdauern von vermutlich mehreren Monaten möglich. Die Fähigkeit, Perioden ohne Oberflächenwasser zu Überleben, scheint bei Chironomiden permanenter Gewässer weit verbreitet zu sein und ist als präadaptive Ausgangssituation für die Entwicklung einer Austrocknungstoleranz zu werten. Die Untersuchung zeigte, dass *L. asquamatus*, *P. hydrophilus* und *P. tritum* speziell an das Überleben im ausgetrockneten Substrat angepasst sind. Die Fähigkeit, sich auch noch unter terrestrischen Bedingungen in eine Puppe und danach in eine Imago umwandeln zu

können (**terrestrischer Schlupf**), ist nach derzeitiger Datenlage ebenfalls als Anpassung zu werten. Einen terrestrischen Schlupf nach erfolgter Austrocknung (bis zu 61 % der Larvenpopulation im vierten Larvenstadium) wurde bei *P. hydrophilus*, *P. tritum* und *C. dorsalis* nachgewiesen.

Die wichtigsten Ergebnisse der **autökologischen Analyse der Freilanddaten** können wie folgend zusammengefasst werden:

- Erste beobachtete Emergenz/letzte beobachtete Emergenz/Anzahl möglicher Generationen: 27.3./Ende Oktober/bis zu sieben (*L. asquamatus*); 27.3./Beginn Oktober/bis zu sieben (*P. hydrophilus*), Beginn Mai/Beginn Oktober/~fünf (*C. dorsalis*); 20.4./16.9./drei (bis vier?) (*P. tritum*);
- Die Tiere der ersten Frühjahrsgeneration waren die Größten, was mit den Ergebnissen der Laborstudie in Einklang steht;
- Mit Hilfe der im Labor ermittelten Temperaturcharakteristika und den in den natürlichen Gewässern aufgezeichneten Wassertemperaturen wurden für *P. hydrophilus* und *P. tritum* die Emergenzperioden prognostiziert und mit den beobachteten Emergenzmustern verglichen. Es ergab sich eine hohe Übereinstimmung der Freilandbefunde mit den Labordaten;
- Die im Labor ermittelten Daten zur Temperaturabhängigkeit der Gesamtentwicklung von *L. asquamatus* waren fragmentarisch und stimmten darüber hinaus nicht gut mit den Freilanddaten überein. Daher wurden die ‘Tag-Grade’ (kumulierte Tagesmittel über 0 °C, da der Entwicklungsnullpunkt nicht bekannt war), die zur Vollendung der Gesamtentwicklung bis zum Erst-, 50 %- und Letztschlupf benötigt werden, aus den Freilanddaten abgeleitet: sie betrugen 350/~450/~550 ‘Tag-Grade’;
- *P. hydrophilus* und etwas undeutlicher *P. tritum*, waren im Freiland quasi bivoltin. Die Anzahl der nach dem Schlupf der zweiten Generation schlüpfenden Imagines war sehr gering. Weiterhin waren die nach der zweiten Generation schlüpfenden Imagines extrem klein. Obwohl die Körpergröße der Imagines im Freiland stark mit der Temperatur korreliert war, ergab der Vergleich mit den Labordaten, dass die Temperatur als Hauptursache des Zwergwuchses ausgeschlossen werden kann. Der Sauerstoffgehalt in den Gewässern wurde in fünf Tagesgängen exemplarisch gemessen und die Gehalte überstiegen nie 2 mg/l. Die täglichen Mittel lagen zwischen 0,1 und 1,0 mg/l. Solche Sauerstoffgehalte sind als extrem niedrig einzustufen. Zudem ist bekannt, dass die Sauerstoffgehalte stark mit der Wassertemperatur korreliert sind. Daher ist anzunehmen, dass kritische Sauerstoffgehalte zu einer deutlichen Wachstums- und Entwicklungsverschlechterung- und letztlich zu dem imaginalen Zwergwuchs geführt hatten.
- In manchen Jahren fielen die Larven von *P. hydrophilus* und *P. tritum* bereits nach dem Schlupf der ersten oder zweiten Frühjahrsgeneration in Dormanz, obwohl noch genügend Wasser für eine Weiterentwicklung vorhanden gewesen wäre. Diese Dormanz wurde vermutlich ebenfalls durch niedrige Sauerstoffgehalte ausgelöst;

- Intensive Austrocknungsperioden (sehr lang und/oder starke Herabsetzung der Substratrestwassergehalte) verursachten hohe Mortalitäten unter den überdauernden Larven. Daher sind die Überdauerer oftmals stark von der Rekrutierung einer zweiten Generation abhängig, die die 'Bank' überdauernder Larven wieder auffüllt und daher hohe Populationsdichten im Folgejahr ermöglicht;
- Die Populationsdichten von *Chironomus dorsalis* steigen nach erfolgter Initialbesiedlung eines Besiedlungsbehäters schnell an, was vermutlich eine dichteabhängige Reduktion der imaginalen Körpergröße nach sich zieht. Eine dichteinduzierte larvale Dormanz wird diskutiert.

Die vorliegende Untersuchung zeigte, dass die untersuchten Arten temporärer Tümpel sehr flexibel auf die sich verändernden Verhältnisse in den Gewässern reagieren. Die hohe Plastizität der Lebensgeschichten wird durch die fakultative larvale Dormanz ermöglicht, die mittels einer Vielzahl von Faktoren ausgelöst werden kann (Austrocknung, Nahrung, Tageslänge, Sauerstoff (?), Dichte (?)). Spezifische Anpassungen erfolgten hinsichtlich der Austrocknung (Austrocknungstoleranz, terrestrischer Schlupf, Entwicklungsbeschleunigung) und bei C. *dorsalis* besonders zugunsten eines hohen Ausbreitungsvermögens. In räumlich konstanten temporären Tümpeln werden Überdauerer begünstigt (*L.asquamatus, P. hydrophilus, P. tritum*) in räumlich inkonstanten Lachen die Besiedlungsspezialisten wie *C. dorsalis*.

7. References

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8. Appendix

Appendix 1: Water depths, conductivity and pH measured in pools 1-3.

Date	Depth site 1	Depth site 1b	Depth site 1c	Depth site 2	Depth site 3	Cond. (µS/cm) site 2	pH site 2
Pool 1							
29.5.93	8			15	8		
2.6.93	8			13		240	7,3
6.6.93	0			2	0		
7.10.93	8			12	7	195	
14.10.93	8			14	9	271	5,7
25.10.93	9			16	11	270	6,2
10.11.93	9			15	10		
14.12.93	10			16	11		
26.1.94						156	5,3
11.3.94	21			29	21		
11.4.94	24			32	23		
22.4.94	21			28	21		7,1
28.5.94	22			30	22	92	7,2
23.5.95				20	20	110	6,6
26.5.95				14	14	84	6,6
27.5.95						94	6,4
28.5.95							6,7
30.5.95						76	6,4
1.6.95						105	6,6
2.6.95				22	20	102	6,2
3.6.95						112	7,7
6.6.95				27	20		
8.6.95				27	20	91	6,9
10.6.95						116	7
11.6.95						228	6,7
12.6.95				20	20	131	6,7
13.6.95						76	6,4
15.6.95				20	20		
22.6.95				23	23		
26.6.95				20	15		
28.6.95				20	20	105	6,2
29.6.95				20	20	102	6,2
30.6.95				15	15		
2.7.95				14	7	112	7,7
3.7.95				16	10		
6.7.95				20	20	91	6,9
8.7.95				13	13	116	7
9.7.95				12	8		
10.7.95				10	9	131	6,5
11.7.95				10	5		
13.7.95				10			
17.7.95				10			
20.7.95				0			
16.4.96	10			20	20		
14.6.96						180	7
18.6.96				12	7		
26.6.96				8	10	245	6,97
10.7.96				12	19		
16.7.96				9	12	252	6,8
23.7.96				0	0		
31.7.96				0	0		
6.8.96				0	0		
14.8.96				0	0		
10.9.96				0	0		
30.9.96				0	0		
18.10.96				15	16		
1.11.96				17	20	191	6,3
18.11.96				19	20		
20.12.96				25	25	155	6,6
18.3.97				25	25	142	6,5
5.4.97				25	28		
11.4.97				26	28	161	6,9
19.4.97				25	23		
26.4.97				25	22		
3.5.97				26	21		
10.5.97				35	30		
14.5.97				30	28	126	7
22.5.97				25	23		

Appendix 1 (continued) (pool 1).

Date	Depth site 1	Depth site 1b	Depth site 1c	Depth site 2	Depth site 3	Cond. (µS/cm) site 2	pH site 2
30.5.97				21	20		
3.6.97						260	7,1
5.6.97				20	16		
12.6.97				14	10		
19.6.97				7	0		
28.6.97				14	10		
5.7.97				14	10	121	7,45
11.7.97				0	0		
19.7.97				0	0		
26.7.97				0	0		
5.8.97				0	0		
14.8.97				0	0		
23.8.97				0	0		
30.9.97				0	0		
5.11.97				0	0		
6.12.97				5	3		
5.1.98	12			22	20	157	6,57
23.3.98	13			20	20	160	6,46
30.3.98	12			20	20		
7.4.98	15			24	24		
15.4.98	14			21	23		
22.4.98	16			24	25	123	6,78
30.4.98	15			23	25		
6.5.98	15			22	23		
13.5.98	10			18	20		
20.5.98	5			13	14		
27.5.98	5			13	15		
3.6.98	10			20	20		
10.6.98	15			22,5	25		
17.6.98	13			20	22,5		
25.6.98	10			17	19	97	6,54
2.7.98	10			18	20		
9.7.98	7			15	17		
17.7.98	12			20	21	103	6,69
24.7.98	10			16	18		
3.8.98	10			18	19		
10.8.98	5			13	14		
18.8.98	0			4	2	138	6,68
26.8.98	0			5	7		
2.9.98	0			0,5	0,5		
11.9.98	0			9	9		
21.9.98	10			18	21	112	6,31
30.9.98	9			15	20		
9.10.98	13			20	21		
19.10.98	13			20	22	142	6,51
2.11.98	15			22	26		
10.2.99				26		141	6,5
6.4.99	15		9,0	23	25	150	6,77
16.4.99	15	8,0	9,0	25	29		
24.4.99	11	6,0	6,0	23	24		
30.4.99	13	7,0	7,0	20	24		
7.5.99	15	8,0	8,0	22	24		
19.5.99	11	5,0	8,0	20	20	150	6,66
27.5.99	10	6,0	9,0	19,5	20		
28.5.99						169	6,32
2.6.99	12	6,0	8,0	20	20,5		
9.6.99	12	8,0	9,0	20	22,5		
18.6.99	8	0,0	0,0	15	20		
25.6.99		0,0	0,0	12,5	14,5		
1.7.99	0	0,0	0,0	5	0		
8.7.99	6	1,0	0,0	14	14		
18.7.99	0	0,0	0,0	4	0		
27.7.99	0	0,0	0,0	0	0		
1.8.99	0	0,0	0,0	0	0		

Appendix 1 (continued).

Date	Depth site 4	Depth site 5	Depth site 6	Cond. (µS/cm) site 5	pH site 5
			Pool 2		
6.6.93	4		27	540	6,9
9.6.93	0		24		7,7
14.6.93	0		20		
18.6.93	0		23	503	7,5
21.6.93	0		20	547	7,9
29.6.93	0		12	670	6,9
3.7.93	0		0		
7.7.93	0		0		
12.7.93	0		0		
17.7.93	0		0		
21.7.93	0		0		
26.7.93	0		0	1620	6
30.7.93	0		0		
4.8.93	0		17	634	6,5
9.8.93	0		13	663	6,5
13.8.93	0		10	733	7
18.8.93	0		4	700	6,6
23.8.93	0		0	903	
28.8.93	0		0		
1.9.93	0		0		
6.9.93	0		0		
11.9.93	0		0		
16.9.93	0		8	665	4,8
24.9.93	0		10	701	6,4
1.10.93	0		15		
7.10.93	23		38	490	
14.10.93	20		36	445	6,4
25.10.93	21		35	459	6,3
10.11.93	18		33		
14.12.93	25		40		
26.1.94	26		41	302	6,4
11.4.93	27		42		
22.4.94	27		42		7,4
28.5.94	26		43	420	7
16.4.96			30		
14.6.96				738	7,6
18.6.96	0	25	13		
26.6.96	0	17	12	613	7,2
10.7.96	4	24	16		
16.7.96	1	20	11	565	7,2
23.7.96	0	4	0	940	6,8
31.7.96	0	18	8	645	6,9
6.8.96	0	0	0		
14.8.96	4	19	11		
28.8.96	0	16	10	450	6,8
10.9.96	0	5	2	610	6,2
30.9.96	0	18	8	532	7,3
18.10.96	18	35	26		
1.11.96	24	41	40	550	6,6
18.11.96		37	35,5		
20.12.96		40	35	681	7
18.3.97	20	45	40	590	6,9
5.4.97	15	42	31		
11.4.97	19	40	29	638	7
19.4.97	15	36	25		
26.4.97	14	35	20		
3.5.97	22	45	30		
10.5.97	36	59	44		
14.5.97				537	7,5
15.5.97	19	55	40		
22.5.97					
30.5.97	5	35	20		
3.6.97				640	7,1
5.6.97	0	25	9		
12.6.97	0	0	0		
19.6.97	0	0	0		
28.6.97	0	15	0		
5.7.97	0	10	7	895	7,2

Appendix 1 (continued) (pool 2).

Date	Depth site 4	Depth site 5	Depth site 6	Cond. (µS/cm) site 5	pH site 5
11.7.97	0	0	0		
19.7.97	0	0	0		
26.7.97	0	0	0		
5.8.97	0	0	0		
14.8.97		0	0		
23.8.97	0	0	0		
30.9.97	0	0	0		
5.11.97	0	0	0		
6.12.97	0	12	9		
5.1.98	25	45	36	592	7,33
23.3.98	16	40	30	546	7,22
30.3.98	16	34	30		
7.4.98	25	37	36		
15.4.98	22	40	38		
22.4.98	28	40	41	571	7,46
30.4.98	28	40	39		
6.5.98	27	38	37		
13.5.98	16	28	26		
20.5.98	6	15,5	14		
27.5.98	3	12,5	10		
3.6.98	25	39	35		
10.6.98	27	41	35		
17.6.98	25	39	35		
25.6.98	19	30	28	585	7,07
2.7.98	19	30	29		
9.7.98	12	25	24		
17.7.98	25	39	36	425	7,08
24.7.98	20	31	30		
3.8.98	20	31	28		
10.8.98	13	26	24		
18.8.98	4	14	12	550	7,28
26.8.98	7	20	15		
2.9.98	5	18	14		
11.9.98	12	25	20		
21.9.98	26	40	35	477	6,85
30.9.98	26	40	35		
9.10.98	25	40	35		
19.10.98	25	41	35	520	7,31
2.11.98	30	43	37		

Appendix 1 (continued).

Date	Depth site 7	Depth site 8	Depth site 9	Depth site 10	Cond. (µS/cm) site 8	Cond. (µS/cm) site 9	Cond. (µS/cm) site 10	pH site 8	pH site 9	pH site 10
Pool 3										
26.5.95	28			4		122	108		5,3	5,2
2.6.95	40		17	20						
3.6.95	35		20	20						
6.6.95						120	106		6	4,2
8.6.95	33		18	20		98	101		5,4	4,4
12.6.95	35		10	13					5,5	4,4
15.6.95	35		17	20						
22.6.95	25		10	10		80	90		5,4	4,8
26.6.95	20		0	0						
28.6.95	13		0	0		103			5	
29.6.95	13		0	0		140			5,4	
30.6.95	0		0	0						
2.7.95	3		0	0		150			5,6	
4.7.95	5		0	0		190			6,4	
6.7.95	5		0	0		211			5,5	
10.7.95	0		0	0						
18.11.96	0	0	0							
25.11.96	10	0	0							
20.12.96	34	40	7		380			6,4		
28.3.97	50	45	20		245			6,35		
5.4.97	35	37	10							
11.4.97	35	35	10		357			6,7		
19.4.97	25	25	0							
26.4.97	25	29	0							
3.5.97	20	29	0							
10.5.97	34	45	12							
14.5.97					340			6		
15.5.97	25	30	0							
22.5.97	0	14	0							
30.5.97	0	0	0							
5.6.97	0	0	0							
12.6.97	0	0	0							
19.6.97	0	0	0							
28.6.97	0	0	0							
5.7.97	0	0	0							
11.7.97	0	0	0							
21.7.97	0	0	0							
26.7.97	0	0	0							
5.8.97	0	0	0							
14.8.97	0	0	0							
23.8.97	0	0	0							

Appendix 1 (continued) (pool 3).

Date	Depth site 7	Depth site 8	Depth site 9	Depth site 10	Cond. (µS/cm) site 8	Cond. (µS/cm) site 9	Cond. (µS/cm) site 10	pH site 8	pH site 9	pH site 10
30.9.97	0	0	0							
5.11.97	0	0	0							
6.12.97	5	5	0							
5.1.98	25	18	0		417			6,6		
23.3.98	24	22	0		343			6,5		
30.3.98	20	20	0							
7.4.98	27	25	0							
15.4.98	41	36	15							
22.4.98	45	32	20		229			6,75		
30.4.98	46	45	25							
6.5.98	44	44	24							
13.5.98	30	30	10							
20.5.98	9,5	7	0							
27.5.98	10	7	0							
3.6.98	20	18	0							
10.6.98	20	17	0							
17.6.98	10	10	0							
25.6.98	0	0	0							
2.7.98	0	0	0							
9.7.98	0	0	0							
17.7.98	0	0	0							
24.7.98	0	0	0							
3.8.98	0	0	0							
10.8.98	0	0	0							
21.9.98	0	0	0							
9.10.98	15	10								
19.10.98	17	14,5			222			5,33		
2.11.98	55	55	30							

Appendix 2: Daily means of water temperatures in pools 1-3.

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
25.11.96	3,7	a			2,5	a
26.11.96	3,7	a			3,3	a
27.11.96	3,5	a			3,4	a
28.11.96	3,5	a			3,0	a
29.11.96	3,5	a			2,1	a
30.11.96	3,2	a			2,1	a
1.12.96	3,1	a			3,1	a
2.12.96	3,1	a			3,8	a
3.12.96	3,4	a			4,1	a
4.12.96	3,7	a			4,3	a
5.12.96	4,1	a			4,8	a
6.12.96	4,1	a			5,0	a
7.12.96	3,8	a			4,6	a
8.12.96	3,5	a			4,5	a
9.12.96	3,2	a			4,2	a
10.12.96	3,1	a			3,9	a
11.12.96	2,9	a			3,9	a
12.12.96	2,7	a			3,5	a
13.12.96	2,7	a			3,5	a
14.12.96	2,7	a			3,4	a
15.12.96	2,3	a			3,1	a
16.12.96	2,3	a			2,9	a
17.12.96	2,3	a			3,4	a
18.12.96	2,3	a			3,7	a
19.12.96	2,3	a			4,1	a
20.12.96	2,5	a			4,3	a
21.12.96	2,4	a			3,9	a
22.12.96	2,3	a			3,9	a
23.12.96	2,3	a			3,5	a
24.12.96	1,9	a			3,5	a
25.12.96	1,5	a			3,1	a
26.12.96	1,2	a			2,8	a
27.12.96	1,1	a			2,7	a
28.12.96	0,7	a			2,3	a
29.12.96	0,4	a			2,2	a
30.12.96	0,3	a			1,9	a
31.12.96	0,2	a			1,9	a
1.1.97	-0,1	a			1,5	a
2.1.97	-0,1	a			1,2	a
3.1.97	-0,6	a			1,1	a
4.1.97	-0,3	a			1,4	a
5.1.97	-0,1	a			1,5	a
6.1.97	-0,1	a			1,5	a
7.1.97	-0,1	a			1,4	a
8.1.97	-0,6	a			1,1	a
9.1.97	-0,6	a			1,1	a
10.1.97	-0,6	a			1,1	a
11.1.97	-0,5	a			1,1	a
12.1.97	-0,1	a			1,1	a
13.1.97	-0,6	a			0,7	a
14.1.97	-0,6	a			0,4	a
15.1.97	-0,6	a			0,0	a
16.1.97	-1,0	a			-0,5	a
17.1.97	-1,0	a			-0,9	a
18.1.97	-0,8	a			-0,8	a
19.1.97	-0,6	a			-0,2	a
20.1.97	-0,6	a			0,1	a
21.1.97	-0,6	a			0,4	a
22.1.97	-0,6	a			0,8	a
23.1.97	-0,6	a			1,1	a
24.1.97	-0,3	a			1,3	a
25.1.97	-0,1	a			1,7	a
26.1.97	-0,1	a			1,5	a
27.1.97	-0,1	a			1,5	a
28.1.97	-0,1	a			1,5	a
29.1.97	-0,1	a			1,5	a
30.1.97	-0,1	a			1,5	a
31.1.97	-0,1	a			1,5	a
1.2.97	-0,1	a			1,5	a
2.2.97	-0,1	a			1,4	a
3.2.97	-0,1	a			1,1	a
4.2.97	-0,1	a			1,1	a
5.2.97	-0,1	a			1,1	a
6.2.97	0,0	a			1,3	a

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
7.2.97	0,0	a			1,4	a
8.2.97	-0,1	a			1,4	a
9.2.97	0,0	a			1,5	a
10.2.97	0,1	a			1,6	a
11.2.97	0,2	a			1,5	a
12.2.97	0,2	a			1,4	a
13.2.97	0,3	a			1,3	a
14.2.97	0,3	a			1,3	a
15.2.97	0,3	a			1,8	a
16.2.97	0,3	a			2,0	a
17.2.97	0,3	a			2,0	a
18.2.97	0,3	a			2,1	a
19.2.97	0,3	a			2,7	a
20.2.97	0,3	a			3,1	a
21.2.97	0,3	a			3,4	a
22.2.97	0,3	a			3,7	a
23.2.97	0,4	a			4,1	a
24.2.97	0,9	a			4,3	a
25.2.97	2,2	a			4,3	a
26.2.97	2,4	a			4,5	a
27.2.97	2,7	a			4,6	a
28.2.97	2,8	a			4,6	a
1.3.97	3,2	a			4,8	a
2.3.97	3,7	a			5,0	a
3.3.97	4,3	a			5,1	a
4.3.97	4,6	a			5,4	a
5.3.97	4,6	a			5,6	a
6.3.97	5,0	a			5,8	a
7.3.97	5,4	a			5,8	a
8.3.97	5,4	a			6,1	a
9.3.97	5,4	a			5,9	a
10.3.97	5,3	a			5,8	a
11.3.97	5,2	a			5,8	a
12.3.97	5,4	a			5,9	a
13.3.97	5,2	a			6,2	a
14.3.97	5,4	a			6,2	a
15.3.97	5,4	a			6,2	a
16.3.97	5,7	a			6,2	a
17.3.97	6,3	a			6,4	a
18.3.97	6,5	a	6,5	a	6,5	a
19.3.97	6,5	a	6,5	a	6,5	a
20.3.97	6,2	a	6,5	a	6,3	a
21.3.97	5,7	a	6,2	a	5,9	a
22.3.97	6,0	a	6,3	a	5,8	a
23.3.97	5,9	a	6,5	a	5,4	a
24.3.97	5,8	a	6,5	a	5,4	a
25.3.97	5,8	a	6,5	a	5,4	a
26.3.97	6,1	a	6,5	a	5,5	a
27.3.97	7,0	a	6,9	a	5,9	a
28.3.97	7,8	a	7,4	a	6,4	a
29.3.97	6,6	a	7,1	a	6,3	a
30.3.97	6,2	a	6,9	a	6,2	a
31.3.97	6,7	a	7,1	a	6,2	a
1.4.97	7,2	a	7,4	a	6,3	a
2.4.97	7,7	a	7,6	a	6,6	a
3.4.97	7,7	a	7,6	a	6,9	a
4.4.97	7,0	a	7,1	a	6,4	a
5.4.97	5,8	a	6,6	a	5,5	a
6.4.97	6,2	a	6,4	a	5,4	a
7.4.97	6,5	a	6,6	a	5,3	a
8.4.97	6,5	a	6,7	a	5,2	a
9.4.97	6,6	a	6,8	a	5,4	a
10.4.97	7,3	a	7,2	a	6,1	a
11.4.97	7,4	a	7,1	a	6,9	a
12.4.97	6,1	a	6,4	a	6,0	a
13.4.97	6,4	a	6,4	a	5,6	a
14.4.97	7,1	a	6,8	a	5,9	a
15.4.97	7,0	a	6,8	a	6,2	a
16.4.97	6,8	a	6,6	a	5,9	a
17.4.97	6,8	a	6,5	a	5,7	a
18.4.97	7,3	a	6,8	a	5,9	a
19.4.97	7,5	a	7,2	a	6,3	a
20.4.97	6,2	a	6,5	a	6,0	a
21.4.97	6,3	a	6,2	a	5,3	a

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
22.4.97	6,3	a	6,2	a	5,5	a
23.4.97	6,7	a	6,3	a	5,5	a
24.4.97	6,9	a	6,6	a	5,7	a
25.4.97	8,1	a	7,4	a	6,9	a
26.4.97	8,2	a	7,9	a	7,4	a
27.4.97	8,3	a	8,4	a	7,5	a
28.4.97	9,0	a	9,1	a	7,9	a
29.4.97	9,0	a	9,1	a	8,0	a
30.4.97	9,1	a	9,1	a	8,0	a
1.5.97	9,2	a	9,3	a	7,9	a
2.5.97	9,9	a	10,0	a	8,5	a
3.5.97	11,0	a	10,8	a	9,3	a
4.5.97	12,2	a	11,9	a	10,4	a
5.5.97	12,0	a	12,1	a	10,7	a
6.5.97	11,1	a	11,4	a	10,0	a
7.5.97	8,8	a	9,9	a	8,7	a
8.5.97	8,6	a	9,6	a	8,0	a
9.5.97	8,2	a	9,4	a	7,8	a
10.5.97	8,3	a	9,3	a	7,7	a
11.5.97	9,3	a	10,0	a	8,0	a
12.5.97	10,6	a	11,1	a	8,7	a
13.5.97	10,8	a	11,6	a	9,2	a
14.5.97	11,7	a	12,3	a	10,1	a
15.5.97	12,1	a	13,1	a	11,0	a
16.5.97	12,3	a	14,0	a	12,1	a
17.5.97	13,4	a	15,2	a	13,6	a
18.5.97	13,6	a	15,4	a	14,0	a
19.5.97	13,6	a	15,4	a	14,3	a
20.5.97	13,6	a	15,2	a	14,1	a
21.5.97	12,8	a	14,2	a	12,7	a
22.5.97	12,1	a	13,4	a	11,6	a
23.5.97	11,3	a	12,2	a	10,7	a
24.5.97	10,6	a	11,4	a	10,3	a
25.5.97	10,2	a	11,3	a	10,7	a
26.5.97	10,5	a	11,5	a	10,9	t/sa
27.5.97	10,9	a	12,1	a	11,3	t/sa
28.5.97	10,7	a	11,9	a	10,3	t/sa
29.5.97	10,8	a	11,7	a	11,0	t/sa
30.5.97	11,3	a	12,2	a	12,1	t/sa
31.5.97	11,2	a	12,1	a	11,0	t/sa
1.6.97	10,3	a	11,3	a	10,0	t/sa
2.6.97	10,8	a	12,0	a	11,4	t/sa
3.6.97	12,7	a	13,7	a	13,0	t/sa
4.6.97	13,1	a	14,2	a	13,8	t/sa
5.6.97	13,5	a	15,0	a	14,5	t/sa
6.6.97	14,1	a	16,3	a	15,2	t/sa
7.6.97	14,9	a	17,0	a	16,0	t/sa
8.6.97	14,5	a	15,8	a	15,1	t/sa
9.6.97	14,7	a	16,3	a	15,4	t/sa
10.6.97	15,3	a	16,9	a	16,1	t/sa
11.6.97	16,4	a	17,1	t/sa	16,0	t/sa
12.6.97	16,4	a	17,7	t/sa	16,6	t/sa
13.6.97	15,8	a	15,8	t/sa	15,2	t/sa
14.6.97	15,3	a	16,5	t/sa	15,7	t/sa
15.6.97	14,9	a	15,4	t/sa	14,3	t/sa
16.6.97	14,2	a	15,0	t/sa	14,0	t/sa
17.6.97	13,9	a	14,7	t/sa	13,7	t/sa
18.6.97	12,9	a	13,6	t/sa	13,0	t/sa
19.6.97	12,2	a	13,4	t/sa	12,9	t/sa
20.6.97	12,3	a	13,8	t/sa	12,9	t/sa
21.6.97	12,7	a	13,9	t/sa	13,0	t/sa
22.6.97	12,7	a	14,4	a	13,1	t/sa
23.6.97	12,4	a	13,5	a	12,5	t/sa
24.6.97	11,9	a	13,1	a	12,3	t/sa
25.6.97	12,2	a	13,1	a	12,5	t/sa
26.6.97	12,3	a	13,6	a	12,7	t/sa
27.6.97	13,2	a	14,9	a	13,7	t/sa
28.6.97	13,3	a	14,7	a	13,8	t/sa
29.6.97	14,9	a	17,0	a	15,8	t/sa
30.6.97	14,2	a	15,5	a	14,3	t/sa
1.7.97	14,0	a	15,5	a	14,2	t/sa
2.7.97	14,6	a	16,0	a	14,9	t/sa
3.7.97	15,1	a	16,7	a	15,3	t/sa
4.7.97	14,7	a	15,7	a	14,2	t/sa

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
5.7.97	14,3	a	14,7	a	13,8	t/sa
6.7.97	13,9	a	14,5	a	13,5	t/sa
7.7.97	13,7	a	14,8	a	14,1	t/sa
8.7.97	13,8	a	14,8	a	14,5	t/sa
9.7.97	14,1	a	15,8	a	15,4	t/sa
10.7.97	14,8	a	16,2	t/sa	15,5	t/sa
11.7.97	15,6	t/sa	17,3	t/sa	16,5	t/sa
12.7.97	15,7	t/sa	16,4	t/sa	16,2	t/sa
13.7.97	16,1	t/sa	17,0	t/sa	16,7	t/sa
14.7.97	16,2	t/sa	16,4	t/sa	16,1	t/sa
15.7.97	15,7	t/sa	17,0	t/sa	16,4	t/sa
16.7.97	15,8	t/sa	16,8	t/sa	16,3	t/sa
17.7.97	15,8	t/sa	17,1	t/sa	16,4	t/sa
18.7.97	15,2	t/sa	16,3	t/sa	15,7	t/sa
19.7.97	14,9	t/sa	15,9	t/sa	15,6	t/sa
20.7.97	14,8	t/sa	15,6	t/sa	15,3	t/sa
21.7.97	14,6	t/sa	15,6	t/sa	15,1	t/sa
22.7.97	15,4	t/sa	16,8	t/sa	16,0	t/sa
23.7.97	16,4	t/sa	17,2	t/sa	16,5	t/sa
24.7.97	16,1	t/sa	16,1	t/sa	15,9	t/sa
25.7.97	15,2	t/sa	15,9	t/sa	15,7	t/sa
26.7.97	14,7	t/sa	15,3	t/sa	15,1	t/sa
27.7.97	15,5	t/sa	16,6	t/sa	16,3	t/sa
28.7.97	15,1	t/sa	15,1	t/sa	15,4	t/sa
29.7.97	15,5	t/sa	15,6	t/sa	15,7	t/sa
30.7.97	15,9	t/sa	16,0	t/sa	16,1	t/sa
31.7.97	15,2	t/sa	15,6	t/sa	15,4	t/sa
1.8.97	14,5	t/sa	15,2	t/sa	14,8	t/sa
2.8.97	14,7	t/sa	15,2	t/sa	14,7	t/sa
3.8.97	15,1	t/sa	16,2	t/sa	15,7	t/sa
4.8.97	17,0	t/sa	17,6	t/sa	17,0	t/sa
5.8.97	17,1	t/sa	17,8	t/sa	17,2	t/sa
6.8.97	16,8	t/sa	16,9	t/sa	16,7	t/sa
7.8.97	16,9	t/sa	17,2	t/sa	16,8	t/sa
8.8.97	17,1	t/sa	17,1	t/sa	17,0	t/sa
9.8.97	17,0	t/sa	16,9	t/sa	17,0	t/sa
10.8.97	17,4	t/sa	17,4	t/sa	17,4	t/sa
11.8.97	17,2	t/sa	17,1	t/sa	17,3	t/sa
12.8.97	17,2	t/sa	17,0	t/sa	17,3	t/sa
13.8.97	17,3	t/sa	17,3	t/sa	17,5	t/sa
14.8.97	17,7	t/sa	17,6	t/sa	17,4	t/sa
15.8.97	17,7	t/sa	17,6	t/sa	17,4	t/sa
16.8.97	17,7	t/sa	17,6	t/sa	17,4	t/sa
17.8.97	16,2	t/sa	17,6	t/sa	16,6	t/sa
18.8.97	16,2	t/sa	16,3	t/sa	16,6	t/sa
19.8.97	15,7	t/sa	15,3	t/sa	15,5	t/sa
20.8.97	16,5	t/sa	16,2	t/sa	16,2	t/sa
21.8.97	17,4	t/sa	16,4	t/sa	16,5	t/sa
22.8.97	17,1	t/sa	16,3	t/sa	16,5	t/sa
23.8.97	18,0	t/sa	17,6	t/sa	17,5	t/sa
24.8.97	18,4	t/sa	17,6	t/sa	17,9	t/sa
25.8.97	18,6	t/sa	17,6	t/sa	17,7	t/sa
26.8.97	18,0	t/sa	17,3	t/sa	17,6	t/sa
27.8.97	18,1	t/sa	17,9	t/sa	17,7	t/sa
28.8.97	16,5	t/sa	16,2	t/sa	16,4	t/sa
29.8.97	15,0	t/sa	14,8	t/sa	14,8	t/sa
30.8.97	14,6	t/sa	13,6	t/sa	13,8	t/sa
31.8.97	16,1	t/sa	15,7	t/sa	15,3	t/sa
1.9.97	16,6	t/sa	15,6	t/sa	15,7	t/sa
2.9.97	16,3	t/sa	15,7	t/sa	15,9	t/sa
3.9.97	15,6	t/sa	15,4	t/sa	15,4	t/sa
4.9.97	16,3	t/sa	15,4	t/sa	15,6	t/sa
5.9.97	16,6	t/sa	15,8	t/sa	15,8	t/sa
6.9.97	16,0	t/sa	15,2	t/sa	15,4	t/sa
7.9.97	13,8	t/sa	13,0	t/sa	13,5	t/sa
8.9.97	14,3	t/sa	14,0	t/sa	13,9	t/sa
9.9.97	13,8	t/sa	13,5	t/sa	13,8	t/sa
10.9.97	12,6	t/sa	11,9	t/sa	12,2	t/sa
11.9.97	12,5	t/sa	11,6	t/sa	11,9	t/sa
12.9.97	13,9	t/sa	12,8	t/sa	12,9	t/sa
13.9.97	13,1	t/sa	12,5	t/sa	12,9	t/sa
14.9.97	11,2	t/sa	10,3	t/sa	11,0	t/sa
15.9.97	11,1	t/sa	10,2	t/sa	10,7	t/sa
16.9.97	11,3	t/sa	10,4	t/sa	11,1	t/sa

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
17.9.97	12,2	t/sa	11,3	t/sa	11,9	t/sa
18.9.97	13,1	t/sa	12,0	t/sa	12,6	t/sa
19.9.97	12,2	t/sa	11,6	t/sa	12,6	t/sa
20.9.97	10,6	t/sa	9,6	t/sa	10,4	t/sa
21.9.97	10,2	t/sa	9,5	t/sa	9,8	t/sa
22.9.97	10,1	t/sa	9,2	t/sa	9,7	t/sa
23.9.97	11,1	t/sa	10,0	t/sa	10,3	t/sa
24.9.97	10,9	t/sa	10,4	t/sa	10,9	t/sa
25.9.97	10,7	t/sa	9,7	t/sa	10,4	t/sa
26.9.97	11,3	t/sa	10,2	t/sa	10,8	t/sa
27.9.97	10,2	t/sa	9,7	t/sa	10,7	t/sa
28.9.97	9,9	t/sa	9,2	t/sa	10,2	t/sa
29.9.97	11,0	t/sa	9,9	t/sa	10,6	t/sa
30.9.97	12,2	t/sa	11,2	t/sa	12,0	t/sa
1.10.97	12,9	t/sa	12,3	t/sa	12,7	t/sa
2.10.97	11,5	t/sa	11,1	t/sa	12,1	t/sa
3.10.97	10,2	t/sa	9,6	t/sa	10,7	t/sa
4.10.97	10,1	t/sa	9,5	t/sa	10,4	t/sa
5.10.97	9,7	t/sa	9,0	t/sa	10,4	t/sa
6.10.97	10,0	t/sa	9,3	t/sa	10,3	t/sa
7.10.97	12,1	t/sa	11,4	t/sa	11,8	t/sa
8.10.97	12,0	t/sa	11,4	t/sa	12,1	t/sa
9.10.97	13,4	t/sa	12,9	t/sa	13,3	t/sa
10.10.97	12,0	t/sa	11,8	t/sa	12,7	t/sa
11.10.97	10,7	t/sa	10,4	t/sa	11,4	t/sa
12.10.97	9,7	t/sa	9,7	t/sa	10,5	t/sa
13.10.97	8,5	t/sa	8,1	t/sa	9,3	t/sa
14.10.97	8,2	t/sa	7,4	t/sa	8,8	t/sa
15.10.97	8,0	t/sa	7,1	t/sa	8,5	t/sa
16.10.97	7,6	t/sa	6,6	t/sa	8,1	t/sa
17.10.97	7,7	t/sa	6,5	t/sa	8,4	t/sa
18.10.97	7,5	t/sa	6,2	t/sa	8,3	t/sa
19.10.97	7,6	t/sa	6,1	t/sa	8,5	t/sa
20.10.97	7,3	t/sa	6,2	t/sa	8,2	t/sa
21.10.97	5,1	t/sa	4,3	t/sa	6,8	t/sa
22.10.97	3,9	t/sa	2,2	t/sa	5,3	t/sa
23.10.97	4,6	t/sa	1,9	t/sa	5,3	t/sa
24.10.97	5,6	t/sa	3,7	t/sa	6,2	t/sa
25.10.97	6,0	t/sa	4,6	t/sa	6,6	t/sa
26.10.97	5,9	t/sa	4,5	t/sa	6,6	t/sa
27.10.97	4,2	t/sa	3,4	t/sa	5,8	t/sa
28.10.97	2,3	t/sa	1,4	t/sa	4,0	t/sa
29.10.97	1,9	t/sa	0,5	t/sa	3,5	t/sa
30.10.97	2,9	t/sa	0,6	t/sa	3,7	t/sa
31.10.97	3,3	t/sa	0,9	t/sa	4,0	t/sa
1.11.97	3,4	t/sa	1,5	t/sa	4,3	t/sa
2.11.97	2,9	t/sa	0,8	t/sa	4,0	t/sa
3.11.97	4,2	t/sa	2,4	t/sa	5,0	t/sa
4.11.97	3,1	t/sa	1,7	t/sa	4,5	t/sa
5.11.97	5,0	t/sa	3,7	t/sa	5,5	t/sa
6.11.97	6,3	a	5,6	a	6,9	t/sa
7.11.97	6,6	a	6,0	a	6,5	t/sa
8.11.97	5,5	a	5,0	a	6,5	t/sa
9.11.97	5,8	a	4,9	a	5,8	t/sa
10.11.97	6,5	a	5,5	a	6,6	t/sa
11.11.97	6,0	a	5,6	a	5,6	t/sa
12.11.97	5,5	a	5,4	a	6,6	t/sa
13.11.97	6,1	a	5,5	a	6,4	a
14.11.97	5,1	a	5,1	a	6,2	a
15.11.97	5,5	a	5,1	a	7,1	a
16.11.97	6,3	a	5,5	a	6,6	a
17.11.97	5,3	a	5,5	a	6,0	a
18.11.97	4,7	a	5,0	a	6,6	a
19.11.97	3,5	a	4,6	a	5,8	a
20.11.97	2,3	a	3,9	a	6,4	a
21.11.97	1,9	a	3,4	a	6,3	a
22.11.97	2,3	a	3,1	a	6,3	a
23.11.97	3,3	a	3,2	a	5,9	a
24.11.97	3,3	a	3,5	a	4,6	a
25.11.97	2,6	a	3,5	a	5,1	a
26.11.97	2,3	a	3,2	a	5,5	a
27.11.97	2,6	a	3,1	a	5,4	a
28.11.97	2,8	a	3,2	a	6,0	a
29.11.97	4,2	a	3,7	a	6,2	a

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
30.11.97	5,0	a	4,2	a	6,6	a
1.12.97	5,1	a	4,6	a	6,8	a
2.12.97	3,5	a	4,3	a	5,3	a
3.12.97	2,1	a	3,7	a	4,9	a
4.12.97	1,6	a	3,2	a	5,0	a
5.12.97	1,7	a	3,1	a	5,0	a
6.12.97	1,8	a	2,8	a	5,2	a
7.12.97	1,8	a	2,7	a	4,1	a
8.12.97	1,7	a	2,7	a	3,1	a
9.12.97	1,7	a	2,7	a	2,8	a
10.12.97	2,4	a	2,7	a	2,3	a
11.12.97	3,8	a	3,0	a	2,3	a
12.12.97	4,5	a	3,4	a	2,4	a
13.12.97	4,6	a	3,9	a	2,7	a
14.12.97	4,6	a	4,0	a	3,2	a
15.12.97	4,2	a	4,3	a	3,6	a
16.12.97	3,6	a	4,3	a	4,1	a
17.12.97	3,2	a	4,2	a	4,4	a
18.12.97	2,7	a	3,9	a	4,4	a
19.12.97	2,6	a	3,9	a	4,5	a
20.12.97	2,3	a	3,9	a	4,0	a
21.12.97	2,3	a	3,6	a	4,1	a
22.12.97	2,3	a	3,5	a	4,2	a
23.12.97	2,0	a	3,5	a	3,6	a
24.12.97	1,9	a	3,3	a	3,9	a
25.12.97	2,0	a	3,1	a	3,5	a
26.12.97	2,5	a	3,4	a	3,1	a
27.12.97	3,2	a	3,7	a	3,9	a
28.12.97	3,5	a	3,9	a	3,9	a
29.12.97	3,5	a	4,0	a	3,9	a
30.12.97	3,5	a	4,3	a	3,9	a
31.12.97	3,5	a	4,3	a	3,9	a
1.1.98	3,7	a	4,3	a	4,2	a
2.1.98	3,9	a	4,3	a	4,5	a
3.1.98	4,2	a	4,3	a	5,1	a
4.1.98	4,2	a	4,4	a	5,9	a
5.1.98	4,0	a	4,6	a	5,7	a
6.1.98	4,0	a	4,6	a	5,9	a
7.1.98	4,0	a	4,6	a	6,2	a
8.1.98	4,3	a	4,6	a	5,8	a
9.1.98	4,6	a	4,6	a	5,0	a
10.1.98	4,8	a	4,6	a	3,6	a
11.1.98	4,3	a	4,6	a	3,1	a
12.1.98	3,7	a	4,6	a	3,1	a
13.1.98	3,2	a	4,6	a	3,1	a
14.1.98	3,1	a	4,3	a	3,1	a
15.1.98	3,1	a	4,2	a	3,1	a
16.1.98	3,5	a	3,9	a	3,1	a
17.1.98	3,9	a	3,9	a	3,1	a
18.1.98	3,8	a	4,3	a	3,0	a
19.1.98	3,5	a	4,1	a	2,5	a
20.1.98	3,5	a	3,9	a	2,7	a
21.1.98	3,2	a	3,9	a	2,7	a
22.1.98	3,1	a	3,9	a	2,7	a
23.1.98	2,8	a	3,9	a	2,7	a
24.1.98	2,7	a	3,9	a	2,7	a
25.1.98	2,4	a	3,8	a	2,7	a
26.1.98	2,3	a	3,5	a	2,4	a
27.1.98	2,3	a	3,5	a	2,6	a
28.1.98	2,0	a	3,3	a	2,7	a
29.1.98	1,9	a	3,1	a	2,7	a
30.1.98	1,7	a	3,1	a	2,8	a
31.1.98	1,5	a	3,0	a	3,1	a
1.2.98	1,5	a	2,7	a	4,1	a
2.2.98	1,1	a	2,7	a	5,0	a
3.2.98	1,1	a	2,4	a	5,4	a
4.2.98	0,7	a	2,3	a	6,2	a
5.2.98	0,7	a	2,3	a	6,0	a
6.2.98	0,7	a	2,3	a	5,8	a
7.2.98	0,7	a	1,9	a	5,9	a
8.2.98	0,7	a	1,9	a	5,3	a
9.2.98	0,7	a	1,9	a	5,1	a
10.2.98	0,7	a	1,9	a	5,0	a
11.2.98	0,7	a	1,9	a	4,7	a

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
12.2.98	0,7	a	1,9	a	4,5	a
13.2.98	0,7	a	1,9	a	3,8	a
14.2.98	0,8	a	1,9	a	3,5	a
15.2.98	0,9	a	1,9	a	2,9	a
16.2.98	0,8	a	1,9	a	2,5	a
17.2.98	0,9	a	1,9	a	2,0	a
18.2.98	1,4	a	2,0	a	1,4	a
19.2.98	1,7	a	2,3	a	0,8	a
20.2.98	2,4	a	2,3	a	1,1	a
21.2.98	3,4	a	2,5	a	1,3	a
22.2.98	4,1	a	2,9	a	1,5	a
23.2.98	4,6	a	3,3	a	1,5	a
24.2.98	4,7	a	3,6	a	1,5	a
25.2.98	5,2	a	3,9	a	1,5	a
26.2.98	5,6	a	4,2	a	1,7	a
27.2.98	5,5	a	4,6	a	1,9	a
28.2.98	5,4	a	4,6	a	1,9	a
1.3.98	5,0	a	4,4	a	1,6	a
2.3.98	4,7	a	4,3	a	1,8	a
3.3.98	4,8	a	4,3	a	1,9	a
4.3.98	5,1	a	4,3	a	1,9	a
5.3.98	5,4	a	4,4	a	1,9	a
6.3.98	5,0	a	4,6	a	1,9	a
7.3.98	4,8	a	4,3	a	2,3	a
8.3.98	5,0	a	4,5	a	2,3	a
9.3.98	5,1	a	4,6	a	2,3	a
10.3.98	4,9	a	4,5	a	3,2	a
11.3.98	4,6	a	4,3	a	4,2	a
12.3.98	4,6	a	4,3	a	4,7	a
13.3.98	4,6	a	4,3	a	5,7	a
14.3.98	4,7	a	4,3	a	6,0	a
15.3.98	5,1	a	4,3	a	5,5	a
16.3.98	5,5	a	4,5	a	5,4	a
17.3.98	6,2	a	4,6	a	5,0	a
18.3.98	6,1	a	5,0	a	5,2	a
19.3.98	6,1	a	5,0	a	4,8	a
20.3.98	5,6	a	5,2	a	4,6	a
21.3.98	5,8	a	5,4	a	4,7	a
22.3.98	5,7	a	5,1	a	4,5	a
23.3.98	5,4	a	5,0	a	4,5	a
24.3.98	4,6	a	5,0	a	5,0	a
25.3.98	4,8	a	4,6	a	5,0	a
26.3.98	5,1	a	4,6	a	5,0	a
27.3.98	5,4	a	4,8	a	5,2	a
28.3.98	5,9	a	5,0	a	5,6	a
29.3.98	6,4	a	5,4	a	6,2	a
30.3.98	7,2	a	5,7	a	6,7	a
31.3.98	7,8	a	6,2	a	7,5	a
1.4.98	8,2	a	6,5	a	8,0	a
2.4.98	8,4	a	6,8	a	8,2	a
3.4.98	8,8	a	7,7	a	8,2	a
4.4.98	8,5	a	7,6	a	8,0	a
5.4.98	8,3	a	7,3	a	7,7	a
6.4.98	8,1	a	7,3	a	7,6	a
7.4.98	8,1	a	7,3	a	7,7	a
8.4.98	7,4	a	7,1	a	7,2	a
9.4.98	7,7	a	6,9	a	7,0	a
10.4.98	7,6	a	6,7	a	6,9	a
11.4.98	7,5	a	6,7	a	7,2	a
12.4.98	7,5	a	6,6	a	6,7	a
13.4.98	7,2	a	6,2	a	6,3	a
14.4.98	6,8	a	6,2	a	6,1	a
15.4.98	6,2	a	6,2	a	5,9	a
16.4.98	6,4	a	6,1	a	6,0	a
17.4.98	6,8	a	6,2	a	6,2	a
18.4.98	7,1	a	6,3	a	6,2	a
19.4.98	7,8	a	6,7	a	6,6	a
20.4.98	7,9	a	7,0	a	6,9	a
21.4.98	8,3	a	7,3	a	7,1	a
22.4.98	8,6	a	7,6	a	7,5	a
23.4.98	8,8	a	7,7	a	7,9	a
24.4.98	9,8	a	8,1	a	8,2	a
25.4.98	9,2	a	8,4	a	8,4	a
26.4.98	9,6	a	8,4	a	8,4	a

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
27.4.98	9,3	a	8,4	a	8,7	a
28.4.98	9,5	a	8,4	a	8,8	a
29.4.98	9,2	a	8,4	a	8,8	a
30.4.98	9,6	a	8,5	a	8,7	a
1.5.98	10,8	a	9,1	a	8,8	a
2.5.98	11,2	a	9,5	a	8,9	a
3.5.98	11,0	a	9,9	a	9,1	a
4.5.98	9,9	a	9,7	a	9,1	a
5.5.98	9,2	a	9,2	a	8,9	a
6.5.98	9,8	a	9,2	a	8,8	a
7.5.98	9,9	a	9,5	a	8,8	a
8.5.98	10,5	a	9,6	a	8,8	a
9.5.98	11,7	a	10,1	a	8,9	a
10.5.98	12,4	a	10,7	a	9,2	a
11.5.98	13,7	a	11,4	a	9,7	a
12.5.98	14,2	a	12,1	a	10,1	a
13.5.98	15,0	a	12,8	a	10,8	a
14.5.98	13,9	a	12,7	a	11,3	a
15.5.98	13,1	a	12,4	a	11,3	a
16.5.98	12,7	a	12,1	a	11,3	a
17.5.98	12,5	a	11,7	a	11,2	a
18.5.98	12,9	a	11,6	a	11,3	a
19.5.98	13,4	a	11,7	a	11,7	a
20.5.98	14,1	a	11,9	a	12,1	a
21.5.98	13,0	a	12,1	a	11,9	a
22.5.98	10,9	a	11,3	a	10,5	a
23.5.98	10,6	a	10,6	a	10,2	a
24.5.98	11,1	a	11,0	a	10,5	a
25.5.98	11,7	a	11,3	a	11,0	t/sa
26.5.98	12,4	a	11,9	a	12,1	t/sa
27.5.98	12,1	a	12,1	a	11,2	a
28.5.98	12,0	a	11,7	a	11,0	a
29.5.98	13,3	a	12,6	a	12,1	a
30.5.98	13,3	a	12,8	a	12,2	a
31.5.98	13,3	a	12,9	a	12,5	a
1.6.98	13,2	a	12,9	a	12,1	a
2.6.98	12,6	a	12,6	a	12,0	a
3.6.98	13,5	a	12,5	a	12,2	a
4.6.98	13,8	a	13,1	a	12,6	a
5.6.98	14,4	a	13,1	a	13,0	a
6.6.98	15,4	a	13,4	a	14,3	a
7.6.98	15,7	a	13,9	a	14,8	a
8.6.98	14,8	a	14,2	a	13,8	a
9.6.98	14,1	a	14,0	a	13,3	a
10.6.98	14,2	a	13,8	a	13,1	a
11.6.98	13,7	a	13,4	a	12,6	a
12.6.98	12,9	a	13,1	a	12,3	a
13.6.98	11,6	a	12,6	a	10,9	a
14.6.98	11,4	a	12,1	a	10,6	a
15.6.98	11,6	a	12,0	a	11,1	a
16.6.98	11,9	a	12,0	a	11,4	a
17.6.98	12,1	a	12,0	a	11,8	a
18.6.98	12,1	a	12,4	a	11,5	a
19.6.98	12,2	a	12,4	a	11,8	a
20.6.98	13,2	a	12,5	a	13,2	a
21.6.98	14,4	a	12,9	a	15,4	a
22.6.98	15,5	a	13,5	a	16,3	t/sa
23.6.98	14,6	a	13,8	a	14,5	t/sa
24.6.98	14,4	a	13,8	a	15,1	t/sa
25.6.98	14,8	a	14,0	a	16,5	t/sa
26.6.98	15,0	a	14,2	a	16,5	t/sa
27.6.98	15,3	a	14,3	a	17,0	t/sa
28.6.98	15,4	a	14,5	a	15,5	t/sa
29.6.98	14,5	a	14,5	a	14,9	t/sa
30.6.98	14,4	a	14,2	a	14,4	t/sa
1.7.98	14,3	a	14,2	a	14,6	t/sa
2.7.98	13,9	a	13,9	a	14,5	t/sa
3.7.98	14,0	a	13,8	a	14,4	t/sa
4.7.98	13,7	a	13,8	a	13,7	t/sa
5.7.98	13,6	a	13,8	a	14,0	t/sa
6.7.98	13,7	a	13,8	a	13,9	t/sa
7.7.98	13,4	a	13,8	a	13,1	t/sa
8.7.98	12,4	a	13,6	a	12,2	t/sa
9.7.98	12,0	a	13,3	a	11,8	t/sa

