Institut für Hydrobiologie, Technische Universität Dresden

Population dynamics of *Daphnia galeata* in the biomanipulated Bautzen Reservoir: life history strategies against food deficiency and predation

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Abstract

The population dynamics and demography of *Daphnia galeata* was analysed in a five year study in the biomanipulated Bautzen Reservoir. Samples were taken two times a week during the period May-July in the pelagic zone of this highly eutrophic water. Major bottom-up and top-down factors were determined during the study period and analysed with regard to their influence on *Daphnia* dynamics and life history. Field data on fecundity and population structure of *D. galeata* were combined with results from life table and growth experiments performed under approximately *in situ* conditions to gain insight into the mechanisms leading to a midsummer decline of this cladoceran species which dominates the zooplankton community in Bautzen Reservoir.

Two main patterns of *Daphnia* dynamics emerged: In years without a midsummer decline the population increased slowly in spring, starting from low densities. High water transparency was observed already during the build-up of the population of *D. galeata*. Despite considerable fluctuations, *Daphnia* abundance remained on a high level throughout summer. In years with a midsummer decline the population started from relatively high densities in early May and more than doubled during one week. Peak densities were reached before the clear-water stage emerged. At the end of this period the population declined to low values which lasted for the rest of the summer.

Fecundity of the Population of *D. galeata* declined, whereas the mean egg volume increased at the beginning of the clear-water stage as a result of declining food levels. The size at maturity (SAM) remained high during this period. Additionally, juvenile growth was reduced and the age at maturity was retarded. Survival probability was low for those daphnids born shortly before or during the clear-water stage compared to those born later. It can be concluded from these results that recruitment to adult stages is strongly reduced during the clear-water stage. The end of this period is marked by an alternation in generations. Only at that time can SAM be reduced because the new generation of adults matures at a smaller size, carrying small eggs. A high impact of non-predatory adult mortality can be expected when the population is dominated by a strong peak-cohort during the clear-water stage according to recruitment patterns during the build-up of the population.

The most drastic decline both of *Daphnia* abundance and SAM was observed in those years when the biomass of juvenile fish exceeded 20 kg ha^{-1} at the end of the clear-water stage. Due to gape-size limitation juvenile fish mainly feed on juvenile daphnids during this period and thus, they reinforce bottom-up effects on the *Daphnia* population. When fish change their size selection towards adult daphnids at the time when the new generation takes over, this seems to represent the worst case for the *Daphnia* population. Consequently, the timing between bottom-up effects and the feeding pressure of juvenile fish determines the extent of the decline.

1 General introduction

The genus *Daphnia* has attracted scientific interest ever since the 17th century (reviewed by Edmondson 1987) and is considered as a model organism in aquatic ecology (Lampert and Sommer 1993). The most obvious reason for this attractiveness is that daphnids dominate the zooplankton community in many temperate meso- to eutrophic water bodies. Apart from that, practical reasons may explain the popularity. *Daphnia* has an appropriate size for being used in laboratory cultures, it is easy to cultivate and has short generation times. As an (relatively) unspecific filter feeder, able to feed on a broad size range of particles in the water (Burns 1968; Wagner 1998), *Daphnia* is able to increase water transparency significantly. Uhlmann (1954) was the first to notice that high densities of *Daphnia* may turn waste water ponds from a turbid into a clear-water state due to their filtering activity. The high importance of daphnids for the development of a clear-water stage has been confirmed in many studies (see review by Lampert 1988 a). This potentially high grazing pressure of *Daphnia* on phytoplankton and other seston-particles has drawn considerable attraction to this particular group of cladocera in biomanipulation experiments.

Biomanipulation is an ecotechnological strategy to improve water quality of eutroficated systems via top-down manipulation of the food web (Shapiro et al. 1975; Benndorf 1988, 1995). Strong top-down effects of fish on the species composition of the zooplankton community had first been demonstrated by Hrbáček (1958) and Hrbáček et al. (1961). The mechanism behind this observation later was formulated in the size-efficiency hypothesis by Brooks and Dodson (1965), stating that size-selective feeding of fish eliminates large-bodied zooplankton, which in the absence of predation would be superior competitors compared to smaller species. Some early biomanipulation experiments were carried out by poisoning the whole fish stock (Hrbáček 1958; Stenson et al. 1978; Shapiro and Wright 1984). The observed (short-term) responses met the expectations: In the absence of planktivorous fish high stocks of large daphnids developed and water transparency increased due to high grazing rates.

Besides this radical method being dubious from an ethical point of view, it has been shown that the complete elimination of fish is not effective in the long run. Even if fish are not able to recolonise the habitat, sooner or later the free ecological niche will be taken by an invertebrate predator (Edmondson and Abella 1988; Wissel and Benndorf 1998, Benndorf et al. 2000). These findings support the view that an “optimal” biomass rather than the complete elimination of planktivorous fish is desirable in biomanipulation experiments (Benndorf 1990, 1995). The numerical value of this optimal biomass should be lake-specific and on the one hand high enough to suppress invertebrate predators but on the other hand not too high to suppress *Daphnia* (Wissel et al. 2000). This goal probably can only be achieved by a more complex strategy of food web management, which may involve stocking of piscivorous fish of various species and sizes and catch restrictions (Benndorf 1990, 1995), improvement of conditions for reproduction of desirable fish (Edmondson and Abella 1988), increasing habitat diversity (Skov and Berg 1999) and selective catches of planktivorous fish (Kasprzak et al. 1988).

The general approach that manipulations at the top of pelagic food webs cascade down to lower trophic levels (Carpenter et al. 1985) has been confirmed in numerous experiments and case studies (see reviews by Benndorf 1990; Reynolds 1994; Drenner and Hambright 1999). However, the proposed chain: high stock of piscivores➔low stock of planktivores➔high stock of large-bodied grazers (*Daphnia*)➔low phytoplankton biovolume and high water transparency in many cases could not be confirmed concerning lower trophic levels and was found to be a much too simplified model (McQueen et al. 1986; DeMelo et al. 1992). The success of biomanipulation in improving water quality depends on many factors. In shallow lakes, clear-water states (initiated by grazers) may be stabilised by a variety of mechanisms connected with macrophytes (competition for nutrients and allelopathic interactions with phytoplankton, providing refuges for grazers, reduced resuspension of sediment) despite of high nutrient loadings (see reviews by Jeppesen et al. 1997; Scheffer 1998; Meijer 2000).

In deep lakes, however, a reduction of mean summer phytoplankton biomass may probably only be achieved if the nutrient (namely phosphorus) loading is below a “biomanipulation-efficiency threshold of the P-loading” (BETP-hypothesis, Benndorf 1987, 1990). This threshold should lake-specifically range between 0.5 and 2.0 g total P m^{-2} y^{-1} (Benndorf 1990; Jeppesen et al. 1990). If the P-loading falls below this threshold, biomanipulation-induced indirect effects stabilise top-down effects on water quality (Benndorf 1992). Increased P-sedimentation (exuviae, fecal material) leads to decreasing total P concentrations in the epilimnion and subsequently declining phytoplankton biomass (Benndorf 1997). This proposed mechanism indeed was confirmed by Rüter et al. (2000) in a whole-lake biomanipulation experiment (flooded quarry in Gräfenhain, see Benndorf et al. 1984; Benndorf 1995). If the P-loading is too high in deep waters, no sustained improvements of water quality can be achieved by biomanipulation. Mean summer phytoplankton biomass will not decline but the phytoplankton size distribution may be shifted to larger species and temporal clear-water phases may develop (Gliwicz 1990; Benndorf and Faltin 1995; Böing et al. 1998). However, even a shift to larger phytoplankton species may result in improved water transparency and thus may be regarded as a success of biomanipulation.

What becomes evident from these results is that in deep waters the effects of biomanipulation (both direct and indirect) exclusively depend on grazers, whereas in shallow lakes additional mechanisms may enhance or maintain water clarity. Thus, the maintenance of high *Daphnia* densities (in terms of biomass) must be regarded as a key factor in biomanipulation experiments in deep waters (Lampert 1988 a; Dawidowicz 1990; Kasprzak et al. 1999). Only in hardwater lakes calcite precipitation may provide an additional mechanism to control eutrophication also in deep waters (Koschel et al. 1983).

In temperate lakes zooplankton dynamics are mainly governed by temperature, food availability and predation. A detailed discussion of the seasonal succession of these steering factors is provided in Chapter 3. Obviously, biomanipulation (apart from some feedback mechanisms) can only influence predation and thus minimise predatory mortality. However, enhancement of the piscivorous fish stock (in order to reduce planktivorous fish) also involves negative feedbacks. The juveniles of these piscivores (at least in the case of zander, *Stizostedion lucioperca* and perch, *Perca fluviatilis*) are themselves planktivores during their first summer. Perch, although not stocked but only indirectly controlled (see below), due to its potentially early piscivory may become a key species in biomanipulated food webs (Mehner et al. 1996 a, 1997; Dörner et al. 1999, in press). The occurrence of juvenile percids in spring usually coincides with the clear-water phase and high *Daphnia* densities. This period of high water transparency (and thus, low food availability for daphnids) is often followed by a drastic decline of *Daphnia* abundance and low densities throughout summer (midsummer decline), resulting in massive algal blooms and low water transparency. This pattern of *Daphnia* dynamics is common in temperate waters and has been described in the PEG (Plankton Ecology Group) model (Sommer et al. 1986). The question as to how bottom-up and top-down effects contribute to the midsummer decline of *Daphnia* certainly is of great importance for biomanipulation experiments and is a central part of this study. A detailed discussion of mortality factors possibly inducing a midsummer decline is given in the following Chapters.

The main objective of this study is the detailed analysis of the population dynamics of *Daphnia galeata* in the biomanipulated Bautzen Reservoir. Special attention has been paid to the life history characteristics of the population and how they are adapted to different bottom-up and top-down factors, posing the following questions: How do the daphnids react to environmental factors, how fast do these reactions take place and how successful are they? With regard to the main goal of biomanipulation, the implementation of a continuously high grazing pressure on phytoplankton, the “successful“ adaptation of *Daphnia* life history would mean the sustenance of high densities, able to exert high filtration rates.

The study comprises several steps, which are described in the following chapters. Chapter 2 contains a brief introduction to the biomanipulation experiment in Bautzen Reservoir, describing the background of this investigation. Chapter 3 contains an overview of the main bottom-up and top down influences on *D. galeata* in Bautzen Reservoir during the period of this study from 1995 to 1999. These factors are evaluated with regard to different patterns of *Daphnia* dynamics. The influence of food conditions on fecundity and reproduction of

D. galeata as determined in field samples is analysed in Chapter 4. This involves a critical evaluation of different reproductive parameters which are used to describe the fecundity of cladocerans. Laboratory experiments concerning bottom-up influences on *Daphnia* fitness during the population development in spring and early summer are presented in Chapter 5. Juvenile growth was estimated in flow-through chambers and life table experiments were performed under approximately *in situ* conditions (excluding predation) to determine demographic responses to changing bottom-up influences. In Chapter 6 field data are presented concerning life history characteristics and demography of *D. galeata* in relation to food conditions and density of age-0 fish. Of special importance is the timing of bottom-up and top-down impacts because this may result in conflicting life history strategies. In Chapter 7 an attempt has been made to determine the importance of non-consumptive mortality on the dynamics of *D. galeata*. Sediment traps were used to estimate non-consumptive mortality in the field. By combining laboratory-derived growth rates with field data, juvenile and adult mortality of *D. galeata* was calculated separately. Additionally, age-specific mortality as determined in life table experiments was used to model *Daphnia* dynamics in the absence of predation. Finally, Chapter 8 contains a general discussion of all the results and the conclusions.

2 Introduction to the biomanipulation experiment in Bautzen Reservoir

Bautzen reservoir is a man-made lake (first impoundment 1974) situated about 70 km northeast of Dresden (Saxony, Germany). Initially, it served as a supply of cooling water for a power plant and additionally was used for flood protection and recreational purposes. Nowadays, the high demands of the public on water quality are due to the extensive use of the reservoir for recreation (fishing, sailing, swimming, surfing). The reservoir has a surface area of 533 ha, a mean depth of 7.4 m and a maximum depth of approximately 12 m. Due to high exposure to wind, Bautzen Reservoir stratifies only for short periods in summer. Usually, thermal stratification develops for a short period in May but is disturbed by mixing events. In June and July, further stratification periods may occur, but often the vertical temperature gradient from the surface to the bottom is only a few degrees or even absent (Chapter 3, compare Benndorf and Henning 1989; Köhler 1992). The inflowing river Spree was characterised by a very high nutrient loading especially during the 1980s (Benndorf 1995). Since 1989 the discharge of wastewater was reduced, but even recently (1996/1997), the phosphorus load amounted to 3.3-3.5 g P m^{-2} y^{-1} (Benndorf et al. 1998). Due to this high nutrient burden the reservoir was in a hypertrophic state with extensive algal blooms and permanently low water transparency during the growing season right after impoundment.