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
10.7.98	12,4	a	13,1	a	14,0	t/sa
11.7.98	13,1	a	13,1	a	13,9	t/sa
12.7.98	13,0	a	13,5	a	13,7	t/sa
13.7.98	13,3	a	13,5	a	14,1	t/sa
14.7.98	13,1	a	13,5	a	13,1	t/sa
15.7.98	12,8	a	13,5	a	13,5	t/sa
16.7.98	12,9	a	13,5	a	12,7	t/sa
17.7.98	13,0	a	13,5	a	13,7	t/sa
18.7.98	13,4	a	13,5	a	14,3	t/sa
19.7.98	13,7	a	13,5	a	14,7	t/sa
20.7.98	14,2	a	13,6	a	17,5	t/sa
21.7.98	15,6	a	13,9	a	18,8	t/sa
22.7.98	15,8	a	14,4	a	17,1	t/sa
23.7.98	15,7	a	14,5	a	16,5	t/sa
24.7.98	15,7	a	14,6	a	16,6	t/sa
25.7.98	15,5	a	14,5	a	16,0	t/sa
26.7.98	15,1	a	14,5	a	16,1	t/sa
27.7.98	15,5	a	14,5	a	16,2	t/sa
28.7.98	15,2	a	14,5	a	15,3	t/sa
29.7.98	14,7	a	14,5	a	14,4	t/sa
30.7.98	14,6	a	14,5	a	14,8	t/sa
31.7.98	14,2	a	14,5	a	13,8	t/sa
1.8.98	14,2	a	14,3	a	14,6	t/sa
2.8.98	14,6	a	14,2	a	14,5	t/sa
3.8.98	14,4	a	14,4	a	15,4	t/sa
4.8.98	14,5	a	14,5	a	14,8	t/sa
5.8.98	14,1	a	14,4	a	14,2	t/sa
6.8.98	14,0	a	14,2	a	15,1	t/sa
7.8.98	14,4	a	14,2	a	16,0	t/sa
8.8.98	15,3	a	14,3	a	17,4	t/sa
9.8.98	15,8	a	14,7	a	17,3	t/sa
10.8.98	15,5	a	14,9	a	17,2	t/sa
11.8.98	16,5	a	14,9	a		
12.8.98	17,3	a	15,4	a		
13.8.98	17,3	a	15,6	a		
14.8.98	15,3	a	15,1	a		
15.8.98	15,6	a	14,7	a		
16.8.98	16,6	a	14,9	a		
17.8.98	16,0	a	15,0	a		
18.8.98	15,7	a	14,7	a		
19.8.98	15,9	t/sa	14,9	a		
20.8.98	15,0	t/sa	14,6	a		
21.8.98	14,2	t/sa	14,4	a		
22.8.98	13,5	t/sa	14,0	a		
23.8.98	12,9	a	13,6	a		
24.8.98	13,4	a	13,5	a		
25.8.98	12,5	a	13,3	a		
26.8.98	13,0	a	13,1	a		
27.8.98	12,6	a	13,1	a		
28.8.98	11,7	a	12,7	a		
29.8.98	11,7	t/sa	12,4	a		
30.8.98	12,1	t/sa	12,4	a		
31.8.98	12,4	t/sa	12,4	a		
1.9.98	12,4	t/sa	12,4	a		
2.9.98	13,8	a	12,4	a		
3.9.98	13,8	a	12,8	a		
4.9.98	13,7	a	12,9	a		
5.9.98	13,5	a	13,1	a		
6.9.98	13,3	a	13,1	a		
7.9.98	13,6	a	13,1	a		
8.9.98	13,7	a	13,4	a		
9.9.98	14,0	a	13,5	a		
10.9.98	14,5	a	13,7	a		
11.9.98	14,3	a	13,8	a		
12.9.98	13,4	a	13,8	a		
13.9.98	11,8	a	13,4	a		
14.9.98	10,8	a	12,7	a		
15.9.98	10,8	a	12,1	a		
16.9.98	11,3	a	12,0	a		
17.9.98	11,2	a	12,0	a		
18.9.98	11,3	a	12,0	a		
19.9.98	11,0	a	12,0	a		
20.9.98	11,2	a	11,7	a		
21.9.98	11,3	a	11,7	a		

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
22.9.98	11,5	a	11,7	a		
23.9.98	11,4	a	11,7	a		
24.9.98	11,2	a	11,7	a		
25.9.98	11,0	a	11,7	a		
26.9.98	11,4	a	11,4	a		
27.9.98	12,0	a	11,7	a		
28.9.98	12,0	a	11,7	a		
29.9.98	12,1	a	11,8	a		
30.9.98	11,9	a	12,0	a		
1.10.98	11,8	a	12,0	a		
2.10.98	10,6	a	11,9	a		
3.10.98	8,6	a	11,5	a		
4.10.98	8,4	a	10,9	a		
5.10.98	8,3	a	10,6	a		
6.10.98	8,6	a	10,3	a		
7.10.98	8,2	a	10,2	a		
8.10.98	8,6	a	10,2	a		
9.10.98	8,9	a	10,1	a		
10.10.98	9,1	a	9,9	a		
11.10.98	9,1	a	10,2	a		
12.10.98	9,2	a	10,2	a		
13.10.98	9,1	a	10,1	a		
14.10.98	9,1	a	9,9	a		
15.10.98	9,6	a	10,0	a		
16.10.98	9,3	a	10,2	a		
17.10.98	9,3	a	9,9	a		
18.10.98	9,5	a	9,9	a		
19.10.98	8,6	a	10,1	a		
20.10.98	8,2	a	9,9	a		
21.10.98	7,8	a	9,5	a		
22.10.98	8,2	a	9,2	a		
23.10.98	8,9	a	9,1	a		
24.10.98	9,2	a	9,5	a		
25.10.98	9,1	a	9,5	a		
26.10.98	8,6	a	9,5	a		
27.10.98	7,9	a	9,4	a		
28.10.98	8,2	a	9,1	a		
29.10.98	8,8	a	9,4	a		
30.10.98	8,2	a	9,3	a		
31.10.98	7,7	a	9,0	a		
1.11.98	7,7	a	8,9	a		
2.11.98	7,5	a	8,8	a		
3.11.98	7,3	a	8,8	a		
4.11.98	7,0	a	8,6	a		
5.11.98	6,7	a	8,2	a		
6.11.98	6,5	a	8,0	a		
7.11.98	6,0	a	7,9	a		
8.11.98	5,8	a	7,7	a		
9.11.98	6,3	a	7,7	a		
10.11.98	7,1	a	7,8	a		
11.11.98	6,9	a	8,0	a		
12.11.98	5,8	a	7,6	a		
13.11.98	5,4	a	7,3	a		
14.11.98	5,4	a	7,2	a		
15.11.98	5,4	a	6,9	a		
16.11.98	5,4	a	6,9	a		
17.11.98	5,2	a	6,8	a		
18.11.98	4,6	a	6,5	a		
19.11.98	4,3	a	6,2	a		
20.11.98	3,9	a	6,2	a		
21.11.98	3,9	a	6,0	a		
22.11.98	3,7	a	5,8	a		
23.11.98	3,5	a	5,5	a		
24.11.98	3,2	a	5,4	a		
25.11.98	3,1	a	5,2	a		
26.11.98	3,0	a	5,0	a		
27.11.98	2,7	a	5,0	a		
28.11.98	2,7	a	4,8	a		
29.11.98	2,7	a	4,6	a		
30.11.98	2,7	a	4,6	a		
1.12.98	2,7	a	4,6	a		
2.12.98	2,5	a	4,6	a		
3.12.98	2,3	a	4,5	a		
4.12.98	2,3	a	4,3	a		

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
5.12.98	2,3	a	4,3	a		
6.12.98	2,3	a	4,3	a		
7.12.98	2,3	a	4,3	a		
8.12.98	1,9	a	3,9	a		
9.12.98	1,9	a	3,9	a		
10.12.98	1,9	a	3,9	a		
11.12.98	1,9	a	3,9	a		
12.12.98	1,9	a	3,9	a		
13.12.98	1,7	a	3,7	a		
14.12.98	1,5	a	3,5	a		
15.12.98	1,7	a	3,6	a		
16.12.98	1,9	a	3,9	a		
17.12.98	1,9	a	3,9	a		
18.12.98	1,9	a	3,9	a		
19.12.98	1,9	a	3,9	a		
20.12.98	1,9	a	3,9	a		
21.12.98	1,9	a	3,9	a		
22.12.98	1,9	a	3,9	a		
23.12.98	1,9	a	3,9	a		
24.12.98	1,9	a	3,5	a		
25.12.98	1,9	a	3,5	a		
26.12.98	1,9	a	3,5	a		
27.12.98	2,2	a	3,6	a		
28.12.98	2,6	a	3,9	a		
29.12.98	3,1	a	4,3	a		
30.12.98	2,7	a	4,2	a		
31.12.98	2,4	a	3,9	a		
1.1.99	2,3	a	3,9	a		
2.1.99	2,3	a	3,7	a		
3.1.99	2,1	a	3,5	a		
4.1.99	2,0	a	3,5	a		
5.1.99	2,5	a	3,8	a		
6.1.99	3,1	a	4,1	a		
7.1.99	3,1	a	4,3	a		
8.1.99	3,1	a	4,3	a		
9.1.99	3,1	a	4,3	a		
10.1.99	3,1	a	4,2	a		
11.1.99	2,8	a	3,9	a		
12.1.99	2,5	a	3,9	a		
13.1.99	2,3	a	3,7	a		
14.1.99	2,3	a	3,5	a		
15.1.99	2,0	a	3,5	a		
16.1.99	2,0	a	3,5	a		
17.1.99	2,5	a	3,5	a		
18.1.99	3,1	a	3,9	a		
19.1.99	3,1	a	3,9	a		
20.1.99	3,1	a	3,9	a		
21.1.99	3,1	a	3,9	a		
22.1.99	3,1	a	3,9	a		
23.1.99	3,3	a	3,9	a		
24.1.99	3,2	a	3,9	a		
25.1.99	3,2	a	3,9	a		
26.1.99	3,8	a	3,9	a		
27.1.99	3,7	a	3,9	a		
28.1.99	3,3	a	3,9	a		
29.1.99	3,1	a	3,9	a		
30.1.99	2,8	a	3,7	a		
31.1.99	2,7	a	3,5	a		
1.2.99	2,5	a				
2.2.99	2,4	a				
3.2.99	2,4	a				
4.2.99	2,2	a				
5.2.99	2,2	a				
6.2.99	2,0	a				
7.2.99	2,0	a				
8.2.99	2,1	a				
9.2.99	1,9	a				
10.2.99	2,0	a				
11.2.99	1,9	a				
12.2.99	1,9	a				
13.2.99	1,9	a				
14.2.99	1,6	a				
15.2.99	1,5	a				
16.2.99	1,5	a				

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
17.2.99	1,5	a				
18.2.99	1,5	a				
19.2.99	1,5	a				
20.2.99	1,5	a				
21.2.99	1,5	a				
22.2.99	1,5	a				
23.2.99	1,5	a				
24.2.99	1,5	a				
25.2.99	1,5	a				
26.2.99	1,5	a				
27.2.99	1,5	a				
28.2.99	1,6	a				
1.3.99	1,9	a				
2.3.99	2,3	a				
3.3.99	3,1	a				
4.3.99	3,8	a				
5.3.99	4,3	a				
6.3.99	4,3	a				
7.3.99	4,0	a				
8.3.99	3,9	a				
9.3.99	4,0	a				
10.3.99	4,3	a				
11.3.99	4,1	a				
12.3.99	4,0	a				
13.3.99	4,4	a				
14.3.99	4,9	a				
15.3.99	5,2	a				
16.3.99	5,1	a				
17.3.99	4,8	a				
18.3.99	4,8	a				
19.3.99	5,1	a				
20.3.99	5,2	a				
21.3.99	5,1	a				
22.3.99	5,0	a				
23.3.99	5,0	a				
24.3.99	5,1	a				
25.3.99	5,6	a				
26.3.99	6,4	a				
27.3.99	6,9	a				
28.3.99	6,2	a				
29.3.99	6,0	a				
30.3.99	6,3	a				
31.3.99	6,3	a				
1.4.99	6,7	a				
2.4.99	7,2	a				
3.4.99	7,3	a				
4.4.99	7,9	a				
5.4.99	8,2	a				
6.4.99	9,2	a				
7.4.99	9,7	a				
8.4.99	8,5	a				
9.4.99	8,1	a				
10.4.99	8,3	a				
11.4.99	8,9	a				
12.4.99	8,1	a				
13.4.99	7,5	a				
14.4.99	7,1	a				
15.4.99	6,0	a				
16.4.99	6,0	a				
17.4.99	6,3	a				
18.4.99	6,6	a				
19.4.99	6,5	a				
20.4.99	6,2	a				
21.4.99	6,7	a				
22.4.99	7,4	a				
23.4.99	7,8	a				
24.4.99	8,3	a				
25.4.99	8,5	a				
26.4.99	9,1	a				
27.4.99	9,5	a				
28.4.99	9,6	a				
29.4.99	9,4	a				
30.4.99	9,6	a				
1.5.99	10,1	a				

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
2.5.99	10,4	a				
3.5.99	10,2	a				
4.5.99	10,0	a				
5.5.99	9,3	a				
6.5.99	8,9	a				
7.5.99	8,9	a				
8.5.99	9,6	a				
9.5.99	10,0	a				
10.5.99	10,4	a				
11.5.99	10,7	a				
12.5.99	11,0	a				
13.5.99	10,8	a				
14.5.99	10,8	a				
15.5.99	10,6	a				
16.5.99	9,7	a				
17.5.99	9,7	a				
18.5.99	10,1	a				
19.5.99	10,8	a				
20.5.99	11,3	a				
21.5.99	11,7	a				
22.5.99	11,8	a				
23.5.99	11,0	a				
24.5.99	11,6	a				
25.5.99	11,9	a				
26.5.99	11,9	a				
27.5.99	12,6	a				
28.5.99	13,7	a				
29.5.99	14,1	a				
30.5.99	14,6	a				
31.5.99	14,6	a				
1.6.99	13,9	a				
2.6.99	14,6	a				
3.6.99	14,9	a				
4.6.99	14,4	a				
5.6.99	13,7	a				
6.6.99	12,9	a				
7.6.99	12,4	a				
8.6.99	12,9	a				
9.6.99	12,4	a				
10.6.99	12,7	a				
11.6.99	13,0	a				
12.6.99	12,6	a				
13.6.99	12,6	a				
14.6.99	13,3	a				
15.6.99	13,9	a				
16.6.99	14,4	a				
17.6.99	14,6	a				
18.6.99	14,5	a				
19.6.99	13,4	a				
20.6.99	13,5	a				
21.6.99	13,5	a				
22.6.99	12,7	a				
23.6.99	12,2	a				
24.6.99	12,4	a				
25.6.99	12,9	a				
26.6.99	13,3	a				
27.6.99	14,3	a				
28.6.99	14,2	a				
29.6.99	13,7	a				
30.6.99	14,7	a				
1.7.99	14,6	a				
2.7.99	14,9	a				
3.7.99	16,0	a				
4.7.99	16,7	a				
5.7.99	17,5	a				
6.7.99	16,1	a				
7.7.99	15,3	a				
8.7.99	15,3	a				
9.7.99	15,7	a				
10.7.99	15,7	a				
11.7.99	16,8	a				
12.7.99	17,1	a				
13.7.99	16,8	a				
14.7.99	16,6	a				

Appendix 2 (continued).

Date	Pool 1 (°C)	Phase pool 1	Pool 2 (°C)	Phase pool 2	Pool 3 (°C)	Phase pool 3
15.7.99	15,4	a				
16.7.99	14,9	a				
17.7.99	15,1	a				
18.7.99	16,0	a				
19.7.99	17,1	t/sa				
20.7.99	17,5	t/sa				
21.7.99	16,7	t/sa				
22.7.99	15,1	t/sa				
23.7.99	14,4	t/sa				
24.7.99	14,3	t/sa				
25.7.99	15,6	t/sa				
26.7.99	16,1	t/sa				
27.7.99	15,9	t/sa				
28.7.99	15,8	t/sa				
29.7.99	16,0	t/sa				
30.7.99	16,2	t/sa				
31.7.99	16,2	t/sa				
1.8.99	16,1	t/sa				

Abbreviations:

Pool 1,2,3 (°C) = daily means of water temperatures in pools 1-3 (see section 4.1.);
Phase pool 1,2,3: a = aquatic phase; t/sa = terrestrial and semiaquatic phase (see Table 1 p 16).
For further explanations see section 3.1.1.2..

Appendix 3: Database of chironomid emergence recorded in pools 1-3 and the colonizing experiments in 1993 (C1) and 1998 (C2). (Abbreviations see 'explanations and comments on Tables 23-25 and 27' on p 68 and at the end of this appendix.)

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
					Tanypodinae						
					1. *Monopelopia tenuicalar* (KIEFFER, 1918)						
Determination: FITTKAU 1962. (A very weak r_{2+3} present). 1 ♂ coll. Murray, 1♂,1♀ coll. ADK.											
Ecology: KREUZER 1940, FITTKAU, 1962, MOLLER PILLOT & BUSKENS 1990. (above all an inhabitant of boggy waters).											
19.5	19.5.99	1999	2	1	1						5,0
19.5	19.5.99	1999	3	1		1					5,0
3.8	3.8.98	1998	3	1	1						5,0
					2. *Natarsia punctata* (MEIGEN, 1804)						
Determination: FITTKAU 1962. 5♂♂+5♀♀ ZSM , rest coll. ADK.											
Ecology: FITTKAU 1962, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990.											
7.5	7.5.99	1999	1c	1	1						5,0
19.5	19.5.99	1999	1c	1	2	6					4,0
27.5	27.5.99	1999	1b	1	1						4,5
27.5	27.5.99	1999	1c	1	8	4					4,0
2.6	2.6.99	1999	1b	1	2	1					5,0
2.6	2.6.99	1999	1c	1	2	6					4,5
9.6	9.6.99	1999	1c	1	3	3					4,5
18.6	18.6.99	1999	1c	1	2	9					3,0
25.6	25.6.99	1999	1b	1	1	2					3,0
25.6	25.6.99	1999	1c	1		1					3,0
1.7	1.7.99	1999	1b	1	1	1					2,5
3.8	3.8.98	1998	3	1	1						5,0
					3. *Procladius choreus* (MEIGEN, 1804)						
Determination: PINDER 1978 and consequences from KOBAYASHI 1998 & 2000. 1 ♂ ZSM, rest coll. ADK.											
Ecology: THIENEMANN 1954, LEARNER & POTTER 1974, POTTER & LEARNER 1974, PARMA & KREBS 1977, FITTKAU & REISS 1978, FRITZ 1981 & 1982a, PINDER 1983, HOLLESEN-KÖRBER 1984, MOLLER PILLOT 1984a, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990, BECKER 1995, DETTINGER-KLEMM 1995b, HEINMÜLLER et al. 1998, SCHNABEL 1999 (very tolerant in respect to water pollution).											
7.5	7.5.99	1999	3	1		1					5,0
19.5	19.5.99	1999	3	1		1					5,0
26.5	26.5.93	1993	2	1	1						5,0
10.6	10.6.92	1992	2	1	3						5,0
14.6	14.6.93	1993	6	2	1						5,0
17.6	17.6.98	1998	3	1		1					5,0
25.6	25.6.98	1998	3	1	1						5,0
25.6	25.6.98	1998	5	2		1					5,0
25.6	25.6.98	1998	6	2	2						5,0
2.7	2.7.98	1998	5	2		1					5,0
5.7	5.7.97	1997	2	1		1					5,0
5.7	5.7.97	1997	5	2	1	1					5,0
10.7	10.7.96	1996	2	1		1					5,0
10.7	10.7.96	1996	3	1	1						5,0
11.7	11.7.97	1997	2	1		1					3,0
16.7	16.7.96	1996	2	1		1					4,0
21.7	21.7.98	1998	C2P8	C2	2	1					5,0
23.7	23.7.96	1996	3	1		1					2,5
					4. *Psectrotanypus varius* (FABRICIUS, 1787)						
Determination: Fittkau 1962. L, P, Pex, ♂♂ + ♀♀ ZSM, rest coll. ADK											
Ecology: KREUZER, 1940, THIENEMANN 1954; FITTKAU 1962, SMITH & YOUNG 1973, PARMA & KREBS 1977, WIGGINS et al. 1980, FRITZ 1981, MOLLER PILLOT 1984a, SCHLEUTER 1986, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990, DETTINGER.KLEMM 1995a+b, BAZANTI et al. 1996, SCHNABEL 1999 (very tolerant in respect to water pollution).											
8.4	8.4.99	1999	net	1						1	5,0
30.4	30.4.99	1999	2	1		1					5,0
7.5	7.5.99	1999	2	1	1	2					5,0
19.5	19.5.99	1999	2	1	2	1					5,0
22.5	22.5.97	1997	net	1					4		5,0
27.5	27.5.99	1999	2	1	1						5,0
2.6	2.6.99	1999	1b	1	4						5,0
3.6	3.6.98	1998	2	1	6	8					5,0
5.6	5.6.97	1997	2	1	1						5,0
6.6	6.6.93	1993	5	2		1					5,0
9.6	9.6.99	1999	1b	1	2	1					5,0
9.6	9.6.93	1993	net	2					6		5,0
10.6	10.6.98	1998	2	1	2	1					5,0
10.6	10.6.98	1998	3	1	3	6					5,0
10.6	10.6.98	1998	6	2	1						5,0
12.6	12.6.97	1997	2	1		2					4,5
12.6	12.6.97	1997	5	2	8	10					3,0
14.6	14.6.96	1996	2	1	1						2,0
17.6	17.6.98	1998	3	1	2	1					5,0
17.6	17.6.98	1998	6	2	1						5,0
18.6	18.6.96	1996	2	1	4						5,0
18.6	18.6.96	1996	3	1	1						4,0

Appendix 3 (continued) (*Psectrotanypus varius*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
18.6	18.6.99	1999	1b	1	6	8					3,0
18.6	18.6.96	1996	w	1				1			5,0
19.6	19.6.97	1997	2	1	6	11					4,0
19.6	19.6.97	1997	3	1		1					3,0
19.6	19.6.97	1997	5	2	1	2					3,0
25.6	25.6.98	1998	2	1		2					5,0
25.6	25.6.98	1998	3	1	4	3					5,0
25.6	25.6.98	1998	5	2	1						5,0
26.6	26.6.96	1996	2	1	1	4					4,5
26.6	26.6.96	1996	3	1	3	2					4,0
28.6	28.6.97	1997	2	1	16	13					5,0
28.6	28.6.97	1997	3	1	1						4,0
29.6	29.6.93	1993	net	2					3	5	4,0
2.7	2.7.96	1996	2	1	3	5					5,0
2.7	2.7.96	1996	3	1	3	4					4,0
2.7	2.7.98	1998	3	1		1					5,0
5.7	5.7.97	1997	2	1	24	32					5,0
5.7	5.7.97	1997	5	2	4	1					5,0
5.7	5.7.97	1997	6	2	1						5,0
8.7	8.7.92	1992	2	1		1					5,0
8.7	8.7.92	1992	5	2	1						5,0
9.7	9.7.98	1998	5	2	1						5,0
10.7	10.7.96	1996	2	1	7	5					5,0
10.7	10.7.96	1996	3	1	2						5,0
11.7	11.7.97	1997	2	1	4	9					3,0
11.7	11.7.97	1997	5	2	4	3					2,5
11.7	11.7.97	1997	6	2	3	1					2,5
16.7	16.7.96	1996	2	1	8	10					4,0
17.7	17.7.96	1996	net	1					37		4,0
17.7	17.7.96	1996	net	2					3		5,0
23.7	23.7.96	1996	2	1	3	4					2,5
24.7	24.7.92	1992	2	1	1						5,0
11.8	11.8.98	1998	C2P4	C2	2	1					5,0
23.8	23.8.93	1993	net	2	1				1	1	3,0
11.9	11.9.98	1998	2	1		1					5,0
21.9	21.9.98	1998	2	1		1					5,0
30.9	30.9.96	1996	5	2	1	1					5,0

5. *Xenopelopia falcigera* (KIEFFER, 1911)

Determination: FITTKAU 1962. 22 ♂♂ ZSM, rest coll. ADK.

Ecology: KREUZER 1940, MÜNCHBERG 1956, FITTKAU 1962, LEARNER & POTTER 1974, HAVELKA & RIEDER 1979, HAVELKA et al. 1980, HOLLESEN-KÖRBER 1984, DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996, HEINMÜLLER et al. 1998.

29.5	29.5.93	1993	3	1	1						5,0
29.5	29.5.93	1993	6	2	1						5,0
2.6	2.6.93	1993	6	2	21						5,0
6.6	6.6.93	1993	5	2	4						5,0
6.6	6.6.93	1993	6	2	12						5,0
9.6	9.6.99	1999	2	1	4						5,0
9.6	9.6.99	1999	3	1	4						5,0
9.6	9.6.93	1993	5	2	16						5,0
9.6	9.6.93	1993	6	2	1						5,0
14.6	14.6.93	1993	5	2	3						5,0
14.6	14.6.93	1993	6	2	12						5,0
18.6	18.6.99	1999	2	1	9						5,0
18.6	18.6.99	1999	3	1	1						5,0
18.6	18.6.93	1993	5	2	1						5,0
18.6	18.6.93	1993	6	2	11						5,0
21.6	21.6.93	1993	5	2	2						5,0
21.6	21.6.93	1993	6	2	10						5,0
25.6	25.6.99	1999	2	1	6						5,0
25.6	25.6.99	1999	3	1	1						5,0
25.6	25.6.93	1993	6	2	7						5,0
29.6	29.6.93	1993	6	2	11						4,0
29.6	29.6.93	1993	net	2	2						4,0
1.7	1.7.99	1999	3	1	1						3,0
2.7	2.7.98	1998	6	2	1						5,0
7.7	7.7.93	1993	net	2	8						3,0
9.7	9.7.98	1998	3	1	1						5,0
9.7	9.7.98	1998	6	2	1						5,0
16.7	16.7.92	1992	2	1	11						5,0
17.7	17.7.98	1998	3	1	1						5,0
19.7	19.7.93	1993	In	2	5						2,0
24.7	24.7.98	1998	3	1	3						5,0
3.8	3.8.98	1998	3	1	4						5,0
3.8	3.8.98	1998	6	2	1						5,0
10.8	10.8.98	1998	3	1	2						5,0
10.8	10.8.98	1998	6	2	1						5,0
18.8	18.8.98	1998	6	2	1						5,0
18.8	18.8.93	1993	C1P3	C1	2						5,0
26.8	26.8.98	1998	6	2	1						5,0
11.9	11.9.98	1998	2	1	1						5,0
24.9	24.9.93	1993	C1P4	C1	3						5,0

6. *Xenopelopia nigricans* (GOETGHEBUER, 1927)

Determination: FITTKAU 1962, LANGTON 1991. 10 ♂♂ ZSM, 1P* PL, rest coll. ADK.* With LANGTON's key the pupa should be *X. falcigera.* But I believe that the characters mentioned in LANGTON 1991 do not hold up and should be restudied (e.g. the shape of the thorax comb seems to be an appropriate character for the separation between pupae of *X. falcigera* and *X. nigricans)*. Adult members of the first spring generation are much darker and larger than those of subsequent generations.

Appendix 3 (continued) (*Xenopelopia nigricans*):

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
Ecology: FITTKAU 1962, FRITZ 1981,1982b, DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996, HAVELKA & RIEDER 1979, HAVELKA et al. 1980.											
8.4	8.4.99	1999	net	1						3	5,0
16.4	16.4.99	1999	2	1	1						5,0
24.4	24.4.99	1999	2	1	1						5,0
24.4	24.4.99	1999	3	1	1						5,0
30.4	30.4.99	1999	3	1	1						5,0
7.5	7.5.99	1999	3	1	1						5,0
26.5	26.5.93	1993	6	2	3						5,0
27.5	27.5.99	1999	3	1	2						5,0
28.5	28.5.94	1994	6	2	1						5,0
28.5	28.5.96	1996	6	2	1						5,0
29.5	29.5.93	1993	3	1	1						5,0
29.5	29.5.93	1993	6	2	14						5,0
30.5	30.5.97	1997	5	2	1						5,0
2.6	2.6.99	1999	2	1	3						5,0
2.6	2.6.99	1999	3	1	13						5,0
2.6	2.6.93	1993	6	2	8						5,0
2.6	2.6.99	1999	1b	1	1						5,0
3.6	3.6.98	1998	2	1	1						5,0
3.6	3.6.98	1998	3	1	1						5,0
3.6	3.6.98	1998	5	2	2						5,0
3.6	3.6.98	1998	6	2	7						5,0
5.6	5.6.97	1997	6	2	3						5,0
6.6	6.6.93	1993	2	1	1						4,0
6.6	6.6.93	1993	5	2	1						5,0
6.6	6.6.93	1993	6	2	3						5,0
9.6	9.6.99	1999	2	1	10						5,0
9.6	9.6.99	1999	3	1	4						5,0
9.6	9.6.93	1993	4	2	1						4,0
9.6	9.6.93	1993	5	2	4						5,0
9.6	9.6.93	1993	6	2	1						5,0
9.6	9.6.99	1999	1b	1	2						5,0
9.6	9.6.93	1993	net	2	3						5,0
10.6	10.6.98	1998	2	1	1						5,0
10.6	10.6.98	1998	6	2	1						5,0
14.6	14.6.93	1993	6	2	4						5,0
17.6	17.6.98	1998	2	1	1						5,0
17.6	17.6.98	1998	3	1	1						5,0
18.6	18.6.99	1999	2	1	2						5,0
18.6	18.6.99	1999	3	1	2						5,0
18.6	18.6.93	1993	6	2	4						5,0
18.6	18.6.99	1999	1b	1	6						3,0
21.6	21.6.93	1993	6	2	7						5,0
22.6	22.6.92	1992	2	1	1						5,0
25.6	25.6.98	1998	3	1	1						5,0
25.6	25.6.99	1999	3	1	1						5,0
25.6	25.6.93	1993	6	2	2						5,0
25.6	25.6.99	1999	1b	1	1						3,0
29.6	29.6.93	1993	5	2	1						4,0
29.6	29.6.93	1993	6	2	7						4,0
29.6	29.6.93	1993	net	2	2						4,0
1.7	1.7.99	1999	3	1	1						3,0
2.7	2.7.96	1996	2	1	1						5,0
2.7	2.7.98	1998	5	2	1						5,0
2.7	2.7.98	1998	6	2	1						5,0
3.7	3.7.93	1993	6	2	1						3,0
7.7	7.7.93	1993	6	2	2						3,0
7.7	7.7.93	1993	net	2	4						3,0
9.7	9.7.98	1998	3	1	2						5,0
9.7	9.7.98	1998	6	2	2						5,0
17.7	17.7.98	1998	3	1	1						5,0
17.7	17.7.98	1998	5	2	3						5,0
17.7	17.7.98	1998	6	2	3						5,0
18.7	18.7.99	1999	2	1	3						4,0
19.7	19.7.93	1993	In	2	1						2,0
24.7	24.7.98	1998	3	1	3						5,0
24.7	24.7.98	1998	5	2	2						5,0
24.7	24.7.98	1998	6	2	2						5,0
30.7	30.7.92	1992	2	1	1						5,0
3.8	3.8.98	1998	3	1	3						5,0
3.8	3.8.98	1998	6	2	6						5,0
10.8	10.8.98	1998	2	1	1						5,0
10.8	10.8.98	1998	3	1	6						5,0
10.8	10.8.98	1998	5	2	2						5,0
10.8	10.8.98	1998	6	2	2						5,0
13.8	13.8.93	1993	6	2	1						5,0
18.8	18.8.98	1998	2	1	1						4,0
18.8	18.8.98	1998	3	1	3						3,5
18.8	18.8.98	1998	5	2	2						5,0
18.8	18.8.93	1993	6	2	2						4,0
18.8	18.8.98	1998	6	2	10						5,0
18.8	18.8.93	1993	net	2	1						4,0
18.8	18.8.98	1998	net	2						1	5,0
26.8	26.8.98	1998	5	2	2						5,0
26.8	26.8.98	1998	6	2	2						5,0
2.9	2.9.98	1998	2	1	3						4,0
2.9	2.9.98	1998	6	2	2						5,0
10.9	10.9.96	1996	5	2	1						4,0
11.9	11.9.98	1998	2	1	33						5,0
11.9	11.9.98	1998	5	2	2						5,0
11.9	11.9.98	1998	6	2	1						5,0

Appendix 3 (continued) (*Xenopelopia nigricans*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
21.9	21.9.98	1998	2	1	23						5,0
21.9	21.9.98	1998	3	1	1						5,0
21.9	21.9.98	1998	6	2	1						5,0
30.9	30.9.98	1998	2	1	3						5,0
19.10	19.10.98	1998	2	1	1						5,0
Xenopelopia falcigera/nigricans ♀♀/Pex/L											
Determination: FITTKAU 1962, LANGTON 1991, MOLLER PILLOT 1984a. 28 ♀♀, 1 Pex ZSM, rest coll. ADK.											
16.4	16.4.99	1999	2	1		1					5,0
24.4	24.4.99	1999	2	1		1					5,0
24.4	24.4.99	1999	3	1		1					5,0
30.4	30.4.99	1999	2	1		1					5,0
7.5	7.5.99	1999	2	1		1					5,0
7.5	7.5.99	1999	3	1		1					5,0
26.5	26.5.93	1993	6	2		2					5,0
27.5	27.5.99	1999	3	1		1					5,0
29.5	29.5.93	1993	6	2		6					5,0
2.6	2.6.92	1992	2	1		1					4,0
2.6	2.6.99	1999	2	1		2					5,0
2.6	2.6.99	1999	3	1		10					5,0
2.6	2.6.93	1993	6	2		18					5,0
3.6	3.6.98	1998	3	1		2					5,0
3.6	3.6.98	1998	5	2		1					5,0
3.6	3.6.98	1998	6	2		11					5,0
5.6	5.6.97	1997	6	2		2					5,0
6.6	6.6.93	1993	2	1		1					4,0
6.6	6.6.93	1993	3	1		1					3,0
6.6	6.6.93	1993	4	2		1					5,0
6.6	6.6.93	1993	5	2		6					5,0
6.6	6.6.93	1993	6	2		16					5,0
9.6	9.6.99	1999	2	1		13					5,0
9.6	9.6.99	1999	3	1		16					5,0
9.6	9.6.93	1993	4	2		1					4,0
9.6	9.6.93	1993	5	2		28					5,0
9.6	9.6.93	1993	6	2		8					5,0
9.6	9.6.99	1999	1b	1		4					5,0
9.6	9.6.93	1993	net	2		2			4	6	5,0
10.6	10.6.98	1998	5	2		2					5,0
10.6	10.6.98	1998	6	2		3					5,0
12.6	12.6.97	1997	6	2		2					3,0
14.6	14.6.93	1993	4	2		3					3,0
14.6	14.6.93	1993	5	2		9					5,0
14.6	14.6.93	1993	6	2		26					5,0
17.6	17.6.98	1998	2	1		1					5,0
17.6	17.6.98	1998	6	2		6					5,0
18.6	18.6.99	1999	2	1		12					5,0
18.6	18.6.96	1996	3	1		1					4,0
18.6	18.6.99	1999	3	1		3					5,0
18.6	18.6.93	1993	5	2		1					5,0
18.6	18.6.93	1993	6	2		14					5,0
18.6	18.6.99	1999	1b	1		2					3,0
21.6	21.6.93	1993	5	2		7					5,0
21.6	21.6.93	1993	6	2		6					5,0
21.6	21.6.93	1993	net	2		1					3,0
25.6	25.6.99	1999	2	1		2					5,0
25.6	25.6.98	1998	3	1		1					5,0
25.6	25.6.99	1999	3	1		3					5,0
25.6	25.6.93	1993	4	2		1					2,0
25.6	25.6.93	1993	6	2		15					5,0
25.6	25.6.98	1998	6	2		1					5,0
29.6	29.6.93	1993	5	2		3					4,0
29.6	29.6.93	1993	6	2		19					4,0
29.6	29.6.93	1993	net	2		4			2	13	4,0
1.7	1.7.99	1999	3	1		1					3,0
3.7	3.7.93	1993	5	2		2					3,0
3.7	3.7.93	1993	6	2		5					3,0
7.7	7.7.93	1993	net	2		17				10	3,0
9.7	9.7.98	1998	3	1		1					5,0
9.7	9.7.98	1998	5	2		1					5,0
9.7	9.7.98	1998	6	2		2					5,0
10.7	10.7.96	1996	2	1		4					5,0
10.7	10.7.96	1996	3	1		1					5,0
11.7	11.7.97	1997	6	2		1					2,5
16.7	16.7.96	1996	3	1		1					3,5
17.7	17.7.98	1998	3	1		4					5,0
17.7	17.7.98	1998	5	2		4					5,0
17.7	17.7.98	1998	6	2		3					5,0
18.7	18.7.99	1999	2	1		4					4,0
18.7	18.7.99	1999	3	1		2					3,0
19.7	19.7.93	1993	In	2		7					2,0
20.7	20.7.92	1992	2	1		1					5,0
24.7	24.7.92	1992	2	1		3					5,0
24.7	24.7.98	1998	2	1		1					5,0
24.7	24.7.98	1998	3	1		2					5,0
24.7	24.7.98	1998	5	2		1					5,0
24.7	24.7.98	1998	6	2		4					5,0
30.7	30.7.92	1992	2	1		9					5,0
3.8	3.8.98	1998	2	1		1					5,0
3.8	3.8.98	1998	3	1		6					5,0
3.8	3.8.98	1998	5	2		2					5,0
3.8	3.8.98	1998	6	2		1					5,0
9.8	9.8.93	1993	net	2		1					5,0

Appendix 3 (continued) (*Xenopelopia falcigera/nigricans* ♀♀/Pex/L).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
10.8	10.8.98	1998	2	1		1					5,0
10.8	10.8.98	1998	3	1		4					5,0
10.8	10.8.98	1998	6	2		1					5,0
18.8	18.8.98	1998	2	1		2					4,0
18.8	18.8.98	1998	3	1		1					3,5
18.8	18.8.93	1993	5	2		2					3,0
18.8	18.8.98	1998	5	2		1					5,0
18.8	18.8.93	1993	6	2		5					4,0
18.8	18.8.98	1998	6	2		4					5,0
18.8	18.8.93	1993	C1P3	C1		2					5,0
23.8	23.8.93	1993	6	2		1					3,0
26.8	26.8.98	1998	6	2		1					5,0
2.9	2.9.98	1998	2	1		6					4,0
2.9	2.9.98	1998	5	2		1					5,0
11.9	11.9.98	1998	2	1		35					5,0
11.9	11.9.98	1998	6	2		2					5,0
21.9	21.9.98	1998	2	1		33					5,0
21.9	21.9.98	1998	5	2		1					5,0
24.9	24.9.93	1993	C1P4	C1		2					5,0
30.9	30.9.98	1998	2	1		5					5,0
30.9	30.9.98	1998	6	2		1					5,0
18.10	18.10.96	1996	6	2		2					5,0

7. *Zavrelimyia* cf. *nubila* (MEIGEN, 1830)

Determination: FITTKAU 1962, LANGTON 1991. I think that adult specimens that are preserved in alcohol are not separable from *Z. barbatipes*. Following the characters given by FITTKAU, it is more likely that the species was *Z. barbatipes* (see also SCHLEUTER 1986). But the pupa found in pool 2 was clearly *Z. nubila*. I therefore assigned all specimens to *Z. nubila.* 4 ♂♂, 18 ♀♀ ZSM, rest coll. ADK.

Ecology: FITTKAU 1962, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986, DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996.

28.5	28.5.94	1994	4	2	1						5,0
9.6	9.6.93	1993	net	2						1	5,0
18.6	18.6.99	1999	2	1	3	1					5,0
25.6	25.6.99	1999	2	1	2	2					5,0
1.7	1.7.99	1999	2	1		1					4,5
7.7	7.7.98	1998	C2P2	C2	5	0					5,0
7.7	7.7.98	1998	C2P3	C2	2	0					5,0
15.7	15.7.98	1998	C2P2	C2	13	19					5,0
15.7	15.7.98	1998	C2P3	C2	14	13					5,0
15.7	15.7.98	1998	C2P5	C2	2	1					5,0
21.7	21.7.98	1998	C2P2	C2	0	1					5,0
21.7	21.7.98	1998	C2P3	C2	3	10					5,0
21.7	21.7.98	1998	C2P5	C2	0	1					5,0
30.7	30.7.92	1992	2	1		1					5,0
23.8	23.8.93	1993	C1P3	C1	14	6					5,0
28.8	28.8.93	1993	C1P3	C1	2	18					5,0
28.8	28.8.93	1993	C1P4	C1	3						5,0
1.9	1.9.93	1993	C1P3	C1		6					4,0
1.9	1.9.93	1993	C1P4	C1	4	2					5,0
6.9	6.9.93	1993	C1P3	C1	1	4					4,0
6.9	6.9.93	1993	C1P4	C1	3	3					5,0
11.9	11.9.98	1998	6	2	1						5,0
11.9	11.9.93	1993	C1P4	C1	1	4					5,0
16.9	16.9.93	1993	C1P4	C1		1					5,0
21.9	21.9.98	1998	2	1	2						5,0
24.9	24.9.93	1993	C1P4	C1	2						5,0
1.10	1.10.93	1993	C1P4	C1	1	2					5,0
7.10	7.10.93	1993	C1P4	C1	1						5,0

Zavrelimyia spec. (FITTKAU, 1962)

6.8	6.8.96	1996	8	3		1					1,0

Tanypodinae gen. spec.

16.4	16.4.96	1996	2	1		1					5,0
19.5	19.5.93	1993	6	2		1					5,0
19.5	19.5.94	1994	6	2		1					5,0
5.6	5.6.97	1997	2	1		1					5,0
14.6	14.6.93	1993	4	2		1					3,0
3.7	3.7.93	1993	4	2		1					2,0
28.8	28.8.96	1996	5	2		1					5,0
11.9	11.9.93	1993	6	2		1					3,0

Prodiamesinae

8. *Prodiamesa olivacea* (MEIGEN, 1818)

Determination: BRUNDIN 1952, PINDER 1978. 1♂ coll. ADK.

Ecology: LEHMANN 1971, MOLLER PILLOT & BUSKENS 1990.

8.4	8.4.97	1997	m	3	1						5,0

Orthocladiinae

9. *Acricotopus lucens* (ZETTERSTEDT, 1850)

Determination: HIRVENOJA 1973, SÆTHER et al. 2000. 1 ♂ ZSM, rest coll. ADK.

Ecology: KREUZER 1940, REISS 1968, HIRVENOJA 1973, FRIZT 1982b, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990.

30.3	30.3.98	1998	2	1		1?					5,0
3.5	3.5.96	1996	net	1	1					1	5,0

Appendix 3 (continued) (*Acricotopus lucens*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
19.5	19.5.93	1993	2	1	2						5,0
22.5	22.5.97	1997	3	1	1						5,0
22.5	22.5.97	1997	5	2		1					5,0
28.5	28.5.96	1996	m	1	1						
2.6	2.6.93	1993	2	1	2						5,0
5.6	5.6.97	1997	2	1	1						5,0
31.7	31.7.96	1996	5	2	1						5,0
1.11	1.11.96	1996	6	2		1					5,0

10. *Brilia modesta* (MEIGEN, 1830)

Determination: PINDER 1978, OLIVER & RUSSEL 1983, COBO et al. 1995. 1♂ coll. ADK.

Ecology: CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990.

9.5	9.5.95	1995	10	3	1						5,0

11. *Bryophaenocladius ictericus* (MEIGEN, 1830)

Determination: PINDER 1978. The genus is in need of revision (SÆTHER et al. 2000). 1♂ coll. ADK.

Ecology: STRENZKE 1950, FRITZ ,1882b, CASPERS & SCHLEUTER 1986.

9.5	9.5.95	1995	10	3	1						5,0

12. *Bryophaenocladius illimbatus* (EDWARDS, 1929)

Determination: PINDER 1978, BRUNDIN 1947 & 56. The genus is in need of revision (SÆTHER et al. 2000) (no acrostichals, squama bare AR ~ 1.5). FRITZ 1982b (page 176) mentions that his *B. illimbatus* (see. FRITZ 1983) is actually *B. inconstans.* Therefore *B. illimbatus* was listed in SAMIETZ 1996a mistakenly who only referred to the wrong statement made by FRITZ. But in the ZSM there are specimens from three different locations in Germany (SPIES pers. comm.). 1♂, 1♀ ZMB, 1m ZSM, 1♂ coll. ADK.

Ecology: Not known (see statements on determination).

21.7	21.7.98	1998	C2P9	C2	1	0					5,0
11.8	11.8.98	1998	C2P4	C2	2	1					5,0

13. *Bryophaenocladius* spec. (similar to *B. virgo* (THIENEMANN & STRENZKE, 1940) and *B. trifurcatus* (GOETGHEBUER 1943))

Determination: SÆTHER 1977, THIENEMANN & STRENZKE 1940, GOETGHEBUER 1940 - 50. 2♀♀ coll. ADK. Mid (!!) and hind tibia with tibial combs; lenghts of palpomeres 2-4 in µm (5th palpomere shrivelled): 43, 160, 112; lengths of flagellomeres 4 and 5 in µm: 87, 131; AR = 0.32; sensilla chaetica of antenna forked near its base similar to virgo. With GOETGHEBUER one ends with *B. trifurcatus*. But this species is listed as nomen dubium in ASHE & CRANSTON 1990. It is therefore not possible to determine the species at the moment. 2♀♀ coll ADK.

Ecology: If it is *B. virgo* see THIEMNEMANN & STRENZKE 1940, STRENZKE 1950 and MOLLER PILLOT 1984b.

22.5	22.5.96	1996	7	3		1					3,5
1.6	1.6.96	1996	7	3		1					3,0

14. *Corynoneura scutellata* (WINNERTZ, 1846)

Determination: SCHLEE 1968, HIRVENOJA & HIRVENOJA 1988. 22 ♀♀ ZSM, 40♀♀ ZMB, rest coll. ADK.

Ecology: KREUZER 1940, BRUNDIN 1956, REISS 1968, HIRVENOJA & HIRVENOJA 1988, MOLLER PILLOT & BUSKENS 1990, LECHTHALER 1993.

11.4	11.4.94	1994	2	1		1					5,0
16.4	16.4.99	1999	3	1		1					5,0
22.4	22.4.94	1994	2	1		2					5,0
6.5	6.5.98	1998	3	1		4					5,0
7.5	7.5.99	1999	3	1		1					5,0
10.5	10.5.97	1997	3	1		6					5,0
13.5	13.5.98	1998	2	1		8					5,0
13.5	13.5.98	1998	3	1		4					5,0
13.5	13.5.98	1998	6	2		3					5,0
15.5	15.5.97	1997	3	1	1	11					5,0
15.5	15.5.97	1997	6	2		1					5,0
19.5	19.5.99	1999	2	1		41					5,0
19.5	19.5.99	1999	3	1		10					5,0
19.5	19.5.99	1999	1b	1		1					5,0
20.5	20.5.98	1998	3	1		1					5,0
20.5	20.5.98	1998	5	2		1					5,0
22.5	22.5.96	1996	2	1		3					5,0
27.5	27.5.98	1998	2	1		1					5,0
27.5	27.5.99	1999	2	1		3					5,0
27.5	27.5.98	1998	3	1		4					5,0
28.5	28.5.94	1994	1	1		1					5,0
28.5	28.5.96	1996	5	2		2					5,0
30.5	30.5.97	1997	6	2		4					5,0
1.6	1.6.96	1996	6	2		1					5,0
2.6	2.6.99	1999	2	1		11					5,0
2.6	2.6.95	1995	9	3		2					5,0
3.6	3.6.98	1998	2	1		68					5,0
3.6	3.6.98	1998	3	1		35					5,0
3.6	3.6.98	1998	5	2		9					5,0
3.6	3.6.98	1998	6	2		7					5,0
5.6	5.6.97	1997	2	1		8					5,0
5.6	5.6.97	1997	3	1		41					5,0
5.6	5.6.97	1997	5	2		2					5,0
5.6	5.6.97	1997	6	2		9					5,0
9.6	9.6.99	1999	2	1		5					5,0

Appendix 3 (continued) (*Corynoneura scutellata*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
9.6	9.6.99	1999	3	1		5					5,0
10.6	10.6.98	1998	2	1		46					5,0
10.6	10.6.98	1998	3	1		5					5,0
10.6	10.6.98	1998	5	2		20					5,0
10.6	10.6.98	1998	6	2		7					5,0
12.6	12.6.97	1997	2	1		1					4,5
12.6	12.6.97	1997	5	2		13					3,0
14.6	14.6.96	1996	2	1		1					5,0
14.6	14.6.96	1996	8	3		1					2,0
17.6	17.6.98	1998	2	1		1					5,0
17.6	17.6.98	1998	3	1		2					5,0
17.6	17.6.98	1998	5	2		2					5,0
17.6	17.6.98	1998	6	2		4					5,0
17.6	17.6.98	1998	C2P9	C2	0	1					5,0
18.6	18.6.96	1996	2	1		4					5,0
18.6	18.6.99	1999	2	1		2					5,0
18.6	18.6.99	1999	3	1		2					5,0
18.6	18.6.96	1996	5	2		8					5,0
18.6	18.6.96	1996	6	2		1					5,0
19.6	19.6.97	1997	3	1		2					3,0
19.6	19.6.97	1997	5	2		1					3,0
19.6	19.6.97	1997	6	2		1					3,0
21.6	21.6.93	1993	net	2		1					5,0
24.6	24.6.98	1998	C2P2	C2	0	3					5,0
25.6	25.6.98	1998	2	1		5					5,0
25.6	25.6.99	1999	2	1		1					5,0
25.6	25.6.98	1998	3	1		10					5,0
25.6	25.6.98	1998	5	2		9					5,0
25.6	25.6.98	1998	6	2		13					5,0
26.6	26.6.96	1996	2	1		2					4,5
26.6	26.6.96	1996	5	2		1					4,5
28.6	28.6.97	1997	5	2		1					4,5
29.6	29.6.93	1993	6	2		6					4,0
2.7	2.7.98	1998	2	1		5					5,0
2.7	2.7.98	1998	3	1		3					5,0
2.7	2.7.98	1998	5	2		43					5,0
2.7	2.7.98	1998	6	2		53					5,0
2.7	2.7.98	1998	C2P10	C2	0	13					5,0
2.7	2.7.98	1998	C2P2	C2	0	6					5,0
3.7	3.7.93	1993	5	2		1					3,0
5.7	5.7.97	1997	3	1		1					4,5
7.7	7.7.93	1993	6	2		2					3,0
7.7	7.7.98	1998	C2P10	C2	0	1					5,0
7.7	7.7.98	1998	C2P2	C2	0	6					5,0
7.7	7.7.98	1998	C2P9	C2	0	17					5,0
9.7	9.7.98	1998	2	1		1					5,0
9.7	9.7.98	1998	3	1		2					5,0
9.7	9.7.98	1998	5	2		12					5,0
9.7	9.7.98	1998	6	2		15					5,0
15.7	15.7.98	1998	C2P10	C2	0	1					5,0
15.7	15.7.98	1998	C2P2	C2	0	37					5,0
15.7	15.7.98	1998	C2P3	C2	0	2					5,0
15.7	15.7.98	1998	C2P9	C2	0	2					5,0
16.7	16.7.96	1996	5	2		2					5,0
17.7	17.7.98	1998	5	2		5					5,0
17.7	17.7.98	1998	6	2		3					5,0
18.7	18.7.99	1999	2	1		1					4,0
19.7	19.7.97	1997	5	2		1					3,0
19.7	19.7.93	1993	In	2		7					2,0
21.7	21.7.93	1993	5	2		1					4,0
21.7	21.7.93	1993	6	2		1					4,0
21.7	21.7.98	1998	C2P10	C2	0	24					5,0
21.7	21.7.98	1998	C2P2	C2	0	12					5,0
21.7	21.7.98	1998	C2P3	C2	0	2					5,0
21.7	21.7.98	1998	C2P5	C2	0	1					5,0
21.7	21.7.98	1998	C2P8	C2	0	2					5,0
21.7	21.7.98	1998	C2P9	C2	0	68					5,0
24.7	24.7.98	1998	2	1		8					5,0
24.7	24.7.98	1998	3	1		7					5,0
24.7	24.7.98	1998	5	2		6					5,0
24.7	24.7.98	1998	6	2		2					5,0
3.8	3.8.98	1998	2	1		3					5,0
3.8	3.8.98	1998	3	1		2					5,0
3.8	3.8.98	1998	5	2		36					5,0
3.8	3.8.98	1998	6	2		23					5,0
10.8	10.8.98	1998	2	1		3					5,0
10.8	10.8.98	1998	3	1		3					5,0
10.8	10.8.98	1998	5	2		33					5,0
10.8	10.8.98	1998	6	2		13					5,0
11.8	11.8.98	1998	C2P4	C2		14					5,0
13.8	13.8.93	1993	C1P4	C1		12					5,0
18.8	18.8.98	1998	2	1		8					4,0
18.8	18.8.98	1998	3	1		3					3,5
18.8	18.8.98	1998	5	2		15					5,0
18.8	18.8.98	1998	6	2		4					5,0
18.8	18.8.93	1993	C1P4	C1		4					5,0
26.8	26.8.98	1998	5	2		2					5,0
26.8	26.8.98	1998	6	2		6					5,0
28.8	28.8.93	1993	C1P4	C1		11					5,0
1.9	1.9.93	1993	C1P3	C1		2					4,0
1.9	1.9.93	1993	C1P4	C1		2					5,0
2.9	2.9.98	1998	5	2		3					5,0
6.9	6.9.93	1993	C1P4	C1		1					5,0

Appendix 3 (continued) (*Corynoneura scutellata*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
6.9	6.9.93	1993	In	2		1					2,0
6.9	6.9.93	1993	In	3		1					2,0
11.9	11.9.98	1998	5	2		6					5,0
11.9	11.9.98	1998	6	2		3					5,0
11.9	11.9.93	1993	C1P4	C1		2					5,0
21.9	21.9.98	1998	5	2		5					5,0
21.9	21.9.98	1998	6	2		4					5,0
24.9	24.9.93	1993	C1P4	C1		18					5,0
30.9	30.9.98	1998	5	2		9					5,0
30.9	30.9.98	1998	6	2		2					5,0
1.10	1.10.93	1993	C1P4	C1		44					5,0
7.10	7.10.93	1993	C1P4	C1		14					5,0
9.10	9.10.98	1998	6	2		1					5,0
14.10	14.10.93	1993	C1P4	C1		4					5,0
19.10	19.10.98	1998	3	1		1					5,0
19.10	19.10.98	1998	5	2		2					5,0
19.10	19.10.98	1998	net	2					1		5,0

15. *Cricotopus sylvestris* (FABRICIUS, 1794)

Determination: HIRVENOJA 1973. 2♂♂, 1♀♀ ZSM, rest coll. ADK.

Ecology: KIEFFER & THIENEMANN 1909, REMMERT 1955, REISS 1968, HIRVENOJA 1973, LEARNER & POTTER 1974, SÆTHER 1979, MENZIE 1981, FRITZ 1982b, CASPERS 1983a, SCHLEUTER 1986, LEUCHS & CASPERS 1988, MOLLER PILLOT & BUSKENS 1990, LECHTHALER 1993, BECKER 1995, DETTINGER-KLEMM 1995b (very tolerant in respect to water pollution).

11.6	11.6.96	1996	net	1	1						5,0
17.6	17.6.98	1998	C2P7	C2		1					5,0
17.6	17.6.98	1998	C2P9	C2	2	2					5,0
24.6	24.6.98	1998	C2P10	C2	1	10					5,0
2.7	2.7.98	1998	C2P10	C2		1					5,0
10.7	10.7.96	1996	2	1	1						5,0
21.7	21.7.98	1998	C2P1	C2	6						5,0

16. *Gymnometriocnemus* cf. *subnudus* (EDWARDS, 1929)

Determination: Virga short, microtricha of wing as in EDWARS 1929 (Plate XVII, Fig. 9); AR = 0.99 (≠ SÆTHER 1983: 1.34); length terminal flagellomere 353 µm (≠ SÆTHER 1983: 482µm); length of antenna 703µm; WL = 1.34 (SÆTHER 1983: 1.58); LR = 0.62; gonostylus (71µm) 5.4 times as long as megaseta (13.1 µm) . 1 ♂ ZSM, 1 ♂ coll. ADK.

Ecology: STRENZKE 1950.

22.5	22.5.96	1996	m	3	2						4,0

17. *Heleniella ornaticollis* (EDWARS, 1929)

Determination: RINGE 1976. 1♀ coll. ADK.

Ecology: RINGE 1976, MOLLER PILLOT 1984b.

31.5	31.5.95	1995	10	3		1					5,0

18. *Limnophyes asquamatus* (ANDERSEN, 1937)

Determination: SÆTHER 1990 (see also section 4.3.1.1. of this study). ♂♂ + ♀♀ of the bisex. form ZSM + ZMB; 3 ♂♂, 1♀, 1♂Pex of the bisexual form coll. Steinhart; ♂♂, ♀♀, many Pex, many L of the parth. Form (lab rearings) ZSM, rest coll. ADK (see also Appendix 4 and 5).

Ecology: For quotations see DETTINGER-KLEMM 2001.

30.3	30.3.98	1998	3	1		1					5,0
30.3	30.3.98	1998	6	2		1					5,0
5.4	5.4.97	1997	7	3		5					5,0
7.4	7.4.98	1998	7	3	7	4					5,0
11.4	11.4.97	1997	7	3	2	1					5,0
11.4	11.4.94	1994	9	3		10					5,0
15.4	15.4.98	1998	7	3	1	2					5,0
16.4	16.4.96	1996	8	3	1						3,0
19.4	19.4.96	1996	7	3	1	1					3,0
19.4	19.4.97	1997	7	3	1						5,0
19.4	19.4.96	1996	8	3	2	1					3,0
22.4	22.4.94	1994	7	3	2	2					5,0
22.4	22.4.98	1998	7	3	1	2					5,0
22.4	22.4.94	1994	9	3	1	3					5,0
23.4	23.4.96	1996	7	3	2	4					3,0
23.4	23.4.96	1996	8	3	4	8					3,5
25.4	25.4.96	1996	7	3	4	10					3,0
25.4	25.4.96	1996	8	3	9	6					3,0
26.4	26.4.97	1997	7	3		1					5,0
28.4	28.4.94	1994	1	1		1					5,0
28.4	28.4.94	1994	7	3		2					5,0
28.4	28.4.96	1996	7	3	20	14					3,0
28.4	28.4.96	1996	8	3	11	19					3,0
28.4	28.4.94	1994	9	3	2	1					5,0
30.4	30.4.98	1998	7	3		1					5,0
1.5	1.5.96	1996	7	3	14	6					3,0
1.5	1.5.96	1996	8	3	17	19					3,0
2.5	2.5.96	1996	Be	3	6	4			7	2	3,0
3.5	3.5.97	1997	7	3		3					5,0
4.5	4.5.96	1996	7	3	5	6					3,0
4.5	4.5.96	1996	8	3	4	1					3,0
6.5	6.5.94	1994	7	3		2					5,0
6.5	6.5.94	1994	9	3		3					?
7.5	7.5.96	1996	7	3	7	14					4,0
7.5	7.5.96	1996	8	3	2	1					4,0

Appendix 3 (continued) (*Limnophyes asquamatus*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
10.5	10.5.97	1997	7	3		2					5,0
10.5	10.5.97	1997	9	3	1						5,0
11.5	11.5.96	1996	7	3	4	4					3,0
11.5	11.5.96	1996	8	3		1					3,0
13.5	13.5.98	1998	6	2		1					5,0
13.5	13.5.98	1998	7	3	1						5,0
13.5	13.5.98	1998	8	3		2					5,0
15.5	15.5.96	1996	7	3	1	5					3,5
19.5	19.5.94	1994	2	1		1					5,0
19.5	19.5.94	1994	6	2		1					5,0
19.5	19.5.94	1994	7	3		16					5,0
19.5	19.5.94	1994	9	3		11					?
20.5	20.5.98	1998	3	1		1					5,0
20.5	20.5.98	1998	6	2		2					5,0
20.5	20.5.98	1998	7	3		11					5,0
20.5	20.5.98	1998	8	3		2					5,0
22.5	22.5.96	1996	7	3	6	2					3,5
22.5	22.5.96	1996	8	3		2					4,0
27.5	27.5.98	1998	3	1		2					5,0
27.5	27.5.98	1998	6	2		1					5,0
27.5	27.5.98	1998	7	3		10					5,0
27.5	27.5.98	1998	8	3		2					5,0
28.5	28.5.94	1994	1	1		4					5,0
28.5	28.5.94	1994	2	1		8					5,0
28.5	28.5.94	1994	6	2	1						5,0
28.5	28.5.94	1994	7	3		12					5,0
28.5	28.5.96	1996	7	3	5	1					3,0
28.5	28.5.96	1996	8	3	1						3,0
28.5	28.5.94	1994	9	3	1	14					5,0
29.5	29.5.95	1995	10	3		2					5,0
1.6	1.6.96	1996	7	3	4	8					3,0
1.6	1.6.96	1996	8	3	1						3,0
3.6	3.6.98	1998	6	2		1					5,0
5.6	5.6.97	1997	6	2		1					5,0
5.6	5.6.96	1996	7	3	48	42					2,5
5.6	5.6.96	1996	8	3	2	1					2,5
8.6	8.6.95	1995	10	3	1	1					5,0
10.6	10.6.96	1996	7	3	24	40					3,0
10.6	10.6.98	1998	7	3	1	1					5,0
10.6	10.6.96	1996	8	3	10	6					3,0
10.6	10.6.98	1998	8	3		3					5,0
14.6	14.6.96	1996	7	3	3	3					2,0
14.6	14.6.96	1996	8	3	1	4					2,0
15.6	15.6.94	1994	7	3	105	194					?
15.6	15.6.94	1994	9	3	4	8					?
17.6	17.6.98	1998	7	3		3					5,0
17.6	17.6.98	1998	C2P9	C2	0	2					5,0
18.6	18.6.96	1996	5	2		1					5,0
18.6	18.6.96	1996	7	3		1					2,0
18.6	18.6.96	1996	8	3		1					2,0
24.6	24.6.98	1998	C2P4	C2	0	2					5,0
24.6	24.6.98	1998	C2P7	C2		3					5,0
25.6	25.6.98	1998	5	2		1					5,0
25.6	25.6.98	1998	7	3	8	18					3,0
25.6	25.6.98	1998	8	3		3					3,0
26.6	26.6.95	1995	10	3		4					4,0
30.6	30.6.95	1995	10	3		1					3,0
2.7	2.7.98	1998	5	2		1					5,0
2.7	2.7.95	1995	7	3		6					3,0
2.7	2.7.98	1998	7	3	9	11					3,0
2.7	2.7.98	1998	8	3	1	2					3,0
2.7	2.7.95	1995	9	3	1						3,0
2.7	2.7.98	1998	C2P10	C2	0	1					5,0
2.7	2.7.98	1998	C2P4	C2	0	1					5,0
2.7	2.7.98	1998	C2P7	C2	0	1					5,0
3.7	3.7.95	1995	10	3		3					3,0
7.7	7.7.98	1998	C2P7	C2	0	1					5,0
9.7	9.7.98	1998	5	2		1					5,0
9.7	9.7.98	1998	6	2		1					5,0
9.7	9.7.98	1998	7	3	9	15					2,5
9.7	9.7.98	1998	8	3	1	3					2,5
10.7	10.7.95	1995	10	3	1						1,0
11.7	11.7.95	1995	7	3	2	1					2,0
17.7	17.7.95	1995	7	3	8	3					2,0
17.7	17.7.98	1998	7	3	1						3,0
19.7	19.7.93	1993	In	3	69	942					2,0
20.7	20.7.95	1995	7	3	4	2					2,0
26.7	26.7.95	1995	2	1		1					3,0
26.7	26.7.95	1995	7	3	2						1,0
26.7	26.7.95	1995	10	3		1					1,0
11.8	11.8.98	1998	C2P4	C2		15					5,0
26.8	26.8.93	1993	In	3					1		2,0
6.9	6.9.93	1993	In	3		3					2,0
11.9	11.9.93	1993	C1P4	C1		2					5,0
16.9	16.9.93	1993	C1P4	C1		1					5,0
21.9	21.9.98	1998	6	2		1					5,0
24.9	24.9.93	1993	C1P4	C1		1					5,0
30.9	30.9.98	1998	6	2		1					5,0
1.10	1.10.93	1993	C1P2	C1		1					5,0
1.10	1.10.93	1993	C1P3	C1		1					5,0
9.10	9.10.98	1998	6	2		1					5,0

Appendix 3 (continued).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
19. *Limnophyes habilis* (WALKER, 1856)											
Determination: SÆTHER 1990 (≠ SÆTHER: preepisternum with about 8 setae standing in an anterior row and additional with one posterior setae). 2♀♀ coll. ADK.											
Ecology: SÆTHER 1990.											
30.5 15.6.	30.5.97 15.6	1997 16.6	7 7.1	3 3.1		1 1					3,0 ?
20. *Limnophyes minimus*-aggregate sensu meo											
Determination: SÆTHER 1990 (see also section 4.3.1.2. of this study). Many ♂♂+ ♀♀ ZSM + ZMB, 1Pex coll. Steinhart, rest coll. ADK.											
Ecology: STRENZKE 1950, THIENEMANN 1954, REMMERT 1955, DELETTRE & TREHEN 1977, DELETTRE 1978, FRITZ 1982b, CASPERS & SCHLEUTER 1986; CRAFFORD 1986, SCHLEUTER 1996, SÆTHER 1990; DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996, SAMIETZ 1996b, STEINHART 1999, SCHNABEL 1999, SCHNABEL & DETTINGER-KLEMM 2000, 2001, ORENDT 1999, 2000a+b, RODRIGUES (2001).											
13.8.	13.8.93	1993	4	2		16					3,0
30.3	30.3.98	1998	6	2		1					5,0
30.3	30.3.98	1998	7	3	1						5,0
5.4	5.4.97	1997	3	1		1					5,0
5.4	5.4.97	1997	7	3	1	1					5,0
5.4	5.4.97	1997	8	3	1						5,0
7.4	7.4.98	1998	2	1		1					5,0
7.4	7.4.98	1998	3	1	1	1					5,0
7.4	7.4.98	1998	7	3		1					5,0
11.4	11.4.94	1994	2	1	1						5,0
11.4	11.4.94	1994	4	2	1						5,0
11.4	11.4.94	1994	6	2	2	1					5,0
11.4	11.4.97	1997	7	3	3						5,0
15.4	15.4.98	1998	3	1		2					5,0
15.4	15.4.98	1998	6	2		1					5,0
15.4	15.4.98	1998	7	3	11	11	1				5,0
16.4	16.4.96	1996	5	2		3					5,0
16.4	16.4.96	1996	8	3		1					3,0
19.4	19.4.96	1996	7	3	1	17					3,0
19.4	19.4.96	1996	8	3		3					3,0
19.4	19.4.97	1997	9	3	1	2					3,0
19.4	19.4.96	1996	Bo	3						1	3,0
22.4	22.4.98	1998	3	1	1						5,0
22.4	22.4.94	1994	4	2	2						5,0
22.4	22.4.94	1994	6	2	3						5,0
22.4	22.4.94	1994	7	3		2					5,0
22.4	22.4.98	1998	7	3	5	15	1				5,0
22.4	22.4.94	1994	9	3	1	1					5,0
23.4	23.4.96	1996	3	1	2	2					5,0
23.4	23.4.96	1996	7	3	5	43					3,0
23.4	23.4.96	1996	8	3	1	18					3,5
24.4	24.4.99	1999	1c	1		1					5,0
25.4	25.4.96	1996	7	3		2					3,0
25.4	25.4.96	1996	8	3		7					3,0
26.4	26.4.97	1997	9	3		8					3,0
28.4	28.4.94	1994	1	1	1	1					5,0
28.4	28.4.94	1994	2	1		2					5,0
28.4	28.4.94	1994	4	2		1					5,0
28.4	28.4.94	1994	6	2		1					5,0
28.4	28.4.96	1996	7	3	3	6					3,0
28.4	28.4.96	1996	8	3		5					3,0
28.4	28.4.94	1994	9	3		1					5,0
30.4	30.4.98	1998	3	1		3					5,0
30.4	30.4.98	1998	5	2		1					5,0
30.4	30.4.98	1998	7	3	7	15					5,0
30.4	30.4.98	1998	8	3		1					5,0
1.5	1.5.96	1996	7	3		2					3,0
1.5	1.5.96	1996	8	3		2					3,0
2.5	2.5.96	1996	Be	3	3	2			3	1	3,0
3.5	3.5.97	1997	7	3	1	1					5,0
3.5	3.5.97	1997	9	3		3					3,0
4.5	4.5.96	1996	7	3		4					3,0
4.5	4.5.96	1996	8	3		1					3,0
6.5	6.5.94	1994	1	1		1					5,0
6.5	6.5.94	1994	2	1		1					5,0
6.5	6.5.94	1994	7	3		1					5,0
6.5	6.5.98	1998	8	3		1					5,0
6.5	6.5.94	1994	9	3		2					5,0
7.5	7.5.96	1996	8	3		3					4,0
7.5	7.5.99	1999	1c	1		1					5,0
10.5	10.5.97	1997	8	3		1					5,0
10.5	10.5.97	1997	9	3	20	14					5,0
13.5	13.5.98	1998	7	3		1					5,0
15.5	15.5.96	1996	7	3		1					3,5
19.5	19.5.94	1994	2	1		1					5,0
19.5	19.5.99	1999	3	1		1					5,0
19.5	19.5.94	1994	6	2		1					5,0
19.5	19.5.94	1994	7	3		1					5,0
19.5	19.5.94	1994	9	3	1	3					3,0
19.5	19.5.99	1999	1c	1		1					4,0
22.5	22.5.96	1996	7	3		1					3,5

Appendix 3 (continued) (*Limnophyes minimus*-aggregate sensu meo).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
22.5	22.5.97	1997	7	3		1					4,5
26.5	26.5.93	1993	6	2		1					5,0
27.5	27.5.99	1999	32	1		1					5,0
27.5	27.5.98	1998	6	2		1					5,0
27.5	27.5.98	1998	7	3	1						5,0
27.5	27.5.98	1998	8	3		1					5,0
27.5	27.5.99	1999	1b	1		1					4,5
27.5	27.5.99	1999	1c	1		1					4,0
28.5	28.5.94	1994	1	1		2					5,0
28.5	28.5.94	1994	2	1		4					5,0
28.5	28.5.94	1994	6	2		1					5,0
28.5	28.5.94	1994	7	3		5					5,0
28.5	28.5.96	1996	8	3		1					3,0
28.5	28.5.94	1994	9	3		3					5,0
29.5	29.5.93	1993	1	1		1					4,0
29.5	29.5.93	1993	3	1		1					5,0
30.5	30.5.97	1997	7	3		7					3,0
30.5	30.5.97	1997	8	3	1	6					3,0
1.6	1.6.96	1996	6	2		1					5,0
1.6	1.6.96	1996	7	3	2						3,0
2.6	2.6.93	1993	3	1		2					5,0
2.6	2.6.99	1999	3	1		1					5,0
2.6	2.6.93	1993	6	2		1					5,0
2.6	2.6.99	1999	1b	1		4					5,0
2.6	2.6.99	1999	1c	1		1					4,5
3.6	3.6.98	1998	3	1		1					5,0
3.6	3.6.98	1998	5	2		3					5,0
3.6	3.6.98	1998	6	2		1					5,0
5.6	5.6.96	1996	2	1		1					5,0
5.6	5.6.97	1997	2	1		1					5,0
5.6	5.6.97	1997	5	2		21					5,0
5.6	5.6.96	1996	7	3	62	22					2,5
5.6	5.6.97	1997	7	3	2	12					2,0
5.6	5.6.96	1996	8	3		13					2,5
5.6	5.6.97	1997	9	3	76	88					2,0
6.6	6.6.93	1993	2	1		2					4,0
6.6	6.6.93	1993	3	1		1					3,0
6.6	6.6.93	1993	5	2		1					5,0
6.6	6.6.93	1993	6	2		2					5,0
9.6	9.6.93	1993	2	1		4					3,0
9.6	9.6.93	1993	3	1		4					3,0
9.6	9.6.99	1999	1b	1		2					5,0
9.6	9.6.99	1999	1c	1		1					4,5
10.6	10.6.98	1998	5	2		2					5,0
10.6	10.6.96	1996	7	3	106	71					3,0
10.6	10.6.98	1998	7	3		1					5,0
10.6	10.6.96	1996	8	3	26	53					3,0
11.6	11.6.98	1998	C2P4	C2	0	1					5,0
11.6	11.6.98	1998	C2P8	C2	1	0					5,0
12.6	12.6.97	1997	5	2		8					3,0
12.6	12.6.97	1997	6	2		4					3,0
12.6	12.6.97	1997	7	3	1						2,0
12.6	12.6.97	1997	8	3	1	7					2,0
14.6	14.6.93	1993	1	1		1					2,0
14.6	14.6.93	1993	2	1		4					3,0
14.6	14.6.93	1993	3	1		14					3,0
14.6	14.6.93	1993	4	2		6					3,0
14.6	14.6.93	1993	6	2		1					5,0
14.6	14.6.96	1996	7	3	10	13					2,0
14.6	14.6.96	1996	8	3	29	49					2,0
17.6	17.6.98	1998	2	1		2					5,0
17.6	17.6.98	1998	5	2		7					5,0
17.6	17.6.98	1998	6	2		6					5,0
17.6	17.6.98	1998	8	3	2	50					5,0
17.6	17.6.98	1998	C2P10	C2	0	3					5,0
17.6	17.6.98	1998	C2P2	C2	2	0					5,0
17.6	17.6.98	1998	C2P6	C2	0	1					5,0
17.6	17.6.98	1998	C2P7	C2	1	0					5,0
18.6	18.6.93	1993	1	1		2					2,0
18.6	18.6.93	1993	2	1		3					2,0
18.6	18.6.99	1999	2	1		5					5,0
18.6	18.6.93	1993	3	1		6					2,0
18.6	18.6.99	1999	3	1		2					5,0
18.6	18.6.96	1996	5	2	1	1					5,0
18.6	18.6.93	1993	6	2		1					5,0
18.6	18.6.96	1996	7	3	1	4					2,0
18.6	18.6.96	1996	8	3	15	33					2,0
18.6	18.6.99	1999	1b	1		10					3,0
18.6	18.6.99	1999	1c	1		5					3,0
19.6	19.6.97	1997	3	1		2					3,0
19.6	19.6.97	1997	5	2		9					3,0
19.6	19.6.97	1997	6	2		5					3,0
21.6	21.6.93	1993	2	1		4					2,0
21.6	21.6.93	1993	3	1		6					2,0
21.6	21.6.93	1993	4	2		3					3,0
21.6	21.6.93	1993	6	2		2					5,0
21.6	21.6.93	1993	net	2		1					5,0
22.6	22.6.95	1995	7	3		2					5,0
24.6	24.6.98	1998	C2P2	C2	0	5					5,0
25.6	25.6.93	1993	2	1		5					2,0
25.6	25.6.98	1998	2	1		3					5,0
25.6	25.6.98	1998	3	1		1					5,0
25.6	25.6.93	1993	4	2		2					2,0

Appendix 3 (continued) (*Limnophyes minimus*-aggregate sensu meo).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
25.6	25.6.98	1998	5	2		37					5,0
25.6	25.6.93	1993	6	2		1					5,0
25.6	25.6.98	1998	6	2		76					5,0
25.6	25.6.98	1998	7	3		91					3,0
25.6	25.6.99	1999	1b	1		12					3,0
25.6	25.6.99	1999	1c	1		17					3,0
26.6	26.6.95	1995	7	3		1					5,0
26.6	26.6.96	1996	7	3	1	2					2,0
26.6	26.6.96	1996	8	3	5						2,0
26.6	26.6.95	1995	9	3		2					4,0
26.6	26.6.95	1995	10	3		3					4,0
28.6	28.6.97	1997	2	1		1					5,0
28.6	28.6.97	1997	3	1		5					4,0
28.6	28.6.97	1997	5	2		3					4,5
28.6	28.6.97	1997	6	2		2					4,0
28.6	28.6.95	1995	9	3		8					3,0
29.6	29.6.93	1993	1	1		2					2,0
29.6	29.6.93	1993	2	1		33					2,0
29.6	29.6.93	1993	3	1		33					2,0
29.6	29.6.93	1993	4	2		12					2,0
29.6	29.6.93	1993	5	2		1					4,0
29.6	29.6.93	1993	6	2		12					4,0
29.6	29.6.95	1995	10	3		2					4,0
30.6	30.6.95	1995	7	3		2					4,0
30.6	30.6.95	1995	9	3		4					3,0
1.7	1.7.99	1999	2	1		1					4,5
1.7	1.7.99	1999	1b	1		21					2,5
1.7	1.7.99	1999	1c	1		26					2,5
2.7	2.7.96	1996	5	2		12					5,0
2.7	2.7.98	1998	5	2		42					5,0
2.7	2.7.98	1998	6	2		8					5,0
2.7	2.7.98	1998	7	3		33					3,0
2.7	2.7.98	1998	8	3		12					3,0
2.7	2.7.95	1995	9	3		7					3,0
3.7	3.7.93	1993	2	1		45					1,0
3.7	3.7.93	1993	3	1		13					2,0
3.7	3.7.93	1993	4	2		9					2,0
3.7	3.7.93	1993	5	2		7					3,0
3.7	3.7.93	1993	6	2		27					3,0
3.7	3.7.95	1995	9	3		2					3,0
3.7	3.7.95	1995	10	3	1	3					3,0
4.7	4.7.95	1995	7	3		1					5,0
4.7	4.7.95	1995	9	3		4					3,0
5.7	5.7.97	1997	3	1		2					2,0
5.7	5.7.97	1997	6	2		2					5,0
5.7	5.7.95	1995	9	3		1					2,0
5.7	5.7.95	1995	10	3		1					2,0
6.7	6.7.95	1995	9	3		1					2,0
7.7	7.7.93	1993	2	1		2					2,0
7.7	7.7.93	1993	3	1		5					2,0
7.7	7.7.93	1993	4	2		1					2,0
7.7	7.7.93	1993	5	2		1					3,0
7.7	7.7.93	1993	6	2		12					3,0
7.7	7.7.95	1995	7	3		1					2,0
8.7	8.7.99	1999	2	1		2					5,0
8.7	8.7.99	1999	3	1		2					5,0
8.7	8.7.95	1995	10	3		1					2,0
8.7	8.7.99	1999	1b	1		5					4,0
8.7	8.7.99	1999	1c	1		8					3,0
9.7	9.7.98	1998	2	1		1					5,0
9.7	9.7.98	1998	5	2		3					5,0
9.7	9.7.98	1998	6	2		10					5,0
9.7	9.7.98	1998	7	3		10					2,5
9.7	9.7.98	1998	8	3		1					2,5
10.7	10.7.96	1996	7	3		2					2,0
10.7	10.7.96	1996	8	3	5	7					2,0
10.7	10.7.95	1995	9	3		1					1,0
10.7	10.7.95	1995	10	3		1					1,0
11.7	11.7.97	1997	2	1		1					3,0
11.7	11.7.97	1997	3	1		2					3,0
11.7	11.7.97	1997	5	2		3					2,5
11.7	11.7.97	1997	6	2		12					2,5
12.7	12.7.93	1993	3	1		7					2,0
12.7	12.7.93	1993	4	2		3					1,0
12.7	12.7.93	1993	5	2		12					2,0
12.7	12.7.93	1993	6	2		15					2,0
15.7	15.7.98	1998	C2P9	C2	0	1					5,0
17.7	17.7.93	1993	2	1		4					2,0
17.7	17.7.93	1993	3	1		1					2,0
17.7	17.7.93	1993	4	2		2					2,0
17.7	17.7.93	1993	5	2	1	5					3,0
17.7	17.7.98	1998	5	2		1					5,0
17.7	17.7.93	1993	6	2	1	28					3,0
17.7	17.7.98	1998	6	2		3					5,0
17.7	17.7.95	1995	7	3		5					2,0
17.7	17.7.98	1998	7	3		3					3,0
17.7	17.7.98	1998	8	3	1	2					2,5
18.7	18.7.99	1999	2	1		3					4,0
18.7	18.7.99	1999	3	1	1	4					3,0
18.7	18.7.99	1999	1b	1	2	9					2,0
18.7	18.7.99	1999	1c	1	1	1					2,0
19.7	19.7.97	1997	2	1		9					3,0
19.7	19.7.97	1997	5	2		15					3,0

Appendix 3 (continued) (*Limnophyes minimus*-aggregate sensu meo).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
19.7	19.7.93	1993	In	2	1	24					2,0
19.7	19.7.93	1993	In	3	5	46					2,0
20.7	20.7.95	1995	7	3		1					2,0
21.7	21.7.93	1993	1	1		1					2,0
21.7	21.7.93	1993	2	1		9					2,0
21.7	21.7.93	1993	3	1		6					2,0
21.7	21.7.93	1993	4	2		3					2,0
21.7	21.7.93	1993	5	2	4	52					4,0
21.7	21.7.93	1993	6	2	1	24					4,0
23.7	23.7.96	1996	2	1		4					2,5
23.7	23.7.96	1996	3	1	1	79					2,5
23.7	23.7.96	1996	5	2		13					4,0
23.7	23.7.96	1996	6	2		7					3,5
23.7	23.7.96	1996	7	3	2	6					2,0
23.7	23.7.96	1996	8	3	8	53					2,0
24.7	24.7.98	1998	2	1		5					5,0
24.7	24.7.98	1998	3	1		1					5,0
24.7	24.7.98	1998	5	2		5					5,0
24.7	24.7.98	1998	6	2		12					5,0
24.7	24.7.98	1998	7	3	1	40					2,0
24.7	24.7.98	1998	8	3	9	121					2,0
26.7	26.7.93	1993	1	1		5					2,0
26.7	26.7.93	1993	2	1		27					2,0
26.7	26.7.97	1997	2	1		1					3,0
26.7	26.7.93	1993	3	1		11					2,0
26.7	26.7.93	1993	4	2		6					2,0
26.7	26.7.93	1993	5	2	1	41					4,0
26.7	26.7.93	1993	6	2	6	30					4,0
26.7	26.7.95	1995	7	3		2					2,0
27.7	27.7.99	1999	2	1		10					2,5
27.7	27.7.99	1999	3	1	2	5					2,5
27.7	27.7.99	1999	1b	1	3	13					2,0
27.7	27.7.99	1999	1c	1	5	24					2,0
27.7	27.7.93	1993	C1P4	C1		2					5,0
30.7	30.7.93	1993	1	1		3					2,0
30.7	30.7.93	1993	2	1		7					2,0
30.7	30.7.93	1993	3	1		5					2,0
30.7	30.7.93	1993	4	2		11					2,0
30.7	30.7.93	1993	5	2		76					4,0
30.7	30.7.93	1993	6	2	3	36					3,0
31.7	31.7.96	1996	2	1		3					2,5
31.7	31.7.96	1996	3	1		27					3,0
31.7	31.7.96	1996	5	2		6					5,0
31.7	31.7.96	1996	6	2		2					5,0
1.8	1.8.99	1999	2	1		11					2,0
1.8	1.8.99	1999	3	1	1	5					2,0
1.8	1.8.99	1999	1b	1	2	6					2,0
1.8	1.8.99	1999	1c	1	2	5					2,0
2.8	2.8.95	1995	2	1		4					1,5
3.8	3.8.98	1998	2	1		4					5,0
3.8	3.8.98	1998	3	1		8					5,0
3.8	3.8.98	1998	5	2		16					5,0
3.8	3.8.98	1998	6	2		20					5,0
3.8	3.8.98	1998	7	3	17	63					2,0
3.8	3.8.98	1998	8	3	117	337					2,0
4.8	4.8.93	1993	1	1	2	9					1,0
4.8	4.8.93	1993	2	1		22					1,0
4.8	4.8.93	1993	3	1		6					2,0
4.8	4.8.93	1993	4	2		5					5,0
4.8	4.8.93	1993	5	2		31					5,0
4.8	4.8.93	1993	6	2		13					5,0
4.8	4.8.93	1993	C1P1	C1		2					5,0
5.8	5.8.97	1997	2	1		8					2,0
6.8	6.8.96	1996	2	1		4					2,0
6.8	6.8.96	1996	3	1		9					2,0
6.8	6.8.96	1996	6	2	1	1					3,0
6.8	6.8.96	1996	7	3	1	1					1,0
6.8	6.8.96	1996	8	3	2	9					1,0
9.8	9.8.93	1993	1	1	2	8					1,0
9.8	9.8.93	1993	2	1		141					1,0
9.8	9.8.93	1993	3	1	1	4					1,0
9.8	9.8.93	1993	4	2		6					3,0
9.8	9.8.93	1993	5	2		13					5,0
10.8	10.8.98	1998	2	1		7					5,0
10.8	10.8.98	1998	3	1		1					5,0
10.8	10.8.98	1998	5	2		21					5,0
10.8	10.8.98	1998	6	2		13					5,0
10.8	10.8.98	1998	7	3	107	246					2,0
10.8	10.8.98	1998	8	3	31	106					2,0
13.8	13.8.93	1993	1	1		1					1,0
13.8	13.8.93	1993	2	1		39					1,0
13.8	13.8.93	1993	3	1		6					1,0
13.8	13.8.93	1993	5	2		10					5,0
13.8	13.8.93	1993	6	2		11					5,0
13.8	13.8.93	1993	C1P1	C1		8					5,0
13.8	13.8.93	1993	C1P3	C1		8					5,0
13.8	13.8.93	1993	C1P4	C1		3					5,0
14.8	14.8.96	1996	5	2		19					5,0
14.8	14.8.96	1996	6	2		1					5,0
14.8	14.8.96	1996	7	3		1					2,0
14.8	14.8.96	1996	8	3		5					2,0
18.8	18.8.93	1993	1	1		1					1,0
18.8	18.8.93	1993	2	1		9					1,0

Appendix 3 (continued) (*Limnophyes minimus*-aggregate sensu meo).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
18.8	18.8.98	1998	2	1		19					4,0
18.8	18.8.93	1993	3	1		1					1,0
18.8	18.8.98	1998	3	1		10					3,5
18.8	18.8.93	1993	4	2	4	26					2,0
18.8	18.8.93	1993	5	2	1	10					3,0
18.8	18.8.98	1998	5	2		12					5,0
18.8	18.8.93	1993	6	2		3					4,0
18.8	18.8.98	1998	6	2		30					5,0
18.8	18.8.93	1993	C1P1	C1		111					2,0
18.8	18.8.93	1993	C1P3	C1		9					5,0
18.8	18.8.93	1993	C1P4	C1		21					5,0
23.8	23.8.93	1993	1	1		1					2,0
23.8	23.8.93	1993	2	1	1	2					2,0
23.8	23.8.93	1993	3	1	1	3					2,0
23.8	23.8.93	1993	4	2	6	18					2,0
23.8	23.8.93	1993	5	2	1	37					3,0
23.8	23.8.93	1993	6	2		8					3,0
23.8	23.8.94	1994	7	3	611	908					?
23.8	23.8.94	1994	9	3	8	128					?
23.8	23.8.93	1993	C1P1	C1	1	102					2,0
23.8	23.8.93	1993	C1P2	C1		2					4,0
23.8	23.8.93	1993	C1P3	C1		15					5,0
23.8	23.8.93	1993	C1P4	C1		23					5,0
26.8	26.8.98	1998	2	1	1	13					5,0
26.8	26.8.98	1998	3	1		20					4,0
26.8	26.8.98	1998	5	2		6					5,0
26.8	26.8.98	1998	6	2		46					5,0
26.8	26.8.93	1993	Bo	3		1					2,0
28.8	28.8.93	1993	2	1		1					1,0
28.8	28.8.93	1993	4	2		3					2,0
28.8	28.8.93	1993	5	2		13					3,0
28.8	28.8.96	1996	5	2		14					5,0
28.8	28.8.93	1993	6	2		3					3,0
28.8	28.8.96	1996	6	2		1					5,0
28.8	28.8.96	1996	7	3	1	2					2,0
28.8	28.8.96	1996	8	3	1	5					2,0
28.8	28.8.93	1993	C1P1	C1		1					1,0
28.8	28.8.93	1993	C1P3	C1		2					5,0
28.8	28.8.93	1993	C1P4	C1		16					5,0
1.9	1.9.93	1993	4	2		1					2,0
1.9	1.9.93	1993	5	2	2	22					3,0
1.9	1.9.93	1993	6	2		10					3,0
1.9	1.9.93	1993	C1P1	C1		2					1,0
1.9	1.9.93	1993	C1P2	C1		5					2,0
1.9	1.9.93	1993	C1P3	C1		11					4,0
1.9	1.9.93	1993	C1P4	C1		31					5,0
2.9	2.9.98	1998	2	1		11					4,0
2.9	2.9.98	1998	3	1	1	15					3,0
2.9	2.9.98	1998	5	2		5					5,0
2.9	2.9.98	1998	6	2		8					5,0
6.9	6.9.93	1993	4	2		4					1,0
6.9	6.9.93	1993	5	2	1	3					2,0
6.9	6.9.93	1993	6	2		3					2,0
6.9	6.9.93	1993	C1P2	C1		8					2,0
6.9	6.9.93	1993	C1P3	C1		78					4,0
6.9	6.9.93	1993	C1P4	C1		30					5,0
6.9	6.9.93	1993	In	2		9					2,0
6.9	6.9.93	1993	In	3		6					2,0
10.9	10.9.96	1996	5	2		2					4,0
10.9	10.9.96	1996	7	3	3	1					2,0
10.9	10.9.96	1996	8	3		2					2,0
11.9	11.9.98	1998	2	1		52					5,0
11.9	11.9.98	1998	3	1	2	34					4,0
11.9	11.9.93	1993	5	2		8					3,0
11.9	11.9.98	1998	5	2		11					5,0
11.9	11.9.93	1993	6	2	1	4					3,0
11.9	11.9.98	1998	6	2		6					5,0
11.9	11.9.93	1993	C1P1	C1		5					5,0
11.9	11.9.93	1993	C1P2	C1		3					5,0
11.9	11.9.93	1993	C1P3	C1		30					5,0
11.9	11.9.93	1993	C1P4	C1	1	29					5,0
16.9	16.9.93	1993	5	2		2					5,0
16.9	16.9.93	1993	C1P3	C1		3					5,0
16.9	16.9.93	1993	C1P4	C1		8					5,0
21.9	21.9.95	1995	2	1	1	9					1,5
21.9	21.9.98	1998	2	1		90					5,0
21.9	21.9.98	1998	3	1	3	87					5,0
21.9	21.9.98	1998	5	2		4					5,0
21.9	21.9.98	1998	6	2	3	13					5,0
24.9	24.9.93	1993	1	1		2					2,0
24.9	24.9.93	1993	2	1	1	5					3,0
24.9	24.9.93	1993	3	1	2	2					3,0
24.9	24.9.93	1993	4	2	5	4					4,0
24.9	24.9.93	1993	5	2	1	8					5,0
24.9	24.9.93	1993	6	2		2					5,0
24.9	24.9.93	1993	C1P1	C1		10					5,0
24.9	24.9.93	1993	C1P2	C1	2	21					5,0
24.9	24.9.93	1993	C1P3	C1	11	43					5,0
24.9	24.9.93	1993	C1P4	C1	3	48					5,0
24.9	24.9.93	1993	EkIn1	3	3	1					2,0
24.9	24.9.93	1993	EkIn2	3		1					2,0
30.9	30.9.93	1993	1	1	1	1					2,0
30.9	30.9.93	1993	2	1	3	9					2,0

Appendix 3 (continued) (*Limnophyes minimus*-aggregate sensu meo).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
30.9	30.9.98	1998	2	1	1	49					5,0
30.9	30.9.93	1993	3	1		1					2,0
30.9	30.9.98	1998	3	1	6	65					5,0
30.9	30.9.93	1993	4	2	1	2					5,0
30.9	30.9.93	1993	5	2		19					5,0
30.9	30.9.96	1996	5	2	1	3					5,0
30.9	30.9.98	1998	5	2		7					5,0
30.9	30.9.93	1993	6	2		3					5,0
30.9	30.9.96	1996	6	2		1					5,0
30.9	30.9.98	1998	6	2	4	45					5,0
30.9	30.9.96	1996	7	3	5	2					2,0
30.9	30.9.96	1996	8	3	5	2					2,0
1.10	1.10.93	1993	C1P1	C1		2					5,0
1.10	1.10.93	1993	C1P2	C1	2	4					5,0
1.10	1.10.93	1993	C1P4	C1	4	32					5,0
7.10	7.10.93	1993	2	1	1	4					5,0
7.10	7.10.93	1993	4	2	2	9					5,0
7.10	7.10.93	1993	5	2	1	28					5,0
7.10	7.10.93	1993	C1P1	C1		3					5,0
7.10	7.10.93	1993	C1P2	C1		3					5,0
7.10	7.10.93	1993	C1P4	C1	1	19					5,0
7.10	7.10.93	1993	EkIn1	3	1	2					2,0
7.10	7.10.93	1993	EkIn2	3		3					2,0
7.10	7.10.93	1993	net	2	1	2					5,0
9.10	9.10.98	1998	2	1	1	4					5,0
9.10	9.10.98	1998	3	1		3					5,0
9.10	9.10.98	1998	5	2		1					5,0
9.10	9.10.98	1998	6	2	1	13					5,0
14.10	14.10.93	1993	3	1		1					5,0
14.10	14.10.93	1993	4	2		10					5,0
14.10	14.10.93	1993	5	2	1	18					5,0
14.10	14.10.93	1993	6	2		4					5,0
14.10	14.10.93	1993	C1P1	C1		2					5,0
14.10	14.10.93	1993	C1P3	C1	1	2					5,0
14.10	14.10.93	1993	C1P4	C1		11					5,0
14.10	14.10.93	1993	EkIn1	3		1					2,0
18.10	18.10.96	1996	5	2		5					5,0
18.10	18.10.96	1996	6	2		2					5,0
18.10	18.10.96	1996	7	3	8	7					2,0
18.10	18.10.96	1996	8	3	2	5					2,0
19.10	19.10.98	1998	2	1		1					5,0
19.10	19.10.98	1998	3	1	2	9					5,0
19.10	19.10.98	1998	6	2		9					5,0
25.10	25.10.93	1993	2	1		2					5,0
25.10	25.10.93	1993	4	2		7					5,0
25.10	25.10.93	1993	5	2		5					5,0
25.10	25.10.93	1993	6	2		3					5,0
25.10	25.10.93	1993	C1P1	C1		1					5,0
25.10	25.10.93	1993	C1P2	C1		5					5,0
25.10	25.10.93	1993	C1P3	C1		12					5,0
25.10	25.10.93	1993	C1P4	C1		12					5,0
1.11	1.11.96	1996	5	2		4					5,0
1.11	1.11.96	1996	7	3		1					2,0
1.11	1.11.96	1996	8	3	1	1					2,0
2.11	2.11.98	1998	2	1		4					5,0
2.11	2.11.98	1998	3	1		4					5,0
2.11	2.11.98	1998	6	2		6					5,0
10.11	10.11.93	1993	2	1		1					5,0
10.11	10.11.93	1993	3	1		1					5,0

Limnophyes minimus var. nov. sensu meo

Determination: SÆTHER 1990 (similar to *L. minimus* but virga simple. Maybe a new species. The specimens were also checked by SÆTHER and MOLLER PILLOT who agreed with me. 11 ♂♂ of this variation were also found by SCHNABEL (1999)). At the moment all specimens are still in coll. ADK.

Ecology: SCHNABEL 1999.

26.4	26.4.97	1997	6	2	1						5,0
7.5	7.5.96	1996	7	3	1						4,0

21. *Limnophyes natalensis* (KIEFFER 1914)

Determination: SÆTHER 1990 (see also section 4.3.1.2. of this study). 3 ♀♀ coll. ADK.

Ecology: High abundances of larvae in wet substrate overgrown by moss (23.9. + 25.9. 1998, Lahnberge near Marburg (Hesse, Germany), DETTINGER-KLEMM unpublished data). This material was deposited at the following locations: 10 ♂♂, 4♀♀, 17 L, 1 ♂ + Pex (PL), 1 ♂ + Pex, 2L ZMB, 1 ♂ + Pex, 1 ♀ ZSM, 137 ♂♂, 10 ♀♀, 3 ♂♂ + Pex, 2 Pex, 1 P, 20 L coll. ADK. SÆTHER 1990, SCHNABEL 1999, ORENDT 2000b, SCHNABEL & DETTINGER-KLEMM 2000.

29.6	29.6.93	1993	4	2		1					2,0
29.6	29.6.93	1993	6	2		1					4,0
7.10	7.10.93	1993	net	2		1					5,0

22. *Limnophyes pentaplastus* (KIEFFER, 1921)

Determination: SÆTHER 1990. See also section 4.3.1.2. of this study. 2 ♂♂ + 2 ♀♀ ZSM, rest coll. ADK.

Ecology: THIENEMANN 1921, CASPERS & SCHLEUTER 1986, SÆTHER 1990, SCHNABEL 1999, SCHNABEL & DETTINGER-KLEMM 2000.