The fish community during this early phase was characterised by a large, natural population of pike (*Esox lucius*), which quickly declined after the more and more people were fishing. An extremely big year-class of perch developed in 1977. These perch were slow-growing and zooplanktivorous (Schultz et al. 1992). In 1977 a biomanipulation experiment was started (Benndorf et al. 1988). The measures undertaken were: stocking with predacious fish (starting in 1977) and catch restrictions for piscivorous fish (starting in 1980). Almost every year until 1995 pond-raised zander were stocked in autumn. Additional stocking was done with pike, eel (*Anguilla anguilla*) and European catfish (*Silurus glanis*). These measures were aimed at establishing a diverse community of piscivorous fish, which is able to feed on a wide size-range of planktivores. As a result, total fish biomass declined and the percentage of piscivores of the total adult fish biomass increased to 68% in 1997 (Benndorf et al. 1998). Under these conditions, perch become piscivorous as early as in the 1+ year-class or at least in the second year (Dörner et al. in press). Once they are piscivorous, young perch are mainly cannibalistic, feeding on specimens of the new year-class (Dörner et al. 1999). Due to its opportunistic feeding behaviour perch is a key species in the biomanipulation experiment in Bautzen Reservoir and therefore subject of intensive studies (Dörner in prep.).

Since 1981, biomanipulation became effective, leading to the dominance of *D. galeata* in the zooplankton community (Benndorf et al. 1988). Extended clear-water phases developed in spring and mean summer values of Secchi depth increased compared to the pre-manipulation period. However, blooms of inedible algae (mostly *Microcystis* spec.) regularly developed in summer (Miersch 1997). High densities of *Daphnia* in spring were often followed by a midsummer decline (Benndorf et al. 2001; see Chapter 3). The high stocks of zander and piscivorous perch of course imply a high reproductive potential of these species. Usually, perch dominate the age-0 fish community in spring and summer, whereas the proportions of zander and roach (*Rutilus rutilus*) are variable between years (Mehner et al. 1996 a, b, 1998 a). In early summer, age-0 fish extensively feed on daphnids (Mehner et al. 1995) and due to their high density and their high metabolic requirements must be regarded as major vertebrate consumers of *Daphnia* (Mehner et al. 1996 a). Kahl et al. (in press) indeed gave evidence that the remaining population of roach, the most abundant planktivorous species in Bautzen Reservoir (Benndorf et al. 1998), exerts only low predation pressure on daphnids.

As biomanipulation alone was found to be insufficient to reduce algal biomass and prevent cyanobacterial blooms in Bautzen Reservoir due to high nutrient loading, a combined ecotechnological strategy was additionally applied in 1996 and 1997 (Deppe et al. 1999). In the inflow region of the reservoir three pumps were installed which pumped hypolimnetic water rich in CO_2 to the surface. Additionally, they were connected with a tank containing a $FeCl_2$- solution. The iron-salt was mixed with nutrient-rich hypolimnetic water and formed precipitates with phosphorus which settled to the bottom after being dispersed in the epilimnion. By this means, it was intended to lower the P-concentration below the BETP level (Benndorf 1987, 1990). CO_2 enrichment in the surface layers was aimed to prevent or break photosynthetic CO_2 depletion, which is suggested to be one reason for the competitive advantage of cyanobacteria in eutrophic waters (Shapiro 1997). The pumps were run during the growing season in 1996 and 1997. Despite the successful suppression (1996) or delay (1997) of *Microcystis* blooms, the applied ecotechnological strategy did not change the overall trophic state of Bautzen Reservoir by reducing the P-load below the BETP threshold level (Deppe et al. 1999).

With the given characteristics, Bautzen Reservoir is almost perfectly suited for the kind of investigation presented in this study. Due to biomanipulation, the zooplankton community is dominated by *D. galeata,* which regularly develops high densities in spring, but often declines in summer. Age-0 fish are the main vertebrate predators during this period. Due to its morphological and physical characteristics, Bautzen Reservoir on the one hand must be regarded as a deep lake with a truly pelagic zone which is not influenced by macrophytes or sediment resuspension. On the other hand, due to its relative shallowness and wind exposition, it lacks a stable thermal stratification. Thus, predator-avoidance behaviour of the zooplankton is only possible to a very limited extent and life history adaptations must be considered as the major strategy to minimise predation effects.

3 Overview: Bottom-up and top-down factors influencing population dynamics of *Daphnia galeata* in Bautzen Reservoir

3.1 Introduction

Daphnia dynamics in temperate waters are mainly governed by temperature, food conditions and predation. The PEG model (Sommer et al. 1986) describes the sequence of steering factors during the seasonal succession of the plankton community. As ectothermic organisms, daphnids are limited by low temperatures in winter. When the temperature increases in spring, *Daphnia* populations grow rapidly, feeding on high algal biomasses which develop earlier. Increased grazing leads to overexploitation of food resources and consequently food becomes limited during the clear-water phase. At the same time, predation by zooplanktivorous fish increases due to higher activity at high water temperature and the emergence of young of the year fish. The relative importance of food limitation and predation in early summer is still discussed controversially (Benndorf and Horn 1985; Vanni 1987; Lampert 1988 b; Boersma 1994; Mehner et al. 1998 b) and is dealt with in detail in the next Chapters.

With regard to the bottom-up aspect, food conditions for daphnids do not only depend on quantity, but also on quality (Richman and Dodson 1983; Sterner 1993; Müller-Navarra 1995; Gulati and DeMott 1997). Additionally, a structural component has to be considered, as small (edible) particles may be indigestible (Porter 1973) and large (inedible) particles may interfere with *Daphnia* filter screens (Gliwicz and Siedlar 1980; Gliwicz and Lampert 1990). The upper size limited of ingestible particles is not fixed but may be adapted by daphnids in response to food conditions (Wagner 1998). A detailed analysis of interactions between food components and *Daphnia* feeding behaviour in Bautzen Reservoir is not treated here, but is part of another study (Voigt, in prep.), which was carried out simultaneously to this investigation.

Concerning top-down influences, the predation impact of fish may be shaped by size-selection (Gliwicz and Pijanowska 1989; Mehner et al. 1998 c). Invertebrate predators may enhance or even replace the feeding pressure of fish (Wissel and Benndorf 1998; Wojtal et al. 1999). These aspects are discussed in the light of extensive research carried out in Bautzen Reservoir (Mehner et al. 1998 b, c; Janßen 1999; Wagner et al. 1999; Wagner pers. comm.). Concerning invertebrate predators, only *Leptodora kindtii* is considered. *Chaoborus flavicans*, due to its emergence pattern, is only abundant in early spring and later in summer and was found to be of low importance for *Daphnia* dynamics in Bautzen Reservoir (Bollenbach 1998).

Daphnids may also be adversely influenced by oxygen deficiency (Hanazato 1996) and too high or too low pH values (Hansen et al. 1991; Havens 1992). In the highly eutrophic soft water lake Bautzen Reservoir, photosynthetic CO_2 depletion may cause high pH values in the euphotic zone (Benndorf et al. 1988; Deppe et al. 1999) whereas in deep water layers heterotrophic activities may result in oxygen depletion. Further factors that may influence *Daphnia* fitness are UV light (Zellmer 1998; Borgeraas and Hessen 2000) and toxic substances, produced e.g. by cyanobacteria (Lampert 1981; Jungmann 1992; Haney et al. 1994; DeMott 1999). Whereas UV light may only be expected to be important in arctic or high altitude waters and thus can be neglected in the case of Bautzen Reservoir, toxicity may well have an influence, as cyanobacterial blooms frequently occur (Benndorf and Henning 1989; Miersch 1997). However, it has been shown before that *D. galeata* may thrive during *Microcystis* blooms and that this *Daphnia* species is better adapted to food conditions in Bautzen Reservoir than others (Ritter 1997). Infections by parasites, bacteria or fungi may harm daphnids (Ebert 1995; Bittner et al. 1999) and were even suggested to be the main cause of population declines (Gries and Güde 1999). However, these factors are beyond the scope of this study.

In this Chapter, the main bottom-up and top-down factors for *D. galeata* in Bautzen Reservoir are analysed during the course of the study period. The potential impact of single factors is evaluated and related to the development of *Daphnia* abundance.

3.2 Methods

Zooplankton was sampled in the pelagic zone of Bautzen Reservoir at a water depth of 10-12 m twice a week at daytime. Samples were taken at one station in the central part of the reservoir with plankton nets of 100 and 500 µm mesh size, 25 cm in diameter and equipped with a flowmeter (Hydrobios, Germany) in 1995 and 1996. Values of particulate organic carbon (POC) in the fraction < 30 µm were taken from Wagner (1998) for these years. In 1997, 1998 and 1999 a tube sampler with capacity of 2 l (Limnos, Finland) was used to sample daphnids. Single tubes taken in depth intervals of 1 m were integrated by pouring them through a plankton net of 30 µm mesh size. Additionally, samples from 3 horizontally divergent stations (distance between stations 300 to 400 m, similar water depth) were pooled, resulting in one composite sample of the pelagic zone. A subsample of the filtrate (< 30 µm) was used for analysis of POC. Additional samples were taken with a 335 µm net to concentrate adult (and potentially fecund) daphnids in case of low fecundity or low abundance of *D. galeata*. In 1996 tube samples were taken additionally to net tows at only one station. Results of different devices were compared and densities obtained by the tube sampler were found to be at least as high as those estimated from nets (mostly a bit higher, Hülsmann unpubl. data).

Zooplankton was immediately preserved in 3% sucrose-formaldehyde solution (Haney and Hall 1973). At least 100-150 daphnids per sample (usually twice as many in case of low fecundity) were counted and measured from the anterior margin of the head (excluding crests if present) to the base of the tail spine in at least three subsamples (1-10 ml, depending on relative *Daphnia* density) under a Zeiss Laboval microscope (magnification x100). If eggs were present in the brood pouch, they were counted and classified to developmental stages (I-IV) according to Threlkeld (1979) with the modification that Threlkeld´s stages 3 and 4 were classified as stage III because their duration is short and differentiation is difficult. The abundance N (ind. l^{-1}) of eggs and animals was calculated according to the formula:

$$N = \text{No. of counted individuals} \cdot \text{sample volume}/(\text{counted volume} \cdot \text{sampled volume}) \quad (3.1)$$

If eggs were found to look “abnormal“ due to infections (mostly by fungi), they were not included into calculations of egg numbers, but daphnids with infected brood chambers were counted separately. For counting *L. kindtii* the number of sub-samples was usually enhanced. If several sampling devices had been used simultaneously (different mesh-sizes, tube sampler) resulting in different densities, the maximum value was used for this species.

Simultaneously to zooplankton sampling temperature, oxygen concentration and pH was determined in depth intervals of 1 m with digital probes (WTW, Germany). Oxygen values for 1995 and 1996 were provided by Benndorf (unpubl. data). Water transparency was recorded using a Secchi disk. For carbon analysis, the 30 µm filtrate from the tube samples was filtered with pre-combusted glass-fibre filters (Filtrak, GMF 5, Germany), dried for 4 h at 60 °C and analysed in a carbon analyser (Leco, C 200, Germany). Data for 1997 and 1998 were taken from Voigt and Hülsmann (in press), POC values for 1999 were provided by H. Voigt, Inst. of Hydrobiology.

Age-0 fish were sampled once a week at night. A twin-bongo net (35 cm diameter) with mesh sizes of 500 and 780 µm was used until fish reached a total length of 20-25 mm. Double oblique hauls were performed for about 5 min. in the whole water column of the pelagic zone. To catch larger fish, a small trawl net (wing length 6.5 m, 4 mm mesh size in cod end) was used. Samples from 1 m and 6 m water depth (positioned by buoys on the otter boards) were pooled for calculation of abundance and biomass. The filtered water volume was determined by flowmeters. Fish were narcotised with CO_2 and preserved in 3% formaldehyde solution. In the laboratory they were identified to species, measured (total length, TL) and weighted (wet weight, ww). Data on fish were provided by M. Plewa, S. Worischka and A. Wagner, Inst. of Hydrobiology, TU Dresden (partly published in Mehner et al. 1997 and Hülsmann and Wagner 2000). Further details of the fish sampling can be found in Mehner et al. (1998 b, c).

3.3 Results

Physical and chemical factors and food conditions (bottom-up factors)

Mean temperature of the water column, combined for monthly periods, differed from year to year (Figure 3.1). May-temperature was lower in 1995 and 1996 compared to the following years. June-temperatures were lowest in 1995, highest in 1998. Water temperatures in July were highest in 1995 and lowest in 1996.