10.6	10.6.98	1998	2	1		1					5,0
24.6	24.6.98	1998	C2P9	C2	0	2					5,0

Appendix 3 (continued) (*Limnophyes pentaplastus*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
25.6	25.6.98	1998	5	2		1					5,0
25.6	25.6.98	1998	6	2	1						5,0
25.6	25.6.98	1998	7	3	1	1					3,0
25.6	25.6.99	1999	1b	1		1					3,0
2.7	2.7.98	1998	5	2	1						5,0
2.7	2.7.98	1998	C2P2	C2	6	4					5,0
2.7	2.7.98	1998	C2P9	C2		1					5,0
7.7	7.7.98	1998	C2P2	C2	6	8					5,0
15.7	15.7.98	1998	C2P2	C2	5	9					5,0
21.7	21.7.98	1998	C2P2	C2	3	3					5,0
21.7	21.7.98	1998	C2P8	C2	2						5,0
18.8	18.8.98	1998	5	2	1						5,0
1.10	1.10.93	1993	C1P1	C1	1						5,0
23. *Limnophyes pumilio*											
Determination: SÆTHER 1990. 1 ♂ + 1 ♀ coll. ADK.											
Ecology: CASPERS & SCHLEUTER 1986, SÆTHER 1990.											
19.5	19.5.94	1994	6	2	1						5,0
28.5	28.5.94	1994	6	2		1					5,0
Limnophyes spec. (EATON, 1875)											
2.5	2.5.96	1996	Be	3	2	2			2		3,0
7.10	7.10.93	1993	net	2						2	5,0
24. *Metriocnemus* cf. e*urynotus* (HOLMGREN, 1883)											
Determination: SÆTHER 1989, SÆTHER 1995. 2♂♂ ZSM, rest coll. ADK.											
Ecology: THIENEMANN 1954, LEHMANN 1971, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990.											
7.7	7.7.98	1998	C2P2	C2	6						5,0
15.7	15.7.98	1998	C2P2	C2		1					5,0
Metriocnemus spec. (VAN DER WULP, 1874)											
19.5	19.5.99	1999	1b	1		1					5,0
25. *Orthocladius* spec. VAN DER WULP, 1874											
Determination: SÆTHER et al. 2000. 1L coll. ADK.											
26.6	26.6.95	1995	9	3					1		4,0
26. *Paralimnophyes hydrophilus* (GOETGHEBUER, 1921)											
Determination: BRUNDIN 1956, MOLLER PILLOT 1984b, LANGTON 1991, WANG & SÆTHER 2002 . See also section 4.3.2.1.3. 35 ♂♂ + 45 ♀♀ ZSM, rest coll. ADK.											
Ecology: KREUZER 1940, SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990, DETTINGER-KLEMM & BOHLE 1996.											
26.1	26.1.94	1994	net	1					3		5,0
26.1	26.1.94	1994	net	2					1		5,0
30.3	30.3.98	1998	3	1	1	1					5,0
30.3	30.3.98	1998	6	2	1						5,0
5.4	5.4.97	1997	3	1	6	1					5,0
7.4	7.4.98	1998	2	1	1	2					5,0
7.4	7.4.98	1998	3	1	6	7					5,0
7.4	7.4.98	1998	5	2	3	3					5,0
7.4	7.4.98	1998	6	2	3	1					5,0
7.4	7.4.98	1998	7	3		1					5,0
11.4	11.4.94	1994	1	1	10	4					5,0
11.4	11.4.94	1994	2	1	43	26					5,0
11.4	11.4.97	1997	2	1	1	1					5,0
11.4	11.4.97	1997	3	1	1	3					5,0
11.4	11.4.94	1994	6	2	1	3					5,0
11.4	11.4.94	1994	9	3	1						5,0
15.4	15.4.98	1998	2	1	5						5,0
15.4	15.4.98	1998	3	1	10	10					5,0
15.4	15.4.98	1998	5	2	3	3					5,0
15.4	15.4.98	1998	6	2	1	2					5,0
15.4	15.4.98	1998	7	3	3	1					5,0
15.4	15.4.98	1998	8	3		1					5,0
16.4	16.4.96	1996	net	1	1				1		5,0
19.4	19.4.96	1996	7	3	1						3,0
22.4	22.4.94	1994	1	1	7	1					5,0
22.4	22.4.94	1994	2	1	14	2					5,0
22.4	22.4.98	1998	2	1	1	1					5,0
22.4	22.4.98	1998	3	1	1	4					5,0
22.4	22.4.94	1994	4	2	1						5,0
22.4	22.4.98	1998	5	2	2	2					5,0
22.4	22.4.98	1998	6	2	1						5,0
22.4	22.4.94	1994	7	3	1	1					5,0
22.4	22.4.98	1998	7	3	3	1					5,0
22.4	22.4.98	1998	8	3	8	11					5,0
22.4	22.4.94	1994	9	3	3	2					5,0
23.4	23.4.96	1996	3	1	1	1					5,0
23.4	23.4.96	1996	7	3		1					3,0
23.4	23.4.96	1996	8	3	1						3,5
25.4	25.4.96	1996	7	3		2					3,0
28.4	28.4.94	1994	1	1		1					5,0
28.4	28.4.94	1994	2	1		1					5,0
28.4	28.4.94	1994	7	3		1					5,0
28.4	28.4.96	1996	8	3		3					3,0
28.4	28.4.94	1994	9	3		2					5,0
30.4	30.4.98	1998	2	1	2	7					5,0
30.4	30.4.98	1998	6	2	1	1					5,0

Appendix 3 (continued) (*Paralimnophyes hydrophilus*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
30.4	30.4.98	1998	7	3	2						5,0
30.4	30.4.98	1998	8	3	17	24					5,0
1.5	1.5.96	1996	7	3	1	1					3,0
2.5	2.5.96	1996	Be	3					2		3,0
3.5	3.5.96	1996	net	1					9	1	5,0
4.5	4.5.92	1992	2	1	1	3					5,0
6.5	6.5.94	1994	2	1	1						5,0
6.5	6.5.98	1998	7	3	7	3					5,0
9.5	9.5.95	1995	9	3		1					5,0
10.5	10.5.97	1997	3	1	11	3					5,0
12.5	12.5.95	1995	10	3		1					5,0
13.5	13.5.98	1998	3	1	4						5,0
13.5	13.5.98	1998	5	2	3	1					5,0
13.5	13.5.98	1998	6	2	2	2					5,0
13.5	13.5.98	1998	8	3	6	5					5,0
15.5	15.5.97	1997	2	1	2	9					5,0
15.5	15.5.97	1997	3	1	47	46					5,0
15.5	15.5.97	1997	5	2		3					5,0
15.5	15.5.95	1995	7	3	1	1					5,0
15.5	15.5.93	1993	net	1					1		5,0
19.5	19.5.94	1994	1	1	18	6					5,0
19.5	19.5.94	1994	2	1	35	20					5,0
19.5	19.5.94	1994	6	2	6	3					5,0
19.5	19.5.94	1994	7	3	9	14					5,0
19.5	19.5.99	1999	1b	1		1					5,0
20.5	20.5.98	1998	2	1	2	1					5,0
20.5	20.5.98	1998	3	1	21	19					5,0
20.5	20.5.98	1998	5	2	5	9					5,0
20.5	20.5.98	1998	6	2	1	5					5,0
20.5	20.5.98	1998	7	3		2					4,5
20.5	20.5.98	1998	8	3	6	2					4,0
22.5	22.5.97	1997	2	1	14	14					5,0
22.5	22.5.97	1997	3	1	24	31					5,0
22.5	22.5.97	1997	5	2		1					5,0
22.5	22.5.97	1997	6	2	1						5,0
22.5	22.5.95	1995	7	3		1					5,0
22.5	22.5.97	1997	net	1					13		5,0
24.5	24.5.96	1996	net	1					12		5,0
26.5	26.5.95	1995	7	3	13	6					5,0
27.5	27.5.98	1998	3	1	16	15					5,0
27.5	27.5.98	1998	5	2	1	4					5,0
27.5	27.5.98	1998	6	2	4	1					5,0
27.5	27.5.98	1998	7	3	2	10					5,0
27.5	27.5.98	1998	8	3	10	27					5,0
28.5	28.5.94	1994	1	1	14	11					5,0
28.5	28.5.94	1994	2	1	40	29					5,0
28.5	28.5.94	1994	4	2		3					5,0
28.5	28.5.94	1994	6	2	1	3					5,0
28.5	28.5.94	1994	7	3	6	4					5,0
28.5	28.5.94	1994	9	3	18	28					5,0
29.5	29.5.95	1995	7	3		1					5,0
30.5	30.5.97	1997	2	1	6	17					5,0
30.5	30.5.97	1997	3	1	1	1					5,0
30.5	30.5.97	1997	5	2		1					5,0
30.5	30.5.97	1997	6	2	1						5,0
30.5	30.5.97	1997	7	3	2						3,0
30.5	30.5.97	1997	8	3	23	35					3,0
31.5	31.5.95	1995	7	3	1						5,0
1.6	1.6.96	1996	3	1	1						5,0
1.6	1.6.96	1996	8	3		5					3,0
2.6	2.6.95	1995	7	3		1					5,0
3.6	3.6.98	1998	2	1	1	3					5,0
3.6	3.6.98	1998	3	1	4	4					5,0
3.6	3.6.98	1998	5	2	2	1					5,0
3.6	3.6.98	1998	6	2		5					5,0
3.6	3.6.98	1998	7	3		2					5,0
3.6	3.6.98	1998	8	3	2	4					5,0
5.6	5.6.96	1996	2	1	1						5,0
5.6	5.6.97	1997	2	1		1					5,0
5.6	5.6.96	1996	3	1	1	1					5,0
5.6	5.6.97	1997	3	1	1	1					5,0
5.6	5.6.97	1997	5	2		4					5,0
5.6	5.6.97	1997	7	3	2	3					2,0
6.6	6.6.95	1995	7	3	13	3					5,0
6.6	6.6.95	1995	9	3	1	2					5,0
8.6	8.6.95	1995	7	3	4	2					5,0
8.6	8.6.95	1995	9	3	1	4					5,0
10.6	10.6.98	1998	2	1	1	2					5,0
10.6	10.6.98	1998	3	1	3						5,0
10.6	10.6.96	1996	5	2	1						5,0
10.6	10.6.98	1998	5	2		1					5,0
10.6	10.6.98	1998	6	2	2	3					5,0
10.6	10.6.98	1998	7	3	7	3					5,0
10.6	10.6.98	1998	8	3	1	3					5,0
12.6	12.6.97	1997	6	2		1					3,0
12.6	12.6.95	1995	7	3	8	4					5,0
12.6	12.6.97	1997	8	3	18	22					2,0
12.6	12.6.95	1995	9	3	1	3					5,0
14.6	14.6.93	1993	2	1		1					3,0
15.6	15.6.94	1994	7	3	47	102					?
15.6	15.6.94	1994	9	3	9	8					?
15.6	15.6.95	1995	9	3	2	4					5,0
17.6	17.6.98	1998	2	1	1	1					5,0

Appendix 3 (continued) (*Paralimnophyes hydrophilus*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
17.6	17.6.98	1998	5	2		1					5,0
17.6	17.6.98	1998	6	2	2	2					5,0
17.6	17.6.98	1998	7	3	3	5					5,0
18.6	18.6.96	1996	2	1	1						5,0
22.6	22.6.95	1995	7	3	2	2					5,0
22.6	22.6.95	1995	9	3	2	4					5,0
25.6	25.6.98	1998	2	1	2	1					5,0
25.6	25.6.98	1998	5	2	1						5,0
25.6	25.6.98	1998	6	2	8	1					5,0
25.6	25.6.98	1998	7	3	21	22					3,0
25.6	25.6.98	1998	8	3	9	7					3,0
26.6	26.6.95	1995	7	3	1						5,0
26.6	26.6.95	1995	9	3	2	1					4,0
26.6	26.6.95	1995	10	3	2						4,0
28.6	28.6.95	1995	7	3	1	1					3,0
28.6	28.6.95	1995	9	3		1					3,0
29.6	29.6.95	1995	7	3	2	3					5,0
30.6	30.6.95	1995	7	3	1						4,0
2.7	2.7.98	1998	2	1	1						5,0
2.7	2.7.98	1998	5	2	4	2					5,0
2.7	2.7.95	1995	7	3		1					3,0
2.7	2.7.98	1998	7	3		5					3,0
2.7	2.7.98	1998	8	3		7					3,0
3.7	3.7.95	1995	7	3	1	2					5,0
5.7	5.7.95	1995	10	3	1						2,0
9.7	9.7.98	1998	2	1		1					5,0
9.7	9.7.98	1998	5	2		1					5,0
9.7	9.7.98	1998	6	2	2	1					5,0
10.7	10.7.96	1996	2	1	2						5,0
10.7	10.7.96	1996	3	1		1					5,0
11.7	11.7.95	1995	7	3		1					2,0
17.7	17.7.98	1998	3	1	1						5,0
17.7	17.7.98	1998	6	2		1					5,0
19.7	19.7.93	1993	In	1	1						2,0
19.7	19.7.93	1993	In	3	247	413					2,0
23.7	23.7.96	1996	2	1		1					2,5
24.7	24.7.98	1998	2	1	4	1					5,0
24.7	24.7.98	1998	6	2	1						5,0
26.7	26.7.95	1995	7	3	1	1					2,0
31.7	31.7.96	1996	3	1		1					3,0
3.8	3.8.98	1998	2	1	4	1					5,0
3.8	3.8.98	1998	3	1	2	1					5,0
3.8	3.8.98	1998	5	2	1	2					5,0
3.8	3.8.98	1998	6	2	5	1					5,0
10.8	10.8.98	1998	2	1	1						5,0
13.8	13.8.93	1993	6	2	1						5,0
18.8	18.8.98	1998	2	1		1					4,0
18.8	18.8.98	1998	5	2	1	1					5,0
18.8	18.8.98	1998	6	2	4	4					5,0
26.8	26.8.98	1998	2	1	1	1					5,0
26.8	26.8.98	1998	6	2	1	1					5,0
26.8	26.8.93	1993	Bo	3		1			2		2,0
2.9	2.9.98	1998	2	1	1						4,0
6.9	6.9.93	1993	C1P3	C1	1						4,0
11.9	11.9.98	1998	2	1	2						5,0
11.9	11.9.98	1998	6	2	1						5,0
16.9	16.9.93	1993	C1P4	C1	1						5,0
21.9	21.9.98	1998	2	1	6	1					5,0
30.9	30.9.98	1998	2	1	2	2					5,0
30.9	30.9.98	1998	6	2	1						5,0
7.10	7.10.93	1993	net	2					1		5,0

27. *Paraphaenocladius impensus* (WALKER, 1856)

Determination: SÆTHER & WANG 1995. 2 ♂♂ + 2 ♀♀ ZSM, rest coll. ADK.

Ecology: THIENEMANN & STRENZKE 1941, STENZKE 1950, BRUNDIN 1956, MOLLER PILLOT 1984, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990, SCHNABEL 1999.

27.5	27.5.99	1999	1c	1		1					4,0
1.7	1.7.99	1999	1c	1	1	2					2,5
8.7	8.7.99	1999	1b	1	1	1					4,0
8.7	8.7.99	1999	1c	1	4						3,0
18.7	18.7.99	1999	1c	1	2	3					2,0
21.7	21.7.93	1993	5	2	1						4,0
1.8	1.8.99	1999	3	1		1					2,0
1.8	1.8.99	1999	1b	1	2						2,0
18.8	18.8.98	1998	3	1		1					3,5
21.9	21.9.98	1998	3	1	2	2					5,0
7.10	7.10.93	1993	net	2		1					5,0

Paraphaenocladius spec. THIENEMANN, 1924

2.7	2.7.98	1998	C2P7	C2	0	2					5,0

28. *Psectrocladius cf. sordidellus* (ZETTERSTEDT, 1838)

Determination: Following WÜLKER's (1956) key, the determination seemed clear. But comparing the figures illustrating the hypopygia of *P. limbatellus* and *P. sordidellus* in PINDER 1978 a definite identification was not possible. In my collection there is a specimen of *P. edwardsi* (= *P. limbatellus)* determined by SÆTHER (SCHNABEL 1999 and SCHNABEL & DETTINGER-KLEMM 2000), which corresponds well with the description in WÜLKER 1956 and which is clearly different from the specimens of my current study. I therefore named the species *P.* cf. *sordidellus*. However, it might be possible that PINDER 1978 illustrated not *P. limbatellus* and *P. sordidellus* but two somewhat different variations of *P. sordidellus*. 3 ♂♂ + 3 ♀♀ ZSM, rest coll. ADK.

Appendix 3 (continued) (*Psectrocladius* cf. *sordidellus*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
Ecology: WÜLKER 1956, REISS 1968, FITTKAU & REISS 1978, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990, CASPERS 1991, BECKER 1995, BAZZANTI et al. 1996.											
20.5	20.5.98	1998	2	1	1						5,0
22.5	22.5.97	1997	net	1					1		5,0
5.6	5.6.97	1997	5	2					1		5,0
12.6	12.6.97	1997	2	1	1						4,5
12.6	12.6.97	1997	5	2		3					3,0
7.7	7.7.98	1998	C2P10	C2	1	0					5,0
7.7	7.7.98	1998	C2P4	C2	4	0					5,0
15.7	15.7.98	1998	C2P4	C2	4	2					5,0
16.7	16.7.96	1996	5	2	2						5,0
21.7	21.7.98	1998	C2P4	C2	5	3					5,0
23.7	23.7.96	1996	5	2	3						4,0
11.8	11.8.98	1998	C2P4	C2	2	4					5,0

29. *Pseudosmittia spec.* A

Determination: STRENZKE 1950, 1960a. The genus is currently under revision by SÆTHER & FERRINGTON (see SÆTHER & FERRINGTON 2002). The material was also inspected by LANGTON, MOLLER PILLOT and SÆTHER. 'The females are similar to *Ps. angusta* and *Ps. virgo,* the pupa is most similar to *Ps. virgo*. However, the specimens are too pale and the AR is too low for *Ps. angusta* and the AR is also too low for *Ps. virgo*' (LANGTON pers. comm.). We may be able to come to some conclusion as to its idendity when the revision of *Pseudosmittia* is eventually published. 15 ♀♀, 1 L, 1 P (all extracted with the Berlese funnel) PL, many ♀♀ ZMB, ZSM and MP, rest coll. ADK.

Ecology: STRENZKE 1950, 1960.

7.4	7.4.98	1998	2	1		1					5,0
2.5	2.5.96	1996	Be	3		15			4	1	3,0
10.5	10.5.97	1997	9	3		311					5,0
22.5	22.5.96	1996	7	3		5					3,5
22.5	22.5.97	1997	7	3		1					4,5
22.5	22.5.97	1997	9	3		47					3,0
28.5	28.5.96	1996	7	3		14					3,0
30.5	30.5.97	1997	7	3		1					3,0
30.5	30.5.97	1997	8	3		1					3,0
1.6	1.6.96	1996	7	3		52					3,0
1.6	1.6.96	1996	8	3		2					3,0
5.6	5.6.96	1996	7	3		32					2,5
5.6	5.6.97	1997	7	3		6					2,0
5.6	5.6.96	1996	8	3		1					2,5
5.6	5.6.97	1997	9	3		277					2,0
10.6	10.6.96	1996	7	3		212					3,0
10.6	10.6.96	1996	8	3		20					3,0
12.6	12.6.97	1997	7	3		3					2,0
12.6	12.6.97	1997	8	3		61					2,0
12.6	12.6.97	1997	9	3		105					2,0
14.6	14.6.96	1996	7	3		82					2,0
14.6	14.6.96	1996	8	3		76					2,0
18.6	18.6.96	1996	6	2		1					5,0
18.6	18.6.96	1996	7	3		47					2,0
18.6	18.6.96	1996	8	3		76					2,0
19.6	19.6.97	1997	7	3		5					2,0
19.6	19.6.97	1997	8	3		194					2,0
19.6	19.6.97	1997	9	3		45					2,0
26.6	26.6.96	1996	7	3		22					2,0
26.6	26.6.96	1996	8	3		76					2,0
28.6	28.6.97	1997	8	3		308					2,0
2.7	2.7.96	1996	5	2		2					5,0
2.7	2.7.98	1998	7	3		1					3,0
2.7	2.7.98	1998	8	3		2					3,0
4.7	4.7.95	1995	9	3		6					3,0
5.7	5.7.97	1997	7	3		1					2,0
5.7	5.7.97	1997	8	3		239					2,0
5.7	5.7.95	1995	9	3		140					2,0
6.7	6.7.95	1995	9	3		143					2,0
7.7	7.7.95	1995	9	3		15					2,0
8.7	8.7.95	1995	10	3		368					2,0
9.7	9.7.98	1998	7	3		9					2,5
9.7	9.7.98	1998	8	3		34					2,5
9.7	9.7.95	1995	9	3		47					1,0
10.7	10.7.96	1996	7	3		27					2,0
10.7	10.7.96	1996	8	3		162					2,0
10.7	10.7.95	1995	9	3		147					1,0
10.7	10.7.95	1995	10	3		18					1,0
17.7	17.7.98	1998	7	3		50					3,0
17.7	17.7.98	1998	8	3		42					2,5
18.7	18.7.99	1999	3	1		1					3,0
18.7	18.7.99	1999	1b	1		5					2,0
18.7	18.7.99	1999	1c	1		5					2,0
20.7	20.7.95	1995	7	3		1					2,0
23.7	23.7.96	1996	7	3		23					2,0
23.7	23.7.96	1996	8	3		1600					2,0
24.7	24.7.98	1998	7	3		331					2,0
24.7	24.7.98	1998	8	3		1291					2,0
26.7	26.7.95	1995	7	3		1					1,0
27.7	27.7.99	1999	1b	1		15					2,0
27.7	27.7.99	1999	1c	1		2					2,0
31.7	31.7.96	1996	2	1		1					2,5
1.8	1.8.99	1999	1b	1		24					2,0
1.8	1.8.99	1999	1c	1		2					2,0
3.8	3.8.98	1998	7	3		906					2,0

Appendix 3 (continued) (*Pseudosmittia* spec. A).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
3.8	3.8.98	1998	8	3		4082					2,0
6.8	6.8.96	1996	2	1		13					2,0
6.8	6.8.96	1996	7	3		6					1,0
6.8	6.8.96	1996	8	3		1934					1,0
10.8	10.8.98	1998	7	3		1526					2,0
10.8	10.8.98	1998	8	3		807					2,0
14.8	14.8.96	1996	7	3		6					2,0
14.8	14.8.96	1996	8	3		331					2,0
23.8	23.8.94	1994	7	3		402					?
23.8	23.8.94	1994	9	3		227					?
28.8	28.8.96	1996	7	3		3					2,0
28.8	28.8.96	1996	8	3		177					2,0
10.9	10.9.96	1996	8	3		188					2,0
21.9	21.9.95	1995	2	1		1					1,5
30.9	30.9.96	1996	8	3		15					2,0
18.10	18.10.96	1996	7	3		1					2,0
18.10	18.10.96	1996	8	3		21					2,0
1.11	1.11.96	1996	8	3		22					2,0

30. *Pseudosmittia conjuncta* (EDWARDS, 1929) (= *P. brachyptera* GOETGHEBUER 1934)

Determination: EDWARDS 1929, GOETGHEBUER 1940 - 50, SÆTHER & FERRINGTON 2002. The determination was confirmed by LANGTON: '*Pseudosmittia conjuncta*: this is correctly idendified, If the parthenogenetic form has not evolved so far from the bisexual to preclude sexual reproduction. On the basis of 'Lindeberg´s razor' (LINDEBERG 1971) the taxon must at the present be called *Ps. conjuncta* (parthenogenetic form)'. 64 ♀♀ PL, 42 ♀♀ ZSM, rest coll. ADK.

Ecology: No data available except those from my current study.

22.5	22.5.96	1996	7	3		42					3,5
28.5	28.5.96	1996	7	3		164					3,0
1.6	1.6.96	1996	7	3		189					3,0
5.6	5.6.96	1996	7	3		73					2,5
10.6	10.6.96	1996	7	3		64					3,0
14.6	14.6.96	1996	7	3		11					2,0
18.6	18.6.96	1996	7	3		1					2,0
26.6	26.6.96	1996	7	3		1					2,0
26.6	26.6.96	1996	8	3		1					2,0
10.7	10.7.96	1996	7	3		2					2,0
3.8	3.8.98	1998	7	3		1					2,0
3.8	3.8.98	1998	8	3		1					2,0
14.8	14.8.96	1996	8	3		1					2,0

31. *Pseudosmittia curticosta* (EDWARDS, 1929)

Determination: PINDER 1978, STRENZKE 1960c. 2 ♂♂ ZSM, 1 ♂ coll. ADK.

Ecology: STRENZKE 1960c, CASPERS & SCHLEUTER 1986. Emergence trap in spring brook near Mardorf in the vicinity of Marburg (Hesse, Germany) (2 ♂♂, 83 ♀♀coll. ADK, 1 ♂, 19 ♀♀ PL). This data indicate that there may also exist a bisexual and parthenogenetic form in *Ps. curticosta* as in other species of the genus.

14.6	14.6.93	1993	6	2	1						5,0
7.7	7.7.93	1993	4	2	1						2,0
10.7	10.7.96	1996	7	3	1						2,0

32. *Smittia* spec. A HOLMGREN, 1869

Determination: SÆTHER 1977. MOLLER PILLOT (pers. comm., translated): 'For the present, I think it could be a new species. At first glance, the females stand between *S. pratorum* and *S. terrestris*. I am currently trying to establish a key for *Smittia* females of the more common species. I may have identified such females as *S. pratorum*. I intend to study such females in more details. The problem is that a lot *Smittia* females have been incompletely and ofteninreliably described. A new species is therefore not welcome.' 127 ♀♀ coll. Rossaro, 28 ♀♀ ZSM, 125 ♀♀ ZMB, 41 ♀♀ coll. MOLLER PILLOT, rest coll. ADK.

Ecology: DETTINGER-KLEMM 1995a (as 'Orthocladiinae Weibchen Typ b'), DETTINGER-KLEMM & BOHLE 1996 (as '*Smittia* spec.').

5.4	5.4.97	1997	7	3		1					5,0
16.4	16.4.99	1999	2	1		1					5,0
9.6	9.6.93	1993	2	1		1					3,0
9.6	9.6.93	1993	3	1		1					3,0
14.6	14.6.93	1993	3	1		5					3,0
21.6	21.6.93	1993	3	1		1					2,0
21.6	21.6.93	1993	4	2		1					3,0
25.6	25.6.93	1993	2	1		2					2,0
25.6	25.6.99	1999	1c	1		1					3,0
26.6	26.6.96	1996	7	3		1					2,0
28.6	28.6.95	1995	9	3		1					3,0
29.6	29.6.93	1993	2	1		1					2,0
29.6	29.6.93	1993	3	1		11					2,0
3.7	3.7.93	1993	1	1		1					1,0
3.7	3.7.93	1993	2	1		2					1,0
3.7	3.7.93	1993	3	1		4					2,0
3.7	3.7.93	1993	4	2		3					2,0
3.7	3.7.93	1993	5	2		5					3,0
3.7	3.7.95	1995	7	3		1					5,0
7.7	7.7.93	1993	1	1		3					2,0
7.7	7.7.93	1993	3	1		2					2,0
7.7	7.7.93	1993	5	2		1					3,0
8.7	8.7.99	1999	1c	1		1					3,0
12.7	12.7.93	1993	2	1		1					1,0

Appendix 3 (continued) (*Smittia* spec. A).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
12.7	12.7.93	1993	3	1		6					2,0
12.7	12.7.93	1993	5	2		1					2,0
17.7	17.7.93	1993	2	1		5					2,0
17.7	17.7.93	1993	3	1		1					2,0
17.7	17.7.93	1993	5	2		1					3,0
17.7	17.7.95	1995	7	3		2					2,0
19.7	19.7.97	1997	2	1		1					3,0
19.7	19.7.93	1993	In	1		3					2,0
19.7	19.7.93	1993	In	2		1					2,0
19.7	19.7.93	1993	In	3		2					2,0
21.7	21.7.93	1993	1	1		1					2,0
21.7	21.7.93	1993	2	1		10					2,0
21.7	21.7.93	1993	3	1		5					2,0
21.7	21.7.93	1993	5	2		9					4,0
23.7	23.7.96	1996	2	1		7					2,5
23.7	23.7.96	1996	3	1		56					2,5
23.7	23.7.96	1996	8	3		1					2,0
26.7	26.7.93	1993	1	1		1					2,0
26.7	26.7.93	1993	2	1		33					2,0
26.7	26.7.95	1995	2	1		1					3,0
26.7	26.7.93	1993	3	1		2					2,0
26.7	26.7.93	1993	5	2		1					4,0
27.7	27.7.99	1999	2	1		1					2,5
27.7	27.7.99	1999	3	1		3					2,5
27.7	27.7.99	1999	1b	1		3					2,0
27.7	27.7.99	1999	1c	1		2					2,0
30.7	30.7.93	1993	2	1		43					2,0
30.7	30.7.93	1993	3	1		4					2,0
30.7	30.7.93	1993	5	2		2					4,0
31.7	31.7.96	1996	2	1		11					2,5
31.7	31.7.96	1996	3	1		44					3,0
1.8	1.8.99	1999	2	1		2					2,0
1.8	1.8.99	1999	3	1		1					2,0
1.8	1.8.99	1999	1b	1		1					2,0
1.8	1.8.99	1999	1c	1		2					2,0
2.8	2.8.95	1995	2	1		5					1,5
3.8	3.8.98	1998	8	3		7					2,0
4.8	4.8.93	1993	1	1		2					1,0
4.8	4.8.93	1993	2	1		6					1,0
4.8	4.8.93	1993	3	1		5					2,0
4.8	4.8.93	1993	5	2		2					5,0
5.8	5.8.97	1997	2	1		1					2,0
6.8	6.8.96	1996	2	1		1					2,0
6.8	6.8.96	1996	8	3		1					1,0
9.8	9.8.93	1993	1	1		2					1,0
9.8	9.8.93	1993	2	1		25					1,0
9.8	9.8.93	1993	3	1		2					1,0
10.8	10.8.98	1998	7	3		8					2,0
10.8	10.8.98	1998	8	3		1					2,0
13.8	13.8.93	1993	2	1		24					1,0
13.8	13.8.93	1993	3	1		2					1,0
18.8	18.8.93	1993	2	1		16					1,0
18.8	18.8.93	1993	3	1		1					1,0
18.8	18.8.98	1998	3	1		9					3,5
18.8	18.8.93	1993	4	2		2					2,0
23.8	23.8.93	1993	1	1		1					2,0
23.8	23.8.93	1993	2	1		3					2,0
23.8	23.8.93	1993	3	1		1					2,0
23.8	23.8.93	1993	5	2		1					3,0
23.8	23.8.94	1994	7	3		125					?
23.8	23.8.94	1994	9	3		81					?
26.8	26.8.98	1998	2	1		6					5,0
26.8	26.8.98	1998	3	1		55					4,0
28.8	28.8.93	1993	2	1		1					1,0
1.9	1.9.93	1993	5	2		1					3,0
2.9	2.9.98	1998	3	1		1					3,0
21.9	21.9.95	1995	2	1		102					1,5
24.9	24.9.93	1993	2	1		2					3,0
30.9	30.9.93	1993	1	1		1					2,0
30.9	30.9.93	1993	2	1		2					2,0
30.9	30.9.96	1996	7	3		1					2,0
7.10	7.10.93	1993	2	1		1					5,0
14.10	14.10.93	1993	5	2		1					5,0
18.10	18.10.96	1996	7	3		2					2,0
2.11	2.11.98	1998	6	2		1					5,0
					33. *Smittia* spec. B						
Determination: SÆTHER 1977. Different from *Smittia* spec. A. 1 ♀ ZSM.											
Ecology: Not known.											
23.7	23.7.96	1996	6	2		1					3,5
					Orthocladiinae gen. spec.						
16.4	16.4.96	1996	5	2		1					5,0
7.5	7.5.96	1996	7	3		1					4,0
15.5	15.5.95	1995	10	3		2					5,0
16.5	16.5.93	1993	2	1		1					5,0
29.5	29.5.93	1993	2	1		1					5,0
1.6	1.6.96	1996	7	3		1					3,0
6.6	6.6.93	1993	2	1		1					4,0
26.6	26.6.95	1995	10	3		1					4,0
28.6	28.6.95	1995	7	3					1		3,0
29.6	29.6.93	1993	4	2		3					2,0

Appendix 3 (continued) (Orthocladiinae gen. spec.).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
3.7	3.7.93	1993	4	2		1					2,0
3.7	3.7.93	1993	6	2		1					3,0
21.7	21.7.93	1993	5	2		1					4,0
13.8	13.8.93	1993	C1P1	C1		1					3,0
13.8	13.8.93	1993	C1P2	C1		1					5,0
13.8	13.8.93	1993	C1P3	C1		1					5,0
13.8	13.8.93	1993	C1P4	C1		1					5,0
18.8	18.8.93	1993	C1P1	C1		2					2,0
11.9	11.9.93	1993	EkIn2	3		2					2,0
16.9	16.9.93	1993	EkIn2	3		1					2,0
Chironominae/Chironomini											
34. *Chironomus annularius* (MEIGEN 1818)											
Determination: STRENZKE 1959, PINDER 1978, LINDBERG & WIEDERHOLM 1979. 1 ♂ coll. ADK.											
Ecology: KREUZER 1940, STRENZKE 1960b, KRIEGER-WOLF & WÜLKER 1971, PARMA & KREBS 1977, RYSER et al. 1978, RASMUSEN 1984, MATENA 1990, MATENA & FROUZ 2000, DETTINGER-KLEMM 1995b (very tolerant in respect to water pollution).											
2.7	2.7.98	1998	C2P8	C2	1	0					5,0
35. *Chironomus dorsalis* sensu STRENZKE (1959) and KEYL & KEYL (1959)											
Determination: See section 4.3.2.1.1.. 40 ♂♂ + 24 ♀♀ + L, P/Pex ZSM, 5 egg masses reared into L, P/Pex, ♂♂ + ♀♀ coll. VALLENDUUK (see Appendix 8 21.5 °C), rest coll. ADK.											
Ecology: KREUTZER 1940, STRENZKE 1960b, BUCK 1965, KRIEGER-WOLF & WÜLKER 1971, LEARNER & POTTER 1974, RYSER et al. 1978, MATENA 1986 & 2000, DETTINGER-KLEMM 1995a+b, 2000a+b, DETTINGER-KLEMM & BOHLE 1996.											
14.6	14.6.92	1992	2	1	3	2					5,0
17.6	17.6.98	1998	C2P10	C2	113	38					5,0
17.6	17.6.98	1998	C2P2	C2	1	0					5,0
17.6	17.6.98	1998	C2P3	C2	137	21					5,0
17.6	17.6.98	1998	C2P4	C2	72	16					5,0
17.6	17.6.98	1998	C2P7	C2	77	48					5,0
17.6	17.6.98	1998	C2P6	C2	3	2					5,0
17.6	17.6.98	1998	C2P9	C2	9	0					5,0
24.6	24.6.98	1998	C2P1	C2	21	3					5,0
24.6	24.6.98	1998	C2P10	C2	157	87					5,0
24.6	24.6.98	1998	C2P2	C2	74	51					5,0
24.6	24.6.98	1998	C2P3	C2	37	57					5,0
24.6	24.6.98	1998	C2P4	C2	36	73					5,0
24.6	24.6.98	1998	C2P5	C2	14	0					5,0
24.6	24.6.98	1998	C2P6	C2	0	3					5,0
24.6	24.6.98	1998	C2P7	C2	61	17					5,0
24.6	24.6.98	1998	C2P8	C2	78	22					5,0
24.6	24.6.98	1998	C2P9	C2	66	69					5,0
2.7	2.7.98	1998	C2P1	C2	26	13					5,0
2.7	2.7.98	1998	C2P10	C2	49	86					5,0
2.7	2.7.98	1998	C2P2	C2	55	32					5,0
2.7	2.7.98	1998	C2P3	C2	58	43					5,0
2.7	2.7.98	1998	C2P4	C2	36	37					5,0
2.7	2.7.98	1998	C2P5	C2	3	8					5,0
2.7	2.7.98	1998	C2P7	C2	98	136					5,0
2.7	2.7.98	1998	C2P8	C2	21	58					5,0
2.7	2.7.98	1998	C2P9	C2	64	49					5,0
7.7	7.7.98	1998	C2P1	C2	23	11					5,0
7.7	7.7.98	1998	C2P10	C2	32	46					5,0
7.7	7.7.98	1998	C2P2	C2	8	19					5,0
7.7	7.7.98	1998	C2P3	C2	1	32					5,0
7.7	7.7.98	1998	C2P4	C2	2	6					5,0
7.7	7.7.98	1998	C2P6	C2	5	0					5,0
7.7	7.7.98	1998	C2P7	C2	0	5					5,0
7.7	7.7.98	1998	C2P8	C2	32	5					5,0
7.7	7.7.98	1998	C2P9	C2	79	13					5,0
15.7	15.7.98	1998	C2P1	C2	23	17					5,0
15.7	15.7.98	1998	C2P10	C2	81	41					5,0
15.7	15.7.98	1998	C2P2	C2	9	4					5,0
15.7	15.7.98	1998	C2P3	C2	7	42					5,0
15.7	15.7.98	1998	C2P4	C2	5	5					5,0
15.7	15.7.98	1998	C2P6	C2	12	2					5,0
15.7	15.7.98	1998	C2P7	C2	7	3					5,0
15.7	15.7.98	1998	C2P8	C2	47	11					5,0
15.7	15.7.98	1998	C2P9	C2	77	40					5,0
16.7	16.7.92	1992	net	1	1						5,0
21.7	21.7.98	1998	C2P1	C2	29	39					5,0
21.7	21.7.98	1998	C2P10	C2	45	34					5,0
21.7	21.7.98	1998	C2P2	C2	6	10					5,0
21.7	21.7.98	1998	C2P3	C2	5	5					5,0
21.7	21.7.98	1998	C2P4	C2	15	8					5,0
21.7	21.7.98	1998	C2P5	C2	1	0					5,0
21.7	21.7.98	1998	C2P6	C2	3	2					5,0
21.7	21.7.98	1998	C2P7	C2	3	2					5,0
21.7	21.7.98	1998	C2P8	C2	16	21					5,0
21.7	21.7.98	1998	C2P9	C2	28	52					5,0
9.8	9.8.93	1993	C1P4	C1	2						5,0
11.8	11.8.98	1998	C2P4	C2	207	130					5,0
13.8	13.8.93	1993	C1P1	C1	14						3,0

Appendix 3 (continued) (*Chironomus dorsalis*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
13.8	13.8.93	1993	C1P2	C1	31	12					5,0
13.8	13.8.93	1993	C1P3	C1	20						5,0
13.8	13.8.93	1993	C1P4	C1	53	24					5,0
18.8	18.8.93	1993	C1P1	C1	19	4	1				2,0
18.8	18.8.93	1993	C1P2	C1	60	40					4,0
18.8	18.8.93	1993	C1P3	C1	145	32					5,0
18.8	18.8.93	1993	C1P4	C1	43	46					5,0
18.8	18.8.93	1993	net	2	9	4				2	4,0
23.8	23.8.93	1993	C1P2	C1	24	23					4,0
23.8	23.8.93	1993	C1P3	C1	409	217					5,0
23.8	23.8.93	1993	C1P4	C1	14	15					5,0
28.8	28.8.93	1993	C1P3	C1	253	223					5,0
28.8	28.8.93	1993	C1P4	C1	11	10					5,0
1.9	1.9.93	1993	C1P3	C1	130	165					4,0
1.9	1.9.93	1993	C1P4	C1	8	15					5,0
6.9	6.9.93	1993	C1P3	C1	72	141					4,0
6.9	6.9.93	1993	C1P4	C1	39	24					5,0
11.9	11.9.93	1993	C1P3	C1	26	72					5,0
11.9	11.9.93	1993	C1P4	C1	116	68					5,0
16.9	16.9.93	1993	C1P3	C1	2	3					5,0
16.9	16.9.93	1993	C1P4	C1	89	109					5,0
24.9	24.9.93	1993	C1P2	C1	1						5,0
24.9	24.9.93	1993	C1P3	C1	84	52					5,0
24.9	24.9.93	1993	C1P4	C1	72	99					5,0
1.10	1.10.93	1993	C1P2	C1	9	1					5,0
1.10	1.10.93	1993	C1P3	C1	12	9					5,0
1.10	1.10.93	1993	C1P4	C1	9	18					5,0
7.10	7.10.93	1993	C1P2	C1	40	29					5,0
7.10	7.10.93	1993	C1P3	C1	12	12					5,0
7.10	7.10.93	1993	C1P4	C1	3	9					5,0
14.10	14.10.93	1993	C1P2	C1	32	32					5,0
14.10	14.10.93	1993	C1P3	C1	4	5					5,0
14.10	14.10.93	1993	C1P4	C1	1	3					5,0
25.10	25.10.93	1993	C1P2	C1		1					5,0

36. *Chironomus longipes* STAEGER, 1839

Determination: PINDER 1978, SHILOVA 1980, LANGTON 1991, VALLENDUUK & MOLLER PILLOT 1999, SÆTHER et al. 2000. 3 ♂♂ + 1 ♀ ZSM, rest coll. ADK.

Ecology: HOLLESEN-KÖRBER 1984, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986.

9.6	9.6.93	1993	net	2		1					5,0
14.6	14.6.93	1993	5	2	1						5,0
21.6	21.6.93	1993	net	2	3	3					5,0
29.6	29.6.93	1993	5	2	1						4,0
29.6	29.6.93	1993	net	2	3	3				1	4,0
18.8	18.8.98	1998	3	1		1					3,5

Chironomus (cf. *Lobochironomus*) spec.

17.7	17.7.96	1996	net	2					1		5,0

37. *Chironomus luridus* STRENZKE, 1959

Determination: STRENZKE 1959, KEYL 1959, PINDER 1978, LINDBERG & WIEDERHOLM 1979, WEBB & SCHOLL 1985, VALLENDUUK & MOLLER PILLOT 1999. Without a cytological species identification based on the karyotype, the species can be only identified with certainty by the combined use of the morphological characters of the larva and of the adult male. *C. luridus* on the one hand and *C. pseudothummi/uliginosus* on the other are not clearly separable from each other in the larval stage but clearly separable as adults. 24 ♂♂, 56 ♀♀ + L, P/Pex, ♂♂, ♀♀ all reared from egg mass (see Appendix 8) ZSM, rest coll. ADK.

Ecology: STRENZKE 1960b, KRIEGER-WOLF & WÜLKER 1971, RYSER et al., 1978., FRITZ 1982b, MATENA 1986, 1990 & 2000, LEUCHS & CASERS 1988, DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996, SCHNABEL 1999.

7.5	7.5.99	1999	1c	1	1						5,0
15.5	15.5.97	1997	5	2	1						5,0
15.5	15.5.97	1997	6	2		1					5,0
19.5	19.5.99	1999	2	1	1	1					5,0
19.5	19.5.99	1999	3	1	1						5,0
19.5	19.5.99	1999	1b	1	2						5,0
19.5	19.5.99	1999	1c	1	2	1					4,0
19.5	19.5.93	1993	net	1	1						5,0
22.5	22.5.97	1997	5	2	1						5,0
22.5	22.5.97	1997	6	2	1						5,0
2.6	2.6.93	1993	1	1	1						4,0
3.6	3.6.98	1998	2	1	2						5,0
9.6	9.6.93	1993	3	1	1						3,0
9.6	9.6.93	1993	net	2	2	4				5	5,0
10.6	10.6.98	1998	5	2	2						5,0
15.6	15.6.94	1994	7	3		1					?
17.6	17.6.98	1998	5	2	4						5,0
17.6	17.6.98	1998	6	2	1						5,0
18.6	18.6.99	1999	1b	1	1						3,0
19.6	19.6.97	1997	2	1	22	8					4,0
21.6	21.6.93	1993	net	2	12	11					5,0
22.6	22.6.92	1992	2	1	2	3					5,0
22.6	22.6.92	1992	5	2	2	3					5,0
25.6	25.6.98	1998	2	1	1						5,0
25.6	25.6.98	1998	5	2	3						5,0
26.6	26.6.96	1996	2	1	3						4,5

Appendix 3 (continued) (*Chironomus lurids*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
27.6	27.6.92	1992	5	2	1	2					5,0
28.6	28.6.97	1997	2	1	7	8					5,0
28.6	28.6.97	1997	5	2		1					4,5
29.6	29.6.93	1993	net	2	11	8				1	4,0
1.7	1.7.92	1992	2	1	6	12					5,0
2.7	2.7.96	1996	2	1		3					5,0
2.7	2.7.98	1998	5	2	1						5,0
2.7	2.7.98	1998	6	2	2	1					5,0
5.7	5.7.97	1997	2	1	3	11					5,0
8.7	8.7.92	1992	2	1	13						5,0
8.7	8.7.92	1992	5	2	1						5,0
9.7	9.7.98	1998	2	1	2						5,0
9.7	9.7.98	1998	6	2	1						5,0
10.7	10.7.96	1996	2	1	8						5,0
10.7	10.7.96	1996	5	2	1						5,0
10.7	10.7.96	1996	6	2		1					5,0
11.7	11.7.97	1997	2	1		4					3,0
16.7	16.7.92	1992	2	1	3	7					5,0
16.7	16.7.96	1996	2	1	1						4,0
16.7	16.7.92	1992	5	2		1					5,0
16.7	16.7.96	1996	6	2	1						5,0
16.7	16.7.92	1992	net	1	2						5,0
17.7	17.7.98	1998	5	2	2	2					5,0
19.7	19.7.97	1997	2	1		1					3,0
20.7	20.7.92	1992	2	1	3	2					5,0
23.7	23.7.96	1996	5	2	5	3					5,0
23.7	23.7.96	1996	6	2	1						5,0
24.7	24.7.92	1992	2	1	1						5,0
24.7	24.7.98	1998	3	1	1						5,0
24.7	24.7.98	1998	6	2	1						5,0
26.7	26.7.95	1995	2	1	1	2					3,0
30.7	30.7.92	1992	2	1	1						5,0
30.7	30.7.92	1992	5	2	3						5,0
3.8	3.8.98	1998	5	2	1	1					5,0
9.8	9.8.93	1993	4	2		1					3,0
18.8	18.8.93	1993	net	2	4	4				2	4,0
23.8	23.8.93	1993	C1P4	C1		1					5,0
28.8	28.8.93	1993	C1P4	C1	3	1					5,0
1.9	1.9.93	1993	C1P4	C1	9						5,0
6.9	6.9.93	1993	C1P4	C1	32	4					5,0
10.9	10.9.96	1996	6	2	1						5,0
11.9	11.9.98	1998	5	2	1						5,0
11.9	11.9.93	1993	C1P4	C1	43	24					5,0
16.9	16.9.93	1993	C1P4	C1	22	56					5,0
24.9	24.9.93	1993	C1P3	C1	2	1					5,0
24.9	24.9.93	1993	C1P4	C1	15	52					5,0
1.10	1.10.93	1993	C1P4	C1	2	5					5,0
7.10	7.10.93	1993	C1P4	C1		1					5,0
38. *Chironomus piger STENZKE, 1959/riparius MEIGEN, 1808*											
26.6	26.6.96	1996	5	2	1						4,5
7.7	7.7.98	1998	C2P2	C2	1						5,0
21.7	21.7.98	1998	C2P1	C2	1						5,0
male phenotype *'lugubris'* sensu PINDER 1978											
24.6	24.6.98	1998	C2P1	C2	7	1					5,0
24.6	24.6.98	1998	C2P10	C2	4	1					5,0
24.6	24.6.98	1998	C2P2	C2	14	5					5,0
24.6	24.6.98	1998	C2P3	C2	6	0					5,0
24.6	24.6.98	1998	C2P5	C2	1	2					5,0
24.6	24.6.98	1998	C2P7	C2	5						5,0
2.7	2.7.98	1998	C2P1	C2	22	7					5,0
2.7	2.7.98	1998	C2P10	C2	10	6					5,0
2.7	2.7.98	1998	C2P3	C2	38	4					5,0
2.7	2.7.98	1998	C2P4	C2	16	9					5,0
2.7	2.7.98	1998	C2P5	C2	10	2					5,0
2.7	2.7.98	1998	C2P7	C2	1	1					5,0
7.7	7.7.98	1998	C2P1	C2	5	7					5,0
7.7	7.7.98	1998	C2P10	C2	11	8					5,0
7.7	7.7.98	1998	C2P3	C2	4	7					5,0
7.7	7.7.98	1998	C2P4	C2	14	5	1				5,0
7.7	7.7.98	1998	C2P5	C2	4	2					5,0
7.7	7.7.98	1998	C2P7	C2	1	1					5,0

Determination: KEYL & STRENZKE 1956, STRENZKE 1959, KEYL, 1959, PINDER 1978, LINDBERG & WIEDERHOLM 1979, WEBB & SCHOLL 1985, VALLENDUUK & MOLLER PILLOT 1999. Without a cytological species identification based on the karyotype, *C. piger* and *C. riparius* are not separable from each other, not even by the combined use of the morphological characters of the larva and of the adult male. Three specimens seemed to belong to *C. lugubris for* which the karyotype has not yet been described. This could therefore be a dark variant of *C. riparius/piger*. Generally, the males of *C. riparius/piger* can be distinguished from males of *C. luridus* and *C. pseudotummi*-agg. by the patterns and intensity of colouration. In combination with the larval characters this identification (C. riparius/piger) is absolutely clear. 1 ♂ + L, P/Pex, ♂♂, ♀♀ all reared from egg mass ZSM, rest coll. ADK.

Ecology: STRENZKE 1960b, KRIEGER-WOLF & WÜLKER 1971, SCHARF 1972, PARMA & KREBS 1977, RYSER et al., 1978., RASMUSEN 1984, CASPERS & SCHLEUTER 1986, MATENA 1986, 1990 & 2000.

Appendix 3 (continued) (*Chironomus piger/riparius* phaenotype *'piger'*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
7.7	7.7.98	1998	C2P8	C2		3					5,0
15.7	15.7.98	1998	C2P1	C2	13	12					5,0
15.7	15.7.98	1998	C2P10	C2	12	9					5,0
15.7	15.7.98	1998	C2P2	C2	3	3					5,0
15.7	15.7.98	1998	C2P3	C2	4	14					5,0
15.7	15.7.98	1998	C2P4	C2	7	14					5,0
15.7	15.7.98	1998	C2P5	C2	11	2					5,0
15.7	15.7.98	1998	C2P6	C2	3	0					5,0
15.7	15.7.98	1998	C2P7	C2	1	5					5,0
15.7	15.7.98	1998	C2P8	C2	4	1					5,0
21.7	21.7.98	1998	C2P1	C2	12	19					5,0
21.7	21.7.98	1998	C2P10	C2	5	11					5,0
21.7	21.7.98	1998	C2P2	C2	1	2					5,0
21.7	21.7.98	1998	C2P3	C2	8	6					5,0
21.7	21.7.98	1998	C2P4	C2	5	16					5,0
21.7	21.7.98	1998	C2P5	C2	3	3					5,0
21.7	21.7.98	1998	C2P6	C2	1						5,0
21.7	21.7.98	1998	C2P8	C2	5	5					5,0
21.7	21.7.98	1998	C2P9	C2		3					5,0
11.8	11.8.98	1998	C2P4	C2	16	14					5,0
male phaenotype '*riparius*' sensu STRENZKE 1959											
17.6	17.6.98	1998	C2P4	C2	1	0					5,0
17.6	17.6.98	1998	C2P7	C2	5	0					5,0
24.6	24.6.98	1998	C2P10	C2	3						5,0
24.6	24.6.98	1998	C2P2	C2	28	8					5,0
24.6	24.6.98	1998	C2P4	C2	15	0					5,0
24.6	24.6.98	1998	C2P5	C2	5	2					5,0
24.6	24.6.98	1998	C2P7	C2	32						5,0
24.6	24.6.98	1998	C2P9	C2	8	1					5,0
2.7	2.7.98	1998	C2P1	C2	3	2					5,0
2.7	2.7.98	1998	C2P10	C2	14	4					5,0
2.7	2.7.98	1998	C2P2	C2	35	10					5,0
2.7	2.7.98	1998	C2P4	C2	53	41					5,0
2.7	2.7.98	1998	C2P5	C2	7						5,0
2.7	2.7.98	1998	C2P6	C2	13	3					5,0
2.7	2.7.98	1998	C2P7	C2	58	49					5,0
2.7	2.7.98	1998	C2P8	C2	4	5					5,0
2.7	2.7.98	1998	C2P9	C2	12	8					5,0
7.7	7.7.98	1998	C2P1	C2	2	1					5,0
7.7	7.7.98	1998	C2P10	C2	13	9					5,0
7.7	7.7.98	1998	C2P2	C2	8	7					5,0
7.7	7.7.98	1998	C2P3	C2	3						5,0
7.7	7.7.98	1998	C2P4	C2	35	41					5,0
7.7	7.7.98	1998	C2P5	C2	6	1					5,0
7.7	7.7.98	1998	C2P6	C2	4	3					5,0
7.7	7.7.98	1998	C2P7	C2	8	26					5,0
7.7	7.7.98	1998	C2P8	C2	5						5,0
7.7	7.7.98	1998	C2P9	C2	10	1					5,0
15.7	15.7.98	1998	C2P1	C2	14	2					5,0
15.7	15.7.98	1998	C2P10	C2	21	13					5,0
15.7	15.7.98	1998	C2P2	C2	1	6					5,0
15.7	15.7.98	1998	C2P3	C2	6	5					5,0
15.7	15.7.98	1998	C2P4	C2	42	37					5,0
15.7	15.7.98	1998	C2P5	C2	12	3					5,0
15.7	15.7.98	1998	C2P6	C2	24	10					5,0
15.7	15.7.98	1998	C2P7	C2	10	22					5,0
15.7	15.7.98	1998	C2P8	C2	8	4					5,0
15.7	15.7.98	1998	C2P9	C2	9	9					5,0
21.7	21.7.98	1998	C2P1	C2	14	9					5,0
21.7	21.7.98	1998	C2P10	C2	24	16					5,0
21.7	21.7.98	1998	C2P3	C2	6	9					5,0
21.7	21.7.98	1998	C2P4	C2	9	24					5,0
21.7	21.7.98	1998	C2P5	C2	11	5					5,0
21.7	21.7.98	1998	C2P6	C2	20	6					5,0
21.7	21.7.98	1998	C2P7	C2	2	5					5,0
21.7	21.7.98	1998	C2P8	C2	9	6					5,0
21.7	21.7.98	1998	C2P9	C2	6	13					5,0
11.8	11.8.98	1998	C2P4	C2	2	24					5,0
Chironomus piger/riparius phaenotypes not distiguished											
3.5	3.5.96	1996	net	1	1					1	5,0
6.5	6.5.94	1994	4	2	1						5,0
22.5	22.5.97	1997	net	1					1		5,0
5.6	5.6.96	1996	2	1	1						5,0
9.6	9.6.99	1999	1b	1	2	1					5,0
10.6	10.6.96	1996	2	1	12	1					5,0
14.6	14.6.96	1996	2	1	1	9					5,0
18.6	18.6.99	1999	1b	1		1					3,0
18.6	18.6.96	1996	w	1				1			5,0
21.6	21.6.93	1993	net	2	1						5,0
24.6	24.6.98	1998	C2P6	C2	3	0					5,0
26.6	26.6.96	1996	3	1	1						4,0
29.6	29.6.93	1993	net	2	1						4,0
2.7	2.7.96	1996	2	1	1						5,0
7.10	7.10.93	1993	net	2				1			5,0
39. *Chironomus pseudothummi STRENZKE, 1959 /uliginosus KEYL, 1960*											

Determination: STRENZKE 1959, KEYL 1960, PINDER 1978, LINDBERG & WIEDERHOLM 1979, WEBB & SCHOLL 1985, VALLENDUUK & MOLLER PILLOT 1999. Without a cytological species identification based on the karyotype, *C. pseudothummi* and *C. uliginosus* are not separable from each other,

Appendix 3 (continued) (*Chironomus pseudothummi/uliginosus*).

not even by the combined use of the morphological characters of the larva and of the adult male. Generally, the males of *C. acidophilus*, *C. pseudothummi* and *C. uliginosus (= Chironomus pseudothummi*-aggregate*)* can be distinguished from males of *C. luridus* and *C. piger/riparius* by the patterns and intensity of colouration. In combination with the larval characters, *C. acidophilus* can also be clearly excluded. The 4 specimens of the *C. pseudothummi*-agg. which were found by SCHNABEL 1999 in two different inundation pools in the meadow of the river Lahn (Marburg, Hesse, Germany), clearly differed from the specimens caught in the present investigation. Together with the ecological data provided by MATENA 2000, I think that it is most likely that 'my' *pseudothummi/uliginosus* belongs to *C. uliginosus*. 5 ♂♂, 1 ♀ ZSM, rest coll. ADK.

Ecology: STRENZKE 1960b, SMITH & YOUNG 1973, SCHLEUTER 1986, DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996, MATENA 2000.

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
24.4	24.4.99	1999	1b	1	3	3					5,0
13.5	13.5.92	1992	2	1	1						5,0
13.5	13.5.98	1998	5	2	1						5,0
19.5	19.5.99	1999	2	1		1					5,0
20.5	20.5.98	1998	5	2		1					5,0
3.6	3.6.98	1998	2	1	16						5,0
10.6	10.6.92	1992	2	1	3						5,0
10.6	10.6.98	1998	2	1	12	10					5,0
10.6	10.6.98	1998	5	2	7	3					5,0
10.6	10.6.98	1998	6	2	1						5,0
12.6	12.6.97	1997	2	1	3	2					4,5
17.6	17.6.98	1998	2	1	1						5,0
17.6	17.6.98	1998	5	2	3	9					5,0
19.6	19.6.97	1997	2	1	2	4					4,0
19.6	19.6.97	1997	6	2		1					3,0
22.6	22.6.92	1992	5	2	2	1					5,0
25.6	25.6.98	1998	2	1	1						5,0
25.6	25.6.98	1998	5	2	2						5,0
26.6	26.6.96	1996	2	1	1	1					4,5
28.6	28.6.97	1997	2	1	3	1					5,0
1.7	1.7.92	1992	2	1	1	1					5,0
2.7	2.7.96	1996	2	1	2	2					5,0
5.7	5.7.97	1997	2	1		1					5,0
5.7	5.7.97	1997	5	2	1						5,0
8.7	8.7.92	1992	2	1	4						5,0
11.7	11.7.97	1997	2	1	1						3,0
16.7	16.7.92	1992	2	1	1	1					5,0
17.7	17.7.98	1998	6	2	1	1					5,0
24.7	24.7.92	1992	2	1		1					5,0
24.7	24.7.98	1998	2	1	1	1					5,0
30.7	30.7.92	1992	2	1	2	1					5,0
26.8	26.8.98	1998	6	2	1						5,0
Chironomus pseudothummi-aggregate (see 39. *Chironomus pseudothummi/uliginosus*, comments on determination)											
15.6	15.6.94	1994	7	3	1	1					?
23.8	23.8.93	1993	C1P4	C1	2						5,0
28.8	28.8.93	1993	C1P4	C1	4	1					5,0
1.9	1.9.93	1993	C1P4	C1	5	7					5,0
6.9	6.9.93	1993	C1P4	C1	6	12					5,0
11.9	11.9.93	1993	C1P4	C1	3	6					5,0
16.9	16.9.93	1993	C1P4	C1		1					5,0
Chironomus luridus-aggregate sensu VALLENDUUK & MOLLER PILLOT 1999											
22.5	22.5.97	1997	net	1					7		5,0
11.6	11.6.96	1996	net	1					36		5,0
17.7	17.7.96	1996	net	1					25		4,0
17.7	17.7.96	1996	net	2					50		5,0
Chironomus piger/riparius/pseudothummi-aggregate											
18.6	18.6.96	1996	2	1	5	2					5,0
Chironomus spec. (MEIGEN, 1803)											
22.5	22.5.97	1997	3	1		1					5,0
22.5	22.5.97	1997	net	1					3		5,0
5.6	5.6.97	1997	5	2		1					5,0
9.6	9.6.93	1993	net	2		1			4		5,0
12.6	12.6.97	1997	5	2		1					3,0
15.6	15.5.93	1993	net	1						1	5,0
21.6	21.6.93	1993	net	2					6	6	5,0
25.6	25.6.98	1998	2	1		3					5,0
25.6	25.6.98	1998	3	1		1					5,0
25.6	25.6.98	1998	5	2		4					5,0
26.6	26.6.96	1996	2	1		1					4,5
29.6	29.6.93	1993	net	2		2			13	10	4,0
2.7	2.7.96	1996	2	1		6					5,0
2.7	2.7.98	1998	2	1		3					5,0
8.7	8.7.92	1992	2	1		22					5,0
10.7	10.7.96	1996	2	1		9					5,0
10.7	10.7.96	1996	3	1		1					5,0
16.7	16.7.96	1996	2	1		4					4,0
16.7	16.7.96	1996	3	1		1					3,5
16.7	16.7.96	1996	5	2		2					5,0
20.7	20.7.92	1992	5	2		2					5,0
24.7	24.7.98	1998	5	2		1					5,0
24.7	24.7.98	1998	6	2		1					5,0
10.8	10.8.98	1998	3	1		2					5,0
10.8	10.8.98	1998	5	2		1					

Appendix 3 (continued) (*Chironomus* spec.).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
18.8	18.8.98	1998	3	1		1					3,5
7.10	7.10.93	1993	net	2		1					5,0

40. *Dicrotendipes lobiger* (KIEFFER, 1921)

Determination: CONTERAS-LICHTENBERG 1986. 1 ♂ coll. ADK.

Ecology: CONTRERAS-LICHTENBERG 1986, MOLLER PILLOT & BUSKENS 1990, CASPERS & SCHLEUTER 1986.

23.7	23.7.96	1996	5	2	1						4,0

41. *Dicrotendipes notatus* (MEIGEN, 1818)

Determination: CONTERAS-LICHTENBERG 1986. 1 ♂ NHW, rest coll. ADK.

Ecology: CONTRERAS-LICHTENBERG 1986, MOLLER PILLOT & BUSKENS 1990, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986.

21.6	21.6.93	1993	net	2						2	5,0
19.7	19.7.93	1993	In	2	1	3					2,0
18.8	18.8.98	1998	5	2	1						5,0

Dicrotendipes spec. (KIEFFER, 1913)

30.9	30.9.98	1998	5	2		1					5,0

42. *Endochironomus tendens* (FABRICIUS, 1775)

Determination: GOETGHEBUER (1937-1954), PINDER 1978, MOLLER PILLOT 1984a, SÆTHER et al. 2000. 1 ♂ + 1 ♀ ZSM, rest coll. ADK.

Ecology: SÆTHER 1962, REISS 1968, FRITZ 1982b, HOLLESEN-KÖRBER 1984, MOLLER PILLOT 1984a, CASPERS & SCHLEUTER 1986, MOLLER PILLOT & BUSKENS 1990.

22.5	22.5.93	1993	6	2	1						5,0
29.5	29.5.93	1993	6	2	1						5,0
9.6	9.6.93	1993	5	2		2					5,0
14.6	14.6.93	1993	6	2		1					5,0
29.6	29.6.93	1993	6	2		1					4,0

Endochironomus spec. (KIEFFER, 1978)

9.6	9.6.93	1993	net	2					2		5,0
21.6	21.6.93	1993	net	2						2	5,0
29.6	29.6.93	1993	net	2		2			1	5	4,0
7.10	7.10.93	1993	net	2					3		5,0

43. *Microtendipes pedellus* (DE GEER, 1776)

Determination: PINDER 1978, GOETGHEBUER (1937-1954), SÆTHER et al. 2000. 1 ♂ ZSM, 2 ♂♂ coll. ADK.

Ecology: HOLLESEN-KÖRBER 1984, MOLLER PILLOT 1984a, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986; MOLLER PILLOT & BUSKENS 1990, HEINMÜLLER et al. 1998.

15.6	15.6.94	1994	7	3	2						?
2.8	2.8.95	1995	3	1	1						1,5

44. *Parachironomus parilis* (WALKER, 1856)

Determination: LEHMANN 1970, PINDER 1978. 2 ♂♂ + 2 ♀♀ ZSM, rest coll. ADK.

Ecology: LEHMANN 1970, CASPERS & SCHLEUTER 1986.

12.6	12.6.97	1997	5	2	6	3					3,0
12.6	12.6.97	1997	6	2	4						3,0
17.6	17.6.98	1998	2	1	1						5,0
19.6	19.6.97	1997	5	2		1					3,0
24.7	24.7.98	1998	6	2	3	2					5,0

45. *Paratendipes albimanus* (MEIGEN, 1818)

Determination: PINDER 1979, GOETGHEBUER (1937-54). The genus is in need of revision and it is likely that *P. albimanus* and *P. plebejus* should be synonymized (REISS, pers. comm.).

Ecology: THIENEMANN 1954, REISS 1968, LEHMANN 1971, WARD & CUMMINS 1978 & 1979, SCHLEUTER 1996, MOLLER PILLOT & BUSKENS 1990, CASPERS 1991, BECKER 1995, SAMIETZ 1996b, SCHÖLL & BALZER 1998, SCHNABEL 1999.

14.5	14.5.93	1993	2	1	1						5,0
15.7	15.7.98	1998	C2P9	C2	1	2					5,0

46. *Phaenopsectra punctipes* (WIEDEMANN, 1817)

Determination: PINDER 1978, SÆTHER et al. 2000. 1 ♂ (28.8.1993) missidentified as *P. flavipes* in DETTINGER-KLEMM & BOHLE 1996. 2 ♂♂ ZSM, rest coll. ADK.

Ecology: REISS 1968, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986.

2.7	2.7.98	1998	6	2	1						5,0
9.7	9.7.98	1998	5	2	1						5,0
11.7	11.7.97	1997	6	2	2						2,5
17.7	17.7.98	1998	5	2	1	1					5,0
3.8	3.8.98	1998	3	1	1						5,0
3.8	3.8.98	1998	6	2	1						5,0
18.8	18.8.98	1998	3	1	1						3,5
18.8	18.8.98	1998	5	2	1						5,0
28.8	28.8.93	1993	5	2	1						3,0

47. *Polypedilum arundinetum* (GOETGHEBUER, 1921)

Determination: PINDER 1978; SÆTHER et al. 2000. 1 ♂ coll. ADK.

Ecology: FITTKAU & REISS 1978, REISS 1984

25.6	25.6.99	1999	3	1	1						5,0

Appendix 3 (continued).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
48. *Polypedilum tritum* (Walker, 1856)/*Polypedilum uncinatum* Goetghebuer, 1921											
Determination: See section 4.3.2.1.2. L (all instars), P/Pex, ♂♂, ♀♀ ZSM, coll. Rossaro and Gotha, rest coll. ADK.											
Ecology KREUZER 1940, BRUNDIN 1947, THIENEMANN 1954, RAPP 1983, MOLLER PILLOT 1984a, CASPERS & SCHLEUTER 1986, SCHLEUTER 1986, BUSKENS 1987, 1989, BUSKENS & VERWIJMEREN 1989, MOLLER PILLOT & BUSKENS 1990, CASPERS 1991, DETTINGER-KLEMM & BOHLE 1996, HEINMÜLLER et al. 1998, DETTINGER-KLEMM 2000a+b.											
16.4	16.4.96	1996	net	1	6	5					5,0
19.4	19.4.96	1996	Bo	3	1						3,0
24.4	24.4.99	1999	1b	1	1	2					5,0
26.4	26.4.97	1997	2	1	20	5					5,0
26.4	26.4.97	1997	3	1	2						5,0
26.4	26.4.97	1997	7	3	1						5,0
28.4	28.4.94	1994	2	1	41	36					5,0
30.4	30.4.99	1999	2	1	4	1					5,0
30.4	30.4.98	1998	3	1	14	7					5,0
30.4	30.4.99	1999	3	1	1						5,0
30.4	30.4.99	1999	1b	1	15	26					5,0
30.4	30.4.99	1999	1c	1	4	6					5,0
3.5	3.5.97	1997	2	1	64	57					5,0
3.5	3.5.97	1997	3	1	7	8					5,0
3.5	3.5.96	1996	net	1					1		5,0
4.5	4.5.92	1992	2	1	8	6					5,0
4.5	4.5.96	1996	2	1	1						5,0
5.5	5.5.92	1992	2	1	13	6					5,0
5.5	5.5.92	1992	net	1					29	1	5,0
6.5	6.5.94	1994	1	1	23	28					5,0
6.5	6.5.94	1994	2	1	48	55					5,0
6.5	6.5.98	1998	2	1	28	25					5,0
6.5	6.5.98	1998	3	1	27	16					5,0
7.5	7.5.96	1996	2	1	2	1					5,0
7.5	7.5.99	1999	2	1	79	53					5,0
7.5	7.5.99	1999	3	1	8	3					5,0
7.5	7.5.99	1999	1b	1	233	156					5,0
7.5	7.5.99	1999	1c	1	58	29					5,0
9.5	9.5.95	1995	7	3	4	2					5,0
9.5	9.5.95	1995	9	3		1					5,0
10.5	10.5.97	1997	2	1	28	18					5,0
10.5	10.5.97	1997	3	1	7	6					5,0
10.5	10.5.97	1997	6	2	1						5,0
10.5	10.5.97	1997	7	3		2					5,0
13.5	13.5.92	1992	2	1	2	1					5,0
13.5	13.5.98	1998	2	1	7	16					5,0
13.5	13.5.98	1998	3	1	6	10					5,0
13.5	13.5.98	1998	5	2		1					5,0
15.5	15.5.97	1997	2	1	3	6					5,0
15.5	15.5.97	1997	3	1		1					5,0
15.5	15.5.95	1995	7	3	1	3					5,0
15.5	15.5.97	1997	8	3	2						5,0
16.5	16.5.93	1993	1	1	1						5,0
19.5	19.5.94	1994	1	1	9	5					5,0
19.5	19.5.94	1994	2	1	14	21					5,0
19.5	19.5.99	1999	2	1	26	27					5,0
19.5	19.5.99	1999	3	1	5	3					5,0
19.5	19.5.94	1994	6	2	1	1					5,0
19.5	19.5.99	1999	1b	1	218	332					5,0
19.5	19.5.99	1999	1c	1	77	103					4,0
20.5	20.5.98	1998	2	1	4	1					5,0
20.5	20.5.98	1998	6	2		1					5,0
22.5	22.5.96	1996	2	1	1	3					5,0
22.5	22.5.97	1997	2	1	1	6					5,0
22.5	22.5.96	1996	3	1	2	1					5,0
22.5	22.5.95	1995	9	3		1					5,0
24.5	24.5.96	1996	net	1					2		5,0
26.5	26.5.95	1995	7	3	2	1					5,0
26.5	26.5.95	1995	9	3	2	1					4,0
27.5	27.5.99	1999	2	1	1	2					5,0
27.5	27.5.99	1999	1b	1	11	32					4,5
27.5	27.5.99	1999	1c	1	14	25					4,0
28.5	28.5.94	1994	1	1	6	5					5,0
28.5	28.5.94	1994	2	1	2	3					5,0
28.5	28.5.94	1994	7	3	1	1					5,0
28.5	28.5.94	1994	9	3	2	3					5,0
29.5	29.5.93	1993	6	2	2						5,0
30.5	30.5.97	1997	2	1	1	1					5,0
31.5	31.5.95	1995	7	3	1						5,0
1.6	1.6.96	1996	2	1	1						5,0
1.6	1.6.96	1996	3	1	1						5,0
2.6	2.6.99	1999	3	1		1					5,0
2.6	2.6.93	1993	6	2	1						5,0
2.6	2.6.99	1999	1b	1	3	3					5,0
2.6	2.6.99	1999	1c	1		2					4,5
5.6	5.6.96	1996	2	1		1					5,0
6.6	6.6.95	1995	9	3	1						5,0
9.6	9.6.93	1993	2	1	2						3,0
9.6	9.6.93	1993	5	2	1						5,0
10.6	10.6.96	1996	2	1	1	1					5,0
10.6	10.6.98	1998	2	1	11						5,0
10.6	10.6.96	1996	3	1		2					5,0

Appendix 3 (continued) (*Polypedilum tritum*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
10.6	10.6.98	1998	3	1	5	1					5,0
12.6	12.6.97	1997	2	1	11	2					4,5
12.6	12.6.97	1997	3	1	1						4,0
14.6	14.6.93	1993	2	1	2						3,0
15.6	15.6.94	1994	7	3	1						?
17.6	17.6.98	1998	2	1	18	4					5,0
17.6	17.6.98	1998	3	1	23	19					5,0
17.6	17.6.98	1998	7	3	1						5,0
18.6	18.6.99	1999	3	1		1					5,0
18.6	18.6.99	1999	1b	1	1	3					3,0
18.6	18.6.99	1999	1c	1		2					3,0
19.6	19.6.97	1997	2	1	9	11					4,0
19.6	19.6.97	1997	3	1	2	7					3,0
21.6	21.6.93	1993	net	2		1					5,0
22.6	22.6.92	1992	2	1	4	1					5,0
22.6	22.6.95	1995	7	3	13	14					5,0
22.6	22.6.95	1995	9	3		1					5,0
24.6	24.6.98	1998	C2P9	C2	1						5,0
25.6	25.6.98	1998	2	1	47	18					5,0
25.6	25.6.99	1999	2	1	1						5,0
25.6	25.6.98	1998	3	1	85	56					5,0
25.6	25.6.98	1998	5	2	4	2					5,0
25.6	25.6.98	1998	6	2	2						5,0
25.6	25.6.98	1998	7	3	2	1					3,0
26.6	26.6.95	1995	7	3	23	24					5,0
26.6	26.6.95	1995	9	3	1	3					4,0
28.6	28.6.97	1997	2	1	12	3					5,0
28.6	28.6.97	1997	3	1	3	1					4,0
28.6	28.6.95	1995	7	3	9	10					3,0
28.6	28.6.95	1995	9	3	3						3,0
29.6	29.6.95	1995	7	3	1	5					5,0
30.6	30.6.95	1995	7	3	4	8					4,0
30.6	30.6.95	1995	9	3	1						3,0
1.7	1.7.92	1992	2	1	24	10					5,0
1.7	1.7.99	1999	2	1	1	2					4,5
1.7	1.7.99	1999	1b	1	2						2,5
2.7	2.7.98	1998	2	1	13	8					5,0
2.7	2.7.96	1996	3	1	1	1					4,0
2.7	2.7.98	1998	3	1	62	74					5,0
2.7	2.7.98	1998	5	2	4	2					5,0
2.7	2.7.98	1998	6	2	6	6					5,0
2.7	2.7.95	1995	7	3	5	79					3,0
2.7	2.7.98	1998	7	3		1					3,0
2.7	2.7.98	1998	C2P9	C2	1	2					5,0
3.7	3.7.95	1995	7	3		20					5,0
5.7	5.7.97	1997	2	1	11	13					5,0
5.7	5.7.97	1997	3	1	1	1					4,5
5.7	5.7.95	1995	7	3	1	1					3,0
6.7	6.7.95	1995	7	3	1	1					4,0
7.7	7.7.95	1995	7	3	2	2					4,0
8.7	8.7.92	1992	2	1	17	33					5,0
8.7	8.7.99	1999	2	1		1					5,0
8.7	8.7.95	1995	7	3		4					3,0
9.7	9.7.98	1998	2	1	5	3					5,0
9.7	9.7.98	1998	3	1	35	25					5,0
9.7	9.7.98	1998	5	2	4	5					5,0
9.7	9.7.98	1998	6	2	2	1					5,0
10.7	10.7.96	1996	2	1	2	2					5,0
10.7	10.7.96	1996	3	1	1						5,0
10.7	10.7.95	1995	7	3	1	2					2,0
11.7	11.7.97	1997	2	1	12	2					3,0
11.7	11.7.97	1997	3	1	1	2					3,0
11.7	11.7.97	1997	5	2		1					2,5
11.7	11.7.95	1995	7	3		6					2,0
16.7	16.7.92	1992	2	1	31	28					5,0
16.7	16.7.96	1996	2	1		1					4,0
16.7	16.7.96	1996	3	1	1	1					3,5
17.7	17.7.98	1998	2	1	6	3					5,0
17.7	17.7.98	1998	3	1	30	28					5,0
17.7	17.7.98	1998	5	2	3	1					5,0
17.7	17.7.95	1995	7	3	1	3					2,0
18.7	18.7.99	1999	2	1	4						4,0
18.7	18.7.99	1999	1b	1	1						2,0
19.7	19.7.97	1997	2	1	9	5					3,0
19.7	19.7.97	1997	5	2		1					3,0
19.7	19.7.93	1993	In	1	23	13					2,0
19.7	19.7.93	1993	In	2	1						2,0
20.7	20.7.92	1992	2	1	7	10					5,0
21.7	21.7.98	1998	C2P7	C2	1	0					5,0
21.7	21.7.98	1998	C2P8	C2	2	0					5,0
21.7	21.7.98	1998	C2P9	C2	2	0					5,0
23.7	23.7.96	1996	2	1	1						2,5
23.7	23.7.96	1996	3	1	2	4					2,5
24.7	24.7.92	1992	2	1	1	9					5,0
24.7	24.7.98	1998	2	1	6	2					5,0
24.7	24.7.98	1998	3	1	21	32					5,0
24.7	24.7.98	1998	5	2	1	3					5,0
24.7	24.7.98	1998	6	2	3						5,0
26.7	26.7.97	1997	2	1	2	1					3,0
26.7	26.7.95	1995	7	3	1	1					2,0
30.7	30.7.92	1992	2	1	9	7					5,0
31.7	31.7.96	1996	3	1	1						3,0
3.8	3.8.98	1998	2	1	2	5					5,0

Appendix 3 (continued) (*Polypedilum tritum*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
3.8	3.8.98	1998	3	1	12	15					5,0
3.8	3.8.98	1998	5	2	3	1					5,0
3.8	3.8.98	1998	6	2	1						5,0
5.8	5.8.97	1997	2	1		3					2,0
10.8	10.8.98	1998	2	1	8	2					5,0
10.8	10.8.98	1998	3	1	5	8					5,0
10.8	10.8.98	1998	5	2		1					5,0
10.8	10.8.98	1998	6	2		2					5,0
11.8	11.8.98	1998	C2P4	C2		1					5,0
18.8	18.8.98	1998	2	1	9	3					4,0
18.8	18.8.98	1998	3	1	17	8					3,5
18.8	18.8.93	1993	C1P1	C1	2						2,0
23.8	23.8.93	1993	5	2		1					3,0
23.8	23.8.93	1993	6	2	1						3,0
26.8	26.8.98	1998	2	1	2						5,0
26.8	26.8.98	1998	3	1	3	2					4,0
26.8	26.8.98	1998	5	2		1					5,0
26.8	26.8.98	1998	6	2	1						5,0
28.8	28.8.93	1993	5	2	1						3,0
1.9	1.9.93	1993	5	2		1					3,0
1.9	1.9.93	1993	6	2	1						3,0
2.9	2.9.98	1998	2	1	2						4,0
2.9	2.9.98	1998	3	1	3	1					3,0
11.9	11.9.98	1998	2	1	8	11					5,0
11.9	11.9.98	1998	3	1	2	2					4,0
21.9	21.9.98	1998	2	1		1					5,0
21.9	21.9.98	1998	3	1	1	2					5,0
1.10	1.10.93	1993	C1P4	C1	1						5,0
7.10	7.10.93	1993	C1P4	C1		6					5,0

49. Synendotendipes *impar* (WALKER, 1856)

Determination: GOETGHEBUER (1937-1954), LENZ (1954-1962), LENZ (1955), PINDER (1978), KALUGINA (1961), GRODHAUS (1987), MOLLER PILLOT 1984a, SÆTHER et al. 2000. 1 ♂ + 1 ♀ ZSM, rest coll. ADK.

Ecology: BRUNDIN 1949, REISS 1968, HOLLESEN-KÖRBER 1984, CASPERS & SCHLEUTER 1986.

30.4	30.4.99	1999	3	1	1						5,0
15.5	15.5.97	1997	6	2		1					5,0
19.5	19.5.94	1994	4	2		1					5,0
22.5	22.5.93	1993	6	2		1					5,0
22.5	22.5.97	1997	6	2		2					5,0
26.5	26.5.93	1993	6	2	1						5,0
2.6	2.6.93	1993	6	2		1					5,0
6.6	6.6.93	1993	6	2	1						5,0
9.6	9.6.93	1993	6	2	1						5,0
9.6	9.6.93	1993	net	2	1						5,0
21.6	21.6.93	1993	net	2	6	5					5,0
29.6	29.6.93	1993	net	2		2					4,0
17.7	17.7.98	1998	5	2	1						5,0
19.7	19.7.93	1993	In	2	1						2,0
24.7	24.7.98	1998	5	2	1						5,0
3.8	3.8.98	1998	5	2	2	1					5,0
3.8	3.8.98	1998	6	2	1						5,0
10.8	10.8.98	1998	5	2	1	4					5,0
18.8	18.8.98	1998	5	2	1						5,0
18.8	18.8.98	1998	6	2	1						5,0

50. Synendotendipes *lepidus* (MEIGEN, 1830)

Determination: see S. *impar*. 1 ♂ ZSM.

Ecology: CASPERS & SCHLEUTER 1986, v. d. VELDE & HIDDINK 1987, MOLLER PILLOT & BUSKENS 1990.

21.6	21.6.93	1993	net	2	1						5,0

Synendotendipes spec. *GRODHAUS, 1987*

17.7	17.7.96	1996	net	2					1		5,0

Chironomini gen. spec.

28.5	28.5.94	1994	4	2	1						5,0
2.6	2.6.93	1993	6	2		1					5,0
6.6	6.6.93	1993	6	2		1					5,0
13.8	13.8.93	1993	4	2		1					5,0
30.9	30.9.93	1993	5	2		1					5,0

Chironominae/Tanytarsini

51. *Cladotanytarsus* spec. KIEFFER, 1921

Determination: SÆTHER et al. 2000. REISS (pers. comm. translated): 'The adult male of *Cladotanytarsus* is 'standard' and I dare - as for decades - no definite determination. A revision of the genus is still to appear.' 5 ♂♂ + 5 ♀♀ ZSM, rest coll. ADK.

24.6	24.6.98	1998	C2P7	C2	1						5,0
2.7	2.7.98	1998	C2P7	C2	5	14					5,0
7.7	7.7.98	1998	C2P4	C2	4	5					5,0
7.7	7.7.98	1998	C2P7	C2	1	2					5,0
15.7	15.7.98	1998	C2P4	C2	4	0					5,0
15.7	15.7.98	1998	C2P4	C2		5					5,0
11.8	11.8.98	1998	C2P4	C2	2	2					5,0

Appendix 3 (continued).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
52. *Micropsectra lindrothi* GOETGHEBUER, 1931											
Determination: PINDER 1978, SÄWEDAL 1976. 5 ♂♂ + 5 ♀♀ ZSM, rest coll. ADK.											
Ecology: SÄWEDAL 1976, CASPERS & SCHLEUTER 1886.											
24.6	24.6.98	1998	C2P3	C2	1	0					5,0
2.7	2.7.98	1998	C2P3	C2	7	0					5,0
7.7	7.7.98	1998	C2P3	C2	1	3					5,0
7.7	7.7.98	1998	C2P4	C2	1						5,0
15.7	15.7.98	1998	C2P3	C2	4	10					5,0
15.7	15.7.98	1998	C2P4	C2	31	26					5,0
15.7	15.7.98	1998	C2P8	C2	1	0					5,0
21.7	21.7.98	1998	C2P3	C2	0	4					5,0
21.7	21.7.98	1998	C2P4	C2	6	14					5,0
21.7	21.7.98	1998	C2P8	C2	4	1					5,0
11.8	11.8.98	1998	C2P4	C2	7	7					5,0
53. *Paratanytarsus grimmii* (SCHNEIDER, 1885)											
Determination: SÆTHER 1977, LANGTON et al. 1988, LANGTON 1991. 50 ♀♀ + 4 ♀♀, 1L, 1Pex, 1P (collected from water filled tyre (Großseelheim, Hesse, Germany) on 24. 10. 1996, then reared in the lab (Table 40 p 139) and preserved on 30.12.1996) ZSM, rest coll. ADK.											
Ecology: LANGTON et al. 1988, LANGTON 1991.											
7.7	7.7.98	1998	C2P4	C2	0	4					5,0
15.7	15.7.98	1998	C2P4	C2		11					5,0
11.8	11.8.98	1998	C2P4	C2		294					5,0
54. *Paratanytarsus tenellulus* (GOETGHEBUER, 1921)											
Determination: REISS & SÄWEDAL 1981. There is a clear seasonal dimorphism in this species. Members of the first spring generation were much larger than the members of the succeeding generations. Furthermore they bore dark brown colourations on the thorax (e.g. vittae), whereas individuals that had emerged during summer were uninformingly white when alcohol preserved (alive presumably green). 5 ♂♂ + 5 ♀♀ ZSM, rest coll. ADK.											
Ecology: SÄWEDAL & LANGTON 1977, FITTKAU & REISS 1978, CASPERS & SCHLEUTER 1986.											
30.4	30.4.99	1999	3	1	1	1					5,0
7.5	7.5.99	1999	2	1		1					5,0
7.5	7.5.99	1999	3	1		1					5,0
19.5	19.5.99	1999	2	1	4	4					5,0
19.5	19.5.99	1999	3	1	5	3					5,0
10.6	10.6.98	1998	2	1	2						5,0
17.6	17.6.98	1998	2	1	1						5,0
25.6	25.6.99	1999	2	1	1	1					5,0
2.7	2.7.98	1998	6	2	1						5,0
10.7	10.7.96	1996	2	1		1					5,0
10.7	10.7.96	1996	5	2	1						5,0
19.7	19.7.97	1997	5	2	1	1					3,0
10.8	10.8.98	1998	2	1		2					5,0
10.8	10.8.98	1998	5	2	1						5,0
18.8	18.8.98	1998	2	1		2					4,0
18.8	18.8.98	1998	6	2		1					5,0
23.8	23.8.93	1993	5	2	1						3,0
26.8	26.8.98	1998	5	2		1					5,0
1.9	1.9.93	1993	5	2	1						3,0
2.9	2.9.98	1998	5	2	1						5,0
11.9	11.9.98	1998	2	1	1						5,0
11.9	11.9.98	1998	3	1	1						4,0
11.9	11.9.98	1998	5	2	1	3					5,0
11.9	11.9.98	1998	6	2	2						5,0
21.9	21.9.98	1998	6	2	1						5,0
55. *Tanytarsus buchonius* REISS & FITTKAU, 1971											
Determination: REISS & FITTKAU 1971. 26 ♂♂ + 42 ♀♀ ZSM, rest coll. ADK.											
Ecology: REISS & FITTKAU 1971, CASPERS & SCHLEUTER 1986, DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996, ORENDT 2000a+b.											
24.6	24.6.98	1998	C2P2	C2	3						5,0
24.6	24.6.98	1998	C2P9	C2	0	4					5,0
2.7	2.7.98	1998	C2P2	C2	90	38					5,0
2.7	2.7.98	1998	C2P3	C2	18	10					5,0
2.7	2.7.98	1998	C2P4	C2	25	21					5,0
2.7	2.7.98	1998	C2P7	C2	0	1					5,0
2.7	2.7.98	1998	C2P8	C2	8	1					5,0
2.7	2.7.98	1998	C2P9	C2	2	0					5,0
7.7	7.7.98	1998	C2P10	C2	1	0					5,0
7.7	7.7.98	1998	C2P2	C2	164	104					5,0
7.7	7.7.98	1998	C2P3	C2	6	2					5,0
7.7	7.7.98	1998	C2P4	C2	8	37					5,0
7.7	7.7.98	1998	C2P7	C2	3	6					5,0
7.7	7.7.98	1998	C2P8	C2	20	13					5,0
7.7	7.7.98	1998	C2P9	C2	1	3					5,0
15.7	15.7.98	1998	C2P10	C2	2	3					5,0
15.7	15.7.98	1998	C2P2	C2	49	92					5,0
15.7	15.7.98	1998	C2P3	C2	4	7					5,0
15.7	15.7.98	1998	C2P4	C2	12	23					5,0
15.7	15.7.98	1998	C2P7	C2	1	7					5,0
15.7	15.7.98	1998	C2P8	C2	4	13					5,0
15.7	15.7.98	1998	C2P9	C2	4	5					5,0
21.7	21.7.98	1998	C2P1	C2	1	0					5,0
21.7	21.7.98	1998	C2P10	C2	6	0					5,0
21.7	21.7.98	1998	C2P2	C2	19	7					5,0
21.7	21.7.98	1998	C2P3	C2	0	3					5,0

Appendix 3 (continued) (*Tanytarsus buchonius*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
21.7	21.7.98	1998	C2P4	C2	3	2					5,0
21.7	21.7.98	1998	C2P8	C2	9	4					5,0
21.7	21.7.98	1998	C2P9	C2	13	19					5,0
11.8	11.8.98	1998	C2P4	C2	151	135					5,0
28.8	28.8.93	1993	C1P4	C1	1						5,0
1.9	1.9.93	1993	C1P4	C1		1					5,0
6.9	6.9.93	1993	C1P4	C1	5	4					5,0
11.9	11.9.93	1993	C1P4	C1	18	29					5,0
16.9	16.9.93	1993	C1P4	C1	8	13					5,0
24.9	24.9.93	1993	C1P2	C1		1					5,0
24.9	24.9.93	1993	C1P4	C1	9	12					5,0
1.10	1.10.93	1993	C1P2	C1	1	1					5,0
1.10	1.10.93	1993	C1P4	C1	2	3					5,0
7.10	7.10.93	1993	C1P2	C1	2	4					5,0
14.10	14.10.93	1993	C1P2	C1	4	2					5,0
14.10	14.10.93	1993	C1P4	C1	1	1					5,0
25.10	25.10.93	1993	C1P3	C1		1					5,0
25.10	25.10.93	1993	C1P4	C1		1					5,0
				56. *Tanytarsus eminulus* (WALKER, 1856)							
Determination: FITTKAU & REISS 1971, determination checked by F. REISS. 1 ♂ coll. ADK.											
Ecology: REISS & FITTKAU 1971, CASPERS & SCHLEUTER 1986.											
15.6	15.6.94	1994	7	3	1						?
				57. *Tanytarsus usmaensis* PAGAST, 1931							
Determination: FITTKAU & REISS 1971, determination checked by F. REISS. 1 ♂ coll. ADK.											
Ecology: REIS & FITTKAU 1971, FITTKAU & REISS 1978, CASPERS & SCHLEUTER 1986, HEINMÜLLER et al. 1998.											
12.7	12.7.93	1993	3	1	1						2,0
				Tanytarsus spec. (VAN DER VULP, 1874)							
15.4	15.4.98	1998	2	1		1					5,0
24.6	24.6.98	1998	C2P4	C2	0	4					5,0
25.6	25.6.98	1998	3	1		1					5,0
				Tanytarsini gen. spec.							
30.5	30.5.97	1997	6	2		1					5,0
19.7	19.7.93	1993	In	2		1					2,0
				Chironominae gen. spec.							
15.5	15.5.96	1996	2		1	1					5,0
16.5	16.5.93	1993	2	1		1					5,0
15.6	15.6.94	1994	7	3		5					?
7.7	7.7.98	1998	C2P8	C2	0	1					5,0
10.7	10.7.95	1995	10	3	1						1,0
11.7	11.7.95	1995	7	3		1					2,0
19.7	19.7.93	1993	Bo	3					8		2,0
6.9	6.9.93	1993	1	1		1					1,0
				Culicidae (this family is only listed for the colonizing experiment 1998 (= C2)							
				1. *Culex pipiens* LINNAEUS, 1758 (only males)							
11.6	11.6.98	1998	C2P4	C2	77	0					5,0
11.6	11.6.98	1998	C2P9	C2	45	0					5,0
17.6	17.6.98	1998	C2P1	C2	6	0					5,0
17.6	17.6.98	1998	C2P10	C2	1	0					5,0
17.6	17.6.98	1998	C2P8	C2	12	0					5,0
17.6	17.6.98	1998	C2P9	C2	28	0					5,0
2.7	2.7.98	1998	C2P6	C2	178	0					5,0
2.7	2.7.98	1998	C2P7	C2	12	0					5,0
2.7	2.7.98	1998	C2P9	C2	2	0					5,0
7.7	7.7.98	1998	C2P10	C2	3	0					5,0
7.7	7.7.98	1998	C2P5	C2	4	0					5,0
7.7	7.7.98	1998	C2P6	C2	38	0					5,0
7.7	7.7.98	1998	C2P7	C2	11	0					5,0
15.7	15.7.98	1998	C2P10	C2	23	0					5,0
15.7	15.7.98	1998	C2P4	C2	1	0					5,0
15.7	15.7.98	1998	C2P6	C2	5	0					5,0
15.7	15.7.98	1998	C2P7	C2	60	0					5,0
15.7	15.7.98	1998	C2P8	C2	3	0					5,0
21.7	21.7.98	1998	C2P10	C2	4	0					5,0
21.7	21.7.98	1998	C2P5	C2	2	0					5,0
21.7	21.7.98	1998	C2P7	C2	3	0					5,0
21.7	21.7.98	1998	C2P8	C2	1	0					5,0
21.7	21.7.98	1998	C2P9	C2	1	0					5,0
				2. *Culex torrentium* MARTINI, 1924 (only males)							
11.6	11.6.98	1998	C2P5	C2	1	0					5,0
17.6	17.6.98	1998	C2P1	C2	57	0					5,0
17.6	17.6.98	1998	C2P10	C2	8	0					5,0
17.6	17.6.98	1998	C2P5	C2	8	0					5,0
17.6	17.6.98	1998	C2P6	C2	3	0					5,0
17.6	17.6.98	1998	C2P9	C2	41	0					5,0
24.6	24.6.98	1998	C2P1	C2	58	0					5,0
24.6	24.6.98	1998	C2P2	C2	12	0					5,0
24.6	24.6.98	1998	C2P4	C2	63	0					5,0
24.6	24.6.98	1998	C2P5	C2	72	0					5,0
24.6	24.6.98	1998	C2P6	C2	28	0					5,0
24.6	24.6.98	1998	C2P9	C2	43	0					5,0
2.7	2.7.98	1998	C2P1	C2	42	0					5,0
2.7	2.7.98	1998	C2P10	C2	97	0					5,0
2.7	2.7.98	1998	C2P2	C2	26	0					5,0
2.7	2.7.98	1998	C2P3	C2	9	0					5,0
2.7	2.7.98	1998	C2P4	C2	2	0					5,0
2.7	2.7.98	1998	C2P6	C2	48	0					5,0
2.7	2.7.98	1998	C2P7	C2	58	0					5,0
2.7	2.7.98	1998	C2P8	C2	6	0					5,0

Appendix 3 (continued) (*Culex torrentium*).

Date 1	Date 2	Year	Site/method	Pool	♂	♀	G	M	L	P/Pex	Humidity
2.7	2.7.98	1998	C2P9	C2	21	0					5,0
7.7	7.7.98	1998	C2P1	C2	23	0					5,0
7.7	7.7.98	1998	C2P10	C2	18	0					5,0
7.7	7.7.98	1998	C2P3	C2	4	0					5,0
7.7	7.7.98	1998	C2P4	C2	6	0					5,0
7.7	7.7.98	1998	C2P5	C2	9	0					5,0
7.7	7.7.98	1998	C2P6	C2	2						5,0
7.7	7.7.98	1998	C2P7	C2	6	0					5,0
7.7	7.7.98	1998	C2P8	C2	3	0					5,0
7.7	7.7.98	1998	C2P9	C2	26	0					5,0
15.7	15.7.98	1998	C2P1	C2	104	0					5,0
15.7	15.7.98	1998	C2P2	C2	10	0					5,0
15.7	15.7.98	1998	C2P3	C2	1	0					5,0
15.7	15.7.98	1998	C2P4	C2	7	0					5,0
15.7	15.7.98	1998	C2P5	C2	14	0					5,0
15.7	15.7.98	1998	C2P7	C2	43	0					5,0
15.7	15.7.98	1998	C2P8	C2	4	0					5,0
15.7	15.7.98	1998	C2P9	C2	31	0					5,0
21.7	21.7.98	1998	C2P1	C2	31	0					5,0
21.7	21.7.98	1998	C2P3	C2	6	0					5,0
21.7	21.7.98	1998	C2P4	C2	7	0					5,0
21.7	21.7.98	1998	C2P5	C2	8	0					5,0
21.7	21.7.98	1998	C2P7	C2	35	0					5,0
21.7	21.7.98	1998	C2P9	C2	7	0					5,0
11.8	11.8.98	1998	C2P4	C2	7						5,0
					Culex torrentium/*pipiens* females						
11.6	11.6.98	1998	C2P4	C2	0	28					5,0
11.6	11.6.98	1998	C2P9	C2	0	14					5,0
17.6	17.6.98	1998	C2P1	C2	0	18					5,0
17.6	17.6.98	1998	C2P10	C2	0	9					5,0
17.6	17.6.98	1998	C2P4	C2	0	21					5,0
17.6	17.6.98	1998	C2P5	C2	0	3					5,0
17.6	17.6.98	1998	C2P6	C2	0	1					5,0
17.6	17.6.98	1998	C2P8	C2	0	5					5,0
17.6	17.6.98	1998	C2P9	C2	0	20					5,0
24.6	24.6.98	1998	C2P1	C2	0	74					5,0
24.6	24.6.98	1998	C2P2	C2	0	6					5,0
24.6	24.6.98	1998	C2P4	C2	0	37					5,0
24.6	24.6.98	1998	C2P5	C2	0	26					5,0
24.6	24.6.98	1998	C2P6	C2	0	2					5,0
24.6	24.6.98	1998	C2P9	C2	0	44					5,0
2.7	2.7.98	1998	C2P1	C2	0	85					5,0
2.7	2.7.98	1998	C2P10	C2	0	29					5,0
2.7	2.7.98	1998	C2P2	C2	0	23					5,0
2.7	2.7.98	1998	C2P3	C2	0	3					5,0
2.7	2.7.98	1998	C2P4	C2	0	11					5,0
2.7	2.7.98	1998	C2P6	C2	0	98					5,0
2.7	2.7.98	1998	C2P7	C2	0	55					5,0
2.7	2.7.98	1998	C2P8	C2	0	8					5,0
2.7	2.7.98	1998	C2P9	C2	0	44					5,0
7.7	7.7.98	1998	C2P1	C2	0	18					5,0
7.7	7.7.98	1998	C2P10	C2	0	22					5,0
7.7	7.7.98	1998	C2P3	C2	0	1					5,0
7.7	7.7.98	1998	C2P4	C2	0	1					5,0
7.7	7.7.98	1998	C2P6	C2	0	62					5,0
7.7	7.7.98	1998	C2P7	C2	0	18					5,0
7.7	7.7.98	1998	C2P8	C2	0	1					5,0
7.7	7.7.98	1998	C2P9	C2	0	7					5,0
15.7	15.7.98	1998	C2P1	C2	0	72					5,0
15.7	15.7.98	1998	C2P10	C2	0	18					5,0
15.7	15.7.98	1998	C2P2	C2	0	10					5,0
15.7	15.7.98	1998	C2P3	C2	0	5					5,0
15.7	15.7.98	1998	C2P4	C2	0	7					5,0
15.7	15.7.98	1998	C2P5	C2	0	13					5,0
15.7	15.7.98	1998	C2P6	C2	0	13					5,0
15.7	15.7.98	1998	C2P7	C2	0	30					5,0
15.7	15.7.98	1998	C2P8	C2	0	14					5,0
15.7	15.7.98	1998	C2P9	C2	0	45					5,0
21.7	21.7.98	1998	C2P1	C2	0	55					5,0
21.7	21.7.98	1998	C2P10	C2		3					5,0
21.7	21.7.98	1998	C2P2	C2	0	2					5,0
21.7	21.7.98	1998	C2P3	C2	0	2					5,0
21.7	21.7.98	1998	C2P4	C2	0	4					5,0
21.7	21.7.98	1998	C2P5	C2	0	12					5,0
21.7	21.7.98	1998	C2P7	C2	0	24					5,0
21.7	21.7.98	1998	C2P8	C2	0	6					5,0
21.7	21.7.98	1998	C2P9	C2	0	2					5,0
11.8	11.8.98	1998	C2P4	C2		5					5,0

Appendix 3 (continued).

Abbreviations:

Site/method: 1, 1b, 1c, 2, 3 = sites of pool 1 (Figure 9 p 42); 4, 5, 6 = sites of pool 2 (Figure 11 p 44); 7, 8, 9, 10 = sites of pool 3 (Figure 13 p 45); CxPy: C1 = colonizing exoperiment 1993 (see DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996); C2 = colonizing experiment 1998 (section 3.2.); Py = number of the colonizing pool.

Pool: 1, 2, 3 = pools 1 - 3 (section 4.1.1.); C1 + C2 = colonizing experiment 1993 (see DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996) and 1998 (section 3.2.).

♂, ♀, G, M, L, P/Pex = number of males, females, intersexes (gynander), egg masses (reared into the adults),larvae, pupae/pupal exuviae.

Humidity = grade of humidity (Table 1 p 15).

Determination:

1. the literature used for determination is listed;
2. comments on the material were often made,
3. deposition of the material:

coll. ADK = private collection of Paul-Martin Andreas Dettinger-Klemm, Plattenhof, 64560 Riedstadt-Erfelden, Germany; or: Weinbergweg 72, 70568 Stuttgart, Germany.

coll. Langton = private collection of Peter H. Langton, 5 Kylebeg Avenue, Colerain, BT52 1 JN, Northern Ireland.

coll. Moller Pillot = private collection of Henk Moller Pillot, Leyparkweg 37, 5022 AA Tilburg, The Netherlands.

coll. Murray = collection of Declan Murray, University College Dublin, Belfield, Department of Zoology, Stillorgan Road, Dublin 4, Ireland.

coll. Rossaro = collection of Bruno Rossaro, Department of Biology, Section Ecology, University of Milano, Via Celoria 26, 20133 Milano, Italy.

coll. Steinhart = private collection of Martina Steinhart, Adalbert Stifter Straße 18, 79102 Freiburg, Germany.

coll. Vallenduuk = private collection of Henk Vallenduuk, De Cock van Neerijnenstraat 9, 5482 GR Schijndel, The Netherlands.

Gotha = Museum der Natur Gotha, Parkallee 15, 99867 Gotha, Germany.

NHW = Naturhistorisches Museum Wien, 2. Zoologische Abteilung, Burgring 7, 1014 Wien, Austria.

ZMB = University of Bergen, Museum of Zoology, Muséplass 3, 5007 Bergen, Norway.

ZSM = Zoologische Staatssammlung München, Münchhausenstraße 21, 81247 München, Germany.

Ecology: literature on the species' ecology is listed, sometimes with notes on the species'ecology written by the present author.

Appendix 4. Overview of the material studied and collected for *Limnophyes asquamatus*.

Origin of specimens	I	II	III	IV	I?	Lex	L	P		Pex		♂♂			♀♀			Ind. Nr.	**Total**
	Sl	Sl	Sl	Sl	Sl	Sl	Alc	Sl	Alc	Sl	Alc	sSl	gSl	Alc	sSl	gSl	Alc		
Germany/surroundings of Marburg (Hesse)																			
Emergence pool 1																17	2	**595, 622 - 633, 1495 - 1498**	**19**
Emergence pool 2												1 ZSM				16		**594, 1384, 1399, 1499 - 1511**	**17**
Emergence pool 3													225	166		640		**542 - 593, 596 - 621, 634 - 845, 880, 851 - 879, 881 - 1321, 1385 - 1398, 1400 - 1494,**	**1031**
hand netting pool 3																3		**1524 - 1526**	**3**
Inund. exp. 1993, pool 3#												3 + 2 ZSM + 2 ZMB		26 + 36 ZSM	5 + 2 ZSM, 1 ZMB	386 + 47 ZSM	504	**1 - 449, 848 - 850**	**1014**
Berlese/soil sample p. 3		3	3	2						1♀ + 1♂B		1, + 3B + 1Sch				1		**1322; L4 - L10, L13**	**16**
⇒parth. lab rear. pool 3	17	14	46	33	30		54 + 10 ZSM	5	1	3* + 4	3* + 34 ZSM				3* + 8	138	3* + 50 ZSM	**1512 - 1516, 1523, 1527 - 1661; L14 - 94, L99 - 125, L127 - 139, L 141, L146 - 150, L155 - 167**	**456**
⇒„bisex“ lab 1996, p. 3													43		5	12		**1323 - 1383**	**60**
Colon. experiment 1993#																2	3	**846 - 847**	**5**
Colon. experiment 1998																9	2	**533 - 541**	**11**
Inund. pool Wehrda##															1	2		**527 - 529**	**3**
cut-off Sichertshausen##																3		**530 - 532**	**3**
Germany/floodplains of the "Untere Odertal" near Schwedt###. Collected and reared by Martina Steinhart																			
parth. lab cultures						4									6			**1517 - 1522; L151 - 154**	**10**
The Netherlans, collected by Henk Moller Pillot (see Appendix 5)																			
Diverse locations				4			1			2*		4	1	1	2* + 20	50	1	**450 - 526; L142 - 145**	**86**
Total	**17**	**17**	**49**	**39**	**30**	**4**	**65**	**5**	**1**	**11**	**37**	**17**	**269**	**229**	**53**	**1326**	**565**		**2734**

Comments and Abbreviations: .

Column names: **I - IV** = Instar I - IV, **I?** = not possible to determine the instar, **Lex** = larval exuviae; **L** = larva, **P** = pupae; **Pex** = pupal exuviae; **Ind. Nr**. = individual numbers of mounted adults and larvae (L); **Sl** = specimens mounted on slides; **Alc** = preserved in alcohol, **sSl** = specimens mounted singly on slides as explained in PINDER (1989), **gSl** = macerated but undisected specimens mounted in groups on slides.

Abbreviations within the cells: * = associated with the adult/pupa. **B** = private collection of Dr. Martina Steinhart (Freiburg), **Sch** = private collection of Silke Schnabel (Marburg), **ZMB** = Museum of Zoology in Bergen, **ZSM** = Zoologische Staatssammlung München. Rest of the material is located at the private collection of Andreas Dettinger-Klemm; # = see DETTINGER-KLEMM & BOHLE (1996) and Appendix 3; ## = see SCHNABEL & DETTINGER-KLEMM (2000); ### = see STEINHART (1999); ⇒ see also Tables 5 and 6 pp 23 and 24-26, respectively).

Appendix 5: Overview of the *Limnophyes* material from The Netherlands with notes by HENK MOLLER PILLOT on the localities and the material.

Date/Sample	Ind. Nr.	Specimens in the spot check
´S Herzogenbosch: Soil sample on peaty, very wet grassland that is inundated once in winter. Up to the end of May, 78 ♀♀ and no ♂♂ were reared from the wet soil of the sample. Up to September 2 further parthenogenetic generations developed within the culture vessel ⇒ **parthenogenetic** individuals.		
9.4.1995/35155	450 - 461	12 ♀♀ *L. asquamatus*
Haarsteeg: Wet border of a temporary trench with thin (33156) and thick (33199) layer of not decomposed organic material on loamy soil. The trench was located in a meadow. The material was reared from wet soil in the laboratory. 24 ♀♀ emerged from this sample (parthenogenetic ?)		
6.4.1993, 9.9.1993/33156, 33199	462 - 470	9 ♀♀ *L. asquamatus*
Tilburg: The medow 'Leyparkweg' had not been fertilized for at least 5 years but probably remains rather rich in nitrogen. The peat dries up in summer and then probably starts decomposing. There are two trenches in the meadow, which dry up in dry summers. In total more than 40 samples were taken between 1992 and 1997. The individuals were extracted/reared from the soil samples by a Tullgren funnel and in very small emergence traps (= mini-em.tr) in which a soil sample of 2.5 dm² was transferred and kept humid. When the study site was inundated, the specimens were also captured by hand netting in the shallow water on the grassland. *L. asquamatus* was frequent on places with wet soils. Two specimens were also captured from drier localities, which had been inundated (and then dried up again) after strong rainfalls a few weeks before. After the inundation of the grassland during winter and spring, the larvae were common but not numerous. After a long inundation of the grassland in spring 1995 a larval density of 100 - 200 larvae per m² was determined at the edge of the inundated area. After inundations and frost in winter 1997, only one dead larva was found. During very dry periods the species was only found in humid to wet soils of the trenches, which had dried up before. Mostly females and occasionally males were encountered. Fourteen females emerged on one occasion from a soil sample that produced a second parthenogenetic generation of > 100 females in the lab.		
29.4.1994, 2.4.1995, 9.8.1996/ 34130, 35154, 36130, 26130a	471 - 502	1 ♂ + 32 ♀♀ *L. asquamatus*
Vogelenzang: Semi-permanent pools which were located in dune valleys. The soil consisted mainly of peaty sand (pH 5-6), rather poor in nitrogen. A total of about 30 samples were taken. *L. asquamatus* had been only encountered from 7 samples with a total of 20 larvae from which 18 developed into females and none into males (parthenogenetic population ?). However on May 4, 1993 one male was caught in a hand net and was not possible to identify (no preepisternals, no anal point !) but was possibly *L. asquamatus*. The species was only found in samples near the edge of the water, except in one case where it was found in a very thick layer of mosses, 25 cm above the water level and more than one meter in distance from the water's edge.		
24.3.1993/33143b	503 - 504	2 ♀♀ with pupal exuviae *L. asquamatus*
Riethoven: Wet and humic sand that is never inundated by the adjacent (3m distance) permanent pool. Pioneer vegetation grew in the direct surroundings of the sampling site. A total of 36 ♂♂ and 13 ♀♀ was reared from this sample by mini-em. tr (see Tilburg). In the shallow water of the permanent pool also 2 larvae were found.		
8.3.1997/37121	505 - 514	2 ♂♂ + 8 ♀♀ L. asquamatus
Ospel: Bog pit (~ 10 m²) overgrown with *Sphagnum* spec. (pH 3.7 - 4.7). > 17 larvae, 9 ♀♀ and 5 ♂♂. Larvae were netted in the water and then transferred into glass vials and partly reared into the adult.		
20.2.1988, 4.3.1989/28029, 29008	515 - 119 L142 - 145	2 ♂♂, 4 ♀♀, 4 larvae *L. asquamatus,* **1♀ + 1 larva with deviant characters:** ♀ with fine and relatively many H+Dc, clearly lighter in colouration; larva with broader antenna (see Fig. 44 section 4.3.1.2.2.)⇒ **new species ?** (section 4.3.1.1.8.)
Rijsbergen: The samples were taken from the edges of shallow permanent pools, which were strongly fluctuating due to the expansion and shrinkage of water. The substrate was partly humic sand. 12 ♂♂ + 27 ♀♀ were reared in the lab from soil samples and hand nettings in the shallow water. Most specimens came from wet soils near the water's edge. But 3 ♂♂ and 3 ♀♀ were reared from a locality with humid soil and about 4 m away from the water's edge (sandy peat), which had never been flooded.		
23.7.1997/37144	520 - 526	1 ♂ + 6 ♀♀ *L. asquamatus*
Elslo: Wet gravel at the edge of a permanent forest brook. The specimens were reared by mini-em. tr (see Tilburg). Some of the specimens belong to a new species.		
15.2.1997/37115		1 ♀ *L. natalensis*, 1 ♀ *L. pentaplastus*, 2 ♂♂ + 1 ♀ *L.* spec. nov.*

Abbreviations and comments:

Column names: Date/sample = sampling date/running number of sampling by Henk Moller Pillot; **Ind. Nr.** = individual number of the mounted adults and larvae (L) in the present study; **specimens in the spot check** = number of specimens and species in the spot check, with comments of the present author.