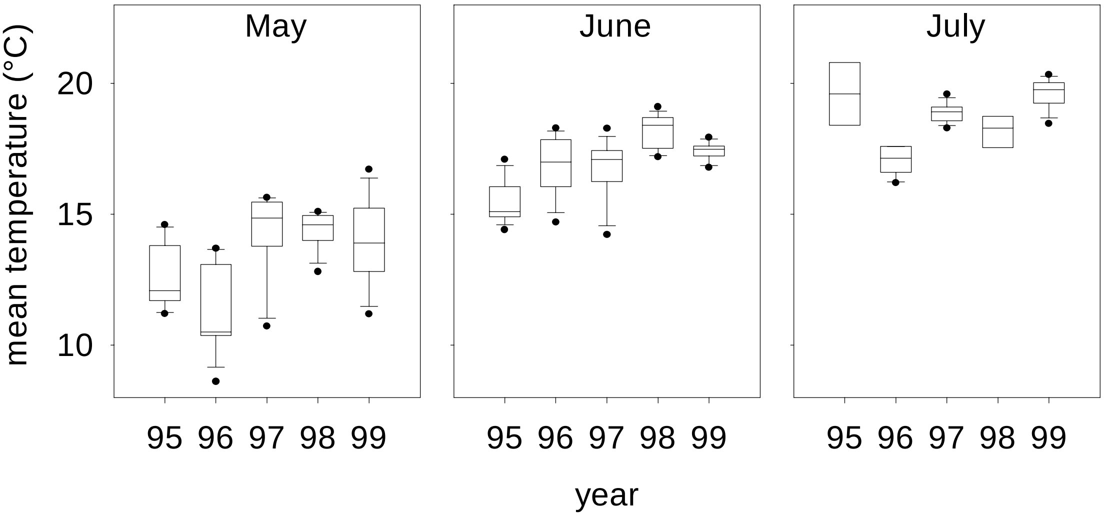

Figure 3.1. Water temperature (vertical means) in Bautzen Reservoir in May, June and July from 1995 to 1999. Box plots display the median and the 10th, 25th, 75th and 90th percentiles.

The stratification pattern differed more from year to year than mean temperatures (Figure 3.2). The main abiotic factors that may influence *Daphnia* dynamics in Bautzen Reservoir (temperature, oxygen concentrations, pH), depending on the stratification pattern, may have considerable vertical gradients. While pH in highly eutrophic waters may increase to sublethal values in surface layers due to photosynthetic CO_2 depletion, oxygen is likely to be depleted in the hypolimnion. By comparing the temperature in 2 m and 10 m depth, the development and the stability of thermal stratification was analysed. Increasing gradients and slow increases of the bottom-temperature indicate high stability of stratification, as well as decreasing oxygen concentrations in 10 m depth. Such a situation was found in 1995 and 1999 from the middle of May onwards. In 1996 stratification started at the beginning of June and was disturbed one month later. However, this was not reflected in oxygen concentration which suggests that the deepest water layers were not intensively mixed. It has to be kept in mind though that in 1996 oxygen was measured at a station which was slightly deeper than the station where temperature was determined and not exactly at the same dates (data provided by workgroup Limnology, Institute of Hydrobiology, TU Dresden).

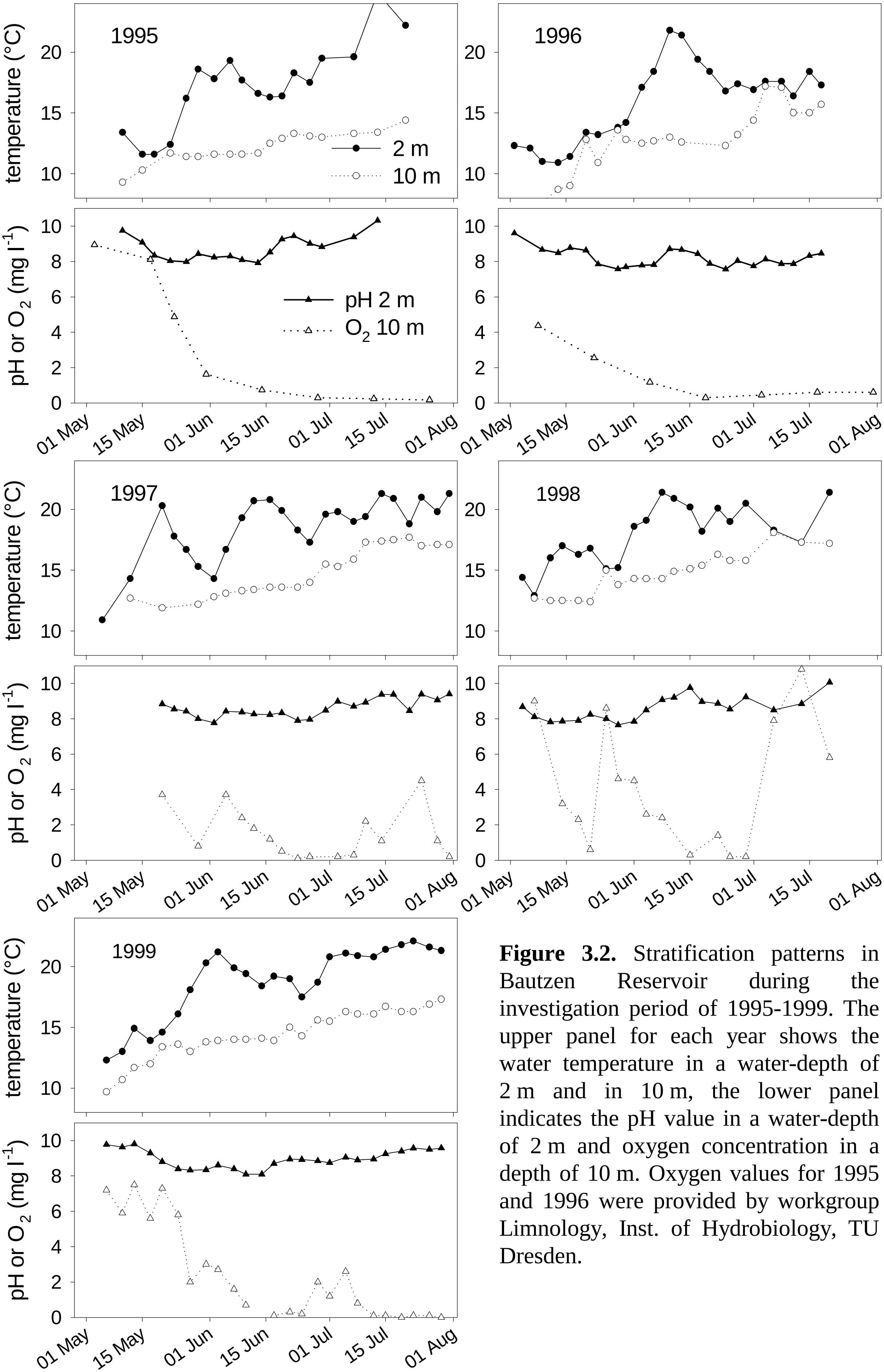

Figure 3.2. Stratification patterns in Bautzen Reservoir during the investigation period of 1995-1999. The upper panel for each year shows the water temperature in a water-depth of 2 m and in 10 m, the lower panel indicates the pH value in a water-depth of 2 m and oxygen concentration in a depth of 10 m. Oxygen values for 1995 and 1996 were provided by workgroup Limnology, Inst. of Hydrobiology, TU Dresden.

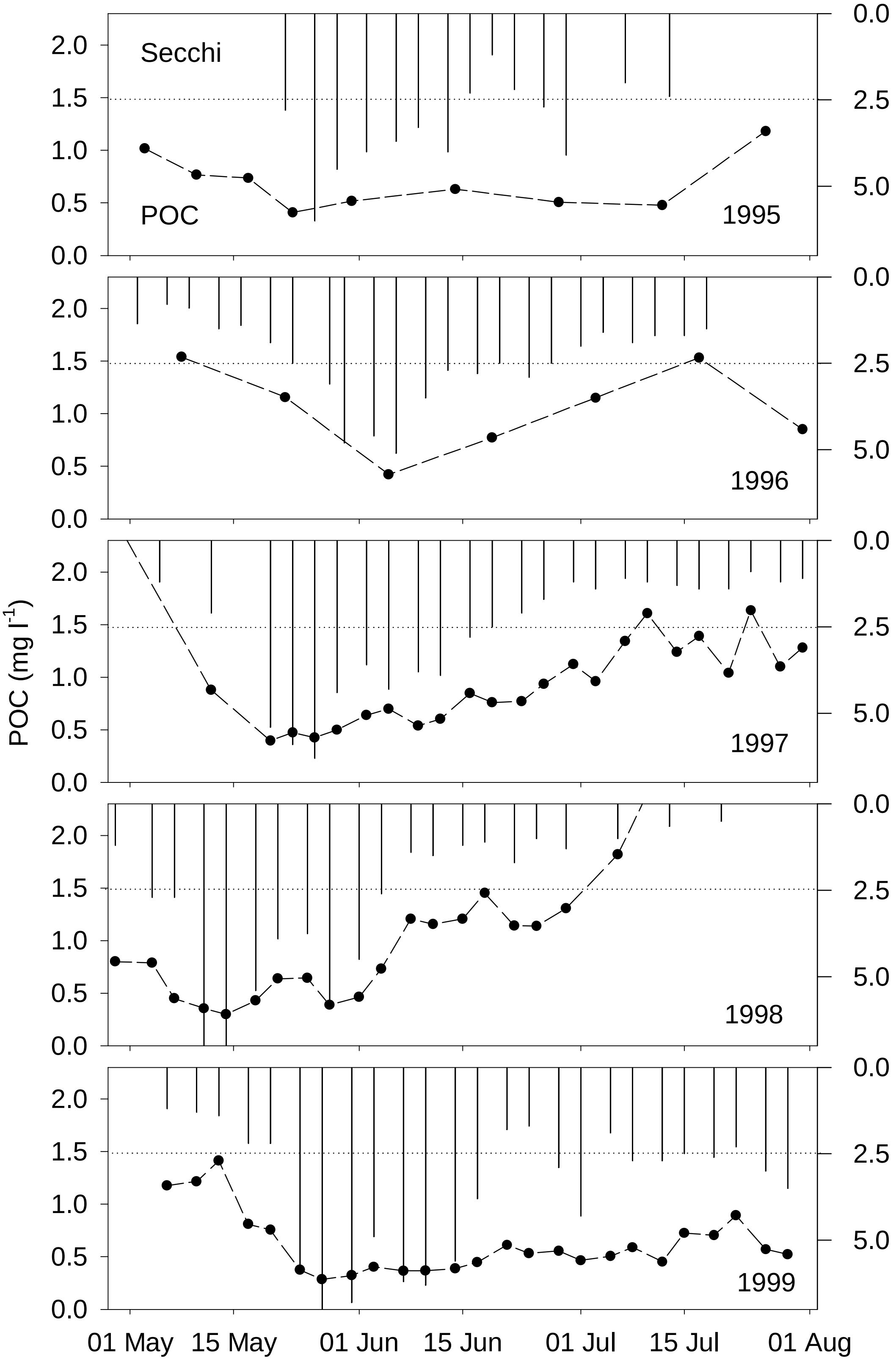

Figure 3.3. Temporal development of POC$_{<30\mu m}$ (mg l^{-1}) and Secchi depth (m) in Bautzen Reservoir during the investigation period of 1995-1999. The dotted lines indicate a water-depth of 2.5 m, which was defined as the threshold level for a clear-water stage. POC$_{<30\mu m}$ values were taken from Wagner (1998), Voigt and Hülsmann (in press) or provided by Voigt (pers. comm.).

In 1997 stratification was frequently disturbed by mixing events which mostly did not reach down to the bottom though. This, in contrast, was observed in late May and mid-July 1998. Summing up, stratification was relatively strong in 1995 and 1999 and weaker in the other years, especially in 1998. Epilimnetic pH values (at 2 m depth) always ranged between 8 and 10 during the investigation period.

$POC_{<30\mu m}$ values showed a strong decrease at the beginning of the clear-water phase (defined as period with Secchi depth > 2.5 m) in each year (Figure 3.3). Minimum values (0.4 mg C l^{-1} in 1997, 0.3 mg C l^{-1} in 1998 and 1999) corresponded to the maxima in Secchi depth (> 5 m) and Secchi depth readings > 2.5 m generally were associated with $POC_{<30\mu m}$ values < 0.8 mg C l^{-1}. The relation between the sestonic carbon content ($POC_{<30\mu m}$) and Secchi depth could be characterised by an exponential function (Figure 3.4). Although POC data for 1995 and 1996 were only available in weekly or biweekly intervals (data from Wagner, 1998), during this early period (May-June) they follow the same pattern as in the other years (Figure 3.3). In 1998 the succession of “planktonic events“ (characterised by the clear-water stage) started about two weeks earlier as in the other years. A strong increase of $POC_{<30\mu m}$ values was recorded at the end of the clear-water phase in 1996, 1997 and especially in 1998. In 1995 and 1999 the end of the clear-water phase was not as clearly defined. The temporal drop in Secchi depth in mid-June in 1995 was caused by a high water event flushing high amounts of detritus particles into the reservoir. In July 1995 a low water transparency was found despite low $POC_{<30\mu m}$ concentrations. At that time a bloom of *Microcystis* with large colonies had developed (Böing et al. 1998). Thus, the period 22 May through the end of June was considered to represent the clear-water stage in that year. In mid-June 1999 a slight increase of $POC_{<30\mu m}$ was associated with a temporal drop in water transparency. Secchi depth readings recovered in July, fluctuating around the threshold value (defining the clear-water stage) of 2.5 m but hardly exceeding it. Thus, it can be assumed that only the period with high Secchi depth readings in May/June 1999 can be compared to the clear-water phase in other years.

Age-0 fish, invertebrate predators (top-down factors) and Daphnia dynamics

Biomass of age-0 fish (pooled data for all species, only pelagic samples) clearly differed between years, being low in 1995 and 1996 compared to 1997 and 1998 (Figure 3.5). For 1999 no data were available. In the first two years of the investigation biomass of young fish increased slowly and reached maximum values of 128 and 161 mg ww m^{-3} in late June 1995 and July 1996, respectively. Age-0 fish biomass strongly increased in June 1997 to its maximum value of 478 mg ww m^{-3}. The same strong increase occurred about two weeks earlier in 1998 (maximum value: 545 mg ww m^{-3}).

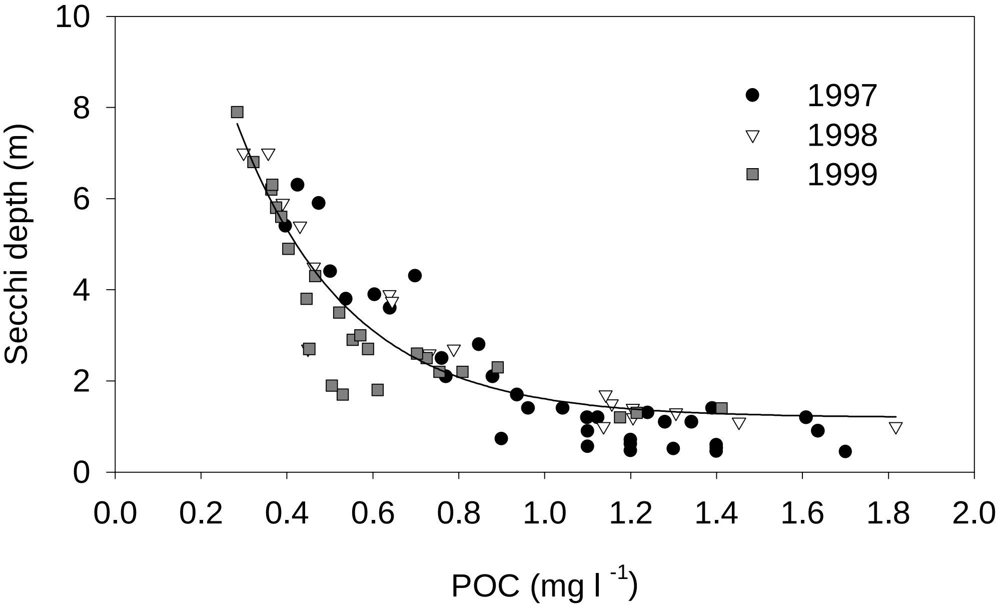

Figure 3.4. Relation between $POC_{<30\mu m}$ (mg l^{-1}) and Secchi depth in Bautzen Reservoir during the investigation period of 1997-1999. For the regression pooled data from all years were used: y = 1.196 + 19.253 exp(-3.851 x), $r^2 = 0.857$, $p < 0.0001$.

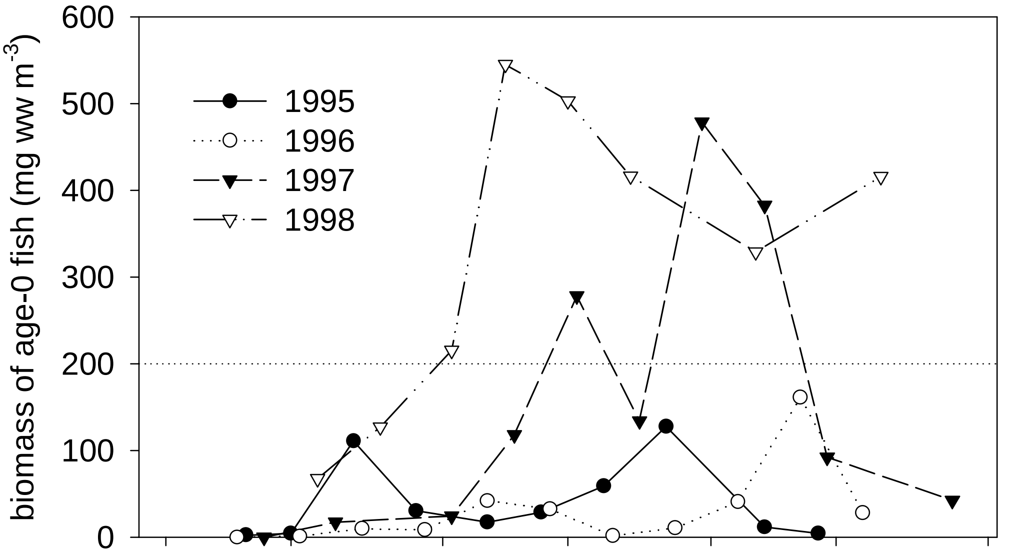

Figure 3.5. Temporal development of biomass of juvenile fish (mg ww m^{-3}) in Bautzen Reservoir during the investigation period of 1995-1998 (sum of all species, only pelagic samples, no data available for 1999). The dotted line indicates the approximate threshold level of 20 kg ha^{-1} as proposed by Mills and Forney (1983). See text for further explanation. Data were taken from Mehner et al. (1997), Worischka (1997) and Hülsmann and Wagner (2000).

L. kindtii was virtually absent until June and reached higher densities only from the middle of June onwards in all years of investigation (Figure 3.6). However, the density levels achieved differed from year to year. Abundance was generally low (< 1 ind. l^{-1}) in 1995 and 1998. In 1996 an outstanding high value was found in June (2.6 ind. l^{-1}), later densities ranged from 1-1.5 ind. l^{-1}. In July 1999 they were in the same range, fluctuating more strongly though. Highest densities of *Leptodora* were found in 1997.

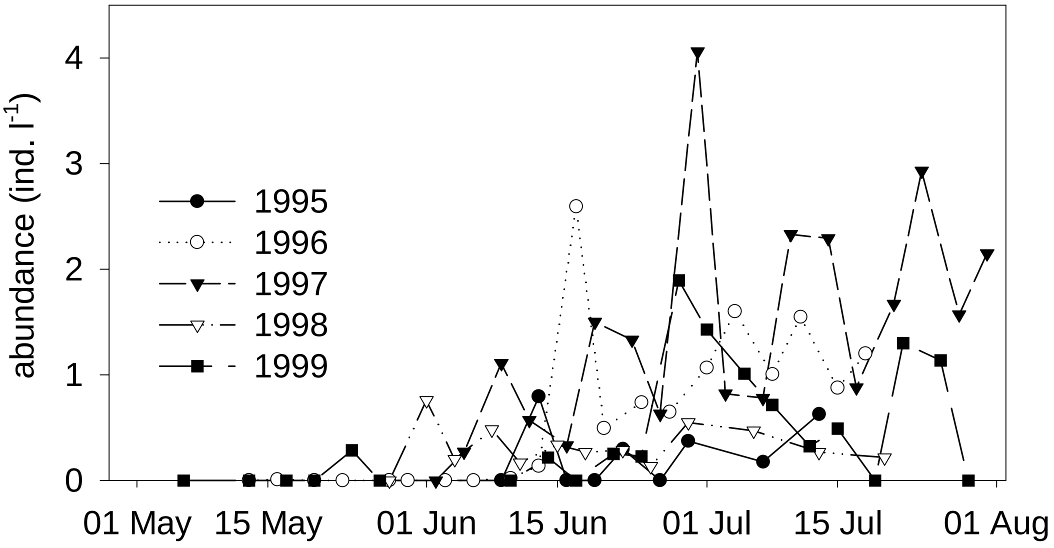

Figure 3.6. Abundance (ind. l^{-1}) of *L. kindtii* during the investigation period of 1995-1999 in Bautzen Reservoir.

In all the years of this investigation there was a phase of high *Daphnia* densities during the study period from May to July (Figure 3.7). However, *Daphnia* population dynamics differed in several aspects between years. With regard to the key mechanism of biomanipulation, the stabilisation of high *Daphnia* abundance, the years can be classified into those without a midsummer decline (1995, 1999) and those with a midsummer decline (1996, 1997, 1998)(for definition of midsummer decline see below). Years without a midsummer decline were characterised by a slow increase of abundance in spring, starting from low densities in early May (< 10 ind. l^{-1}). Peak densities were reached in the middle of June (1995) or in July (1999). In contrast, in years with a midsummer decline the *Daphnia* population increased fast and early to its maximum abundance. This was most obvious in 1997 and 1998 when the population development in May started from relatively high densities (35 and 45 ind. l^{-1}, respectively) and increased about threefold in one week. With some fluctuations abundance remained high for about four weeks and then declined rapidly to low values (~10 ind. l^{-1} in 1997, < 1 ind. l^{-1} in 1998) which lasted until the end of the investigation period.

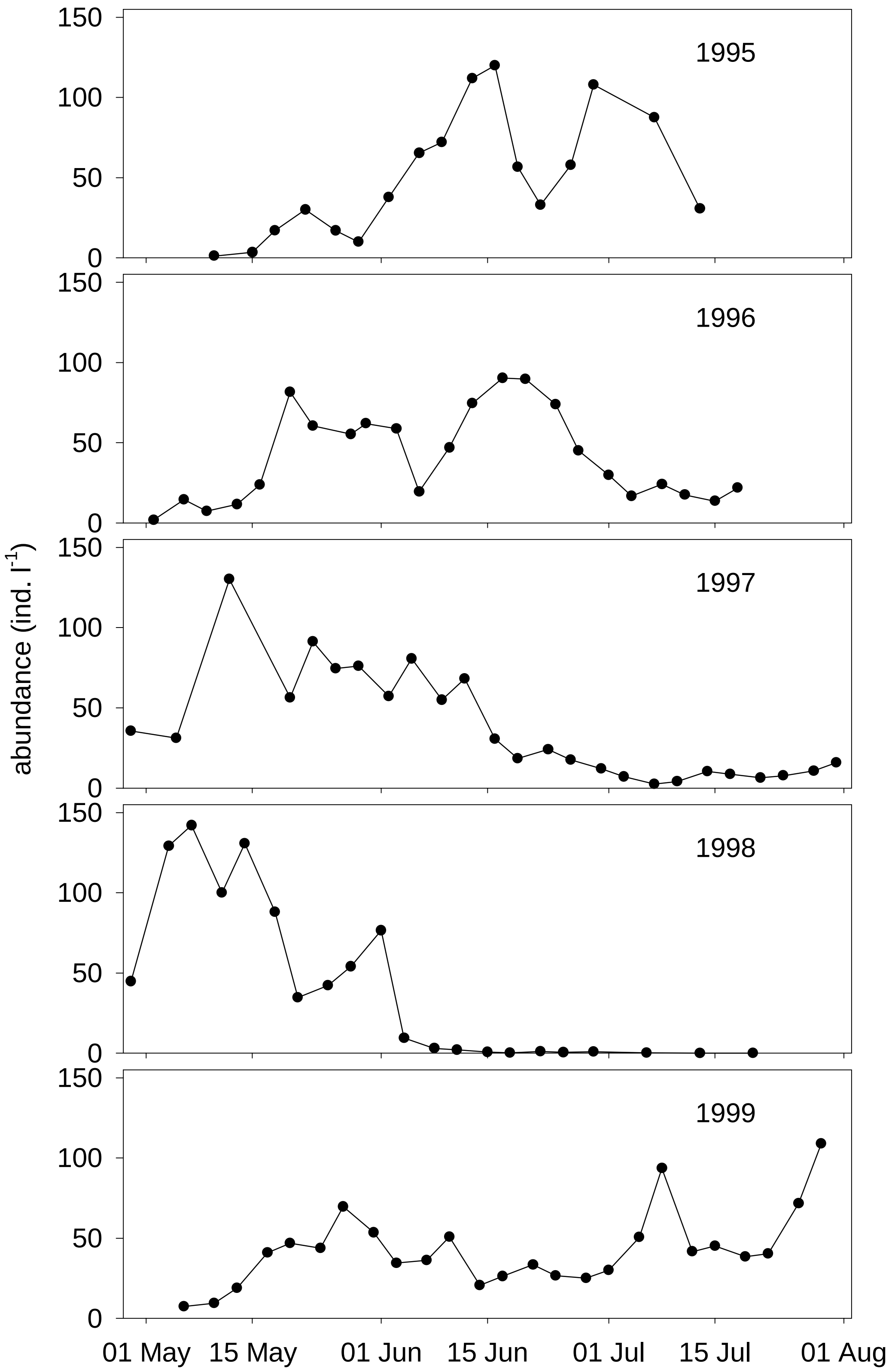

Figure 3.7. Abundance (ind. l^{-1}) of *D. galeata* during the investigation period of 1995-1999 in Bautzen Reservoir.

The population development in 1996 was in between those found in years with or without a midsummer decline. The increase in early May, similarly to years without a midsummer decline, was very low and started from a low density. After that, however, population dynamics more resembled patterns observed in years with a midsummer decline: A strong increase during one week was followed by a period of high abundance and a subsequent (but moderate) decline.