* This is the same species I identified as *Limnophyes* spec. nov. in SCHNABEL 1999 and SCHNABEL & DETTINGER-KLEMM (2000). The species will probably be named *L. mechthildae* spec. nov..

Appendix 6: Measurements of some diagnostic characters of *P. tritum/P. uncinatum*. (see section 4.3.2.1.2.).

Nr.	Date	Box Nr.	Sex	App. ratio	Shape app. 1	Shape apex of anal point	LR	AR	WL (mm)	ThL (mm)	TL (mm)
I11		93	m	0.47	knob	rounded	1.41	1.63	2.00	0.91	3.33
I12		93	m	0.50	knob indistinct	rounded	1.30	1.63	2.05	0.91	3.38
I13		93	m	0.50	without	rounded	1.50	1.67	1.98	0.89	3.19
I14		94	m	0.58	weak fold	rounded	1.24	1.70	2.07	0.89	3.56
I15		94	m	0.50	without, ± straight (dorsal view)	rounded	1.33	1.71	2.05	0.91	3.21
I53	1.1.97	98	m	0.46			1.21	1.63	2.05	0.91	3.11
I54	1.1.97	98	m	0.66			1.35		2.03	0.89	3.04
I56	1.1.97	98	m					1.61	1.95	0.86	
I57	30.12.96	100	m	0.50			1.30	1.73	2.10	0.91	3.38
I31	4.10.97	101	m	0.60		rounded	1.33	1.83	2.32	1.01	3.61
I32	4.10.97	101	m	0.47	without, angled	expanded distally, rounded	1.29	1.83	2.30	1.04	3.71
I33	4.10.97	101	m	0.53	weak fold	rounded	1.28	1.71	2.27	1.01	3.58
I36	26.9.97	102	m	0.57	± even	expanded distally, rounded	1.35	1.87	2.27	1.01	3.36
I37	15.8.97	103	m	0.50		rounded	1.46	1.77	2.22	1.01	3.41
I70	16.12.96	104	m	0.62	sickle shaped	rounded	1.39	1.69	2.00	0.91	3.04
I71	16.12.96	104	m	0.56	angled	rounded	1.41	1.66	1.95	0.90	3.16
I72	18.12.96	105	m	0.62	± even		1.29	1,63	2.10	0.91	3.19
I75	16.12.96	106	m	0.62	± even	rounded	1.41		1.90	0.91	3.01
I76	16.12.96	106	m					1.60	1.98	0.89	
I78	18.12.96	107	m	0.65	± straight	rounded	1.40	1.66	2.05	0.89	3.04
I91	5.12.96	108	m	0.57	± even		1.49	1.55	1.75	0.79	2.72
I92	5.12.96	108	m	0.45	± even		1.41		1.65	0.82	2.84
I93	18.12.96	109	m	0.51	± even	rounded	1.53	1.58	1.56	0.74	2.54
I94	17.12.96	109	m					1.52	1.61	0.82	
I97	17.12.96	110	m	0.59	straight (dorsal view)	rounded	1.49	1.54	1.70	0.79	3.01
I100	5.12.96	111	m	0.59	± even		1.54	1.52	1.68	0.82	2.89
I108	4.12.96	112	m	0.47	constricted, angled	rounded		1.50		0.79	
I109	4.12.96	113	m	0.53	left: constricted + angled; right: even, fold	expanded distally, rounded	1.56	1.57	1.70	0.82	2.74
I110	5.12.96	113	m	0.51			1.46	1.54	1.51	0.79	2.82
I111	5.12.96	113	m				1.43		1.65	0.79	2.74
I114	17.12.96	114	m	0.45	± straight	rounded	1.68	1.43	1.51	0.77	2.77
I115	17.12.96	114	m	0.58	constricted + angled	rounded	1.50	1.50	1.68	0.79	2.71
I124	12.8.97	116	m	0.48	constricted + angled	rounded	1.46	1.58	1.70	0.82	2.62
I125	11.8.97	116	m	0.50	constricted + angled	rounded	1.41		1.65	0.82	
I126	11.8.97	116	m	0.53	constricted + angled	rounded	1.36	1.54	1.63	0.82	2.82
I127	12.8.97	116	m					1.54	1.63	0.79	2.49
I131	9.8.97	117	m	0.49	left: angled; right: ± even	rounded	1.50	1.65	1.53	0.82	2.67
I132	11.8.97	117	m	0.50	constricted + angled		1.47	1.48	1.43	0.77	2.91

Appendix 6 (continued).

Nr.	Date	Box Nr.	Sex	App. ratio	Shape app. 1	Shape apex of anal point	LR	AR	WL (mm)	ThL (mm)	TL (mm)
I135*	27.6.97	AI Sichertshausen	m	0.54	± even	rounded	1.43	1.60	2.00	0.91	
I136**	27.6.97	AI Sichertshausen	m	0.53	left: ± even (lateral view); right: ± straight (dorsal view)		1.64	1.50	1.83	0.89	
I137	12.5.97	Borkener See	m	0.75	± straight + apical bend	rounded	1.42	1.56	2.05	0.96	
I138	12.5.97	Borkener See	m	0.66	± straight + apical bend, week knob	rounded	1.52	1.73	2.05	0.94	
I140	2.9.98	Pool 1 em. trap	m	0.70	± even	rounded	1.41	1.62	1.90	0.86	
I141	24.4.99	Pool 1 em. trap	m	0.38	constricted, ± even	rounded	1.24	1.61	2.27	0.99	
I142	19.6.96	Pool 1 net. samp.	m	0.67	± even	rounded	1.56	1.61	1.80	0.77	
I143	14.6.96	Pool 1 net samp.	m	0.55	± even	pointed (lateral view)	1.51	1.53	1.85	0.89	
I139	6.5.98	Pool 2 em trap	m	0.55	left: ± even; right: apical bend	rounded	1.34	1.80	2.30	1.01	
I6		93	f				1.50		2.10	0.96	2.84
I7		93	f				1.32		2.22	0.99	2.59
I1		94	f				1.24		2.22	0.99	2.82
I2		94	f				1.23		1.53	0.89	3.09
I3		94	f				1.33		2.20	0.99	2.67
I41	27.12.96	97	f				1.49		1.75	0.77	2.05
I42	27.12.96	97	f				1.48		1.61	0.72	2.30
I43	1.1.97	98	f				1.41		1.95	0.86	2.32
I44	2.1.97	98	f				1.47		1.85	0.86	2.37
I45	3.1.97	98	f				1.39		1.85	0.86	2.07
I46	31.12.96	100	f				1.39		2.27	0.96	2.77
I47	31.12.96	100	f				1.41		2.10	0.94	2.71
I48	31.12.96	100	f				1.35		2.37	0.99	2.84
I21	16.8.97	101	f				1.26		2.47	1.01	2.72
I22	4.10.97	101	f				1.32		2.35	0.99	2.84
I23	4.10.97	101	f				1.37		2.40	1.04	2.94
I24	4.10.97	101	f				1.31		2.30	1.04	2.87
I25	4.10.97	101	f				1.31		2.40	1.09	2.72
I26	4.10.97	102	f				1.41		2.27	0.99	2.69
I27	4.10.97	102	f				1.30		2.32	1.04	2.64
I28	4.10.97	102	f				1.39		2.27	1.01	2.62
I29	4.10.97	102	f				1.33		2.27	1.01	2.79
I30	15.8.97	103	f				1.28		2.25	1.01	2.69
I61	16.12.96	104	f				1.39		1.78	0.79	2.17
I62	18.12.96	104	f				1.40		1.88	0.89	1.98
I63	18.12.96	104	f				1.47		1.61	0.86	2.00
I64	18.12.96	105	f				1.33		2.05	0.96	2.45
I65	18.12.96	105	f				1.48		1.85	0.91	2.15
I66	18.12.96	106	f				1.43		1.90	0.84	2.10
I67	18.12.96	106	f				1.52			0.79	2.10

Appendix 6 (continued).

Nr.	Date	Box Nr.	Sex	App. ratio	Shape app. 1	Shape apex of anal point	LR	AR	WL (mm)	ThL (mm)	TL (mm)
I68	18.12.96	I06	f				1.44		1.78	0.86	2.27
I69	18.12.96	I07	f				1.44		1.98	0.84	2.42
I81	17.12.96	I08	f				1.44		1.80	0.86	2.00
I82	18.12.96	I09	f				1.59		1.70	0.82	2.12
I83	18.12.96	I09	f				1.45		1.95	0.89	2.45
I84	17.12.96	I10	f				1.52		1.56	0.77	1.88
I85	18.12.96	I10	f				1.53		1.51	0.74	2.07
I86	18.12.96	I10	f				1.52		1.51	0.77	2.10
I87	18.12.96	I10	f				1.53		1.51	0.74	1.95
I88	17.12.96	I10	f				1.48		1.43	0.72	1.75
I89	17.12.96	I10	f				1.53		1.61	0.77	2.05
I101	17.12.96	I12	f				1.41		1.70	0.89	2.17
I102	4.12.96	I12	f				1.50			0.82	2.25
I103	17.12.96	I14	f				1.61		1.48	0.72	1.68
I104	17.12.96	I14	f				1.57		1.31	0.67	1.73
I105	17.12.96	I14	f				1.55		1.36	0.69	1.73
I106	17.12.96	I14	f				1.59		1.56	0.74	1.80
I107	17.12.96	I15	f				1.48		1.41	0.72	1.78
I118	12.8.97	I16	f				1.37		1.53	0.82	2.03
I120	9.8.97	I17	f				1.57		1.43	0.77	1.78
I121	9.8.97	I17	f				1.48		1.46	0.79	
I122	8.9.97	I17	f				1.57		1.36	0.74	2.05
I123	8.9.97	I17	f				1.60		1.48	0.79	

Abbreviations and comments:

Nr. = individual number; date = date of preservation.

Box Nr. = (a) number of culture vessel (see Appendix 8) and (b) sampling locality: AI Sichertshausen = temporary cut-off of the Lahn near Marburg (Hesse, Germany) (Altarm I Sichertshausen (SCHNABEL & DETTINGER-KLEMM 2000); Borkener See = lake in a former open-cast brown coal mine in Borken (Hesse, Germany) (HEINMÜLLER et al. 1998); pool 1/pool 2 em. trap/net sampling = trapped in pool 1 or 2 by emergence trap or by net sampling of larvae which were then reared into adults.

Sex: m = male; f = female.

App. ratio = appendage ratio (see section 4.3.2.1.2.).

Shape app. 1 = comments on the shape of the appendage 1: the appendage 1 may have a knob and/or fold distally or not (= without). It seemed to be more or less straight, angled, evenly bend from base to tip (= even), sickle shaped or more or less straight with stronger bend only apically (apical bend). These variations observed are partly due to different views (see comments on different shape of the left and right appendage 1). In some cases the appendage 1 was constricted from insertion of lateral seta until tip.

Shape of anal point: see section 4.3.2.1.2..

LR/AR/WL//ThL/TL = leg ratio/antennal ratio/wing length/thorax length/total length (see SÆTHER 1980).

* determined as *P. uncinatum* by F.REISS (see section 4.3.2.1.2.).

** determined as *P. tritum* by F. REISS (see section 4.3.2.1.2.).

Appendix7: Thorax length (THL), body length (BL), wing length (WL) and wing width (WW) for four species of *Chironomus* (see section 4.3.3.).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
			Chironomus dorsalis			
11.10.1996	m	9.5 °C LD	1,4	5,45	3,3	0,9
11.10.1996	m	9.5 °C LD	1,525	6,275	3,45	0,95
02.08.1996	m	16.0 °C LD	1,6	6,15	3,4	0,9
02.08.1996	m	16.0 °C LD	1,55	5,5	3,4	0,9
22.08.1997	m	13.8 °C SD	1,7	6,2	3,65	0,95
04.11.1997	m	13.8 °C SD	1,55	6	3,3	0,9
17.06.1998	m	C2P1	1,3	5,5	2,95	0
17.06.1998	m	C2P1	1,4	5,5	3,05	0,8
17.06.1998	m	C2P1	1,35	5,2	3,05	0,75
17.06.1998	m	C2P1	1,3	5	2,9	0,75
17.06.1998	m	C2P1	1,4	5,75	3	0,8
24.06.1998	m	C2P1	1,15	4,6	2,45	0,675
24.06.1998	m	C2P1	1,2	5,15	2,45	0
24.06.1998	m	C2P1	1,25	5,25	3	0,8
24.06.1998	m	C2P1	1,25	5,1	2,7	0,75
24.06.1998	m	C2P1	1,25	5,35	2,85	0,75
02.07.1998	m	C2P1	1,25	4,75	2,45	0
02.07.1998	m	C2P1	1,2	4,75	2,4	0
02.07.1998	m	C2P1	1,4		2,55	0,75
02.07.1998	m	C2P1	1,2		2,5	0
02.07.1998	m	C2P1	1,15		2,45	0
07.07.1998	m	C2P1	1,25	5	2,6	0,7
07.07.1998	m	C2P1	1,225		2,6	0,7
07.07.1998	m	C2P1	1,2	4,9	2,55	0,7
07.07.1998	m	C2P1	1,2	5	2,55	0,7
07.07.1998	m	C2P1	1,2	4,75	2,5	0,7
15.07.1998	m	C2P1	1,25		2,7	0,7
15.07.1998	m	C2P1	1,2	4,85	2,6	0
15.07.1998	m	C2P1	1,3	5,25	2,75	0,75
15.07.1998	m	C2P1	1,15	4,75	2,5	0,7
15.07.1998	m	C2P1	1,2	4,75	2,65	0,7
21.07.1998	m	C2P1	1,1		2,5	0,65
21.07.1998	m	C2P1	1,2	4,85	2,55	0,7
21.07.1998	m	C2P1	1,25	5,2	2,6	0,7
21.07.1998	m	C2P1	1,25	5,25	2,75	0
21.07.1998	m	C2P1	1,2		2,55	0,65
17.06.1998	m	C2P2	1,7	6,3	3,65	1,05
24.06.1998	m	C2P2	1,45	6,2	3,3	0
24.06.1998	m	C2P2	1,45	5,9	3,25	0,85
24.06.1998	m	C2P2	1,4		3,25	0,85
24.06.1998	m	C2P2	1,5	6	3,25	0,85
24.06.1998	m	C2P2	1,45	6	3,15	0,8
02.07.1998	m	C2P2	1,35		2,55	0
02.07.1998	m	C2P2	1,3	4,9	2,6	0,7
02.07.1998	m	C2P2	1,3		2,5	0,7
07.07.1998	m	C2P2	1,25	5,1	2,7	0,75
07.07.1998	m	C2P2	1,35		2,9	0,8
07.07.1998	m	C2P2	1,25	4,75	2,75	0
07.07.1998	m	C2P2	1,3	5,25	2,8	0,8
07.07.1998	m	C2P2	1,3		2,75	0,75
15.07.1998	m	C2P2	1,35		2,95	0,85
15.07.1998	m	C2P2	1,3	5,4	2,9	0,8
15.07.1998	m	C2P2	1,4		2,9	0,85
15.07.1998	m	C2P2	1,3		2,85	0,8
15.07.1998	m	C2P2	1,3	5,05	2,75	0,75
21.07.1998	m	C2P2	1,4		2,9	0,8
21.07.1998	m	C2P2	1,35	6,2	3,1	0,8
21.07.1998	m	C2P2	1,4	5,85	3	0,75
21.07.1998	m	C2P2	1,4	5,75	3,05	0,8
21.07.1998	m	C2P2	1,35		3	0,8
24.06.1998	m	C2P3	1,45	5,8	3,2	0,8
24.06.1998	m	C2P3	1,3	5,25	2,85	0,7
24.06.1998	m	C2P3	1,4	5,5	3	0,75
24.06.1998	m	C2P3	1,5	6,15	3,4	0,9
24.06.1998	m	C2P3	1,45	6,5	3,4	0,9
02.07.1998	m	C2P3	1,35	5,5	3	0,85
02.07.1998	m	C2P3	1,35	5,7	2,85	0,8
02.07.1998	m	C2P3	1,35	5,95	2,95	0
02.07.1998	m	C2P3	1,4	5,65	2,9	0
02.07.1998	m	C2P3	1,4	5,3	2,95	0
07.07.1998	m	C2P3	1,35	5,5	2,85	0,75
15.07.1998	m	C2P3	1,45	6,75	3,25	0,85
15.07.1998	m	C2P3	1,45	6,25	3,1	0
15.07.1998	m	C2P3	1,4	5,25	3,1	0
15.07.1998	m	C2P3	1,4	5,4	3	0
15.07.1998	m	C2P3	1,45		3,15	0,825
21.07.1998	m	C2P3	1,45	6	3,1	0,8
21.07.1998	m	C2P3	1,4		3,15	0,85
21.07.1998	m	C2P3	1,45	6,25	3,15	0
21.07.1998	m	C2P3	1,45		3,1	0,75
21.07.1998	m	C2P3	1,45	6,5	3,2	0,85
17.06.1998	m	C2P4	1,4	5,25	3,05	0

Appendix 7 (continued) (*Chironomus dorsalis*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
17.06.1998	m	C2P4	1,35	5,75	3,05	0,8
17.06.1998	m	C2P4	1,4		3	0,75
17.06.1998	m	C2P4	1,45		3,1	0,85
17.06.1998	m	C2P4	1,4	5,6	3,15	0,75
24.06.1998	m	C2P4	1,35	5,4	2,95	0
24.06.1998	m	C2P4	1,4	6,05	2,85	0
24.06.1998	m	C2P4	1,4	5,35	3,1	0
24.06.1998	m	C2P4	1,35	5,15	3,05	0
24.06.1998	m	C2P4	1,35	5,25	2,85	0
02.07.1998	m	C2P4	1,3	4,95	2,75	0,7
02.07.1998	m	C2P4	1,3	5,25	2,9	0,75
02.07.1998	m	C2P4	1,45	5,5	2,9	0
02.07.1998	m	C2P4	1,4	5,6	2,95	0
02.07.1998	m	C2P4	1,3	5,35	2,8	0
07.07.1998	m	C2P4	1,45	5,4	2,95	0
07.07.1998	m	C2P4	1,4	5,7	3	0,8
15.07.1998	m	C2P4	1,45		3,2	0,75
15.07.1998	m	C2P4	1,4	5,85	3,15	0,8
15.07.1998	m	C2P4	1,35	5,6	3,15	0,8
15.07.1998	m	C2P4	1,45		3,15	0,85
15.07.1998	m	C2P4	1,5		3,1	0,85
21.07.1998	m	C2P4	1,45	5,75	3,2	0
21.07.1998	m	C2P4	1,4	5,75	3,15	0,8
21.07.1998	m	C2P4	1,4		3,05	0
21.07.1998	m	C2P4	1,4	5,75	3,1	0,85
21.07.1998	m	C2P4	1,5	6	3,2	0,85
11.08.1998	m	C2P4	1,4	5,55	3	0
11.08.1998	m	C2P4	1,4	5,6	3	0,8
11.08.1998	m	C2P4	1,4	5,45	3	0,75
11.08.1998	m	C2P4	1,35	5,5	0	0
11.08.1998	m	C2P4	1,3	5,5	0	0
24.06.1998	m	C2P5	1,3		2,85	0,85
24.06.1998	m	C2P5	1,3	5,3	2,65	0
24.06.1998	m	C2P5	1,35	5,5	2,75	0
24.06.1998	m	C2P5	1,3	5,75	2,9	0,8
24.06.1998	m	C2P5	1,3	5,1	2,85	0,8
02.07.1998	m	C2P5	1,25		2,95	0,775
02.07.1998	m	C2P5	1,3		2,75	0
02.07.1998	m	C2P5	1,3	5,05	2,85	0,75
02.07.1998	m	C2P5	1,3		2,85	0,75
02.07.1998	m	C2P5	1,25		2,75	0,775
21.07.1998	m	C2P5	1,3		2,9	0,8
17.06.1998	m	C2P6	1,45	5,85	2,9	0,8
17.06.1998	m	C2P6	1,4		3	0
17.06.1998	m	C2P6	1,4	5,75	3,05	0,75
07.07.1998	m	C2P6	1,35		2,95	0
07.07.1998	m	C2P6	1,35		2,9	0,7
07.07.1998	m	C2P6	1,3	5	2,85	0,75
07.07.1998	m	C2P6	1,35		2,85	0,75
07.07.1998	m	C2P6	1,4	5,5	2,85	0
15.07.1998	m	C2P6	1,35	5,5	2,85	0,75
15.07.1998	m	C2P6	1,35		2,75	0,75
15.07.1998	m	C2P6	1,35	5,5	3	0,75
15.07.1998	m	C2P6	1,35		2,9	0,8
15.07.1998	m	C2P6	1,35		2,85	0,75
21.07.1998	m	C2P6	1,3		2,9	0,75
21.07.1998	m	C2P6	1,3	5,25	2,7	0,7
17.06.1998	m	C2P7	1,5	6,3	3,25	0
17.06.1998	m	C2P7	1,5	5,75	3,1	0
17.06.1998	m	C2P7	1,5	5,7	3,15	0
17.06.1998	m	C2P7	1,45	5,6	3,1	0,75
17.06.1998	m	C2P7	1,45	6,4	3,05	0,75
24.06.1998	m	C2P7	1,3		2,7	0,75
24.06.1998	m	C2P7	1,35	5,6	2,65	0,8
24.06.1998	m	C2P7	1,35		2,85	0
24.06.1998	m	C2P7	1,4		2,95	0,85
24.06.1998	m	C2P7	1,4		2,9	0,8
02.07.1998	m	C2P7	1,3	5,25	2,75	0
02.07.1998	m	C2P7	1,4	5,8	2,85	0,75
02.07.1998	m	C2P7	1,4	5,5	2,8	0,7
02.07.1998	m	C2P7	1,4	5,5	2,9	0
02.07.1998	m	C2P7	1,35	5,45	2,8	0,8
15.07.1998	m	C2P7	1,4	5,85	3,2	0,85
15.07.1998	m	C2P7	1,4	6,25	3,25	0,8
15.07.1998	m	C2P7	1,4	5,6	3,1	0,8
15.07.1998	m	C2P7	1,4	6,15	3,2	0,8
15.07.1998	m	C2P7	1,5	6	3,05	0,85
21.07.1998	m	C2P7	1,4	6	3,25	0,85
21.07.1998	m	C2P7	1,4	5,75	3,2	0,85
21.07.1998	m	C2P7	1,3	5,85	3,25	0,8
24.06.1998	m	C2P8	1,25	5	2,75	0
24.06.1998	m	C2P8	1,25	5,1	2,6	0
24.06.1998	m	C2P8	1,3		2,75	0,7
24.06.1998	m	C2P8	1,3	4,85	2,75	0
24.06.1998	m	C2P8	1,25	5,1	2,75	0,75
02.07.1998	m	C2P8	1,225	5	0	0

Appendix 7 (continued) (*Chironomus dorsalis*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
02.07.1998	m	C2P8	1,25		0	0
02.07.1998	m	C2P8	1,3		2,65	0
02.07.1998	m	C2P8	1,35	5,15	2,8	0,75
02.07.1998	m	C2P8	1,35	5,55	2,85	0
07.07.1998	m	C2P8	1,3	5,25	2,9	0
07.07.1998	m	C2P8	1,3	5,5	2,95	0
07.07.1998	m	C2P8	1,25	4,85	2,75	0,75
07.07.1998	m	C2P8	1,3	4,9	2,75	0,7
07.07.1998	m	C2P8	1,25	5	2,85	0,75
15.07.1998	m	C2P8	1,3	5	2,7	0,7
15.07.1998	m	C2P8	1,4	5,75	2,95	0,775
15.07.1998	m	C2P8	1,3	5,3	2,9	0,75
15.07.1998	m	C2P8	1,3	5,5	2,95	0,7
15.07.1998	m	C2P8	1,4	6	3	0,75
21.07.1998	m	C2P8	1,25		2,85	0,75
21.07.1998	m	C2P8	1,25	5	2,8	0,75
21.07.1998	m	C2P8	1,3	5,4	2,8	0,75
21.07.1998	m	C2P8	1,3	5,2	2,85	0,75
21.07.1998	m	C2P8	1,2	5	2,75	0,75
24.06.1998	m	C2P9	1,3	5,85	3	0,85
24.06.1998	m	C2P9	1,35		3	0,8
24.06.1998	m	C2P9	1,35	5,8	2,95	0,85
24.06.1998	m	C2P9	1,3	5,6	2,9	0,8
24.06.1998	m	C2P9	1,35	5,5	3	0,8
02.07.1998	m	C2P9	1,3	5,85	2,75	0,7
02.07.1998	m	C2P9	1,3		2,7	0,7
02.07.1998	m	C2P9	1,35		2,75	0,8
02.07.1998	m	C2P9	1,3	5,4	2,8	0,75
02.07.1998	m	C2P9	1,325		2,75	0,75
07.07.1998	m	C2P9	1,3	6	2,75	0,75
07.07.1998	m	C2P9	1,3	5,5	0	0
07.07.1998	m	C2P9	1,25	5,35	2,85	0
07.07.1998	m	C2P9	1,35	5,5	2,85	0,8
07.07.1998	m	C2P9	1,35	5,8	2,85	0,75
15.07.1998	m	C2P9	1,3	5,4	2,7	0,7
15.07.1998	m	C2P9	1,3	5,65	2,8	0,75
15.07.1998	m	C2P9	1,45	6	3,1	0,85
15.07.1998	m	C2P9	1,3	5,5	2,75	0,7
15.07.1998	m	C2P9	1,35	5,5	2,9	0,8
21.07.1998	m	C2P9	1,35	5,75	2,9	0,8
21.07.1998	m	C2P9	1,35	5,45	2,8	0,75
21.07.1998	m	C2P9	1,35	5,75	2,9	0,8
21.07.1998	m	C2P9	1,3	5,45	2,75	0,75
21.07.1998	m	C2P9	1,3	5,4	2,8	0,75
17.06.1998	m	C2P10	1,4	5,8	3,05	0,8
17.06.1998	m	C2P10	1,4		3,05	0
17.06.1998	m	C2P10	1,35	5,2	2,95	0
17.06.1998	m	C2P10	1,3	5,3	3	0,85
17.06.1998	m	C2P10	1,4	5,8	3,05	0,8
24.06.1998	m	C2P10	1,3		2,9	0
24.06.1998	m	C2P10	1,35	5,8	2,9	0,7
24.06.1998	m	C2P10	1,35	5,9	3,1	0,8
24.06.1998	m	C2P10	1,35	5,25	2,75	0,75
24.06.1998	m	C2P10	1,3	5	2,9	0,8
02.07.1998	m	C2P10	1,35		2,95	0
02.07.1998	m	C2P10	1,3		2,75	0,75
02.07.1998	m	C2P10	1,25	5,15	2,75	0,75
02.07.1998	m	C2P10	1,35	5,45	2,9	0
02.07.1998	m	C2P10	1,3		2,85	0,725
07.07.1998	m	C2P10	1,3	5,25	2,8	0,7
07.07.1998	m	C2P10	1,35	5,5	2,95	0,7
07.07.1998	m	C2P10	1,25	5,05	2,7	0,7
07.07.1998	m	C2P10	1,35	5,5	2,8	0,75
07.07.1998	m	C2P10	1,25	5,25	2,75	0,7
15.07.1998	m	C2P10	1,35	5,5	3	0,75
15.07.1998	m	C2P10	1,4	6,4	2,9	0,8
15.07.1998	m	C2P10	1,4		2,95	0
15.07.1998	m	C2P10	1,3		2,95	0,8
15.07.1998	m	C2P10	1,3	5,25	2,8	0,75
21.07.1998	m	C2P10	1,3	5,4	2,95	0,75
21.07.1998	m	C2P10	1,25	5,25	2,8	0,8
21.07.1998	m	C2P10	1,3	5,1	2,85	0,75
21.07.1998	m	C2P10	1,3	5,05	2,85	0,75
21.07.1998	m	C2P10	1,3	5,25	2,75	0,75
14.06.1992	m	Natural	1,5			
14.06.1992	m	Natural	1,4			
16.07.1992	m	Natural	1,45	5,25	2,9	0,8
16.07.1992	m	Natural	1,35	5	2,95	0,8
24.07.1992	m	Natural	1,35			
24.07.1992	m	Natural	1,4			
24.07.1992	m	Natural	1,45			
24.07.1992	m	Natural	1,45			
01.07.1992	m	Natural	1,45			
20.07.1992	m	Natural	1,35			
13.11.1996	w	9.5 °C LD	1,6	5,75	3,65	1,15
23.11.1996	w	9.5 °C LD	1,75	6,6	3,85	1,2

Appendix 7 (continued) (*Chironomus dorsalis*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
05.08.1996	w	16.0 °C LD	1,6	5,1	3,4	1,15
05.08.1996	w	16.0 °C LD	1,65	5,3	3,3	1,2
04.11.1997	w	13.8 °C LD	1,6	5,5	3,35	1,1
04.11.1997	w	13.8 °C LD	1,75	5,8	3,55	1,15
24.06.1998	w	C2P1	1,25	4,25	2,85	1
24.06.1998	w	C2P1	1,3	3,8	2,85	0
24.06.1998	w	C2P1	1,35	5	2,75	1
02.07.1998	w	C2P1	1,3		2,7	0,9
02.07.1998	w	C2P1	1,25		2,7	0
02.07.1998	w	C2P1	1,3		2,6	0
02.07.1998	w	C2P1	1,35	4,3	2,7	0,95
02.07.1998	w	C2P1	1,25		2,65	0
07.07.1998	w	C2P1	1,35		2,7	0,9
07.07.1998	w	C2P1	1,25	4,1	2,55	0,9
07.07.1998	w	C2P1	1,3	4,2	2,65	0,9
07.07.1998	w	C2P1	1,2	4,1	2,5	0,9
07.07.1998	w	C2P1	1,3	4,85	2,75	0,95
15.07.1998	w	C2P1	1,3	4,5	2,85	0,95
15.07.1998	w	C2P1	1,3	4,2	2,75	0,95
15.07.1998	w	C2P1	1,3	4,15	2,75	0,95
15.07.1998	w	C2P1	1,25	4,5	2,7	1
15.07.1998	w	C2P1	1,45	4,5	2,75	0,95
21.07.1998	w	C2P1	1,25	4,35	2,8	0,95
21.07.1998	w	C2P1	1,25	4,1	2,7	0,9
21.07.1998	w	C2P1	1,4		2,8	0,95
21.07.1998	w	C2P1	1,3		2,8	0
21.07.1998	w	C2P1	1,2	4,3	2,8	0,9
24.06.1998	w	C2P2	1,45	4,35	3,05	1,05
24.06.1998	w	C2P2	1,55	4,8	3,15	1,15
24.06.1998	w	C2P2	1,5	5	3,15	1,15
24.06.1998	w	C2P2	1,6	5,2	3,3	1,1
24.06.1998	w	C2P2	1,5	5,1	3,1	1,1
02.07.1998	w	C2P2	1,4	4,05	2,55	0,9
02.07.1998	w	C2P2	1,4	4,3	2,6	0,95
02.07.1998	w	C2P2	1,45		0	0
02.07.1998	w	C2P2	1,45	4,5	2,7	0
02.07.1998	w	C2P2	1,45	4,6	2,6	0,9
07.07.1998	w	C2P2	1,4	4,9	2,95	1
07.07.1998	w	C2P2	1,5		3,15	1,05
07.07.1998	w	C2P2	1,4	5,25	3,05	1
07.07.1998	w	C2P2	1,55	5,55	3	1
07.07.1998	w	C2P2	1,4	4,75	3,05	1,05
15.07.1998	w	C2P2	1,4		3,1	1,05
15.07.1998	w	C2P2	1,35		2,9	1
15.07.1998	w	C2P2	1,3	4,4	2,9	0,9
15.07.1998	w	C2P2	1,4		3,1	1
21.07.1998	w	C2P2	1,45	5,85	3,1	1
21.07.1998	w	C2P2	1,5	5,45	3,2	1
21.07.1998	w	C2P2	1,5	4,85	3,2	1,05
21.07.1998	w	C2P2	1,5	5,5	3,1	1,1
21.07.1998	w	C2P2	1,4	4,5	3	1
24.06.1998	w	C2P3	1,5	5,25	3,3	1,05
24.06.1998	w	C2P3	1,6	6,1	3,55	1,2
24.06.1998	w	C2P3	1,65	6	3,45	1,1
24.06.1998	w	C2P3	1,6	6,1	3,3	1,1
24.06.1998	w	C2P3	1,45	4,95	3,35	1,05
02.07.1998	w	C2P3	1,45	5,15	3,1	1,15
02.07.1998	w	C2P3	1,45	5,6	3,2	0
02.07.1998	w	C2P3	1,45	5,85	3,15	1,1
02.07.1998	w	C2P3	1,55	5,6	3,25	0
02.07.1998	w	C2P3	1,5	5,5	3,15	1
07.07.1998	w	C2P3	1,45		3,15	1,05
07.07.1998	w	C2P3	1,45	5,1	3,15	1,05
07.07.1998	w	C2P3	1,4	4,75	3,05	1,05
07.07.1998	w	C2P3	1,45		3,2	1,05
07.07.1998	w	C2P3	1,55		3,25	1,05
15.07.1998	w	C2P3	1,45		3,3	1,1
15.07.1998	w	C2P3	1,5		3,25	0
15.07.1998	w	C2P3	1,55	5,25	3,25	0
15.07.1998	w	C2P3	1,5		3,3	1,05
15.07.1998	w	C2P3	1,4	5,3	3,3	1,05
21.07.1998	w	C2P3	1,6	6	3,65	1,25
21.07.1998	w	C2P3	1,5		3,3	1,05
21.07.1998	w	C2P3	1,65	5,95	3,65	1,6
21.07.1998	w	C2P3	1,55		3,3	0
17.06.1998	w	C2P4	1,5	5,65	3,25	1,1
17.06.1998	w	C2P4	1,55	5,95	3,35	1,05
17.06.1998	w	C2P4	1,5	5,1	3,25	0
17.06.1998	w	C2P4	1,45	5,2	3,4	1,15
17.06.1998	w	C2P4	1,55	5,45	3,55	1,25
24.06.1998	w	C2P4	1,5	5,4	3,3	0
24.06.1998	w	C2P4	1,45	5	3,15	1,15
24.06.1998	w	C2P4	1,35	4,9	2,95	0
24.06.1998	w	C2P4	1,5	4,75	3,15	0
24.06.1998	w	C2P4	1,5	4,65	3,3	1,15
02.07.1998	w	C2P4	1,45		3,1	1,05

Appendix 7 (continued) (*Chironomus dorsalis*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
02.07.1998	w	C2P4	1,35	4,5	3,1	0
02.07.1998	w	C2P4	1,35	4,5	2,95	0
02.07.1998	w	C2P4	1,45	4,65	2,85	0,95
02.07.1998	w	C2P4	1,4	4,75	2,85	0,95
07.07.1998	w	C2P4	1,5	5,15	2,85	1
07.07.1998	w	C2P4	1,5	4,85	3	0,95
07.07.1998	w	C2P4	1,6	5,25	3,05	1
07.07.1998	w	C2P4	1,6	5,15	3,25	1,05
07.07.1998	w	C2P4	1,55	5,3	3,25	1,05
15.07.1998	w	C2P4	1,5	5,25	3,2	1,05
15.07.1998	w	C2P4	1,45	4,8	0	0
15.07.1998	w	C2P4	1,55		3,4	1,1
15.07.1998	w	C2P4	1,65		3,5	1,15
15.07.1998	w	C2P4	1,6		3,45	1,15
21.07.1998	w	C2P4	1,65	5,35	3,25	0
21.07.1998	w	C2P4	1,5	5,5	3,35	1,15
21.07.1998	w	C2P4	1,6		3,3	1,1
21.07.1998	w	C2P4	1,6	5,75	3,45	1,15
21.07.1998	w	C2P4	1,6	5,4	3,25	1,05
11.08.1998	w	C2P4	1,5	4,75	0	0
11.08.1998	w	C2P4	1,5	5,25	0	0
11.08.1998	w	C2P4	1,5	4,7	3,15	1,05
11.08.1998	w	C2P4	1,4	5,35	0	0
11.08.1998	w	C2P4	1,5	5,2	0	0
02.07.1998	w	C2P5	1,3	4,85	3	1,05
02.07.1998	w	C2P5	1,5		3,1	1,05
02.07.1998	w	C2P5	1,35	5,1	3	0,95
02.07.1998	w	C2P5	1,35	4,65	2,8	0,925
02.07.1998	w	C2P5	1,4	5,1	3	0
17.06.1998	w	C2P6	1,45	4,95	3,15	0
17.06.1998	w	C2P6	1,45	5,35	3,2	0
24.06.1998	w	C2P6	1,45	4,7	3,2	1,05
24.06.1998	w	C2P6	1,45		3,15	1,1
24.06.1998	w	C2P6	1,35	4,45	3	0
15.07.1998	w	C2P6	1,425		3	1,075
15.07.1998	w	C2P6	1,35		2,9	0,95
21.07.1998	w	C2P6	1,3	4,75	2,85	0
21.07.1998	w	C2P6	1,45	4,6	3,05	1,05
21.07.1998	w	C2P6	1,3	4,5	2,9	1
17.06.1998	w	C2P7	1,4	5,25	3,25	0
17.06.1998	w	C2P7	1,4	4,9	3,1	0
17.06.1998	w	C2P7	1,5	5,1	3,25	1,15
17.06.1998	w	C2P7	1,45		3	0
17.06.1998	w	C2P7	1,4	5	3,15	1,05
24.06.1998	w	C2P7	1,45		2,85	0,95
24.06.1998	w	C2P7	1,45	4,95	3	0,95
24.06.1998	w	C2P7	1,6		3,15	1,05
24.06.1998	w	C2P7	1,45	5,5	3,2	1,1
24.06.1998	w	C2P7	1,35		2,85	1,05
02.07.1998	w	C2P7	1,5	4,9	3,15	1,1
02.07.1998	w	C2P7	1,45	5,35	3,05	1
02.07.1998	w	C2P7	1,5	5,3	3,05	1,1
02.07.1998	w	C2P7	1,45	4,7	3	0
02.07.1998	w	C2P7	1,45	4,75	2,9	1
07.07.1998	w	C2P7	1,6		3,15	1,05
07.07.1998	w	C2P7	1,4		3,15	1,05
07.07.1998	w	C2P7	1,375	4,6	2,9	1
07.07.1998	w	C2P7	1,55	6	3,3	1,05
07.07.1998	w	C2P7	1,45	4,75	3	1
15.07.1998	w	C2P7	1,55	5,5	3,45	1,1
15.07.1998	w	C2P7	1,65	6,25	3,6	1,15
15.07.1998	w	C2P7	1,45	5,85	3,3	1,125
21.07.1998	w	C2P7	1,6	5,75	3,5	1,1
21.07.1998	w	C2P7	1,45	5,15	3,3	0
24.06.1998	w	C2P8	1,5	5,15	3,1	1,1
24.06.1998	w	C2P8	1,35	4,25	2,8	0,85
24.06.1998	w	C2P8	1,35	4,9	2,85	0,95
24.06.1998	w	C2P8	1,35	4,5	2,8	0,95
24.06.1998	w	C2P8	1,35	4,25	2,75	0,95
02.07.1998	w	C2P8	1,375	4,35	2,9	0,9
02.07.1998	w	C2P8	1,35	4,75	2,65	0,8
02.07.1998	w	C2P8	1,5	4,9	2,95	0,9
02.07.1998	w	C2P8	1,35	4,5	2,7	0
02.07.1998	w	C2P8	1,25	4,5	2,75	0,825
07.07.1998	w	C2P8	1,35	4,5	3,05	1
07.07.1998	w	C2P8	1,3	4,85	2,85	1
07.07.1998	w	C2P8	1,5	4,8	3,05	0,95
07.07.1998	w	C2P8	1,3	4	2,75	0,9
07.07.1998	w	C2P8	1,35		2,9	0,9
15.07.1998	w	C2P8	1,5	4,75	3,15	1
15.07.1998	w	C2P8	1,475	4,75	3,25	1,075
15.07.1998	w	C2P8	1,45	4,5	3,15	0
15.07.1998	w	C2P8	1,475		3,05	1
15.07.1998	w	C2P8	1,55		3,4	1
21.07.1998	w	C2P8	1,4	4,6	2,9	0
21.07.1998	w	C2P8	1,4	4,75	3,05	0,95

Appendix 7 (continued) (*Chironomus dorsalis*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
21.07.1998	w	C2P8	1,45	4,6	3,05	0,95
21.07.1998	w	C2P8	1,45	4,85	0	0
21.07.1998	w	C2P8	1,5	4,8	3,1	1,05
24.06.1998	w	C2P9	1,45	5,05	3,2	1,1
24.06.1998	w	C2P9	1,5		3,1	1,1
24.06.1998	w	C2P9	1,35	5	2,95	1,05
24.06.1998	w	C2P9	1,45	5,65	3	0
24.06.1998	w	C2P9	1,35	5,1	2,85	0
02.07.1998	w	C2P9	1,4	5,15	2,95	1
02.07.1998	w	C2P9	1,45		2,95	1
02.07.1998	w	C2P9	1,4	4,9	3	0
02.07.1998	w	C2P9	1,45	5	3,05	0
02.07.1998	w	C2P9	1,45	5	3,05	1
07.07.1998	w	C2P9	1,425		2,95	1
07.07.1998	w	C2P9	1,375	4,9	2,85	1
07.07.1998	w	C2P9	1,35		2,9	1
07.07.1998	w	C2P9	1,45		3	0,95
07.07.1998	w	C2P9	1,4	5	2,85	1
15.07.1998	w	C2P9	1,35	5,25	2,95	0,95
15.07.1998	w	C2P9	1,4	4,85	2,9	1
15.07.1998	w	C2P9	1,4	4,95	3	1,05
15.07.1998	w	C2P9	1,35	5,3	3,1	1,05
15.07.1998	w	C2P9	1,35	4,6	2,9	0,95
21.07.1998	w	C2P9	1,4	5,8	3	1
21.07.1998	w	C2P9	1,35	4,25	2,95	0
21.07.1998	w	C2P9	1,3	5,15	2,75	0,95
21.07.1998	w	C2P9	1,35		2,9	0,95
21.07.1998	w	C2P9	1,3	5,35	2,9	1
17.06.1998	w	C2P10	1,5	4,85	3,25	0
17.06.1998	w	C2P10	1,4	5,35	3,3	1,15
17.06.1998	w	C2P10	1,45	5,1	3,3	0
17.06.1998	w	C2P10	1,5	5	3,1	0
17.06.1998	w	C2P10	1,45	5,4	3,25	1,1
24.06.1998	w	C2P10	1,4	4,9	3	1,05
24.06.1998	w	C2P10	1,4		2,85	1
24.06.1998	w	C2P10	1,4		3	1,1
24.06.1998	w	C2P10	1,35	4,85	2,9	1,05
24.06.1998	w	C2P10	1,45	4,75	3,1	1,05
02.07.1998	w	C2P10	1,4	4,4	2,85	0
02.07.1998	w	C2P10	1,4	4,5	2,85	0
02.07.1998	w	C2P10	1,4	4,5	2,9	0
02.07.1998	w	C2P10	1,4	4,6	2,75	0,9
02.07.1998	w	C2P10	1,45	4,75	2,95	0,95
07.07.1998	w	C2P10	1,4	5,1	2,9	0,95
07.07.1998	w	C2P10	1,3	4,6	2,9	1
07.07.1998	w	C2P10	1,35	5	2,9	0
07.07.1998	w	C2P10	1,3	4,65	0	0
07.07.1998	w	C2P10	1,4	4,5	2,85	0,95
15.07.1998	w	C2P10	1,4	4,85	2,95	0,9
15.07.1998	w	C2P10	1,35	4,5	2,9	0,9
15.07.1998	w	C2P10	1,4	5	3	0
15.07.1998	w	C2P10	1,4	4,5	3	0
15.07.1998	w	C2P10	1,45	5,1	3,1	0,95
21.07.1998	w	C2P10	1,45	4,75	2,95	0,95
21.07.1998	w	C2P10	1,4	4,65	0	0
21.07.1998	w	C2P10	1,4	4,55	2,9	1
21.07.1998	w	C2P10	1,5	4,5	3,05	0,85
21.07.1998	w	C2P10	1,35	4,5	2,9	0,95
14.06.1992	w	Natural	1,6			
14.06.1992	w	Natural	1,6			
16.07.1992	w	Natural	1,6	5,1	3,3	1,1
16.07.1992	w	Natural	1,55	4,75	3,15	1,1
24.07.1992	w	Natural	1,6			
24.07.1992	w	Natural	1,5			
24.07.1992	w	Natural	1,55			
24.07.1992	w	Natural	1,45			
01.07.1992	w	Natural	1,6			
01.07.1998	w	Natural	1,5			
		Chironomus luridus				
22.06.1992	m	2	1,6	6,5	3,6	0,95
19.06.1997	m	2	1,45	6,25	3,3	0,85
28.06.1997	m	2	1,45	6,1	3,2	0,9
05.07.1997	m	2	1,5	7	3,5	0,95
25.06.1998	m	2	1,5	6,35	3,45	0,95
19.05.1999	m	1c	2,025	7,75	4,3	1,1
08.07.1992	m	Lahnberge other	1,4	5,35	3,25	0,9
24.09.1993	m	C1P3	1,425	5,85	3,45	0,95
28.08.1993	m	C1P3	1,25	5,35	3,15	0,9
22.06.1992	f	2	1,6	5,2	3,9	1,1
19.06.1997	f	2	1,65	6,4	3,7	1,1
28.06.1997	f	2	1,45	5,1	3,25	1
05.07.1997	f	2	1,55	5,6	3,45	1,05
11.07.1997	f	2	1,45	5,25	3,3	1,05
19.05.1999	f	1c	2	8,05	4,5	1,4

Appendix 7 (continued) (*Chironomus luridus*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
08.07.1992	f	Lahnberge other	1,65	5	3,65	1,1
24.09.1993	f	C1P3	1,4	5,2	3,3	1
28.08.1993	f	C1P3	1,45	4,5	3,25	1,05
Chironomus piger/riparius phaenotype *piger*						
24.06.1998	m	C2P1	1,65	6,25	3,6	0,95
02.07.1998	m	C2P2	1,5	6,05	3,2	0,85
15.07.1998	m	C2P3	1,35	5,3	2,95	0,8
21.07.1998	m	C2P4	1,25	5,1	2,6	0,775
24.06.1998	m	C2P10	1,6	5,95	3,3	0,95
24.06.1998	m	C2P3	1,55	6,25	3,4	0,95
07.07.1998	m	C2P3	1,6	6,3	3,4	0,95
02.07.1998	m	C2P4	1,45	5,75	2,95	0,85
24.06.1998	m	C2P5	1,45	5,65	3,15	0,75
24.06.1998	m	C2P7	1,4	5,25	2,85	0,825
15.07.1998	m	C2P8	1,35	5,3	3	0,8
24.06.1998	f	C2P1	1,4	5,25	2,8	0,85
02.07.1998	f	C2P1	1,55	4,8	3,2	1,05
15.07.1998	f	C2P1	1,25	4,15	2,8	0,95
21.07.1998	f	C2P1	1,3	3,9	2,85	0,95
24.06.1998	f	C2P10	1,85	6,05	3,75	1,2
07.07.1998	f	C2P3	1,6	5,5	3,4	1,15
02.07.1998	f	C2P4	1,55	4,7	3,1	0,9
24.06.1998	f	C2P5	1,45	4,25	2,7	0,9
15.07.1998	f	C2P8	1,5	4,5	3,25	1,1
21.07.1998	f	C2P8	1,5	4,6	3,3	1,05
Chironomus piger/riparius phaenotype *riparius*						
24.06.1998	m	C2P2	1,7	6,8	3,7	1
17.06.1998	m	C2P4	1,55	6,15	3,15	0,9
26.06.1998	m	C2P4	1,45	5,85	3,1	0,8
02.07.1998	m	C2P4	1,45	5,75	2,85	0,85
07.07.1998	m	C2P4	1,55	5,65	3,15	0,85
15.07.1998	m	C2P4	1,6	6,5	3,5	0,9
26.06.1998	m	C2P7	1,45	5,7	2,9	0,85
02.07.1998	m	C2P7	1,5	5,65	3	0,8
24.06.1998	m	C2P9	1,45	6		
21.07.1998	m	C2P9	1,3	5,3	2,75	0,8
21.07.1998	f	C2P10	1,4	4,55	2,9	0,95
24.06.1998	f	C2P2	1,55	5,75	3,3	
02.07.1998	f	C2P4	1,55	4,7	2,9	0,95
07.07.1998	f	C2P4	1,45	4,75	3	0,95
15.07.1998	f	C2P4	1,55	5,2	3,05	1,05
11.08.1998	f	C2P4	1,7	5,65	3,35	1,1
02.07.1998	f	C2P7	1,45	4,95	3	1
21.07.1998	f	C2P7	1,7	5,75	3,45	1,15
24.06.1998	f	C2P9	1,65	5,55		
21.07.1998	f	C2P9	1,45	4,6	2,8	1
Chironomus piger/riparius, localities others than the boxes of the colonizing experiment, 1998						
10.06.1999	m	2	1,65	7,9	3,6	0,95
09.06.1999	m	1b	1,75	7,25	3,9	1
14.10.1993	m	Großseelheim	1,55	5,75	3,05	0,85
21.02.1997	m	Schulte	1,7	6,5	3,65	0,9
27.12.1999	m	Wabern	1,575	6	3,25	0,9
10.06.1999	f	2	1,75	7,6	3,65	1,125
09.06.1999	f	1b	1,7	7,05	3,6	1,2
17.06.1999	f	1b	1,85	6,8	3,85	1,3
14.10.1993	f	Großseelheim	1,6	4,9	3	0,95
21.02.1997	f	Schulte	1,75	5,25	3,6	1,15
Chironomus pseudothummi/uliginosus						
12.06.1997	m	2	1,55	6,25	3,4	1,05
03.06.1998	m	2	1,625	6,75	3,85	1,025
10.06.1998	m	2	1,4	5,85	3,25	0,9
25.06.1998	m	2	1,45	6,85	3,35	0,9
24.07.1998	m	2	1,325	5,55	3,1	0,85
16.07.1992	m	2	1,45	6	3,35	0,9
24.04.1998	m	1b	1,85	8,05	4,3	1,1
24.04.1998	m	1b	1,9	7,85	4,2	1,1
23.08.1993	m	C1P4	1,425	5,55	3,175	0,8
11.09.1993	m	C1P4	1,35	5,6	3,4	0,85
12.06.1997	f	2	1,45	5,7	3,5	1
10.06.1998	f	2	1,45	5,1	3,4	0,95
10.06.1998	f	2	1,55	6	3,55	1,15
24.07.1998	f	2	1,425	5,25	3,3	1,025
24.04.1998	f	1b	2,1	8,35	4,85	1,5
24.04.1998	f	1b	2	6,85	4,55	
06.09.1993	f	C1P4	1,45	4,45	3,25	0,95
01.09.1993	f	C1P4	1,5	5,1	3,5	1

Appendix 7 (continued) (*Chironomus pseudothummi/uliginosus*).

Date	Sex	Site/Experiment	THL (mm)	BL (mm)	WL (mm)	WW (mm)
01.09.1993	f	C1P4	1,4	4,5	3,35	1,1
11.09.1993	f	C1P4	1,5	5,5	3,5	1,1

Abbreviations:

THL = thorax length; **BL** = body length; **WL** = wing length; **WW** = wing width; **CxPy** = Colonizing experiment in 1993 (C1, see DETTINGER-KLEMM 1995a, DETTINGER-KLEMM & BOHLE 1996) or 1998 (C2, this study) and number of the colonizing pool (Py); **Großseelheim** = reared from larvae that were collected in a water-filled car tyre on a farm in Großseelheim (Hesse, Germany); **Lahnberge other** = two small temporary pools near pool 2 (see table 1 in DETTINGER-KLEMM & BOHLE 1996); **Natural** = two puddles on construction site (Lahnberge, Marburg, Hesse, Germany) (see table 1 in DETTINGER-KLEMM & BOHLE 1996); **Schulte** = reared from larvae obtained from an commercial supplier (Schulte, The Netherlands); **Wabern** = reared from larvae that were collected in the sewage ditch of a sugar refinery in Wabern (Hesse, Germany). **Numbers of site**, see section 4.1.; **9.5 °C LD, 16.0 °C LD, 13.8 °C SD** = specimens from the experiments on the impact of temperature and photoperiod on development (section 4.4.1.2. and Appendix 8).