3.4 Discussion

Related to the main objective of this study, the analysis of *Daphnia* population dynamics with regard to successful biomanipulation, the different pattern of population development can be categorised into years with or without a midsummer decline. A midsummer decline under the conditions of Bautzen Reservoir was defined as a decline of *Daphnia* biomass below 1 mg ww l^{-1} by Benndorf et al. (2001). For the specific conditions of this water, this is a reasonable, but nevertheless arbitrarily chosen value. According to this definition, densities presented in this study (when converted to ww) fall below the threshold in 1997 and 1998, but not in 1995 and 1999 and only on one date in 1996. Benndorf et al. (2001) distinguished between a short (< 30 days) and a long midsummer decline (> 30 days), considering the whole growing season and using a fortnightly sampling interval. Since the present study focuses on mechanisms initiating (or preventing) a midsummer decline, the sampling interval was 3-4 days but the investigation period was limited until July. For the purpose of this study and from an extensive literature search on midsummer declines (Chapter 8, Table 8.3), a midsummer decline was defined as a period of at least two weeks of strongly reduced abundance (< 20% of maximum abundance) during June through August. Again, according to this definition, the diagnosis is unambiguous for two years in each category (no midsummer decline in 1995 and 1999, midsummer decline in 1997 and 1998), whereas *Daphnia* densities in July 1996 - with one exception - were slightly above the critical level. This “in between“ pattern in 1996 is discussed below and in the next Chapters. However, since abundance did decline and remained on a comparably low level, 1996 is referred to as “with midsummer decline“.

No clear pattern distinguishing between years with or without a midsummer decline emerged from the comparison of mean water temperature. However, a monthly separation of the sampling period (as in Figure 3.1) may be inappropriate and a phenomenological approach may lead to different results. When the mean temperatures of the clear-water phases (corresponding to the period of high *Daphnia* abundance) of each year are compared, however, still no trend could be detected. Mean temperature during the clear-water phase was the same in 1995 and 1998 (15.0°C) and in 1996 and 1997 (15.9°C), a bit higher in 1999 (16.2°C). Rising temperatures in early May clearly are a prerequisite for a quick population growth, but no direct temperature effects on the initiation of a midsummer decline can be expected according to this study. Benndorf et al. (2001) concluded from an analysis of a long-term data set from Bautzen Reservoir that temperature indirectly influences the initiation of a midsummer decline by two mechanisms. The temperature in winter and early spring determines the timing and the height of the spring peak of daphnids which has consequences for non-predatory mortality due to aging. The temperature in early summer influences the timing of the hatching of young fish and their growth during their first weeks of life. This has a strong influence on the development of the biomass of juvenile fish which determines their feeding impact on *Daphnia* (compare Chapters 7/8).

In contrast to the mean temperature, the stratification pattern differed rather clearly between years with and without a midsummer decline. Years without a midsummer decline were characterised by stable stratification from mid-May onwards. Contrary to this, in years with a midsummer decline, stratification was unstable. This was most obvious in 1998, the year with the most drastic decline of *D. galeata*. Since temperature gradients were small, even in stratified conditions, the most important parameter characterising stratification stability probably was oxygen depletion in deep water layers. This may have effects on the presence or absence of a hypolimnetic refuge for the daphnids (Wright and Shapiro 1984) and is discussed in Chapter 8.

Throughout the study period, pH values hardly exceeded 10 and consequently, neither direct effects on *Daphnia* survival nor decreasing egg viability can be expected due to pH effects (Beklioglu and Moss 1995; Vijverberg et al. 1996; Ritter 1997). Higher pH values were only recorded right at the surface, which was generally avoided by daphnids (personal observation). With regard to *Daphnia* - fish interactions, daphnids may actually benefit from pH values around 10, as fish are more sensitive to high pH than daphnids (Beklioglu and Moss 1995). Only a further increase of pH (≥ 10.5) may also impair *Daphnia* fitness (O´Brien and DeNoyelles 1972; Vijverberg et al. 1996).

Relatively low $POC_{<30\mu m}$ values during the clear-water stage may be regarded as a result of high *Daphnia* grazing (Lampert et al. 1986). Böing et al. (1998) indeed found negative correlations between the biomass of the edible size fraction of the phytoplankton and the clearance rate of *D. galeata* and between phytoplankton biovolume and Secchi depth in Bautzen Reservoir. However, although the clear-water phase certainly was associated with high *Daphnia* densities, the timing between the development of the *Daphnia* population and the onset (or termination) of the clear-water stage differed from year to year. Peak densities of *D. galeata* were recorded shortly before the maximum in Secchi depth in years with a midsummer decline: 1996 (82 ind. l^{-1} in May, 5.1 m), 1997 (130 ind. l^{-1}; 6.3 m) and 1998 (142 ind. l^{-1}; 7.0 m). In years without a midsummer decline (1995, 1999), peak Secchi depth readings (6.0 m and 7.9 m, respectively) were observed already at moderate *Daphnia* densities during the build-up of the population, although neither maximum water transparency nor maximum *Daphnia* abundance (120 ind. l^{-1} in June 1995, 69 and 108 ind. l^{-1} in May and July 1999, respectively) differed from other years (compare Table 8.2). Of course, *Daphnia* abundance does not linearly translate into an effective grazing rate, but depends on population structure and modifications of the individual grazing rate e.g. due to dissolved substances (Wagner 1998). Additionally, grazing effects of other zooplankton species contribute to overall grazing pressure. For the initiation of the clear-water phase in Bautzen Reservoir, in particular *Asplanchna priodonta* grazing on *Asterionella formosa* may be important (Köthe 1995). A detailed analysis of the interactions between food conditions and *Daphnia* grazing in Bautzen Reservoir is provided in Wagner (1998) and Voigt (in prep.). In this study, the food effects on *Daphnia* reproduction and life history are analysed (Chapters 4, 5, 6). The high amplitude of POC dynamics suggests that food conditions have a strong influence, although minimum values were much higher than threshold food concentrations for *Daphnia* reproduction in other systems (e.g. Lampert 1978).

Differences in biomass of juvenile fish in different years indicate an influence of fish predation on *Daphnia* dynamics. Fish biomass was much higher in 1997 and 1998 (when *Daphnia* declined) than in 1995 and 1996 (no, or moderate decline, respectively). However, even in these years, increases of fish biomass coincided with decreases in *Daphnia* density. In 1997 and 1998 the decline of the *Daphnia* population occurred exactly at the time when juvenile fish biomass exceeded 200 mg ww m^{-3}. Assuming a mean depth of the pelagic zone of 10 m, this value converts to 20 kg ha^{-1}. This was estimated as critical age-0 fish biomass by Mills and Forney (1983) who found that *D. pulex* in Oneida Lake declined in those years when this threshold was exceeded.

The coincidence between the increase in fish biomass and the decline of *D. galeata* in Bautzen Reservoir is striking. However, from a rough estimate of Mehner et al. (1995) and results of an enclosure experiment (Hülsmann and Mehner 1997), much higher critical values were suggested for this particular water. It can be suggested that the critical fish density for *Daphnia* depends on the nutrient level of the system (Scheffer et al. 2000) and on additional mortality factors. Unfortunately, no data concerning juvenile fish biomass are available for 1999. However, the comparison of relative catches of age-0 fish with gill-nets, which was done in every year of this investigation in late summer and in November, suggests that the 1999 year-classes of perch and zander (and also roach) were low compared to 1997 and 1998 (Dörner et al. in prep.). Effects of fish on *Daphnia* life history are analysed in Chapter 6. Predatory mortality of *D.galeata* due to juvenile fish is discussed in Chapter 7.

Concerning abundance estimates of invertebrate predators, one has to consider sampling efficiency of different devices. Generally, high sampling volumes are desirable, as densities are smaller compared to mesozooplankton abundance. In an extensive study on invertebrate predators in Bautzen Reservoir, Bollenbach (1998) found that nighttime sampling with a net of 250 µm mesh size was most effective to catch *L. kindtii* and *C. flavicans*. Both species show strong dial migration behaviour, hiding near (or actually on) the bottom during daytime. For the sake of comparability between different years, only daytime catches were considered in this study. However, in contrast to Bollenbach (1998), tube samples (Friedinger type) were also considered. The latter were often found to yield the highest densities. This was most probably due to the vertical distribution of *Leptodora*, because by using a Friedinger bottle, samples were taken very close to the bottom, whereas with nets, at least the lowest half meter (length of the net) was not sampled. Abundance estimates of *Leptodora* in 1997 in this study (max.: 4 ind. l^{-1}) indeed partly are even higher than those found by Bollenbach (1998) (2 ind. l^{-1}). Still, they were in the same order of magnitude. However, relatively strong fluctuations suggest that patchiness and sampling error was higher in daytime catches than in nighttime catches.

Concerning differences between years with or without a midsummer decline of *D. galeata* no clear pattern of *Leptodora* abundance arises. A decline was observed in both years with high densities of *Leptodora* (1996, 1997). However, the strongest decline was observed in 1998, when *Leptodora* was much less abundant. Interestingly though was the highest density of *Leptodora* in 1998 found at the beginning of June when *Daphnia* declined. Results of Bollenbach (1998) suggest that predation impact of *Leptodora* on *Daphnia* is strongest in late summer (which was beyond the scope of this study) and thus may be significant for the duration of a midsummer decline.

In summary, in accordance with Sommer et al. (1986), temperature, food and predation (mostly by age-0 fish) may be considered as decisive factors controlling *Daphnia* dynamics in Bautzen Reservoir during spring and early summer. The main temperature effects on the initiation of a midsummer decline refer to the timing of the spring peak of *Daphnia* and to the development of the biomass of juvenile fish feeding on daphnids (Benndorf et al. 2001). Food conditions decline during the clear-water phase. Towards the end of this period, biomass of juvenile fish may increase strongly. How these factors influence *Daphnia* dynamics and life history and how they interact leading either to a midsummer decline or not is analysed in the next Chapters.

4 Food limitation of fecundity and reproduction of *Daphnia galeata* as determined in field samples

4.1 Introduction

Relating fecundity of cladoceran populations to food conditions in field samples is notoriously problematic. Although it is common sense that food conditions influence fecundity and some studies have shown a clear relation between food concentration and the number of eggs per female (e.g. Lampert 1978; Müller-Navarra and Lampert 1996), it is clear that effects of predation are also of great importance. As reviewed by Gliwicz and Boavida (1996), a reduction of the mean brood size of a given size class of *Daphnia* may similarly be obtained by food limitation, size selective feeding by fish and copepod predation on eggs in brood cavities, although the mechanisms differ. With regard to the mean clutch size in a population, additionally a strong effect of a changing size structure of the population can be expected, as brood size depends on body size (Seitz 1980; Gliwicz and Lampert 1994).

In order to eliminate the effects of body size on clutch size, Hebert (1977) calculated a “standard egg production“, which is the mean clutch size of an animal of standard length. This value is derived from a regression of brood size on body size multiplied by the proportion of egg carrying females (related to the total number of adults). This concept has since been applied in many studies (e.g. Lampert 1988 b; Boersma 1995; Müller-Navarra and Lampert 1996), although its applicability has never really been tested despite obvious flaws. In situations of food limitation, all gravid females of a *Daphnia* population produce only few eggs, irrespective of their size. In these cases, the slope of the regression of brood size versus body size is not significantly different from zero and the mean brood size (mean number of eggs per brood) is used (Lampert 1988 b). When a significant regression is found, the difference between mean brood size and standard brood size depends on the relation between the mean size of egg carrying females and the arbitrarily chosen standard size. Both slope and intercept of these regressions are affected by food levels and possibly even by the size structure of the population (Hall 1964; Duncan 1989; Arbačiauskas and Gasiunaite 1996). Hence, the results depend on the chosen standard length. Moreover, as mean brood size may also be influenced by predation (see above), the calculation of a standard brood size is valid only on condition that the predation impact is equal for all egg carrying size classes of a cladoceran population. This supposition however, will hardly be met and consequently, the standard brood size (or standard egg production) may not be truly size-independent.

The influence of body size on brood size can be regarded as space limitation of the brood pouch in case of excess food conditions and without predation. Thus, a clear relation should exist between body size and maximum brood size (compare Chapman and Burns 1994; Gliwicz and Lampert 1994). Using this relation and relating the actual egg number of a

Daphnia population to a calculated maximum value, should therefore result in a truly size-corrected measure of the reproductive potential of a *Daphnia* population.

In this Chapter, different parameters of *Daphnia* fecundity are compared with regard to possible influences of the changing size structure of the population. Further, these reproductive parameters are related to prevailing food conditions in Bautzen Reservoir, taking into account possible influences of predation. As the reproductive success of a *Daphnia* population, apart from fecundity, is determined by temperature and the population structure (Paloheimo 1974; Polishchuk 1995), the reproductive patterns during the investigation period are analysed. For this purpose another “uncommon“ parameter, potential cumulative recruitment, is introduced.

4.2 Methods

Field sampling of *Daphnia* as well as determination of POC and water temperature are explained in Chapter 3.