Appendix 8: Data of the experiments on the influence of temperature and photoperiod on development.

Temperature	Box	First	Last	Median	Mean	sd	Eggs	Mass	♂♂	♀♀	Vessel	L. mea.	L. pres.	P. mea./pres.	♂♂ mea.	♀♀ mea.	Comment	Survival	Density
***Limnophyes asquamatus* parthenogenetic lab culture**																			
21.5 °C ± 4 LD	143	29	46	38	38.1	3.6	±60	1		30	C		14					V	~11 000
	144	22	32	27	26.9	2.1	±60	1		23	C							III	~11 000
Total *Limnophyes asquamatus* forma *aquaticus*							**±120**	**2**		**53**			**14**						
Paralimnophyes hydrophilus																			
4.5 °C ± 1 LD	50						251	4	(1)***		A							0	11 496
	51	134.5	134.5				96	3	7	2	C	4	4		1	2		9.8	15 091
	52						99	4			C							0	15 563
	53						122	2	(1)***	(1)***	P+C	12	12					0	19 178
	54						317	7			P+C	16	16					0	49 832
9.5 °C ± 1 LD	55	69	111	86	86.9	8.6	379	8	110	85	A	5	5	3	3	3		52.6	17 358
	56	58.5	119	96.5	97.6	9.0	377	11	50	59	C	10	15	1	3	3		30.2	59 264
	57	66.5	108.5	84	85.0	12.6	371	15	5	7	P+C	46	46		2	3		3.7	58 321
	58	69	122	106	99.9	15.6	257	6	31	16	P+C	43	43	1	2	2		22.1	40 400
14.6 °C ± 1 LD	59	30	42	34	33.6	2.1	251	7	59	46	A	11	11		2	1		43.8	11496
	60	28	44	40	37.7	4.5	282	9	36	19	C	17	17		4	5		20.8	44 330
	61	33	52	42	42.7	4.4	268	8	28	23	P+C	47	47			1		23.1	42 130
	62	30	38	31	32.0	2.9	102	4	4	4	P+C	41	41		1	2		13.1	16 034
	63	32	50	45	44.7	3.0	459	16	57	31	P+C	61	61	1	2	1	20 L	22.2	72 155
19.3 °C ± 1 LD	64	17	23	20	19.8	1.4	202	6	63	36	A	5	10	2	4	2		52.1	9 252
	65	17	27	20	21.0	2.5	234	5	42	34	C	24	24		3	1		36.2	36 785
	66	19	41	25	26.6	5.0	298	6	42	52	P+C	84	84		2			43.9	46 846
	67	22	36	30	29.5	4.6	130	3	6	4	P+C	40	40			1		11.1	20436
	68	23	37	27	28.4	3.4	222	9	19	17	P+C	62	62			1		22.5	34.898
25.0 °C ± 0.5 LD	69	12	18	14	14.6	1.4	312	10	45	36	A		6	1	3	1		26.6	14 290
	70	15	19	17.5	17.2	1.2	135	2	9	1	P+C	55	55	1	2	2		12.7	21 222
	71	12	19	14	14.3	1.5	242	6	41	28	C	5	16					30.5	38 042
	72	15	20	17	17.2	1.6	290	8	16	9	P+C	64	64		3	4		11.1	45 588
	73	17	35	22	23.1	4.3	342	7	60	43	P+A		44		2			34.6	15 664
29.1 °C ± 1 LD	74						304	8			A	23	23	4			†	0	13 923
	75						249	5			C	7	7				†	0	39 143
	76						247	7			P+C	25	33				†, 4 L	0	38 828
	77						172	4			P+C	3	3				†	0	27 038
	78						333	17			P+C	17	17	1			†	0	52 348
	79						60	1			P+C	12	12				†	0	9 432
30.2 °C ± 0.5 LD	80						504	10			A	4	4				††	0	23 083
	81						204	5			P+C	4	4				††	0	32 069
33.5 °C ± 1 LD	82						315	7			A						egg†	0	14 427
	83						434	8			C						egg†	0	68 225
	84						326	10			P						egg†	0	51 247
Total *Paralimnophyes hydrophilus*							**9186**	**248**	**730**	**552**		**747**	**826**	**15**	**39**	**35**			

Appendix 8 (continued).

Temperature	Box	First	Last	Median	Mean	sd	Eggs	Mass	♂♂	♀♀	Vessel	L. mea.	L. pres.	P. mea./pres.	♂♂ mea.	♀♀ mea.	Comment	Survival	Density
Chironomus annularius																			
11.0 °C ± 1 SD	85	51	91.5	58.5	61.3	9.5	~350	0.5	51	41	P+A		20		20	12		II	~16 000
11.0 °C ± 1 LD	86	72	227.5	165	151.0	43.1	~350	0.5	70	52	P+A		47		16	13		III	~16 001
	87	68	226.5	137.5	147.0	48.0	~300	1	69	55	P+C+A		45		1	1		IV	~13 700
13.8 °C ± 2 SD/LD	88	47	101.5	76	76.6	10.7	~650	0.5	120	122	P+A		26				#	III	~29 800
	121	34.5	78	64	62.4	6.3	~500	0.5	31	78	P+A		30	1			#	II	~22 900
19.6 °C ± 1 LD	122	24	68.5	54	51.6	11.4	~650	0.5	37	52	P+C+A		65				LP†	II	~29 800
	123	24	65.5	55	52.5	10.4	~500	0.5	6	34	P+C+A		50	1			LP†	I	~22 900
24.2 °C ± 2 LD	124	17	22	18	18.4	1.1	~500	0.5	18	13	P+A		46				LP††	I	~22 900
	125						~650	0,5			P						egg †	0	
30.2 °C ± 0.5 LD	126	16	31	19	20.1	4.0	~500	0.5	54	64	P+C+A		30	1				II	~22 900
	127	16	26	21	20.8	2.6	~650	0.5	46	50	P+C+A		50					II	~29 800
	128	11	25	20	19.2	3.6	~1000	1	21	20	P+C+A		19				egg††	I	~45 800
Total *Chironomus annularius*							**~6 600**	**7**	**523**	**581**			**428**	**3**	**37**	**26**			
Chironomus dorsalis																			
4.5 °C ± 1 LD	1						≈c	1			C						L†	0	
	2						≈d	1			P						L†	0	
	3						≈c	1			P						L†	0	
	4						≈c	1			P						L†	0	
9.5 °C ± 1 LD	5	132	227.5	184	180.6	17.1	≈c	1	118	119	C+A	6	80		1	1		IV	≈23 000
	6	77	186	153	148.6	22.1	≈c	1	121	119	P+C+A	87	102		5	4		V	≈23 000
	7	77	200	169.5	166.7	23.6	≈c	1	112	88	P+A	76	99		4	2		IV	≈23 000
16.0 °C ± ± 1 LD	8	32	44	41	40.2	3.1	≈c	1	7	6	C	0	69		1	3		I	≈79 000
	9	29	48	38	37.4	4.5	≈c	1	101	94	P+A	60	79		5			IV	≈23 000
	10	28	39	32	32.5	2.9	≈c	1	83	62	P+A	54	64		4	5		III	≈23 000
13.8 °C ± 2 SD/LD	11	40.5	95.5	85	83.4	7.5	≈c	1	202	214	P+A	21	21			1	##	V	≈23 000
	12	29	91.5	82	81.6	8.2	≈c	1	253	232	P+A	20	20		5	5	##	V	≈23 000
	13	34	108	86	79.8	16.4	≈c	1	221	254	P+A	0	15		5	4	##	V	≈23 000
	14	27					≈c	1	6	1	P+A		5				##, *		≈23 000
20.0 °C ± 0.5 LD	15	18	23	19.5	19.7	1.5	≈c	1	40	20	C		50					I	≈79 000
	16	20	24	21	21.3	1.3	≈c	1	24	13	C		50	5				I	≈79 000
	17	20	25	22	22.3	1.3	≈c	2	46	36	P+A	81	75		5			I	≈46 000
	18	20	27	23	23.5	1.5	≈c	1	4	70	P+C		102		2	2		II	≈79 000
	19	21	24	22	21.8	0.7	≈b	1	4	17	P+A	6	68	1	1	1		I	≈14 000
	20	21	30	24	24.4	2.1	≈c	1	111	106	P+C+A	76	91	1	2	5		IV	≈23 000

Appendix 8 (continued) (*Chironomus dorsalis*).

Temperature	Box	First	Last	Median	Mean	sd	Eggs	Mass	♂♂	♀♀	Vessel	L. mea.	L. pres.	P. mea./pres.	♂♂ mea.	♀♀ mea.	Comment	Survival	Density
21.5 °C ± 4 LD	V1	17					≈c	1			A						Vallend.		≈23 000
	V2	17					≈c	1			A						Vallend.		≈23 000
	V3	20					≈c	1			A						Vallend.		≈23 000
	V4	20					≈c	1			A						Vallend.		≈23 000
	V5	22					≈c	1			A						Vallend.		≈23 000
25.0 °C ± 0.5 LD	21	17	20	18	18.2	1.0	≈c	1	2	11	C		60					I	≈79 000
	22	16	22	19	19.1	1.3	≈d	1	70	26	P+A	58	74		3	1		II	≈27 500
	23	16	22	18	18.5	1.6	≈c	1	45	51	P+A	49	64	1	2	1		II	≈23 000
	24	15	20	18	17.7	1.0	≈c	1	45	53	P+A	19	59	1	3	1		II	≈23 000
	25	13	17	15	14.9	1.0	≈c	1	27	30	P+C		68	1	1	1		I	≈79 000
	26	13	17	15	14.8	1.1	≈c	1	25	38	P+C		59	1	1			I	≈79 000
	27	14	20	16	16.3	1.5	≈c	1	70	71	P+A		65					III	≈23 000
27.3 °C ± 2 LD	28	12	18	14	14.3	1.6	≈c	1	65	56	P+A		46	2				II	≈23 000
	29	12	17	13	13.4	1.2	≈b	1	66	48	P+A		47	3				IV	≈14 000
	30	12	17	14	14.4	1.3	≈a	1	64	37	P+C+A		50					V	≈9 000
	31	12	17	13	13.5	1.1	≈a	1	45	38	P+C+A		47					IV	≈9 000
	32	11	13	13	12.5	0.6	≈d	1	21	21	P+C		39	1				I	≈94 000
29.1 °C ± 0.5 LD	33	13	22	16	16.7	1.6	500	1	47	53	P+A		35				****	II	22 900
	34	15	22	17	17.1	1.6	500	1	41	23	P+A		41				****	I	22 900
	35	21	26.5	23	23.4	1.5	400	1	30	24	P+C+A		76				****	II	18 320
	36	13	15	14	13.6	0.6	327	1	12	12	P+C		13	3			****	I	51 404
	37	11	13	11	11.6	0.7	168	1	18	5	P+A		9	1			****	I	7 794
30.2 °C ± 0.5 LD	38	14	29	19	19.7	2.7	≈c	1	160	151	P+C+A	47	60		3	3		V	≈23 000
	39	13	20	16	16.4	1.5	≈c	1	144	107	P+C+A	45	55		4	4		IV	≈23 000
	40	12	20	16	15.9	1.6	≈c	1	169	159	P+C+A	36	50		3	3		V	≈23 000
30.4 °C ± 2 LD	41	12	14	13	12.7	0.6	≈c	1	18	18	P+C+A		32	1				I	≈23 000
	42	13	18	15	15.0	1.7	≈c	1	28	26	P+C+A		58					I	≈23 000
	43	12	16	14	14.3	1.0	≈c	1	38	11	P+A		62					I	≈23 000
	44	11	19	15	14.9	2.0	≈c	1	78	59	P+A		45					III	≈23 000
	45	13	25	17	16.9	2.8	≈a+c	2	61	55	P+C+A		69					II	≈32 000
31.1 °C ± 4 LD	46	13	19	16	16.0	1.6	≈c	1	14	11	C		24	2				I	≈79 000
	47	15	20	17	17.1	1.4	≈b	1	28	22	P+A		48	1				II	≈14 000
	48	15	20	18	17.8	1.3	≈c	1	23	16	P+A		65					I	≈23 000
	49	16	22	18	18.5	1.9	≈c	1	40	27	P+A		92					II	≈23 000
33.5 °C ± 2 LD	49a						≈a	1			P		5				†††	0	
	49b						≈a	1			P						†††	0	
	49c						≈d	1			P		5				†††	0	
	49d						≈a	1			P						†††	0	

Appendix 8 (continued) (*Chironomus dorsalis*).

Temperature	Box	First	Last	Median	Mean	sd	Eggs	Mass	♂♂	♀♀	Vessel	L. mea.	L. pres.	P. mea./pres.	♂♂ mea.	♀♀ mea.	Comment	Survival	Density
33.5 °C ± 2 LD	49e						≈a	1			P						†††	0	
35.0 °C ± 1 LD	49f						≈c	1			P						††††	0	
	49g						≈c	1			P						††††	0	
	49h						≈c	1			P						††††	0	
41.0 °C ± 4 LD	49i						≈c	1			P						†††††	0	
	49j						≈c	1			P						†††††	0	
	49k						≈c	1			P						†††††	0	
Total *Chironomus dorsalis*								**67**	**2947**	**2710**		**741**	**2512**	**25**	**60**	**47**			
Chironomus luridus																			
9.5 °C ± 1 LD	129	90	250	206	203.5	25.7	≈d	1	67	45	P+C		89					II	≈94 000
16.0 °C ± 1 LD	130	33	51	44	43.1	4.2	≈d	1	29	26	P+A		70					I	≈94 000
25.0 °C ± 0.5 LD	131	24	28	26	26.0	1.5	≈b	1	2	5	C		36				LP††	I	≈47 000
Total *Chironomus luridus*							**3**		**98**	**76**			**195**						
Polypedilum tritum																			
4.5 °C ± 1 LD	89						500	4			P						egg†	0	
	90						396	4			P						egg†	0	
	91						183	2			C						egg†	0	
	92						597	5			A						egg†	0	
9.5 °C ± 1 LD	93	74.5	116	86	88.3	6.7	550	4	22	40	P+C	49	49	1	3	3		12.4	86 455
	94	78	116	98	98.1	8.0	461	4	62	68	P+C	49	49		3	3		31.6	72 465
	95	78	116	93.5	92.4	7.1	433	4	84	98	C	5	5		2	2		42.5	68 063
	96	84	113	93.5	95.4	7.2	576	5	34	20	A			2	2	2		9.4	26 375
14.6 °C ± 1 LD	97	36	51	46	45.7	3.5	609	5	61	80	P+C	53	53		3	2		25.4	95 729
	98	35	51	42	41.0	3.0	398	4	72	75	P+C	48	60		4	3		43.5	62 562
	99						460	4			C						*	0	72 307
	100	39	51	44	43.8	2.5	555	5	85	75	A				4	4		28.8	25 413
13.8 °C ± 2 SD/LD	101	40	110	90	89.3	11.1	999	9	147	163	A	5	10	1	5	5	#####	31.4	45 744
	102	43	110	90	88.1	8.3	888	8	203	216	A	5	10	4	1	4		47.9	40 662
	103	35	100.5	84.5	78.6	19.1	555	5	59	49	P+C	28	28		4	1		19.7	87 240
19.3 °C ± 1 LD	104	24	35	28	28.6	2.1	412	4	29	31	P+C	3	120		2	3		20.5	64 762
	105	26	35	29	29.3	2.7	428	4	52	39	P+C	116	116		3	2		29.2	67 277
	106	25	42	29	31.8	5.2	364	4	55	49	C	18	18	1	3	3		30.1	57 217
	107	27	38	31	31.3	2.1	526	5	90	110	A	11	11		3	1		38.8	24 086
25.0 °C ± 0.5 LD	108	15	30	18	18.9	3.8	430	4	39	35	P+C	58	58	2	2	1		20.0	67 592
	109	16	32	23	23.0	3.9	491	4	57	87	P+C	62	62	1	4	2		33.6	77 180
	110	17	33	24	23.9	3.7	543	4	129	110	C	10	15		3	7		45.3	85 354
	111	15	33	19	19.7	2.5	481	5	54	64	A	5	5		1			24.8	22 025
29.1 °C ± 0.5 LD	112	14	30	17	19.1	4.1	429	4	36	23	P+C		66		1	2		16.3	67 435
	113	14	27	16	16.6	2.3	310	4	14	24	P+C		65		5			15.5	48 729
	114	14	33	23	22.9	4.0	465	4	130	138	C		10		3	4		58.9	73 093
	115	15	27	17.5	18.3	3.0	590	5	13	11	A		5			1		4.1	27 016

Appendix 8 (continued) (*Polypedilum tritum*).

Temperature	Box	First	Last	Median	Mean	sd	Eggs	Mass	♂♂	♀♀	Vessel	L. mea.	L. pres.	P. mea./pres.	♂♂ mea.	♀♀ mea.	Comment	Survival	Density
	116	35	47	40	39.8	2.7	999	9	63	39	A	19	19		7	3	**	10.4	45 744
30.2 °C ± 0.5 LD	117	30	64	33	39.2	12.0	999	9	10	14	A	14	21	1	3	4	LP††	2.5	45 744
	118						444	4			P+C	41	50					0	69 792
33.5 °C ± 2	119						335	3			P						egg†	0	
LD	120						444	4			P						egg†	0	
Total *Polypedilum tritum*							**16 850**	**152**	**1600**	**1658**		**599**	**905**	**13**	**71**	**62**			

Abbreviations and explanations:

Columns:

Temperature = mean temperature ± range and light-cycle; **Box Nr.** = Number of experimental unit; **First/Last** = First/Last emergence from oviposition (days); **Median/Mean** = Median value/arithmetic mean of emergence (days); **sd** = standard diversity; **Eggs/Mass** = a) number or estimate of eggs/number of egg masses used in the experiment; ♂♂/♀♀ = number of emerged males/females; **Vessel** = type of culture vessel; **L/P** = larvae/pupae; **mea./pres**. = measured/preserved; **Survival** = **a)** %: Adults/(eggs - (L. pres. + P. pres.)) * 100 **b)** estimated survival: I = 0.1 - 15 %, II = 15.1 - 30 %, III = 30.1 - 45 %, IV = 45.1 - 60 %, V = 60.1 - 100 %; **Density** = larvae/m² (= egg number * (1/area of vessel (m²)).

Letters:

A = plastic aquarium (18.2 * 12.0 * 15.0 cm); **C** = crystallizing dishes (diameter 9.0 cm, hight: 5.0 cm); **L** = living larvae at the end of the experiment; **LD** = long-day experiment (16:8 h); **P** = petri plastic dishes (diameter: 8.8 cm, hight: 2.0 cm); **P+C(+A)** = first reared in a petri plastic dish and then the larvae were transferred into a crystallizing dish (or additionally/alternatively in a plastic aquarium); **SD** = short-day experiment (8:16 h).

Vallend. = these egg masses were reared in 1998 only until the first emergence. Then the rearings were finished, about 10 larvae per egg mass were preserved in a solution of 70 % alcohol and lactic acid (3:1 = Karnua) and the pupal skins and the adults were preserved seperately in 70 % alcohol. This material was then send to Henk Vallenduuk (The Netherlands) for his private collection and for his scientific use.

Symbols:

* = vessel fell down and the content spilled onto the floor, all larvae died; ** = after 30 days from hatching, the larvae were kept at 20 °C; *** = after 54 days from hatching no larvae were seen anymore and the vessels were transferred into a 20 °C incubator where the adults (number in parenthesis) eclosed 66.5, 67.5 and 73 days, respectively, from oviposition; **** = until 5 days after oviposition the larvae were erroneously kept under a day-night-cycle of temperature changing from 30 - 25 °C, after 5 days from oviposition the temperature was constant 30 °C. Another error occurred in this experiment until 9 days from oviposition: the air supply switched off during the night

egg† = embryonic development was observed, but the embryos died before hatching; **egg††** = raised mortality during embryonic development; **L†** = raised mortality during embryonic development, larvae did not grow after hatching and died in the long run; **LP†** = raised mortality in the instar IV and pupal stage; **LP††** = very high mortality of larvae**;†** = raised mortality rates already during embryonic development, partial development into pupae but no development into adults; **††** = very high mortality during embryonic development and early larval instars, only single specimens developed into instars IV and none into the pupae; **†††** = all larvae died after hatching; **††††** = all larvae died during hatching; **†††††** = no embryonic development possible;

= SD until 36 days after oviposition, then change to LD; ## = SD until 62 days after oviposition, then change to LD; ### = SD until 115 days after oviposition, then change to SD; #### = At 214 days after oviposition the temperature was changed to 21.5 °C; ##### = SD until 70 days after oviposition, then change to LD.

~ = the number of eggs was approximately estimated from a photography of the egg mass; ≈ = estimation of egg numbers in four categories: a) about 200 b) about 300 c) about 500 d) about 600 (the estimation was done by comparing the egg masses with 5 egg masses of different sizes which eggs had been counted); ± = the number of the eggs was approximately counted using a photography of the egg mass.

Appendix 9: Larval body lengths and growth rates for *Chironomus dorsalis*, *Polypedilum tritum* and *Paralimnophyes hydrophilus*.

Chironomus dorsalis

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
9.5 °C	5	18		2,0	2,98		5
		0	0	1,0	0,85		5
		2	2	1,0	1,05	0,106	3
		4	2	1,0	1,15	0,045	1
		6	2	1,0	1,42	0,107	4
		9	3	1,0	1,64	0,047	5
		12	3	2,0	2,30	0,113	5
9.5 °C	6	15	3	1,8	2,82	0,068	5
		19	4	2,4	3,81	0,076	5
		22	3	3,0	4,67	0,068	5
		29	7	3,0	5,70	0,028	5
		36	7	4,0	6,95	0,028	5
		43	7	3,2	7,02	0,001	5
		50	7	4,0	8,56	0,028	5
Mean 1						**0,060**	
		61	11	4,0	7,79	-0,009	5
		81	20	4,0	10,00	0,012	5
		92	11	4,0	10,82	0,007	5
		105	13	4,0	11,54	0,005	5
		120	15	4,0	11,11	-0,003	5
		138	18	4,0	10,85	-0,001	4
		0	0	1,0	0,86		6
		9	9	1,0	1,72	0,077	5
		12	3	2,0	2,23	0,088	5
		15	3	2,0	3,15	0,115	5
9.5 °C	7	19	4	2,4	3,74	0,043	5
		22	3	3,0	4,55	0,065	5
		29	7	3,0	5,54	0,028	5
		36	7	3,5	5,97	0,011	4
		43	7	3,8	8,13	0,044	6
		50	7	4,0	9,35	0,020	5
Mean 2						**0,055**	
		61	11	4,0	9,46	0,001	5
		81	20	4,0	9,76	0,002	5
		92	11	4,0	10,94	0,010	5
		105	13	4,0	11,30	0,002	5
		120	15	4,0	11,39	0,001	5
		0	0	1,0	0,85		5
13.8 °C SD	11	20	20	4,0	8,58	0,116	5
		56	36	4,0	10,81	0,006	5
		65	9	4,0	9,84	-0,010	6
		0	0	1,0	0.86		
13.8 °C SD	12	19	19	3,6	7,57	0,114	5
		55	36	4,0	11,43	0,011	5
		64	9	4,0	11,69	0,003	5
		1	0	1,0	1,02		5
		4	3	1,6	1,86	0,201	10
		6	2	2,0	2,97	0,234	6
		8	2	2,5	3,60	0,095	4
16.0 °C	9	10	2	2,8	3,99	0,051	5
		12	2	3,2	5,15	0,128	5
		14	2	3,4	6,16	0,090	5
		17	3	3,6	7,16	0,050	5
		19	2	4,0	8,75	0,100	5
Mean 3						**0,119**	
		23	4	4,0	10,50	0,045	5
		26	3	4,0	10,20	-0,010	5
		1	0	1,0	0,97		8
		2	1	1,0	1,15	0,172	4
		3	1	1,0	1,42	0,209	3
		7	4	1,8	2,35	0,126	5
16.0 °C	10	9	2	2,6			5
		11	2	3,0	4,71	0,174	5
		13	2	3,2	5,74	0,099	5
		15	2	4,0	8,04	0,169	4
		18	3	4,0	9,76	0,065	6
Mean 4						**0,145**	

Appendix 9 (continued) (*Chironomus dorsalis*).

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
16.0 °C	10	20	2	4,0	10,21	0,023	5
		24	4	4,0	10,14	-0,002	4
20.0 °C	17	0	0	1,0	0,73		5
		1	1	1,0	0,94	0,252	5
		2	1	1,0	1,35	0,362	5
		3	1	1,3	1,75	0,264	6
		4	1	2,0	2,51	0,356	5
		5	1	2,2	3,02	0,185	5
		7	2	3,0	4,94	0,246	5
		8	1	3,0	5,53	0,113	5
		9	1	3,8	6,21	0,117	5
		10	1	4,0	7,39	0,173	5
		11	1	4,0	8,55	0,146	5
		12	1	4,0	9,29	0,082	5
		13	1	4,0	10,13	0,087	5
		14	1	4,0	11,03	0,086	5
Mean 5						**0,190**	
		15	1	3,8	10,12	-0,086	5
		16	1	4,0	10,11	-0,001	5
20.0 °C	19	0	0	1,0	0,85		1
		1	1	1,0	0,96	0,125	3
		2	1	1,0	0,75	-0,250	1
		3	1	1,0	0,85	0,125	1
20.0 °C	20	1	0	1,0	1,05		2
		2	1	1,0	1,51	0,363	5
		3	1	1,6	1,88	0,218	5
		4	1	2,0	2,52	0,296	5
		5	1	2,0	2,97	0,163	5
		6	1	2,6	3,78	0,242	5
		7	1	3,0	4,98	0,275	5
		8	1	3,0	5,56	0,111	4
		9	1	3,6	6,42	0,143	5
		10	1	4,0	7,22	0,117	5
		11	1	4,0	8,07	0,112	5
		12	1	4,0	7,68	-0,049	5
		13	1	4,0	9,10	0,169	5
Mean 6						**0,180**	
		14	1	4,0	8,48	-0,071	5
		15	1	4,0	9,27	0,089	5
		16	1	4,0	10,28	0,103	5
25.0 °C	22	0	0	1,0	0,97		2
		1	1	1,0	1,25	0,251	5
		2	1	1,8	1,95	0,441	4
		3	1	2,0	2,60	0,289	5
		5	2	2,6	3,50	0,149	5
		6	1	2,6	3,42	-0,024	5
		7	1	2,6	3,71	0,084	5
		8	1	3,2	5,03	0,304	6
		9	1	4,0	7,59	0,411	4
		10	1	4,0	8,28	0,087	3
		11	1	4,0	9,47	0,134	4
Mean 7						**0,212**	
		12	1	4,0	8,44	-0,114	5
		13	1	4,0	9,51	0,119	5
25.0 °C	23	0	0	1,0	0,85		2
		1	1	1,0	1,06	0,223	4
		2	1	1,5	1,70	0,473	4
		3	1	2,0	2,87	0,522	5
		5	2	3,0	4,16	0,186	5
		6	1	3,0	5,10	0,205	5
		7	1	3,4	5,16	0,010	5
		8	1	4,0	7,07	0,315	2
		9	1	3,8	7,73	0,089	4
		10	1	4,0	9,53	0,209	3
		11	1	4,0	10,00	0,048	6
Mean 8						**0,228**	
		12	1	4,0	9,34	-0,068	4
25.0 °C	24	0	0	1,0	0,90		3
		1	1	1,0	1,10	0,201	1

Appendix 9 (continued) (*Chironomus dorsalis*)

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
		2	1	1,0	1,42	0,256	4
25.0°C	24	8	6	4,0	6,64	0,257	3
		9	1	4,0	9,64	0,373	2
Mean 9						**0,272**	
		10	1	4,0	9,17	-0,051	3
		12	2	4,0	10,66	0,075	3
		0	0	1,0	0,77		5
		1	1	1,0	0,84	0,089	4
		2	1	1,0	0,98	0,154	5
30.2 °C	38	3	1	1,0	1,27	0,266	5
		5	2	2,5	3,07	0,440	10
		8	3	3,3	5,84	0,214	9
		11	3	3,9	8,48	0,125	9
		0	0	1,0	0,80		5
		1	1	1,0	0,87	0,089	5
		2	1	1,0	0,98	0,118	6
30.2 °C	39	4	2	2,1	2,82	0,526	8
		7	3	3,5	6,21	0,263	10
		10	3	4,0	8,81	0,116	11
		1	0	1,0	0,98		5
		3	2	1,0	1,32	0,150	11
30.2 °C	40	6	3	3,3	5,64	0,483	10
		9	3	4,0	7,79	0,108	10
			Polypedilum tritum				
		0		1,0	0,51		4
		7	7	1,0	0,74	0,054	5
		14	7	1,0	1,15	0,063	5
9.5 °C	93	22	8	2,0	1,86	0,060	5
		29	7	3,0	2,54	0,045	5
		36	7	3,0	3,36	0,040	5
		45	9	4,0	4,35	0,029	5
		53	8	4,0	5,93	0,039	5
Mean 1						**0,047**	
		60	7	4,0	5,38		5
		69	9	4,0	6,29		5
		0		1,0	0,57		4
		7	7	1,3	0,65	0,018	4
		14	7	1,0	1,09	0,073	4
9.5 °C	94	22	8	2,0	1,65	0,052	5
		29	7	3,0	2,71	0,071	4
		36	7	3,0	3,15	0,021	5
		45	9	3,8	4,13	0,030	5
		53	8	4,0	5,14	0,027	5
Mean 2						**0,042**	
		60	7	4,0	5,32		5
		69	9	4,0	5,51		7
9.5 °C	95	69		3,8	4,90		5
		0		1,0	0,58		3
		1	1	1,0	0,69	0,169	3
		4	3	1,0	0,98	0,115	3
		7	3	1,0	1,17	0,060	4
14.6 °C	97	10	3	2,0	1,47	0,077	5
		13	3	2,2	1,89	0,083	5
		16	3	3,0	2,74	0,124	5
		19	3	3,4	3,46	0,078	5
		22	3	4,0	3,99	0,047	5
		25	3	4,0	4,71	0,055	5
Mean 3						**0,090**	
		28	3	4,0	4,29		5
		32	4	3,8	4,29		5
		0		1,0	0,65		4
		3	3	1,0	0,75	0,047	2
		6	3	1,0	1,16	0,145	4
14.6 °C	98	9	3	2,0	1,55	0,096	4
		12	3	2,0	1,78	0,047	4
		15	3	3,0	2,71	0,140	4
		18	3	3,4	3,61	0,095	5
		21	3	4,0	4,62	0,083	5

Appendix 9 (continued) (*Polypedilum tritum*).

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
14.6 °C	98	24	3	4,0	5,18	0,038	5
Mean 4						**0,086**	
		27	3	4,0	4,89		5
		31	4	4,0	5,07		5
13.8 °C SD	101	72		4,0	5,43		5
13.8 °C SD	102	72		4,0	6,14		5
		0		1,0	0.49		3
		1	1	1,0	0,54		5
		3	2	1,0	0,64		5
13.8 °C SD	103	23	20	3,8	4,71		5
		29	6	4,0	4,67		5
		70	41	4,0	5,53		5
19.3 °C	104	2		1,0	0,91		3
		0		1,0	0,68		5
		1	1	1,0	0,70	0,039	2
		2	1	1,0	0,86	0,207	3
		3	1	1,0	1,13	0,272	4
		4	1	1,0	1,24	0,091	3
		5	1	1,8	1,38	0,103	6
		6	1	2,0	1,76	0,243	4
		7	1	2,2	2,02	0,141	5
		8	1	2,6	2,06	0,019	5
		9	1	2,8	2,62	0,240	5
19.3 °C	105	10	1	3,0	3,03	0,144	4
		11	1	3,0	3,26	0,074	5
		12	1	3,2	3,40	0,041	5
		13	1	3,4	3,36	-0,013	5
		14	1	3,8	3,73	0,106	5
		15	1	3,8	4,06	0,083	5
		16	1	4,0	4,28	0,054	5
		17	1	3,9	4,48	0,045	10
		18	1	4,0	4,73	0,055	5
		19	1	4,0	5,29	0,111	5
Mean 5						**0,108**	
		20	1	4,0	5,26		5
		21	1	4,0	5,34		6
		22	1	4,0	5,29		8
		8		2,0	1,75		4
19.3 °C	106	12	4	3,5	3,24	0,154	4
		21	9	4,0	4,58	0,039	5
		22	1	4,0	5,11		5
19.3 °C	107	22		4,0	5,51		5
		24	2	4,0	5,58		6
		0		1,0	0,73		3
		1	1	1,0	0,97	0,286	4
		2	1	1,3	1,21	0,220	3
		3	1	1,8	1,38	0,130	4
		4	1	2,0	1,83	0,277	5
25.0 °C	108	5	1	2,8	2,67	0,379	5
		6	1	3,2	3,38	0,237	5
		7	1	3,4	3,38	-0,001	5
		8	1	4,0	4,16	0,209	5
		9	1	3,8	3,86	-0,075	5
		10	1	4,0	5,21	0,299	5
Mean 6						**0,196**	
		11	1	4,0	4,83		5
		12	1	4,0	4,95		4
		0		1,0	0,70		5
		2	2	1,3	1,20	0,270	11
		3	1	1,6	1,41	0,165	5
		4	1	2,0	1,75	0,210	6
25.0 °C	109	5	1	2,0	2,13	0,200	4
		6	1	2,6	2,21	0,034	5
		7	1	3,0	3,20	0,373	5
		9	2	3,8	3,49	0,043	5
		10	1	3,8	4,02	0,142	5
Mean 7						**0,180**	
		11	1	3,8	3,52		5
		12	1	4,0	4,10		6

Appendix 9 (continued) (*Paralimnophyes hydrophilus*).

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
25.0 °C	110	6		3,0	2,52		5
		12	6	3,8	4,02		5
25.0 °C	111	12		4,0	4,31		5
30.2 °C	116	11		2,8	2,19		4
		14	3	3,2	2,57		5
		20	6	3,8	4,01		5
		27	7	3,6	3,69		5
30.2 °C	117	10		2,4	2,18		5
		13	3	2,8	2,63		5
		26	13	4,0	4,85		4
30.2 °C	118	0		1,0	0,61		3
		1	1	1,0	0,80		3
		2	1	1,0	1,07		5
		3	1	1,0	1,18		5
		4	1	1,3	1,16		4
		5	1	1,4	1,28		5
		8	3	2,6	1,97		5
		11	3	3,4	3,58		5
		14	3	2,8	2,64		6
Paralimnophyes hydrophilus							
4.5 °C	51	75,5	0	3,0	2,52		1
		97,5	22	3,0	2,59	0,001	1
		124,5	27	4,0	4,41	0,020	2
Mean 1						**0,010**	
4.5 °C	53	1	0	1,0	0,49		3
		10	9	1,0	0,58	0,018	2
		17	7	1,0	0,74	0,034	3
Mean 2						**0,026**	
		31	14	1,0	0,71	-0,003	4
4.5 °C	54	7	0	1,0	0,51		3
		14	7	1,0	0,73	0,052	3
		72	58	2,0	1,56	0,013	1
		94	22	4,0	3,53	0,037	1
		121	27	4,0	3,95	0,004	3
Mean 3						**0,027**	
		123	2	3,4	2,92	-0,151	5
9.5 °C	55	64	0	4,0	3,63		5
9.5 °C	56	37	0	3,4	2,69		5
		44	7	4,0	3,17	0,023	5
		53	9	4,0	3,34	0,006	5
9.5 °C	57	0	0	1,0	0,54		5
		1	1	1,0	0,57	0,042	5
		4	3	1,0	0,62	0,030	4
		10	6	1,0	0,59	-0,010	5
		17	7	1,0	0,75	0,036	3
		24	7	1,6	1,20	0,067	5
		30	6	2,0	1,62	0,050	4
		44	14	2,4	1,84	0,009	5
		53	9	3,8	3,12	0,059	5
Mean 4						**0,035**	
9.5 °C	58	0	0	1,0	0,50		5
		4	4	1,0	0,58	0,036	5
		10	6	1,0	0,66	0,022	6
		17	7	1,0	0,71	0,012	3
		24	7	1,4	1,00	0,048	5
		30	6	2,0	1,40	0,056	5
		37	7	2,0	1,33	-0,007	4
		44	7	3,0	1,96	0,055	5
		53	9	4,0	2,82	0,040	5
Mean 5						**0,033**	
14.6 °C	59	13	0	2,0			1
		17	4	3,0	2,18		5
		26	9	4,0	4,11	0,071	5
14.6 °C	60	8	0	1,0	0,94		1
		10	2	2,3	1,42	0,207	3
		17	7	4,0	3,15	0,114	3
		20	3	4,0	3,15	-0,001	5

Appendix 9 (continued) (*Paralimnophyes hydrophilus*).

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
14.6 °C	60	24	4	4,0	3,49	0,026	5
Mean 6						**0,086**	
		0	0	1,0	0,57		5
		1	1	1,0	0,49	-0,138	4
		2	1	1,0	0,63	0,247	5
		4	2	1,0	0,72	0,063	2
		6	2	1,0	0,85	0,087	3
14.6 °C	61	8	2	1,7	1,14	0,147	3
		11	3	2,0	1,33	0,051	1
		15	4	2,6	1,92	0,091	5
		18	3	2,8	2,23	0,049	5
		21	3	3,3	2,89	0,087	4
		24	3	3,8	3,53	0,067	5
Mean 7						**0,075**	
		27	3	4,0	3,33	-0,020	5
		0	0	1,0	0,61		5
		1	1	1,0	0,60	-0,018	3
		3	2	1,0	0,79	0,137	3
		4	1	1,0	0,77	-0,029	1
		5	1	1,0	0,82	0,063	2
		7	2	1,0	1,04	0,121	1
14.6 °C	62	9	2	2,0	1,28	0,107	3
		11	2	2,3	1,63	0,119	1
		14	3	2,5	1,87	0,045	2
		18	4	4,0	2,95	0,114	3
		21	3	4,0	3,15	0,021	5
		24	3	4,0	4,00	0,080	5
Mean 8						**0,069**	
		27	3	4,0	3,47	-0,047	5
		0	0	1,0	0,49		5
		1	1	1,0	0,59	0,173	5
		3	2	1,0	0,71	0,097	5
		5	2	1,0	0,95	0,147	3
		8	3	1,0	1,05	0,033	3
14.6 °C	63	12	4	2,0	1,45	0,080	5
		15	3	2,2	1,72	0,058	5
		18	3	3,0	2,39	0,109	5
		21	3	2,8	1,91	-0,074	5
		24	3	3,4	2,35	0,069	5
		28	4	4,0	3,00	0,061	5
Mean 9						**0,075**	
		31	3	4,0	2,96	-0,005	5
		41	10	4,0	3,28	0,010	5
19.3 °C	64	15	0	4,0	4,06		5
		11	0	4,0	3,13		5
		12	1	4,0	3,24	0,036	4
19.3 °C	65	13	1	4,0	2,91		5
		15	2	4,0	4,15	0,178	5
		16	1	4,0	3,74	-0,103	5
		0	0	1,0	0,54		5
		1	1	1,0	0,64	0,167	5
		2	1	1,0	0,77	0,186	3
		3	1	1,0	0,96	0,220	5
		4	1	1,0	1,02	0,056	4
		5	1	1,3	1,03	0,017	3
		6	1	2,0	1,40	0,301	5
		7	1	2,0	1,52	0,082	5
19.3 °C	66	8	1	2,6	1,80	0,171	5
		9	1	2,8	1,87	0,041	5
		10	1	3,4	2,36	0,229	5
		11	1	3,6	2,40	0,016	5
		12	1	3,8	2,91	0,195	5
		13	1	3,8	2,80	-0,040	5
		14	1	3,8	2,98	0,064	6
		15	1	4,0	3,60	0,188	3
Mean 10						**0,126**	
		16	1	3,8	2,81	-0,248	5
		18	2	4,0	3,37	0,092	5
19.3 °C	67	1	0	1,0	0,76		3

Appendix 9 (continued) (*Paralimnophyes hydrophilus*).

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
		2	1	1,0	0,81	0,068	4
		4	2	2,0	1,12	0,161	2
		5	1	1,5	1,03	-0,090	4
		7	2	2,0	1,31	0,121	2
19.3 °C	67	9	2	3,0	1,86	0,176	2
		10	1	2,7	1,80	-0,035	3
		12	2	3,0	2,24	0,109	3
		14	2	4,0	3,06	0,157	2
		15	1	4,0	2,72	-0,120	1
		16	1	4,0	3,36	0,212	1
Mean 11						**0,076**	
		18	2	4,0	3,11	-0,038	3
		19	1	4,0	3,39	0,085	3
		20	1	4,0	3,11	-0,086	2
		0	0	1,0	0,54		3
		1	1	1,0	0,62	0,145	4
		2	1	1,0	0,64	0,036	4
		3	1	1,0	0,77	0,185	5
		4	1	1,0	0,91	0,166	5
19.3 °C	68	5	1	1,0	0,86	-0,055	4
		6	1	1,5	1,03	0,180	4
		7	1	2,0	1,42	0,318	3
		8	1	1,8	1,29	-0,092	5
		11	3	2,8	1,90	0,129	5
		12	1	3,4	2,33	0,201	5
		13	1	3,4	2,19	-0,061	5
Mean 12						**0,105**	
		15	2	3,0	2,19	-0,001	5
		20	5	4,0	3,63	0,101	5
		0	0	1,0	0,55		3
		1	1	1,0	0,69	0,224	5
		2	1	1,0	0,99	0,360	1
		3	1	1,4	1,01	0,026	5
		4	1	1,6	1,22	0,182	5
25.0 °C	70	5	1	2,0	1,67	0,319	5
		6	1	2,5	1,79	0,071	4
		7	1	3,0	2,18	0,192	5
		8	1	3,5	2,52	0,145	6
		9	1	3,8	2,50	-0,005	5
		10	1	4,0	3,26	0,265	5
Mean 13						**0,178**	
		11	1	4,0	2,84	-0,138	3
		13	2	4,0	3,33	0,080	3
25.0 °C	71	10	0	4,0	2,91		5
		0	0	1,0	0,56		9
		1	1	1,0	0,74	0,273	1
		2	1	1,0	0,99	0,285	5
		3	1	1,3	1,07	0,081	3
		4	1	2,0	1,26	0,168	5
25.0 °C	72	5	1	2,0	1,58	0,226	5
		6	1	3,0	2,02	0,244	5
		7	1	3,4	2,49	0,208	5
		8	1	4,0	2,62	0,051	5
		9	1	4,0	2,51	-0,043	5
		10	1	4,0	2,95	0,161	6
		11	1	4,0	3,11	0,053	5
Mean 14						**0,155**	
		13	2	4,0	3,07	-0,006	5
		7	0	3,8	2,91		5
		8	1	3,4	2,29	-0,243	5
29.0 °C	74	10	2	3,7	2,62	0,069	3
		11	1	3,8	2,84	0,081	5
		14	3	4,0	3,02	0,020	4
		15	1	4,0	2,89	-0,045	1
29.0 °C	75	7	0	2,6	1,86		5
		17	10	3,5	2,34	0,023	2
		0	0	1,0	0,51		4
29.0 °C	76	1	1	1,0	0,63	0,212	4
		2	1	1,0	0,77	0,204	5

Appendix 9 (continued) (*Paralimnophyes hydrophilus*).

Temperature	Box Nr.	Days after hatching	Days between samplings	Instar*	Body length**	Growth rate***	N
29.0 °C	76	3	1	1,3	0,80	0,037	4
		4	1	1,0	0,99	0,207	1
		5	1	1,0	0,92	-0,067	2
		10	5	3,0	1,85	0,139	1
		15	5	2,3	1,50	-0,042	4
29.0 °C	77	2	0	1,0	0,67		1
		4	2	1,0	0,89	0,144	1
		10	6	2,0	1,51	0,088	1
29.0 °C	78	0	0	1,0	0,55		4
		1	1	1,0	0,61	0,113	5
		3	2	1,0	0,86	0,171	2
		8	5	3,3	2,00	0,168	3
		9	1	4,0	2,79	0,331	1
		16	7	4,0	2,90	0,005	2
29.0 °C	79	0	0	1,0	0,50		5
		1	1	1,0	0,52	0,051	4
		2	1	1,0	0,59	0,123	1
		4	2	1,0	0,65	0,049	2

Explanations:

$$* \quad \sum_{\text{Instar I}}^{\text{Instar IV}} \text{Instar numbers} \Big/ n$$

** geometric mean of body length per sampling (section 3.5.1.);

*** for definition see section 3.5.8.

Mean 1 - x: these mean values were used for calculating the regressions of mean growth rates versus temperatures (section 4.4.1.2.8., Table 41 p 143).

Appendix 10: Results of the experiment on drought tolerance.

Instar	Days	Medium	Begin (%)	End (%)	Class	Survival (%)
			Chironomus dorsalis			
I	3	50 % KOH	63.7	56.1	3	100.0
I	3	50 % KOH	67.7	63.9	4	90.0
I	6	50 % KOH	63.2	27.4	2	93.3
I	6	50 % KOH	81.7	80.4	5	56.7
I	12	50 % KOH	88.3	69.8	4	0.0
I	18	50 % KOH	69.7	4.0	1	0.0
I	18	50 % KOH	79.2	69.9	4	70.0
I	24	50 % KOH	65.5	1.3	1	0.0
I	24	50 % KOH	81.3	58.1	3	0.0
I	30	50 % KOH	78.4	15.8	1	0.0
III/IV	3	50 % KOH	81.2	80.9	5	90.0
III/IV	6	50 % KOH	79.3	78.0	4	80.0
III/IV	12	50 % KOH	79.8	77.0	4	10.0
III/IV	18	50 % KOH	77.0	71.1	4	0.0
III/IV	24	50 % KOH	82.3	76.1	4	0.0
III/IV	30	50 % KOH	81.9	63.3	4	25.0
III/IV	60	50 % KOH	81.6	3.0	1	0.0
IV	3	50 % KOH	81.2	80.5	5	75.0
IV	6	50 % KOH	83.3	82.7	5	0.0
IV	12	50 % KOH	82.7	73.2	4	0.0
IV	18	50 % KOH	83.4	5.0	1	0.0
IV	24	50 % KOH	79.2	43.5	3	0.0
IV	30	50 % KOH	81.2	51.0	3	0.0
IV	60	50 % KOH	83.6	2.0	1	0.0
			***Chironomus plumosus* aggregate**			
I	3	50 % KOH	70.6	65.9	4	63.3
I	6	50 % KOH	56.0	37.3	2	0.0
I	12	50 % KOH	63.1	39.3	2	0.0
I	18	50 % KOH	69.9	8.0	1	0.0
I	24	50 % KOH	57.6	5.8	1	0.0
I	30	50 % KOH	56.1	5.0	1	0.0
II	3	50 % KOH	81.5	81.2	5	35.0
II	6	50 % KOH	85.8	85.5	5	60.0
II	12	50 % KOH	84.9	76.2	4	65.0
II	18	50 % KOH	84.2	77.3	4	30.0
II	24	50 % KOH	83.5	55.0	3	0.0
II	30	50 % KOH	86.1	25.3	2	0.0
III/IV	3	50 % KOH	40.9	40.5	3	80.0
III/IV	6	50 % KOH	54.8	54.0	3	75.0
III/IV	12	50 % KOH	47.1	36.2	2	50.0
III/IV	18	50 % KOH	49.3	33.5	2	0.0
III/IV	24	50 % KOH	48.3	37.7	2	15.0
III/IV	30	50 % KOH	58.8	52.4	3	25.0
III/IV	60	50 % KOH	49.6	16.1	1	0.0
IV	3	50 % KOH	35.6	34.8	2	73.3
IV	6	50 % KOH	34.3	33.4	2	53.3
IV	12	50 % KOH	37.8	27.6	2	26.7
IV	18	50 % KOH	38.0	26.5	2	0.0
IV	24	50 % KOH	37.9	32.0	2	0.0
IV	30	50 % KOH	40.5	36.4	2	10.0
IV	60	50 % KOH	47.1	14.3	1	0.0
			Polypedilum tritum			
I	3	5 % KOH	71.7	71.7	4	76.7
I	3	5 % KOH	75.0	74.2	4	30.8
I	3	50 % KOH	70.9	67.5	4	66.7

Appendix 10 (continued) (*P. tritum*).

Instar	Days	Medium	Begin (%)	End (%)	Class	Survival (%)
I	3	50 % KOH	67.0	55.3	3	41.1
I	3	silicate granulate	83.7	81.7	5	90.0
I	3	silicate granulate	85.3	84.8	5	85.0
I	6	5 % KOH	73.9	70.9	4	73.3
I	6	5 % KOH	79.5	78.9	4	66.7
I	6	50 % KOH	64.6	21.5	2	16.7
I	6	50 % KOH	71.5	65.0	4	46.2
I	6	silicate granulate	85.7	59.1	3	90.0
I	6	silicate granulate	86.4	85.9	5	82.5
I	12	5 % KOH	72.5	66.2	4	73.3
I	12	5 % KOH	80.5	78.8	4	30.8
I	12	50 % KOH	60.4	1.9	1	0.0
I	12	50 % KOH	77.3	32.7	2	20.5
I	12	silicate granulate	84.5	12.6	1	0.0
I	12	silicate granulate	86.2	85.4	5	80.0
I	18	5 % KOH	79.4	76.2	4	66.7
I	18	50 % KOH	58.7	1.9	1	0.0
I	18	50 % KOH	68.6	4.1	1	0.0
I	18	silicate granulate	85.7	83.6	5	70.0
I	24	5 % KOH	70.1	48.8	3	70.0
I	24	5 % KOH	76.1	74.0	4	51.3
I	24	50 % KOH	55.6	2.2	1	0.0
I	24	50 % KOH	70.2	3.3	1	0.0
I	24	silicate granulate	85.3	11.7	1	0.0
I	24	silicate granulate	86.4	79.2	4	67.5
I	30	5 % KOH	75.4	59.1	3	10.0
I	30	5 % KOH	78.3	75.2	4	77.0
I	30	50 % KOH	78.5	3.2	1	0.0
I	30	silicate granulate	83.0	12.3	1	0.0
I	30	silicate granulate	82.7	0.9	1	0.0
I	60	5 % KOH	85.9	82.9	5	66.7
I	60	50 % KOH	86.8	12.2	1	0.0
I	60	silicate granulate	83.0	13.3	1	0.0
I	90	50 % KOH	85.5	12.3	1	0.0
I	90	90 % KOH	86.4	73.8	4	66.7
I	90	silicate granulate	86.7	13.6	1	0.0
I	180	5 % KOH	86.7	84.6	5	25.7
I	180	50 % KOH	82.6	27.9	2	0.0
I	180	silicate granulate	87.1	9.5	1	0.0
III	3	5 % KOH	88.1	88.0	5	50.0
III	3	50 % KOH	80.4	77.4	4	56.7
III	3	silicate granulate	72.8	9.2	1	0.0
III	6	5 % KOH	87.4	87.1	5	63.3
III	6	50 % KOH	82.6	81.3	5	66.7
III	6	silicate granulate	70.6	8.6	1	0.0
III	12	5 % KOH	88.0	87.4	5	66.7
III	12	50 % KOH	80.6	77.5	4	36.7
III	12	silicate granulate	52.5	6.4	1	0.0
III	18	5 % KOH	84.5	83.5	5	80.0
III	18	50 % KOH	81.8	77.4	4	53.3
III	18	silicate granulate	82.9	15.4	1	0.0
III	24	5 % KOH	85.0	83.5	5	26.7
III	24	50 % KOH	78.7	2.9	1	0.0
III	24	silicate granulate	53.3	2.8	1	0.0
III	30	5 % KOH	87.4	84.4	5	36.7
III	30	50 % KOH	81.4	44.9	3	40.0

Appendix 10 (continued) (*P. tritum*).