The proportion of adults in the population of *D. galeata* was estimated after determining the size at maturity (SAM) according to Stibor and Lampert (1993): The proportion of egg-carrying females was calculated for each size class (class width 50 µm). The smallest size in which this proportion was at least 50% of the mean value of definitely adult size classes was defined as SAM. This parameter and the mean size of egg-carrying daphnids was used to characterise the size structure of the *Daphnia* population. SAM was shown to correlate also with mean size and maximum size of *D. galeata* in Bautzen Reservoir, respectively (Mehner et al. 1998 b; Hülsmann and Weiler 2000). A standard brood size (SBS) was calculated for daphnids of 1.4 mm length (this standard size had also been used for *D. galeata* by Lampert 1988 b and Müller-Navarra and Lampert 1996), derived from a linear regression between body length and egg number. Multiplying this value by the proportion of egg-carrying adults (related to the total number of adults) results in a standard clutch size (SCS) (compare Hebert 1977; Lampert 1988 b). The calculation of other reproductive parameters is explained in Table 4.1.

Additionally, in an approach introduced by Vaga et al. (1985) and similarly used by Chapman and Burns (1994) and Gliwicz and Lampert (1994), the reproductive potential of *D. galeata* was calculated as follows: Considering all egg carrying daphnids that have been found in all samples from 1995-1998, the maximum brood size in size classes of 50 µm width was determined. A regression of maximum brood size versus mean body size of each size class was calculated. Taking this function and the abundance of different size classes (50 µm width) of *D. galeata* on every sampling date, the maximum egg number per size class was calculated. Finally, these calculated egg numbers were summed for all adult size classes (according to

SAM). The actual egg number of each sampling date was then expressed as percentage of this calculated value (theoretical maximum egg number, assuming that all adults carry the maximum brood size) and defined as realised reproductive potential (RRP). For example, RRP = 20% means that the population with a given size structure realised only 20% of the egg number it could have realised under favourable conditions.

Table 4.1. Definitions of reproductive parameters and relations between them. A standard size of 1.4 mm was used for *D. galeata* (Lampert 1988 b; Müller-Navarra and Lampert 1996). E = egg number, N_e = Number of egg carrying daphnids, N_a = Number of adult daphnids, N = total number of daphnids, E_{max} = calculated maximum egg number. * introduced as standard egg production (SEP) by Hebert (1977).

Parameter	Calculation	Relationships
Mean brood size (BS)	$= E/N_e$	
Proportion of egg carrying adults (Ad)	$= N_e/N_a$	= CS/BS
Mean clutch size (CS)	$= E/N_a$	= BS Ad
Egg ratio (ER)	= E/N	$= CS\ (N_a/N) = BS\ (N_e/N)$
Standard brood size (SBS)	= BS of standard-sized *Daphnia* (see text)	
Standard clutch size (SCS)*	= CS of standard-sized *Daphnia* (see text)	= SBS Ad
Realised reproductive potential (RRP)	$= E/E_{max}\ 100$ (see text)	

A time shift (delay) of once the egg developmental time (D), calculated from the mean water temperature according to Bottrell et al. (1976), was introduced to relate reproductive parameters to sestonic carbon content. Assuming an even egg age distribution, a time shift of about one D is most reasonable, which is confirmed by a correlation analysis by Seitz (1980) and results of Müller-Navarra and Lampert (1996), who used a time shift of 1.25 D. POC values were linearly interpolated between sampling dates if necessary. Pooled data from 1997 and 1998 (high temporal resolution) were used. Linear regressions of the form $y = m\ x + b$ were calculated for the relation between $POC_{<30\mu m} < 0.8$ mg l^{-1} (clear-water phase) and reproductive parameters. The POC-threshold (Th) for egg production was calculated from the function coefficients if the regression was found to be significant ($p < 0.025$): $Th = -b/m$ (intercept with x-axis).

For comparison of RRP with other reproductive parameters, I will focus on clutch size (CS) and standard clutch size (SCS), as these parameters are most frequently used in studies of *Daphnia* fecundity.

Reproduction of *D. galeata* was analysed using the egg-ratio method. The birth rate was calculated according to Paloheimo (1974):

$b = \ln(E/N + 1)\ 1/D$ (4.1)

As sampling intervals were usually shorter than D, it was possible to calculate the actual recruitment of the population (better: potential recruitment, assuming that all eggs may actually hatch). The approach of Johnsen (1983), as modified by Dorazio (1986), was used to calculate the hatching frequency. According to Threlkeld (1979), eggs spend different portions A_i of total egg development time D in each egg stage i ($A_I = 0.302$, $A_{II} = 0.32$, $A_{III} = 0.218$, $A_{IV} = 0.16$). Thus, the duration D_i of egg stage i is

$$D_i = D \cdot A_i \text{ (d)} \tag{4.2}$$

The proportion P_i of eggs that are going to hatch during the time interval Δt can be calculated for each egg stage (I-IV):

$$\text{if } D_{IV} > \Delta t \quad \text{then } P_{IV} = \Delta t / D_{IV} \text{ and } P_{I\text{-}III} = 0 \quad \text{else } P_{IV} = 1 \tag{4.3}$$

$$\text{if } D_{IV} + D_{III} > \Delta t \quad \text{then } P_{III} = \frac{\Delta t - D_{IV}}{D_{III}} \text{ and } P_{I\text{-}II} = 0 \quad \text{else } P_{III} = 1 \text{ and} \tag{4.4}$$

$$\text{if } D_{IV} + D_{III} + D_{II} > \Delta t \quad \text{then } P_{II} = \frac{\Delta t - (D_{IV} + D_{III})}{D_{II}} \text{ and } P_I = 0 \quad \text{else } P_{II} = 1 \text{ and} \tag{4.5}$$

$$\text{if } D > \Delta t \quad \text{then } P_I = \frac{\Delta t - (D_{IV} + D_{III} + D_{II})}{D_I} \quad \text{else } P_I = 1 \tag{4.6}$$

The total number of eggs (E_h) that are going to hatch during the time interval Δt was calculated from P_i and the observed frequency of each egg stage (F_i):

$$E_h = \sum_{i=I}^{IV} P_i \cdot F_i \tag{4.7}$$

These calculations will result in an underestimation of E_h if $D < \Delta t$. During June and July this was sometimes the case when the sampling interval Δt was 4 days and, depending on temperature, exceeded D by 0.5 to 1 day. In July 1995 and 1998 samples were only taken weekly. Assuming an equal egg age distribution during these sampling intervals, the calculated number of neonates (in these cases equal to the number of eggs present at the beginning of the sampling interval) was multiplied with the factor ($\Delta t/D$) to obtain the potential recruitment. In order to compare recruitment patterns in different years, cumulative recruitment was calculated for each year and added to the start-abundance at the end of April or the beginning of May when field investigations started.

4.3 Results

Relation body size - maximum brood size

A clear relation exists between body size and maximum brood size of *D. galeata* in Bautzen Reservoir (Figure 4.1). Daphnids > 1.8 mm generally were scarce and hence, it should not be overemphasised that in the largest specimens only few eggs were found. Consequently, animals > 2.0 mm were not considered for calculating the regression line. Highest egg numbers in large size classes (defining the limiting line) were found in spring samples in all years investigated (exemplified for one date in 1996 by grey circles). Egg numbers were generally small during the clear-water stage (black triangles), although the same size-classes carried eggs as in spring samples. Small ovigerous daphnids (< 1 mm) were found in summer samples (white squares).

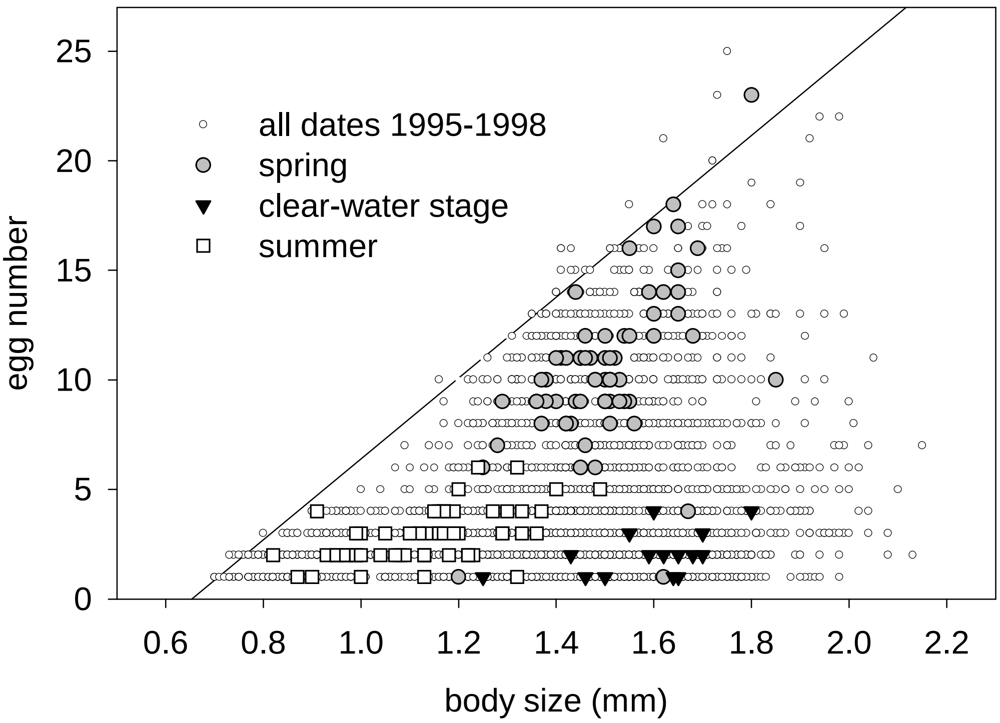

Figure 4.1. Relation between body size (mm) and brood size (number of eggs) of *D. galeata*, considering all egg-carrying daphnids in samples taken from Bautzen Reservoir between May and July of 1995-1998 (dots) and showing examples of this relation at selected dates, representing particular situations (spring: 16 May 1996, clear-water stage: 3 June 1996, summer: 18 July 1996). The regression equation of maximum brood size BS_{max} versus body size (limiting line) was calculated for maximum egg numbers in size classes of 50 µm width: $BS_{max} = 18.45\ L - 12.055$; $r^2 = 0.94$, $p < 0.005$. From Hülsmann (in press).

Size structure of Daphnia population and fecundity

The size structure of the *Daphnia* population was characterised by a high and relatively stable SAM prior to and during the clear-water phase in all years of investigation (Figure 4.2). The mean size of egg-carrying daphnids always reflected the same changes in the size structure as SAM (with some time lags), indicating that the size range of ovigerous females was usually narrow and that small SAM indeed indicates a small size of all egg-carrying animals. In 1995 some fluctuations of SAM occurred at the end of the clear-water phase, but values never fell short of 1.1 mm. In all other years a high SAM (maximum values > 1.5 mm) was found during the clear-water phase, but after that a distinct decrease was recorded. In 1996, a primiparous size of about 1 mm was found in July, whereas in 1997 values dropped to about 0.8 mm during three weeks and in 1998 this decrease took place during only two weeks. Reduction of SAM in 1999 was moderate down to a summer-level of 1.1-1.2 mm.

Concerning *Daphnia* fecundity, similar patterns as well as pronounced differences can be found between different years (Figure 4.3). In all years there was a strong decrease in fecundity related to the decline of $POC_{<30\mu m}$ values (see Figure 3.3) at the beginning of the clear-water stage, irrespective of which reproductive parameter is considered. However, the decline started at different levels, being highest in 1996 and 1999 (CS = 13, SCS = 8, RRP = 89%) and lowest in 1998 (CS = 5, SCS = 4, RRP = 26%). At the beginning of the clear-water phase fecundity was generally low. However, in 1995 and 1999 extremely low values (CS and SCS < 1, RRP < 5%) were seldom recorded but fecundity remained at a relatively low level throughout the rest of the study period. In all other years strong fluctuations occurred already during the clear-water phase and thereafter. Comparing the different reproductive parameters, seasonal fluctuations were similar both in direction and extent of change for most of the investigation period in all years. However, reproductive parameters strongly diverged especially in 1997 and 1998 after SAM declined. SCS was either lower than or equal to CS until SAM declined, henceforward slightly higher. RRP cannot be directly compared to CS or SCS, however, it almost identically followed the same patterns as CS until SAM declined. From then on, RRP increased in comparison to CS and reached values that were comparable to (1997) or even higher (1998) than those before the clear-water phase.

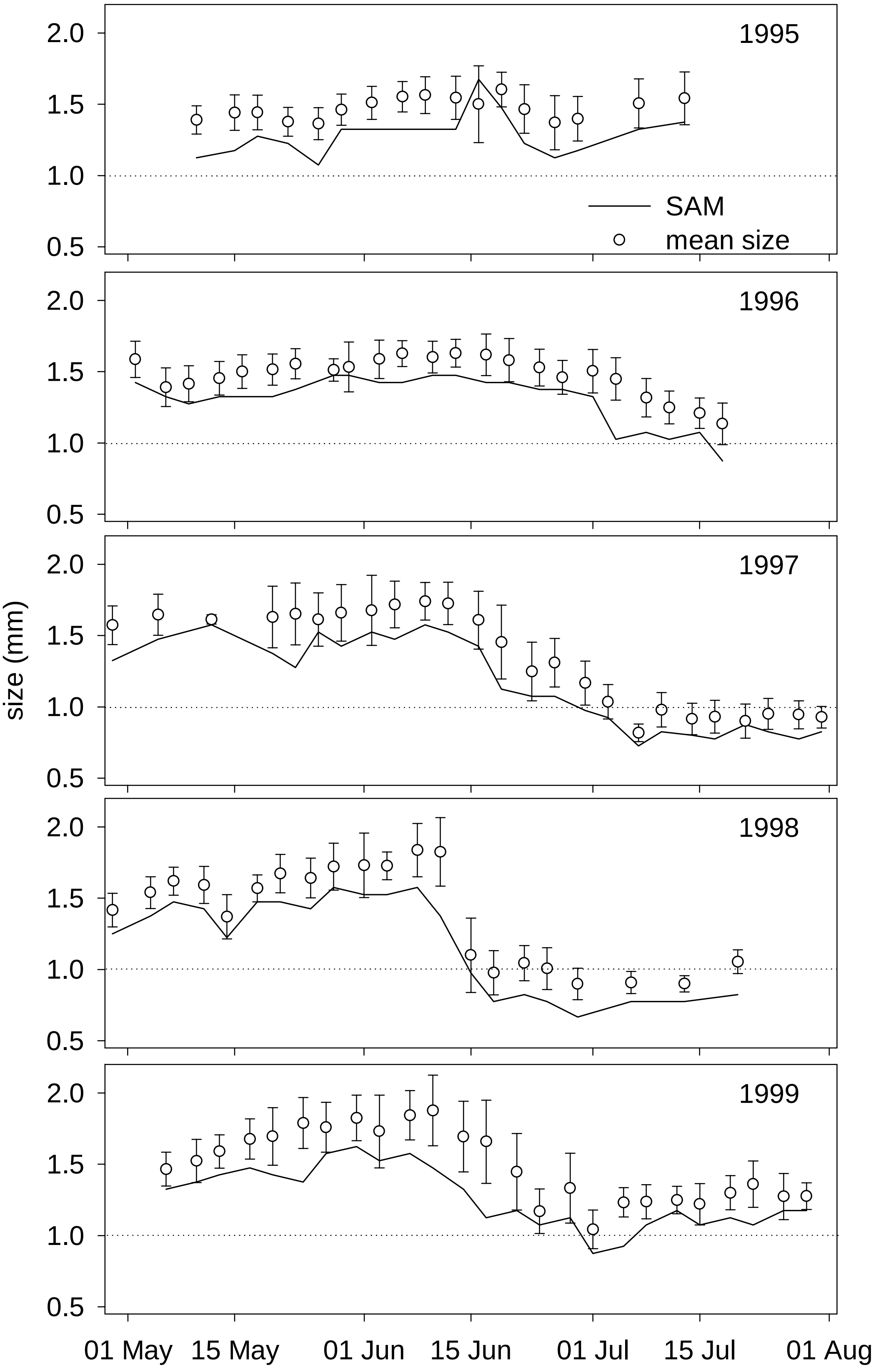

Figure 4.2. Temporal pattern of size at maturity (SAM) and mean size (± SD) of egg-carrying females (mm) of the *Daphnia* population in Bautzen Reservoir during the investigation period of 1995-1999.

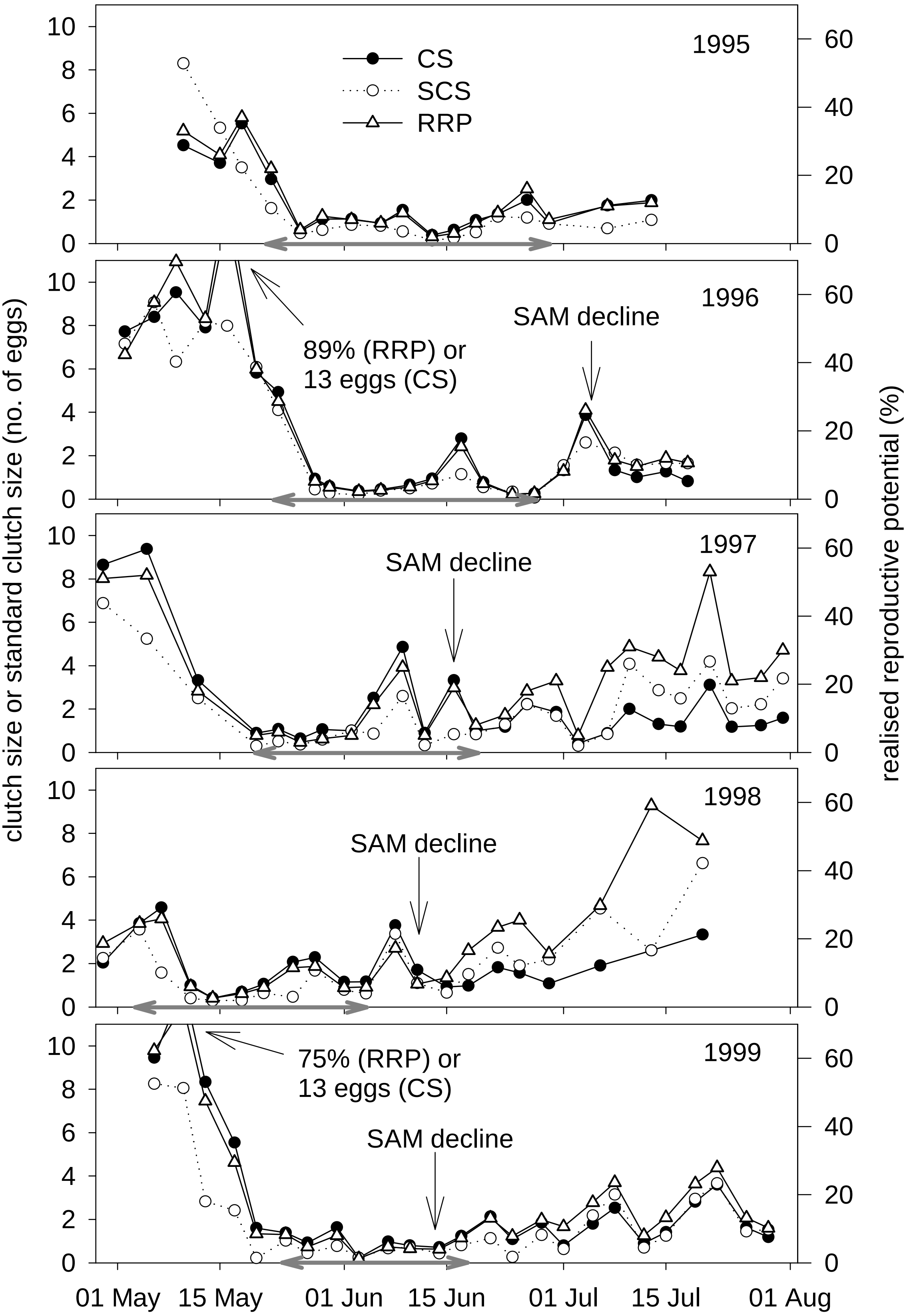

Figure 4.3. Temporal pattern of clutch size (CS), standard clutch size (SCS) and realised reproductive potential (RRP) of *D. galeata* in Bautzen Reservoir during the investigation period of 1995-1999. Grey arrows on the x-axis indicate the clear-water phase with a Secchi depth > 2.5 m.

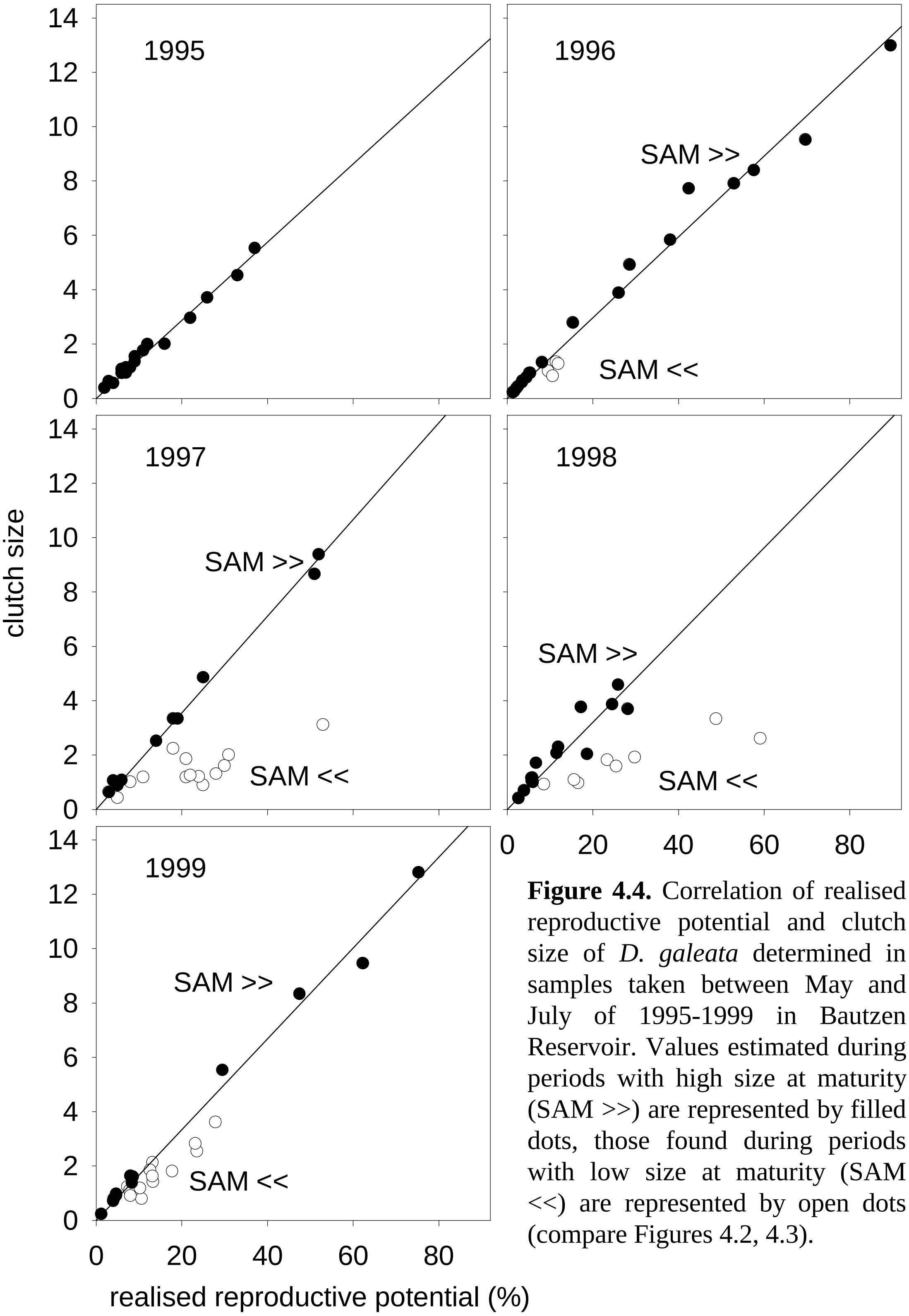

Figure 4.4. Correlation of realised reproductive potential and clutch size of *D. galeata* determined in samples taken between May and July of 1995-1999 in Bautzen Reservoir. Values estimated during periods with high size at maturity (SAM >>) are represented by filled dots, those found during periods with low size at maturity (SAM <<) are represented by open dots (compare Figures 4.2, 4.3).

Correlating RRP with CS in different years reveals that both parameters were closely coupled as long as SAM was high (and relatively stable) (Figure 4.4, Table 4.2). Correlation coefficients were 0.99 for 1995 and 1996 and 0.98 for 1999 regarding all sampling dates. In 1997 and 1998 they were equally high (0.99 and 0.95, respectively) only when considering sampling dates before SAM declined (Table 4.2). The moderate declines of SAM in 1996 and 1999 did not strongly affect the correlation (Figure 4.4), although the same tendency as in 1997 and 1998 becomes obvious: When expressed as clutch size, fecundity in case of low SAM is lower than RRP would suggest. As all reproductive parameters are based on the same raw data (compare Table 4.1), they are closely related and thus, correlation of RRP with other parameters is partly just autocorrelation. However, it is still remarkable that highest r-values (regarding high SAM) were found between RRP and CS in all years investigated, whereas other reproductive parameters correlated less well with RRP (Table 4.2).

Table 4.2. Correlation (r) of RRP with other reproductive parameters of *D. galeata* during the investigation period of 1995-1999 in Bautzen Reservoir. For 1997 and 1998 separate values were calculated considering either all samples (total) or periods with high SAM (SAM>>) or low SAM (SAM<<). Bold values indicates significance with $p < 0.01$. For definitions of parameters refer to Table 1.