Instar	Days	Medium	Begin (%)	End (%)	Class	Survival (%)
III	30	silicate granulate	82.4	28.0	2	53.3
III	60	5 % KOH	85.5	83.0	5	56.7
III	60	50 % KOH	87.5	63.9	4	56.7
III	60	silicate granulate	81.6	68.3	4	46.7
III	90	5 % KOH	88.4	83.8	5	16.7
III	90	50 % KOH	86.7	57.8	3	40.0
III	90	silicate granulate	82.1	66.0	4	50.0
III	180	5 % KOH	89.2	77.1	4	6.7
III	180	50 % KOH	82.2	31.5	2	33.3
III	180	silicate granulate	81.0	13.5	1	0.0
IV	3	5 % KOH	85.6	76.5	4	56.7
IV	3	50 % KOH	69.1	54.7	3	50.0
IV	4	silicate granulate	36.0	8.3	1	36.7
IV	6	5 % KOH	78.1	76.6	4	56.7
IV	6	50 % KOH	55.3	24.8	2	33.3
IV	6	silicate granulate	66.8	62.4	4	26.7
IV	12	5 % KOH	82.3	80.5	5	16.7
IV	12	50 % KOH	75.8	70.6	4	6.7
IV	12	silicate granulate	66.0	23.4	2	3.3
IV	18	5 % KOH	82.0	79.9	4	6.7
IV	18	50 % KOH	77.6	73.2	4	6.7
IV	24	5 % KOH	77.5	70.9	4	43.3
IV	24	50 % KOH	67.0	27.2	2	26.7
IV	24	silicate granulate	55.7	3.2	1	0.0
IV	24	silicate granulate	60.7	4.4	1	0.0
IV	30	5 % KOH	79.6	76.5	4	13.3
IV	30	50 % KOH	78.3	52.8	3	0.0
IV	30	silicate granulate	57.2	28.8	2	33.3
IV	60	5 % KOH	81.5	78.4	4	0.0
IV	60	50 % KOH	50.0	26.1	2	6.7
IV	60	silicate granulate	56.0	28.8	2	0.0
IV	90	5 % KOH	79.6	81.8	5	16.7
IV	90	50 % KOH	65.5	25.4	2	0.0
IV	90	silicate granulate	77.9	87.7	5	3.3
IV	180	5 % KOH	85.8	55.1	3	3.3
IV	180	50 % KOH	71.4	10.0	1	0.0
IV	180	silicate granulate		-	1	0.0
		***Limnophyes asquamatus* parthenogenetic**				
III	3	50 % KOH	75.4	69.1	4	35.0
III	3	silicate granulate	72.8	63.9	4	50.0
III	6	50 % KOH	73.1	54.8	3	60.0
III	6	silicate granulate	73.2	54.4	3	50.0
III	12	50 % KOH	71.4	36.2	2	50.0
III	12	silicate granulate	76.8	42.5	3	60.0
III	18	50 % KOH	68.6	38.4	2	35.0
III	18	silicate granulate	75.5	26.5	2	50.0
III	24	50 % KOH	71.2	40.0	3	60.0
III	24	silicate granulate	79.5	24.1	2	30.0
III	30	50 % KOH	67.2	8.2	1	0.0
III	30	silicate granulate	74.7	25.2	2	45.0
III	60	50 % KOH	68.6	50.4	3	35.0
III	60	silicate granulate	74.3	45.9	3	20.0
III	90	50 % KOH	72.6	30.5	2	25.0
III	90	silicate granulate	68.4	25.2	2	10.0
III	180	50 % KOH	75.5	30.0	2	0.0
III	180	silicate granulate	68.6	46.1	3	45.0

Appendix 10 continued (*L. asquamatus*).

Instar	Days	Medium	Begin (%)	End (%)	Class	Survival (%)
IV	3	50 % KOH	71.6	69.5	4	90.0
IV	3	silicate granulate	62.9	47.3	3	15.0
IV	6	50 % KOH	63.7	50.0	3	80.0
IV	6	silicate granulate	65.6	43.6	3	65.0
IV	12	50 % KOH	69.1	45.8	3	90.0
IV	12	silicate granulate	62.5	39.3	2	75.0
IV	18	50 % KOH	64.6	27.2	2	10.0
IV	18	silicate granulate	67.3	40.0	3	75.0
IV	24	50 % KOH	61.7	5.2	1	0.0
IV	24	silicate granulate	68.3	36.3	2	30.0
IV	30	50 % KOH	55.6	50.1	3	55.0
IV	30	silicate granulate	77.8	17.5	1	0.0
IV	60	50 % KOH	66.0	33.8	2	30.0
IV	60	silicate granulate	64.2	45.2	3	65.0
IV	90	50 % KOH	65.3	43.9	3	60.0
IV	90	silicate granulate	71.3	33.4	2	35.0
IV	180	50 % KOH	58.6	33.8	2	5.0
IV	180	silicate granulate	69.3	57.2	3	10.0
		Paralimnophyes hydrophilus				
I	3	50 % KOH	61.4	57.2	3	80.0
I	3	silicate granulate	68.4	64.2	4	80.0
I	6	50 % KOH	66.6	63.0	4	75.0
I	6	silicate granulate	70.7	65.7	4	60.0
I	12	50 % KOH	66.0	60.8	4	60.0
I	12	silicate granulate	73.1	67.3	4	55.0
I	18	50 % KOH	65.6	52.1	3	55.0
I	18	silicate granulate	71.5	37.6	2	60.0
I	24	50 % KOH	74.4	39.5	2	55.0
I	24	silicate granulate	68.2	22.2	2	0.0
I	30	50 % KOH	72.0	22.9	2	0.0
I	30	silicate granulate	73.7	10.6	1	0.0
I	60	50 % KOH	70.1	28.9	2	40.0
I	60	silicate granulate	68.9	39.3	2	0.0
I	90	50 % KOH		53.7	3	20.0
I	90	silicate granulate	72.1		1	0.0
I	180	silicate granulate	68.7	33.2	2	0.0
II	3	50 % KOH	73.2	71.3	4	75.0
II	3	silicate granulate	71.5	68.8	4	65.0
II	6	50 % KOH	69.4	66.3	4	95.0
II	6	silicate granulate	70.7	63.8	4	70.0
II	12	50 % KOH	79.3	67.1	4	95.0
II	12	silicate granulate	68.1	51.1	3	80.0
II	18	50 % KOH	74.1	40.4	3	95.0
II	18	silicate granulate	64.9	35.7	2	75.0
II	24	50 % KOH	77.3	36.5	2	30.0
II	24	silicate granulate	66.7	28.4	2	35.0
II	30	50 % KOH	68.9	6.9	1	0.0
II	30	silicate granulate	63.9	28.2	2	30.0
II	60	50 % KOH	70.4	34.5	2	20.0
II	60	silicate granulate	72.3	33.2	2	45.0
II	90	50 % KOH	71.6	34.2	2	25.0
II	90	silicate granulate	72.2	25.4	2	15.0
II	180	50 % KOH	69.5	39.1	2	15.0
II	180	silicate granulate	68.5	45.6	3	5.0
III	3	50 % KOH	71.3	70.4	4	70.0
III	3	silicate granulate	65.4	63.6	4	70.0

Appendix 10 continued (*Paralimnophyes hydrophilus*).

Instar	Days	Medium	Begin (%)	End (%)	Class	Survival (%)
III	6	5 % KOH		70.7	68.1	4	100.0
III	6	50 % KOH		66.5	63.0	4	65.0
III	6	silicate granulate		70.0	65.2	4	90.0
III	12	5 % KOH		70.5	49.2	3	45.0
III	12	50 % KOH		75.9	63.8	4	35.0
III	12	silicate granulate		69.3	56.3	3	40.0
III	18	5 % KOH		78.3	57.9	3	25.0
III	18	50 % KOH		69.6	33.3	2	50.0
III	18	silicate granulate		73.9	56.6	3	55.0
III	24	50 % KOH		73.6	36.5	2	20.0
III	24	silicate granulate		75.6	41.1	3	35.0
III	30	5 % KOH		68.0	8.1	1	0.0
III	30	50 % KOH		72.7	7.8	1	0.0
III	30	silicate granulate		65.3	28.0	2	65.0
III	60	5 % KOH		72.2	36.8	2	50.0
III	60	50 % KOH		70.5	33.0	2	30.0
III	60	silicate granulate		70.2	54.4	3	60.0
III	90	5 % KOH		69.9	30.3	2	5.0
III	90	50 % KOH		71.9	31.9	2	10.0
III	90	silicate granulate		68.5	24.3	2	5.0
III	180	5 % KOH		72.2	37.1	2	5.0
III	180	50 % KOH		71.8	31.2	2	0.0
III	180	silicate granulate		72.5	23.2	2	0.0
IV	3	50 % KOH		74.9	72.7	4	40.0
IV	3	silicate granulate		69.1	65.5	4	40.0
IV	6	5 % KOH		67.6	57.3	3	45.0
IV	6	50 % KOH		73.3	70.4	4	40.0
IV	6	silicate granulate		74.2	67.8	4	30.0
IV	12	5 % KOH		70.5	51.0	3	80.0
IV	12	50 % KOH		65.8	48.9	3	40.0
IV	12	silicate granulate		77.2	52.3	3	20.0
IV	18	5 % KOH		71.8	43.7	3	5.0
IV	18	50 % KOH		75.3	50.9	3	15.0
IV	18	silicate granulate		71.9	32.3	2	25.0
IV	24	50 % KOH		70.0	37.1	2	15.0
IV	24	silicate granulate		72.9	29.1	2	5.0
IV	30	5 % KOH		74.0	9.7	1	0.0
IV	30	50 % KOH		70.6	7.6	1	0.0
IV	30	silicate granulate		71.8	14.3	1	0.0
IV	60	5 % KOH		76.4	53.1	3	5.0
IV	60	50 % KOH		73.2	41.9	3	10.0
IV	60	silicate granulate		66.5	31.4	2	15.0
IV	90	5 % KOH		73.2	43.9	3	10.0
IV	90	50 % KOH		73.6	42.8	3	0.0
IV	90	silicate granulate		68.4	23.2	2	0.0
IV	180	5 % KOH		77.9	56.1	3	0.0
IV	180	50 % KOH		73.8	32.9	2	0.0
IV	180	silicate granulate		69.7	34.6	2	0.0

Explanations:

Instar = larval instar: I = instar 1, II = instar 2, III = instar 3, III/IV = instars 3 and some small larvae in the instar 4, IV = instar IV ; Medium = kind of hygroscopic medium used in the experiment; Begin (%)/End (%) = water content (% of mud weight) at the beginning/end of the experiment; Class = class of humidity at the end of the experiment (class 1: 0 - 19.9 %, class 2: 20 - 39.9 %, class 3: 40 - 59.9 %, class 4: 60 - 79.9 %, class 5: 80 - 90 %); survival (%) = percentage of aestivated individuals.

Appendix 11: Chironomidae recorded during temporary pool research studies.

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
Chironominae/Chironomini												
1. *Apedilum elachistus*			NOLTE 1995(f)									not drought-tolerant (colonizer)
2. *Beardius* spec.			4(f)									
Chironomus spec.	11(f), 19(f)				16(f)	12(f),29(-)	14(f)			9(f)	17(-)	
3. C *Chironomus aberratus*	25(-)											
4. *Chironomus alternans*					6(-)							
5. *Chironomus annularius*	19(-),34(-)					18(-)						
6. *Chironomus aprilinus*											17(-)	
7. *Chironomus attenuatus*		13(f)										
8. *Chironomus cingulatus*	3(-),19(-)											
9. *Chironomus conjunctus*					6(-)							
10. *Chironomus curtivalva*					6(-)							
11. *Chironomus decorus*		15(f)										
Chironomus dorsalis prior 1959***	19(f),24(f), 26(-)											
12. *Chironomus dorsalis* posterior 1959***	3(f),20(f), 25(f),34(f)	8(f)				2(-),10(-)						predominantly in puddles i.e. extremely astatic waters (see section 5.3.1.2.)
13. *Chironomus imicola*				30(f)								
14. *Chironomus lacunarius*	25(f),26(f), 27(-)											typical for pools on alpine pastures
15. *Chironomus longipes*	3(-),20(-), 34(-)											
16. *Chironomus luridus*	34(f)					2(f)						
17. Chironomus *lugubris/piger/riparius*	5(f), 23(-), 24(f),34(f)	13(f),				2(f),10(-), 18(-)						
18. *Chironomus pallidivittatus*		13(-)										
19. *Chironomus plumosus* agg.	19(-)					10(f)						
20. *Chironomus pseudothummi* agg	1(-),3(f), 20(f)	13(-),				2(-),10(-)						
21. *Chironomus pulcher*				30(f)								
22. *Chironomus salinarius*											17(-)	
23. *Chironomus staegeri*	13(-)											
24. *Chironomus stigmaterus*		21(-)										at least drought tolerant
25. *Chironomus tentans*		13(-)										
26. *Chironomus tepperi*					6(-)					7(f)		
27. *Chironomus tuxis*		21(-)										at least drought tolerant
28. *Chironomus zealandicus*					22(-)							
29. *Cladopelma* spec.			4(-)							7(f), 9(f)		
Cryptochironomus spec.			4(-)							7(f),9(-)		
30. *Cryptochironomus defectus*						12(-)						
31. *Cryptochironomus rostratus*						10(-)						
32. *Cryptochironomus supplicans*						10(-)						

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
34. *Cryptocladophelma virescens*						10(-)						
34. *Cryptocladophelma laccophila* agg.						10(-)						
35. *Demeijerera brachialis*							14(-)					
Dicrotendipes spec.	23(-)	15(-)			16(-)					9(f)		
36. *Dicrotendipes leucoscelis*						14(-)						
37. *Dicrotendipes lobiger*	3(-),19(-), 34(-)											
38. *Dicrotendipes* cf. *lucifer*							14(-)					
39. *Dicrotendipes modestus*							14(f)					
40. *Dicrotendipes nervosus*/agg.		13(-)				10(-),18(-) 29(-)	14(f)					
41. *Dicrotendipes notatus*	34(-)											
42. *Dicrotendipes* cf. *thanatogratus*							14(-)					
43. *Dicrotendipes* cf. *tritomus*							14(-)					
Einfeldia spec.							14(f)					
44. *Einfeldia dissidens*	25(-)											
45. *Einfeldia pagana*	3(-)	13(-)										
Endochironomus spec.		15(-)				12(-)						
46. *Endochironomus albipennis*						10(f),29(-)						
47. *Endochironomus nigricans*		13(-),21(-)				14(-)						
48. *Endochironomus tendens*	3(-),19(-), 34(-)					10(-),18(-)						
Glyptotendipes spec.		15(-),21(-)				12(-)						
49. *Glyptochironomus barbipes*		13(-)				10(-)					17	
50. *Glyptotendipes dreisbachi*		13(-)										
51. *Glyptotendipes gripekoveni*	19(-)					10(-),12(-)						
52. *Glyptotendipes lobiferus*		13(-)										
53. *Glyptotendipes pallens*	5(f)					10(f),18(-) 29(-)						
54. *Glyptotendipes paripes*	3(-)					10(f)						
55. *Glyptotendipes unacus*		13(-)										
Goeldichironomus spec.			4(f)									
56. *Goeldichironomus holoprasinus*							14(-)					
Harnischia spec.		15(-)										
57. *Harnischia viriduala*		13(-)										
58. *Kiefferulus dux*		13(-)					14(f)					
59. *Kiefferulus martini*										9(-)		
60. *Kiefferulus tendipediformis*						10(-),18(-)					17(-)	
Microchironomus spec.										7(f),9(f)		
61. *Microchironomus deribae*											17(-)	
Microtendipes spec.										9(-)		
62. *Microtendipes chloris* agg.						10(-)						

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
63. *Microtendipes pedellus*	3(-),11(f), 34(-)					10(-)	14(-)					
64. *Omisus pica*							14(-)					
Paraborniella spec.										9(f)		
65. *Paraborniella tonnoiri*					6(f),32(f)							drought resistent (JONES 1975)
Parachironomus spec.	19(-)	8(-),13(-) 21(-)	4(-)		16(f)		14(-)			7(f),9(f)		
66. *Parachironomus arcuatus*						10(f),18(f)						
67. *Parachironomus biannulatus*						10(-)						
68. *Parachironomus digitalis*						2(-)						
69. *Parachironomus parilis*	34(-)											
70. *Paracladopelma laminata* agg.						10(-)						
Paratendipes spec.		15(-)										
71. *Paratendipes albimanus/plebeius*	3(-),34(-)					2(f),10(-), 12(-),29(-)						
Phaenopsectra spec.		8(-),21(-)										at least drought tolerant
72. *Phaenopsectra flavipes*		31(-)				2(f),10(-),12(-)						colonizer (GRODHAUS 1987b)
73. *Phaenopsectra mortensoni*		31(-)										at least drought tolerant (GRODHAUS 1987b)
74. *Phaenopsectra pilicellata*		31(-)										drought resistent, summer-dormant, specific (GRODHAUS 1976, 1980,1987b)
75. *Phaenopsectra profusa*		31(-)										colonizer (GRODHAUS 1987b)
76. *Phaenopsectra punctipes*	34(-)											
Polypedilum spec.	11(-),	8(f), 15(-)	4(-)			12(-)						
77. *Polypedilum arundinetum*	34(-)											
78. *Polypedilum cultellatum*						2(-),18(-)						
79. *Polypedilum* cf. *dewulfi*				30(h)								drought resistent (MILLER 1969)
80. *Polypedilum* gr. *fallax*		21(-)										at least drought tolerant
81. *Polypedilum flavicorne*							14(-)					
82. *Polypedilum leei*										9(f)		
83. *Polypedilum leucopum*						10(-)						
84. *Polypedilum nubeculosum*	1(-),3(-)					10(f),18(-)						
Polypedilum gr. *nubeculosum*						29(-)						
85. *Polypedilum nubifer*	11(-)				6(-),					9(-)		
86. *Polypedilum oresitrophus*										9(-)		
87. *Polypedilum pedestre* agg.						10(-)						
88. *Polypedilum sordens*						2(-),18(-),29(-)						
Polypedilum sordens agg.						10(-)						
89. *Polypedilum trigonus*						14(-)						
90. *Polypedilum tritum/uncinatum*	1(f),3(f),19(-), 20(f),34(f)					2(-),10(-), 29(-)	14(f)					drought tolerant (present study)

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
Polypedilum uncinatum agg.											17(-)	
91. *Polypedilum vanderplanki*				30(f)								cryptobiosis (HINTON 1951, 1960a, 1960b, 1968, ADAMS 1984)
Stenochironomus spec.										9(-)		
92. *Stenochironomus cinctus*							14(-)					
93. *Stictichironomus* spec.	23(-)											
Synendotendipes spec.						10(-),29(-)						
94. *Synendotendipes impar*	3(-),34(-)											
95. *Synendotendipes lepidus*	3(-),34(-)											
96. *Tribelos* spec. a		31(-)										drought resistent, summer-dormant, specific (GRODHAUS 1976, 1980, 1987b)
97. *Tribelos* spec. b		31(-)										at least drought tolerant, specific (GRODHAUS 1980, 1987b)
98. *Tribelos ater*							14(-)					
99. *Wirthiella* spec.		31(-)										at least drought tolerant (GRODHAUS 1980)
100. *Potthastia longimanus*						10(-)						
Diamesinae												
101. Harrisonia petricola				33(-)								
Orthocladiinae												
102. *Acricotopus lucens*	3(-),34(-)					10(-),12(-)					17(-)	
103. *Acricotopus nitidellus*		13(f),21(-)										
104. *Allotrissocladius amphibius*					6(f)							drought resistent (EDWARD 1968)
105. *Cardiocladius* spec.	11(-)											
Chaetocladius spec.						12(-)					17(-)	
106. *Chaetocladius dentiforceps*	1(f)											
Chaetocladius dentiforceps agg.											17(-)	
107. *Chaetocladius perennis*	20(-),23(-)											
108. *Chaetocladius piger* agg.						10(f)					17(-)	
109. *Chaetocladius* gr. *vitellinus*	23(-)											
Corynoneura spec.	1(-),3(f), ,5(-), 11(f), 19(-), 20(f),27(-)	8(f), 15(-)	4(-)			2(-),12(-)	14(-)			9(f)		
110. *Corynoneura brundini*						10(-)						
111. *Corynoneura edwardsi*						10(-)						
112. *Corynoneura lobata*	3(-)											
113. *Corynoneura scutellata*	23(-),25(-), 34(f)					2(-),10(-), 18(f),29(-)						
Corynoneura scutellata agg.						10(f)					17	
Cricotopus spec.	4(-),23(-)	8(f),13(-), 15(-)			16(f)	2(-),12(-),	14(-)			7(f),9(f)		
114. *Cricotopus albitibia*						7(f)						

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
115. *Cricotopus algorum*	26(-)											
116. *Cricotopus annulator*						2(-)						
117. *Cricotopus bicinctus*						2(-),18(-)						
118. *Cricotopus* gr. *cylindraceus*/fe.											17(-)	
119. *Cricotopus flavocinctus*						10(f)						
120. *Cricotopus fuscus*	27(-)											
121. *Cricotopus intersectus*						10(-),18(f)						
122. *Cricotopus ornatus*						18(-)					17(-)	
123. *Cricotopus* cf. *polaris*						2(-)						
124. *Cricotopus sylvestris*	3(-),11(f), 19(-),34(-)	21(-)				2(-),10(f), 12(-),18(f), 29(-)					17(-)	
125. *Cricotopus tibialis*						2(-)					17(-)	
126. *Cricotopus triannulatus*						18(-)						
127. *Cricotopus trifasciatus*	3(-)											
Diplocladius spec.	19(-)											
128. *Diplocladius cultriger*	23(-)										17(-)	
129. *Eukiefferiella* spec.		8(-),21(-)			16(-)							
130. *Heleniella ornaticollis*	34(-)											
131. *Hetterotrissocladius marcidus*	26(-)											
132. *Hydrobaenus* spec. a (*pilipes* sensu GRODHAUS 1980)	31(-)											drought resistent, summer-dormant, specific (GRODHAUS 1980, MOLLER PILLOT pers. comm.)
133. *Hydrobaenus* spec. b	31(-)											at least drought tolerant, summer-dormant (GRODHAUS 1980)
134. *Hydrobaenus* cf. *distylus*	28 [(a)](-)											
135. *Hydrobaenus lugubris*						2(f),10(f), 29(-)						drought resistent (SCHNABEL 1999, STEINHART 1999a)
136. *Hydrobaenus pilipes*		21(-)										at least drought tolerant, summer-dormant (WIGGINS et al. 1980, MOLLER PILLOT pers. comm.)
137. *Krenosmittia* spec.	1(-)											
138. *Lapposmittia parvibarba*	23(-)											only in temporary pools ?
139. *Limnophyes asquamatus*	3(f),34(f)	13(f)				2(-),10(-), 29(-)						drougth tolerant (present study)
140. *Limnophyes mechthildae**						2(f)						drought tolerant (SCHNABEL 1999)
141. *Limnophyes pentaplastus*	34(-)					2(f)						
142. *Limnophyes pumilio*	34(-)					18(-)						
143. *Microcricotopus bicolor*						18(-)						
Metriocnemus spec.	25(-)					12(-)						
144. *Metriocnemus albolineatus*	3(-)					2(-)						
145. *Metriocnemus corticalis***	28[(b)](f)											

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
146. *Metriocnemus eurynotus*	28**[c](-), 34(-)					2(-)						
147. *Metriocnemus fuscipes*	26(-)											
148. *Metriocnemus hirticollis* agg.											17(-)	
14. *Metriocnemus hygropetricus* agg.											17(-)	
150. *Metriocnemus inopinatus*						10(-)						
Metriocnemus inopinatus agg.											17(-)	
151. *Metriocnemus tristellus* agg.											17(-)	
Nanocladius spec.							14(-)			9(f)		
152. *Nanocladius bicolor*						10(f),29(-)						
153. *Nanocladius* cf. *rectinervis*						2(-),10(f)						
Orthocladius spec.						2(-),12(-)					17(-)	
154. *Orthocladius lignicola*						2(-)						
155. *Orthocladius oblidens*						2(-)						
156. *Orthocladius obumbratus*						10(f)						
157. *Orthocladius rivulorum*											17(-)	
158. *Orthocladius rubicundus*						10(-)						
159. *Orthocladius wetterensis*						10(-)						
160. *Parakiefferiella* spec.	11(-)					10(-)				9(f)		
161. *Paralimnophyes albibasis*										9(f)		
162. *Paralimnophyes hydrophilus*	1(f),3(-), 19(f),23(-), 34(f)											drought tolerant (present study)
Parametriocnemus spec.							14(-)					
163. *Parametriocnemus stylatus*						2(-)						
Paratrichocladius spec.	28[d](-)											
164. *Paratrichocladius rufiventris*	23(-)					2(-)						
Psectrocladius (*Allopsectrocladius*) spec.		13(-)				12(-)						
165. *Psectrocladius obvius*	11(f),23(-), 25(-)											
166. *Psectrocladius platypus*	3(-),11(-)										17(-)	
167. *Psectrocladius barbimanus*		13(f)										
168. *Psectrocladius limbatellus*	23(-)					2(-)						
169. *Psectrocladius* gr. *psilopterus*	23(-),25(-)											
170. *Psectrocladius sordidellus*	3(f),11(-), 34(-)					2(-),10(-)						
Psectrocladius sordidellus agg.						10(f),29(-)						
Psectrocladius spec.	1(-),5(f),27(-)	21(-)					14(f)					
Rheocricotopus spec.							14(-)					
171. *Rheocricotopus chalybeatus*						2(-),29(-)						
172. *Rheocricotopus effusus* agg.						10(f)						
173. *Rheocricotopus fuscipes*						2(-)						

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
Thienemaniella spec.							14(-)			9(-)		
174. *Thienemanniella* cf. *obscura*						2(-)						
Trissocladius spec.	8(f),23(-)										17(-)	predominantly in temporary pools
175. *Trissocladius brevipalpis*	3(-)											summer-dormant (MOLLER PILLOT pers. comm.)
176. *Tvetenia calvescens*						2(-)						
Zalutschia spec.	5						14(f)					
177. *Zalutschia humphriesiae*											17(-)	predominantly in temporary pools, summer-dormant (MOLLER PILLOT pers. comm.)
178. *Zalutschia tatrica*	23(-)											
Podonominae												
Lasiodiamesa spec.											17(-)	
179. *Lasiodiamesa gracilis*	23(-)											only known from temporary pools
180. *Trichotanypus posticalis*	23(-)											
Prodiamesinae												
Prodiamesa spec.		21(-)										at least drought tolerant
181. *Prodiamesa olivacea*	19(-),34(-)					2(-)					17(-)	
Pseudochironominae												
182. *Pseudochironomus middlekauffi*							14(-)					
Tanypodinae												
Ablabesmyia spec.		8(-)	4(f)				14(f)			9(f)		
183. *Ablabesmyia longistyla*						2(f)						
184. *Ablabesmyia* cf. *mollochi*							14(-)					
185. *Ablabesmyia monilis*	1(-),3(-),23(-)	21(-)				10(-),12(-), 18(-),29(-)						
186. *Apsectrotanypus trifascipennis*						10(-)						
Clinotanypus spec.			4(-)									
187. *Clinotanypus nervosus*						12(-)						
188. *Coelopynia pruinosa*										9(-)		
189. *Coelotanypus* spec.			4(-)									
190. *Conchapelopia melanops*	20(-),23(-)					2(f)					17(-)	
191. *Conchapelopia pallidula*						12(-)						
192. *Djalmabatista* spec.			4(-)									
Guttipelopia spec.		21(-)					14(-)					at least drought tolerant
193. *Guttipelopia guttipennis*	19(-)										17(-)	
194. *Krenopelopia* spec.						12(-)						
Labrundinia spec.			4(f)									
195. *Labrundinia neopilosella*							14(-)					
Larsia spec.			4(f)				14(-)			9(f),		
196. *Larsia curticalcar*	25(-)											

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
Macropelopia spec.	11(f),	15(-)										
197. *Macropelopia goetghebueri*	5(-),24(-)										17(-)	
198. *Macropelopia nebulosa*	11(-),24(-), 28(f)[(b)]					12(-)					17(-)	
199. *Macropelopia notata*	1(-)											
Monomelopia spec.							14(-)					
200. *Monopelopia tenuicalar*	11(-),19(f), 34(-)					18(-)						
Natarsia spec.							14(-)					drought tolerant ? (FROUZ & MATENA 2000)
201. *Natarsia punctata*	3(-),34(f)									9(f)		drought tolerant ? (FROUZ & MATENA 2000)
202. *Paramerina* spec.										9(f)		
203. *Pentaneura* spec.		15(-)			16(-)							
Procladius spec.	23(-),26(-)	21(-)	4(-)		16(-)					9(f),10(f)	17(-)	
204. *Procladius bellus*							14(-)					
205. *Procladius choreus*-agg	1(-),3(-),11(f), 19(-),20(-), 24(f),26(f), 34(-)					2(f),10(-), 12(f),18(-), 29(-)						
206. *Procladius crassinervis*	1(-)											
207. *Procladius culiciformis*		13(-)										
208. *Procladius flavifrons*						10(-)						
209. *Procladius* cf. *freemani*							14(f)					
210. *Procladius paludicola*					6(f)					7(f)		
211. *Procladius signatus*						10(-)						
Psectrotanypus spec.		8(f)										
212. *Psectrotanypus dyari*		13(-),21(-)				14(f)						
213. *Psectrotanypus johnsoni*		13(-)										
214. *Psectrotanypus guttularis*		13(-)										
215. *Psectrotanypus varius*	1(-),3(f), 11(f),19(-), 20(f),24(-), 25(-),26(f), 34(f)					2(f),12(f), 18(-),29(-)					17(-)	
216. *Reomyia* spec.							14(f)					
217. *Rheopelopia* spec.						10(f)						
218. *Tanypus kraatzi*						10(-)					17(-)	
219. *Tanypus punctipennis*	20(-)					10(-)	14(-)				17(-)	
220. *Telopelopia fascigera*						10(-)						
221. *Telmatopelopia nemorum*	3(-),19(f), 20(f)										17(-)	predominantly in temporary pools
222. *Thienemannimyia vitellina*						2(-)						
223. *Trichotanypus* spec.						12(-)						

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
Xenopelopia spec.											17(-)	
224. Xenopelopia falcigera	3(f),19(f) 34(f)					12(-)						
225. *Xenopelopia nigricans*	20(f),34(f)					10(-),18(-)						
Zavrelimyia spec.	11(f)					12(-)						
226. *Zavreliella marmorata*						10(-),	14(-)					
227. *Zavrelimyia melanura*	19(-)											
228. *Zavrelimyia nubila/barbatipes*	3(f),23(-), 24(-),34(f)										17(-)	
229. *Zavrelimyia signatipennis*						2(-)						
230. *Zavrelimyia sinuosa*							14(-)					
Chironominae/Tanytarsini												
Cladotanytarsus spec.	3(-),34(f)					12(-)				7(f),9(-)		
231. *Cladotanytarsus mancus* agg.						10(f)						
232. *Lauterborniella* spec.		15(-)										
Micropsectra spec.	11(f), 19(-), 25(-)	8(-),13(-)				12(f)	14(-)					
233. *Micropsectra apposita*						12(-)						
234. *Micropsectra atrofasciata*						2(-),10(-), 12(-)						
235. *Micropsectra bidentata*	5(f)					2(-)						
236. *Micropsectra fusca*	1(f),24(f)											
237. *Micropsectra groenlandica*	23(-)											
238. *Micropsectra junci*	24(-),26(-)											
239. *Micropsectra lindrothi*	3(f),34(f)											
240. *Micropsectra notescens*						12(-)						
241. *Micropsectra reoseiventris*	3(f)											
Paratanytarsus spec.	11(f), 27(-)	21(-),31(-)				12(f),29(-)				9(f)		at least drought tolerant (GRODHAUS 1980, WIGGINS et al. 1980)
242. *Paratanytarsus austriacus*	3(f)											
243. *Paratanytarsus boiemicus*						18(f)						
244. *Paratanytarsus confusus*						2(-)						
245. *Paratanytarsus grimmii*	34(f)											
246. *Paratanytarsus inopertus*						18(-)						
247. *Paratanytarsus intricatus*	25(-),26(-)											
248. *Paratanytarsus* cf. *laccophilus*	23(-)	13(-)										
149. *Paratanytarsus laetipes*		13(-)				12(-)						
250. *Paratanytarsus lauterborni*	23(-)											
251. *Paratanytarsus penicillatus*						10(-)						
252. *Paratanytarsus tenellulus*	3(f),20(-), 34(-)											
253. *Paratanytarsus tenuis*						12(-)						

Appendix 11 (continued).

Species	non-wetland					wetland					?	Comment
	PA	NA	NT	AT	A	PA	NA	NT	AT	A	PA	
Rheotanytarsus spec.						10(-),29(-)						
254. *Rheotanytarsus photophilus*						18(-)						
Tanytarsus spec.	11(f),23(-), 24(f),27(-)	13(-),15(-), 21(-),31(-)	4(f)		16(-)	10(f),12(-),29(-)	14(-)			7(f),9(f)		single members of the genus are at least drought tolerant (GRODHAUS 1980)
255. *Tanytarsus brundini*						2(f)						
256. *Tanytarsus buchonius*	3(-),34(f)											
257. *Tanytarsus debilis*	3(-)											
258. *Tanytarsus ejuncidus*						2(-)						
259. *Tanytarsus eminulus*	34(-)					2(-)						
260. *Tanytarsus fuscithorax*					6(-)							
261. *Tanytarsus glabrescens*	26(f)											
262. *Tanytarsus lestagei*-agg.		13(-)				2(-)						
263. *Tanytarsus palidicornis*	1(f),3(-),28(-)					2(f),12(-), 29(-)						
264. *Tanytarsus semibarbitarsus*										7(f)		
265. *Tanytarsus usmaensis*	3(-),34(-)											
266. *Virgatanytarsus* spec.							14(-)					

Abbreviations and Comments:

Column names:

non-wetland = temporary non-wetland pools; **wetland** = temporary wetland pools (see section 5.1.1.); **?** = temporary pools, no separation in wetland and non-wetland pools was possible.

PA = Palaearctic; **NA** = Nearctic; **NT** = Neotropical; **AT** = Afrotropical; **A** = Australian (CRANSTON 1995).

Lines:

Number(s) of the investigation(s) (see below) and frequency of the species in parenthesis: (f) = frequent; (-) = rare or no data on frequency available:

1 = DELETTRE (1989), France; **2** = SCHNABEL (1999), SCHNABEL & DETTINGER-KLEMM (2000a, b), Germany; **3** = SCHLEUTER (1986), Germany; **4** = NOLTE (1989), Bolivia; **5** = JACKSON & MCLACHLAN (1991), England; **6** = EDWARD (1968), Australia; **7** = SUTER et al. (1995), Australia; **8** = WILLIAMS (1983), Canada; **9** = HILLMAN & NIELSEN (1995), Australia; **10** = STEINHART (1999a), Germany; **11** = BAZZANTI et al. (1996, 1997), Italy; **12** = HARNISCH (1922), Poland; **13** = DRIVER (1977), Canada; **14** = LEEPER & TAYLOR (1998), USA; **15** = KENK (1949), USA; **16** = LAKE et al. 1989, Australia; **17** = MOLLER PILLOT & BUSKENS (1990), The Netherlands; **18** = FRITZ (1981), Germany; **19** = KREUZER (1940), Germany; **20** = RAPP (1983), Germany; **21** = WIGGINS et al. (1980), Canada; **22** = BARCLAY (1966), New Zealand; **23** = THIENEMANN (1941), Sweden; **24** = HALL (1951), England; **25** = THIENEMANN (1936) with additions of WÜLKER & KLÖTZLI (1973), Germany; **26** = THIENEMANN (1950), Austria; **27** = PESTA (1948) (study site and collection of the material), THIENEMANN 1950 (determination), Austria, Italy; **28** = temporary pool near Roth (see Roth in Table 70) (DETTINGER-KLEMM unpl. data), Germany; **29** = LECHTHALER (1993), Austria; **30** = MILLER (1969), MCLACHLAN & LADLE (2001), Nigeria and Malawi; **31** = GRODHAUS (1976, 1980, 1987b), USA; **32** = BISHOP 1974, Australia; **33** = HARRISON 1978, South Africa; **34** = present study

Comments:

* see Appendix 5; ** determination checked by OLE SÆTHER; **(a)** ♂♂, ♀♀, larvae and pupal exuviae; **(b)** ♂♂, ♀♀ and pupal exuviae; **(c)** ♂; **(d)** ♀,); ***Prior the revision of STRENZKE (1959) and KEYL & KEYL (1959), the name *Chironomus dorsalis* was used for very different species (e.g. *C. luridus*, see STRENZKE (1959) and KEYL (1962)); the table therefore differs between recordings prior and posterior to 1959.

If necessary all Palearctic species' names were transferred into the present nomenclature using ASHE (1983), ASHE & CRANSTON (1990), SÆTHER et al (2000) and the most recent revisions available. The species' names of all other biogeographical regions were only adjusted to the present placement within a genus (ASHE (1983).

Appendix 12: Developmental zeroes in the Chironomidae.

Species	Author	T_0 (°C)
Tanypodinae		
Ablabesmyia monilis	MACKEY 1977	4.4
Procladius choreus	MACKEY 1977	11.0
Orthocladiinae		
Cricotopus algarum	MACKEY 1977	4.2
Cricotopus bicinctus	MACKEY 1977	3.8
Cricotopus sylvestris	KONSTANTINOV 1958	10.0
	MACKEY 1977	3.8
Corynoneura coronata	MACKEY 1977	4.2
Hydrobaenus lugubris	STEINHART 1999*	3.7
Hydrobaenus kondoi	KONDO 1996	-2.17
Metriocnemus hirticollis	MACKEY 1977	4.3
Microcricotopus bicolor	MACKEY 1977	4.6
Paralimnophyes hydrophilus	present study	3.1
Synorthocladius semivirens	MACKEY 1977	3.5
Chironomini		
Chironomus annularius	KONSTANTINOV 1958	4.5
	present study	5.3
Chironomus decorus	MAIER et al. 1990	~8.0
Chironomus dorsalis	present study	4.6
Chironomus heterodentatus	KONSTANTINOV 1958	8.1
Chironomus kiiensis	SURAKARN & YANO 1995	15.6
Chironomus plumosus	KONSTANTINOV 1958, HILSENHOFF 1966 & REIST & FISCHER 1979	5.0
	OSTROVSKY 1995	6.0
	KONSTANTINOV 1958	6.6
Chironomus riparius	RASMUSSEN 1984	4.1
	SCHARFF 1973*	6.8
Chironomus tepperi	STEVENS 1998	10.4
Dicrotendipes modestus	MACKEY 1977	4.3
Dicrotendipes nervosus	KONSTANTINOV 1958	5.4
Glyptotendipes pallens	KONSTANTINOV 1958	6.0
	MACKEY 1977	-4.0
Glyptotendipes tokunagai	YANO et al. 1991	12.3
Microtendipes chloris	MACKEY 1977	4.1
Parachironomus biannulatus	MACKEY 1977	4.2
Parachironomus spec.	KONSTANTINOV 1958	9.7
Paratendipes albimanus	WARD & CUMMINS 1979	4.0
Phaenopsectra flavipes	MACKEY 1977	2.4
Polypedilum convictum	MACKEY 1977	4.2
Polypedilum nubeculosum	KONSTANTINOV 1958	8.6
	MACKEY 1977	0.5
Polypedilum tritum	present study	5.2
Tanytarsini		
Cladotanytarsus atridorsum	MACKEY 1977	4.4
Paratanytarsus spec.	CLEMENT et al. 1975	12.8
Rheotanytarsus photophilus	MACKEY 1977	4.6
Stempellina spec.	SUNDERMANN & DETTINGER-KLEMM 2002	3.0 - 4.0
Tanytarsus oyamai	OKAZAKI & YANO 1995	12.6

*calculated after the published data by the present author.

The T_0-values of KONSTANTINOV (1958) were taken from MACKEY 1977 who reanalysed the original data.

Appendix 13: The relation of temperature and generation time in Chironomidae.

Species	Author	Generation time (days) in an approximate ambient temperature class					
		5 °C	10 °C	15 °C	20 °C	25 °C	30 °C
Tanypodinae							
Ablabesmyia monilis	MACKEY 1977* **Eu**			F = 17			
Procladius choreus	MACKEY 1977* **Eu**			F = 35			
Paramerina fasciata	JACKSON & SWEENEY 1995 **NT**				F = 40		
Diamesinae							
Pseudodiamesa branickii	NOLTE & HOFFMANN 1992 **Eu**		(8°C): F ≈ 90				
Orthocladiinae							
Acricotopus lucens	present study **Eu**				21.5 °C: F = 15		
Corynoneura coronata	MACKEY 1977* **Eu**			F = 5			
Cricotopus algarum	MACKEY 1977* **Eu**			F = 25			
Cricotopus bicinctus	MACKEY 1977* **Eu**			F = 15			
Cricotopus sylvestris	KONSTANTINOV 1958 **Eu**				18 °C: F = 21 22 °C F = 14		
	MACKEY 1977* **Eu**			F = 18			
	MENZIE 1981 **NA**			F ≈ 30 - 40	F ≈ 17		F ≈ 17
	WOTTON et al. 1992 **Eu**	Slow sand filter beds of the Thames water Plc in west London (August - October): F = 16 - 20 days					
Cricotopus spec.	JACKSON & SWEENEY 1995 **NT**				F = 19		
Eukiefferiella ilkleyensis	STOREY 1987 **Eu**		$\bar{x}$ = 111	$\bar{x}$ = 71	$\bar{x}$ = 75 - 98		
Hydrobaenus kondoi	KONDO 1996 **J**	$\bar{x}$ = 104 (6 °C)	$\bar{x}$ = 82 (8° C)				
Hydrobaenus lugubris	STEINHART 1999a, 2000a,b **Eu**	$\bar{x}$ = 142	$\bar{x}$ = 48	$\bar{x}$ = 21 - 24	$\bar{x}$ = 18 - 29		
Limnophyes asquamatus	present study lab **Eu**				22 °C: F = 22 $\bar{x}$ = 33		
	present study field **Eu**		8 °C: F = 45 11 °C: $\bar{x}$ = 51 12 °C: F = 28				
Limnophyes biverticillatus	REMMERT 1955b **Eu**				Temp ?: F = 20		
Limnophyes minimus s. str.	present study **Eu**			F = 28; $\bar{x}$ = 29			
Limnophyes minimus agg.	STEINHART 1999a, 2000a **Eu**			F = 15; $\bar{x}$ = 29 - 42			
Limnophyes virgo	REMMERT 1955b **Eu**				Temp ?: F = 28		
Metriocnemus hirticollis	MACKEY 1977* **Eu**			F = 14			
Microcricotopus bicolor	MACKEY 1977* **Eu**			F = 6			
Paralimnophyes hydrophilus	present study **Eu**	F = 135	F = 59; $\bar{x}$ = 92	F = 28; $\bar{x}$ = 38	19°C: F = 17 $\bar{x}$ = 25	F = 12; $\bar{x}$ = 17	29 °C: lethal

Appendix 13 (continued).

Species	Author	Generation time (days) in an approximate ambient temperature class					
		5 °C	10 °C	15 °C	20 °C	25 °C	30 °C
Parametriocnemus stylatus	present study **Eu**		dormancy III				
Parametriocnemus spec. 1	JACKSON & SWEENEY 1995 **NT**				F = 30		
Parametriocnemus spec. 2	JACKSON & SWEENEY 1995 **NT**				F = 24		
Parametriocnemus spec. 3	JACKSON & SWEENEY 1995 **NT**				F = 36		
Psectrocladius limbatellus	WOTTON et al. 1992 **Eu**	Slow sand filter beds of the Thames water Plc in west London (August - October): F = 16 - 20 days					
Pseudosmittia arenaria	REMMERT 1955b **Eu**				Temp ?: F = 28		
Pseudosmittia nanseni	STEINHART 1999a **Eu**			$\bar{x}$ = 50 - 68			
Synorthocladius semivirens	MACKEY 1977* **Eu**			F = 9			
		Chironomini					
Apedilum elachistus	NOLTE 1995 **NT**					20 - 26 °C: F = 13	25 - 35 °C: F = <7 - 11
Chironomus anonymus	JACKSON & SWEENEY 1995 **NT**				F = 50		
Chironomus annularius	MACKEY 1977* **Eu**			E = 43			
	present study **Eu**		11°C: F = 51; dormancy LD	14 °C: F = 35 dormancy LD	F = 24	24 °C: F = 17	F = 11
Chironomus bernensis	REIST & FISCHER 1987 **Eu**				$\tilde{x}$ = 26	$\tilde{x}$ =23	
Chironomus decorus	DANKS 1978 **NA**			$\tilde{x}$ = 37 dormancy SD	$\tilde{x}$ = 26		
	MAIER et al. 1990 **NA**		$\bar{x}$ = 111	$\bar{x}$ = 62	$\bar{x}$ = 33	$\bar{x}$ = 27	28 °C = lethal
Chironomus dorsalis	present study **Eu**	lethal	F = 77 dormancy IV	F = 27; $\bar{x}$ = 37 dormancy SD	F = 18; $\bar{x}$ = 22	F = 13; $\bar{x}$ = 17	F = 11; $\bar{x}$ = 16
Chironomus heterodentatus	MACKEY 1977* **Eu**			E = 34			
Chironomus imicola	MCLACHLAN 1988 **AT**					~26 °C: F = 10; $\bar{x}$ = 42	
Chironomus kiiensis	SURAKARN & YANO 1995 **J**				$\bar{x}$ = 21	$\bar{x}$ = 14	$\bar{x}$ = 11
Chironomus luridus	present study **Eu**		F = 90 dormancy IV	16 °C: F = 33; $\bar{x}$ = 43		F = 24; $\bar{x}$ = 26	
Chironomus nuditarsis	REIST & FISCHER 1987 **Eu**				$\tilde{x}$ = 36	$\tilde{x}$ = 22	
	present study **Eu**				F = 30	24 °C: F = 23	F = 17
Chironomus piger	SCHARF 1973 **Eu**		dormancy IV	$\bar{x}$ = 37	$\bar{x}$ = 22	$\bar{x}$ = 17	
Chironomus plumosus	MACKEY 1977* **Eu**			F = 60			
	REIST & FISCHER 1987 **Eu**				$\tilde{x}$ = 55	$\tilde{x}$ = 32	
	present study **Eu**		11 °C: F = 78 dormancy SD				
Chironomus pulcher	MCLACHLAN 1988 **AT**					~23 °C: F = 13; $\bar{x}$ = 56	

Appendix 13 (continued).

Species	Author	Generation time (days) in an approximate ambient temperature class					
		5 °C	10 °C	15 °C	20 °C	25 °C	30 °C
Chironomus riparius	SCHARF 1973 **Eu**		dormancy IV	$\bar{x}$ = 35	$\bar{x}$ = 21	$\bar{x}$ = 16	
	MACKEY 1977* **Eu**			F = 35			
	HOLLOWAY 1983 **Eu**					$\bar{x}$ = 16	
	GODDEERIS et al. 2001 **Eu**			F = 26 - 32 dormancy SD			
Chironomus salinarius	KOSKINEN 1968 **Eu**				18 °C: $\bar{x}$ = 56		
	DRAKE & ARIAS 1995 **Eu**		dormancy ?	$\bar{x}$ = 65	21 °C: $\bar{x}$ = 47		
Chironomus sancticaroli	STRIXINO & STRIXINO 1982 **NT**					19 - 26 °C: F = 15	
Chironomus staegeri	DANKS 1978 **NA**				$\tilde{x}$ = 68		
Chironomus strenzkei	SYRJÄMÄKI 1965 **NT**						28 °C: E = 10 - 12
Chironomus tepperi	STEVENS 1998 **A**		(12.5 °C): $\bar{x}$ = 44	$\bar{x}$ = 35	$\bar{x}$ = 16	$\bar{x}$ = 10	$\bar{x}$ = 10
Chironomus tentans	SIBLEY et al. 1998 **NA**					F ≈ 25; L = 60	
Dicrotentipes modestus	MACKEY 1977* **Eu**			F = 8			
Dicrotendipes nervosus	MACKEY 1977* **Eu**			F = 48			
Dicrotendipes notatus	present study **Eu**				F = 34 $\bar{x}$ = 37		
Endochironomus nigricans	DANKS 1978 **NA**			$\tilde{x}$ = 48	$\tilde{x}$ = 35		
Endotribelos grodhausi	JACKSON & SWEENEY 1995 **NT**				F = 31		
Endotribelos spec. 2	JACKSON & SWEENEY 1995 **NT**				F = 34		
Glyptotendipes foliicola	present study **Eu**					24 °C: F = 33	F = 34
Glyptotendipes pallens	MACKEY 1977* **Eu**			F = 23			
	present study **Eu**				F = 47		
Glyptotendipes tokunagai	YANO et al 1991 **J**		dormancy IV	$\bar{x}$ = 100	$\bar{x}$ = 51	$\bar{x}$ = 31	$\bar{x}$ = 19
Microtendipes chloris	MACKEY 1977* **Eu**			F = 29			
Parachironomus biannulatus	MACKEY 1977* **Eu**			F = 7			
Parachironomus spec.	MACKEY 1977* **Eu**			F = 38			
Phaenopsectra flavipes	MACKEY 1977* **Eu**			F = 36			
Polypedilum convictum	MACKEY 1977* **Eu**			F = 13			
Polypedilum cf. *corniger*	JACKSON & SWEENEY 1995 **NT**				F = 26		
Polypedilum epomis	JACKSON & SWEENEY 1995 **NT**				F = 22		
Polypedilum microzoster	JACKSON & SWEENEY 1995 **NT**				F = 24		
Polypedilum obelos	JACKSON & SWEENEY 1995 **NT**				F = 72		
Polypedilum nubeculosum	MACKEY 1977* **Eu**			F = 35			

Appendix 13 (continued).

Species	Author	Generation time (days) in an approximate ambient temperature class					
		5 °C	10 °C	15 °C	20 °C	25 °C	30 °C
Polypedilum tritum	present study **Eu**	lethal	F = 75; $\bar{x}$ = 94	F = 35; $\bar{x}$ = 44 dormancy SD	F = 24; $\bar{x}$ = 30	F= 15; $\bar{x}$ = 21	lethal
Polypedilum vanderplanki	MCLACHLAN 1983a **AT**					Temp?: F > 40	
Polypedilum spec. 5	JACKSON & SWEENEY 1995 **NT**				F = 26		
Polypedilum spec. 6	JACKSON & SWEENEY 1995 **NT**				F = 40		
Stenochironomus leptopus	JACKSON & SWEENEY 1995 **NT**				F = 33		
Stenochironomus cf. *quadrinotatus*	JACKSON & SWEENEY 1995 **NT**				F = 23		
Stenochironomus spec. 3	JACKSON & SWEENEY 1995 **NT**				F = 30		
Tanytarsini							
Cladotanytarsus atridorsum	MACKEY 1977* **Eu**			F = 10			
Paratanytarsus grimmii	LANGTON et al. 1988 **Eu** present study **Eu**		12.5 °C: F = 32	16 °C: F = 25		25 °C: F = 19 24 °C: F = 13	
Pontomyia oceana	SOONG et al. 1999 **T**					F≈ 30	
Rheotanytarsus photophilus	MACKEY 1977* **Eu**			F = 8			
Stempellina spec.	SUNDERMANN & DETTINGER-KLEMM 2002 **Eu**	Univoltine and summer-dormant. Under exclusion of the period of summer dormancy ~ 1370 effective degree days are needed for total development					
Tanytarsus fimbriatus	WOTTON et al. 1992 **Eu**	Slow sand filter beds of the Thames water Plc in west London (August - October): F = 16 - 20					
Tanytarsus oyamai	OKAZAKI & YANO 1990 **J**			$\bar{x}$ = 57	$\bar{x}$ = 41	$\bar{x}$ = 18	$\bar{x}$ = 12
Tanytarsus pandus	JACKSON & SWEENEY 1995 **NT**				F = 32		

Abbreviations and explanations:

Author column: ***** the figures represent only the development time for the larval period; furthermore the larvae were often of an unknown age at the start of the rearings; temperature regulation remains questionable; **AT** = Africotropis; **Eu** = Europe; = Japan; **NA** = Nearctis; **NT** = Neotropis; **T** = Taiwan.

Temperature columns: **F** = days from oviposition until the first emergence; $\bar{x}$ = mean generation time; $\tilde{x}$ = median generation time; **lethal** = lethal temperature for total development; **dormancy III/IV** = most larvae enter into dormancy during the instar III/IV; **dormancy LD/SD** = most larvae enter into dormancy when kept under long-/short-days; **dormancy ?** = larvae are supposed to enter into dormancy.

Erklärung:

Ich versichere, dass ich vorliegende Dissertation

"Chironomids (Diptera, Nematocera) of Temporary Pools - an Ecological Case Study"

selbst verfasst und mich keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der vorliegenden Form oder einer ähnlichen Form noch nicht zu Prüfungszwecken eingereicht.

Riedstadt, den 19. Oktober 2003