		1995	1996	1997	1998	1999
BS	total	**0.83**	**0.91**	**0.65**	0.30	**0.89**
	SAM>>			**0.97**	**0.76**	
	SAM<<			0.45	**0.93**	
Ad	total	**0.85**	**0.79**	**0.72**	**0.80**	**0.77**
	SAM>>			**0.75**	**0.90**	
	SAM<<			0.65	0.81	
CS	total	**0.99**	**0.99**	**0.73**	**0.58**	**0.98**
	SAM>>			**0.99**	**0.95**	
	SAM<<			**0.77**	**0.86**	
ER	total	**0.86**	0.13	0.44	0.50	**0.79**
	SAM>>			**0.92**	**0.78**	
	SAM<<			0.31	0.07	
SBS	total	**0.82**	**0.91**	**0.82**	**0.55**	**0.83**
	SAM>>			**0.83**	0.45	
	SAM<<			**0.81**	0.51	
SCS	total	**0.84**	**0.93**	**0.92**	**0.76**	**0.95**
	SAM>>			**0.96**	**0.85**	
	SAM<<			**0.85**	0.62	

Dependency of Daphnia fecundity on food conditions

Relating fecundity of *D. galeata* with food conditions, a clear dependency on food concentration was found when only values obtained during the clear-water stage (1997-1999) are considered (Figure 4.5, Table 4.3). Significant regressions could be established between all reproductive parameters and $POC_{<30\mu m}$ values < 0.8 mg C l^{-1}, except SBS (Table 4.3). However, the calculated POC-threshold for egg production was found to be negative in case of the relation POC-BS, although the regression was significant. The POC-threshold for the parameters CS, SCS and RRP were similar (0.2-0.23 mg C l^{-1}). Especially in the case of CS it

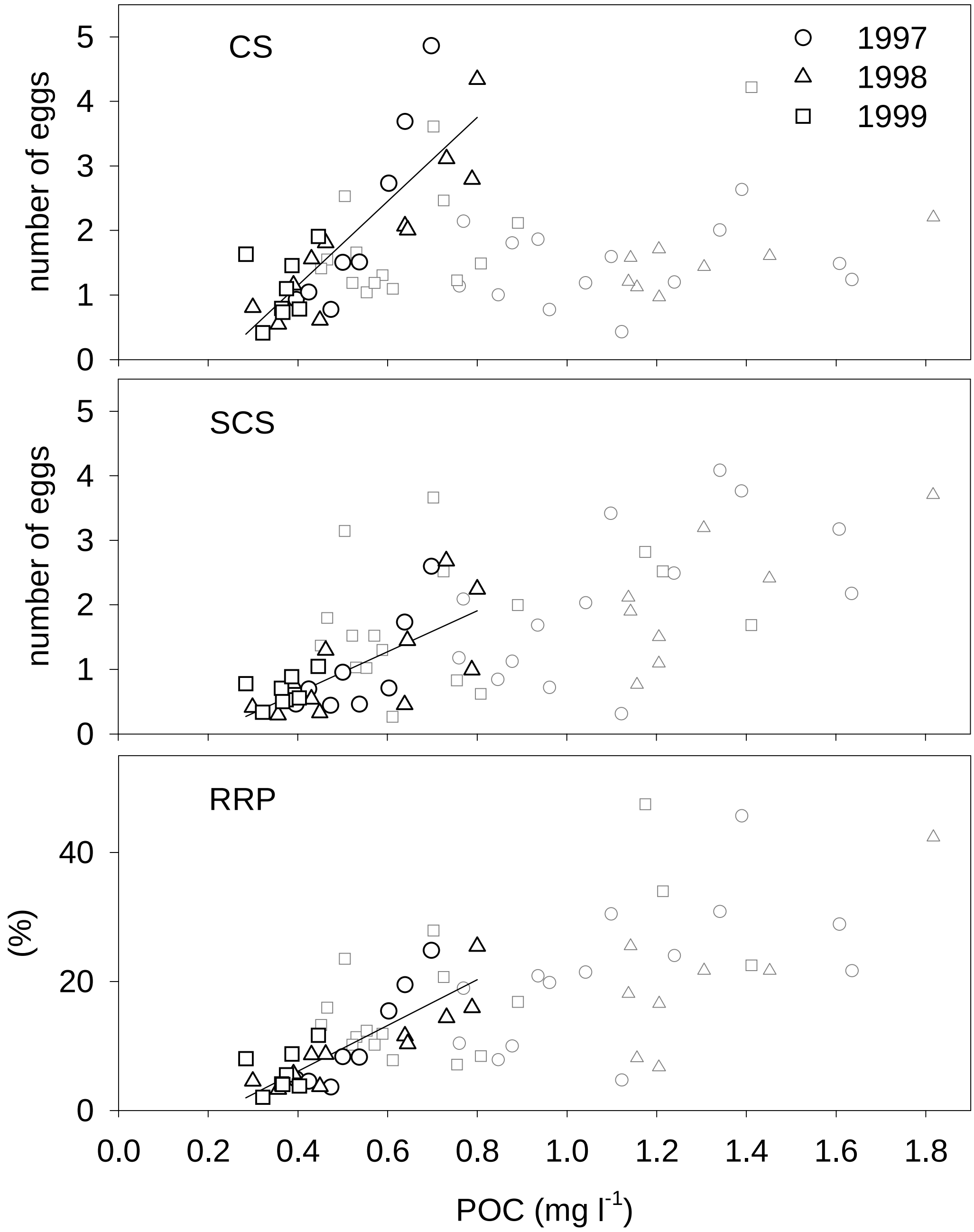

Figure 4.5. Reproductive parameters of *D. galeata* determined in field samples taken from Bautzen Reservoir between May and July of 1997, 1998 and 1999 plotted against POC$_{<30\mu m}$ concentrations (mg l^{-1}). Relations to clutch size (CS), standard clutch size (SCS) and realised reproductive potential (RRP) are shown, using a time shift of once the egg developmental time. Only values from the clear-water stage (pooled data from all three years) were used for calculating the regression line (bold symbols). Refer to Table 4.3 for regression statistics.

is remarkable that a clear relation to POC$_{<30\mu m}$ values < 0.8 mg l^{-1} was found, whereas no relation at all was detectable considering all POC$_{<30\mu m}$ values (< 2 mg l^{-1}). In fact, when POC$_{<30\mu m}$ values were high after the clear water stage in 1997 and 1998, CS was mostly below 2 (Figure 4.3), so seemingly, fecundity declined when POC$_{<30\mu m}$ rose higher than 0.8 mg l^{-1}.

When size-corrected fecundity parameters (SCS, RRP) are considered, still no clear pattern arose in the higher POC-concentration range.

Table 4.3. Coefficients of linear regressions of reproductive parameters of *D. galeata* versus $POC_{<30\mu m}$ concentration (mg l^{-1}), using a time shift of once the egg development time. Only values obtained during the clear-water stage were used (pooled data from 1997-1999). Threshold represents the POC-threshold for reproduction (mg POC l^{-1}), defined as intercept with the x-axis. Negative values (-) are not shown. BS = mean brood size, Ad = proportion of egg-carrying adults, CS = mean clutch size, ER = egg ratio, SBS = standard brood size, SCS = standard clutch size, RRP = realised reproductive potential. For definitions see Table 1.

Parameter	slope	intercept	threshold	r^2	p	n
BS	3.979	0.841	-	0.53	< 0.001	27
Ad	1.098	-0.131	0.12	0.61	< 0.001	27
CS	6.509	-1.457	0.22	0.70	< 0.001	27
ER	0.751	-0.120	0.16	0.46	< 0.001	27
SBS	1.205	1.765	-	0.05	0.27	27
SCS	3.173	-0.632	0.20	0.50	< 0.001	27
RRP	35.467	-8.101	0.23	0.70	< 0.001	27

Daphnia reproduction and potential recruitment

In all years a period of low birth rates during the clear-water stage was observed (Figure 4.6). However, no consistent pattern emerged at the beginning of the clear-water phase and later in summer. In years without a midsummer decline (1995, 1999) the birth rate decreased to about 0.05 d^{-1} at moderate densities (30-50 ind. l^{-1}) during the early population development. In years with a midsummer decline (1996-1998) values still were higher at even higher *Daphnia* densities and then dropped. During the decline phase of the population in 1996-1998 birth rates increased.

Potential cumulative recruitment of *D. galeata* strongly diverged in different years, but revealed distinct patterns (Figure 4.7). In years without a midsummer decline (1995, 1999) cumulative recruitment increased slowly, but continually. The population development started at a low level (< 10 ind. l^{-1}). Until the middle of May the population hardly increased due to recruitment from parthenogenetic eggs in both years. Thereafter, the increase was a bit higher in 1999 than in 1995, but curves were largely parallel up to a strong increase of cumulative recruitment in July 1999. In years with a midsummer decline (1997, 1998), contrary to years without, the strongest increase of recruitment was observed during one week in early May, starting from a relatively high density level (> 30 ind. l^{-1}). This quick increase was followed by extended periods with low recruitment. In 1997 there was a moderate, but steady increase of recruitment from the middle of June onwards.

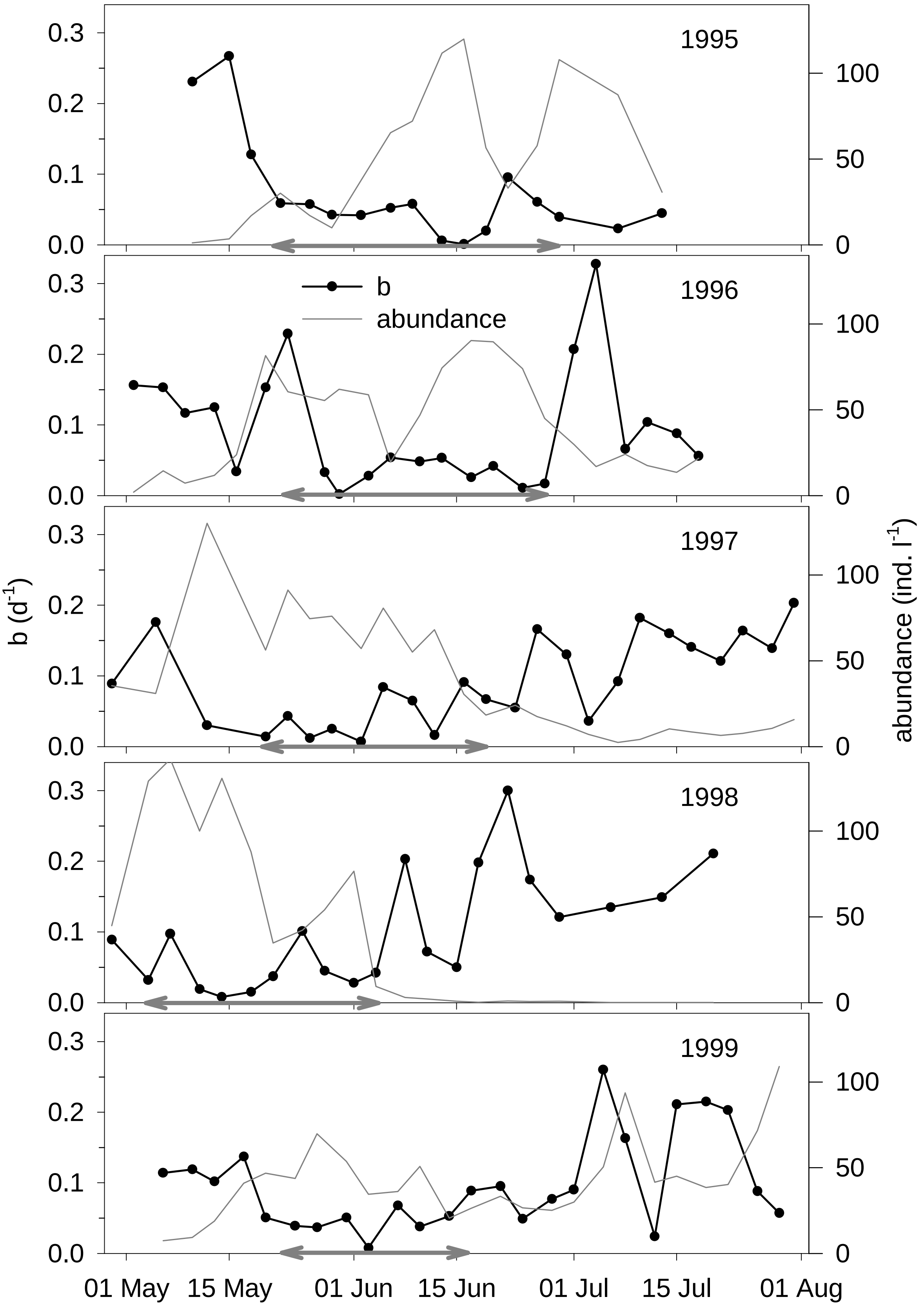

Figure 4.6. Birth rate of *D. galeata* in Bautzen Reservoir during the investigation period of 1995-1999. The abundance patterns of Figure 3.7 are displayed for orientation. Grey arrows on the x-axis indicate the clear-water phase with a Secchi depth > 2.5 m.

In contrast, virtually no further increase took place in June and July 1998. The recruitment pattern in 1996 was in between the one found in years with or without a midsummer decline. The increase in early May, similarly to years without a midsummer decline, was very low. After that, however, recruitment more resembled patterns observed in years with a midsummer decline; a strong increase in about one week was followed by a strong depression of recruitment.

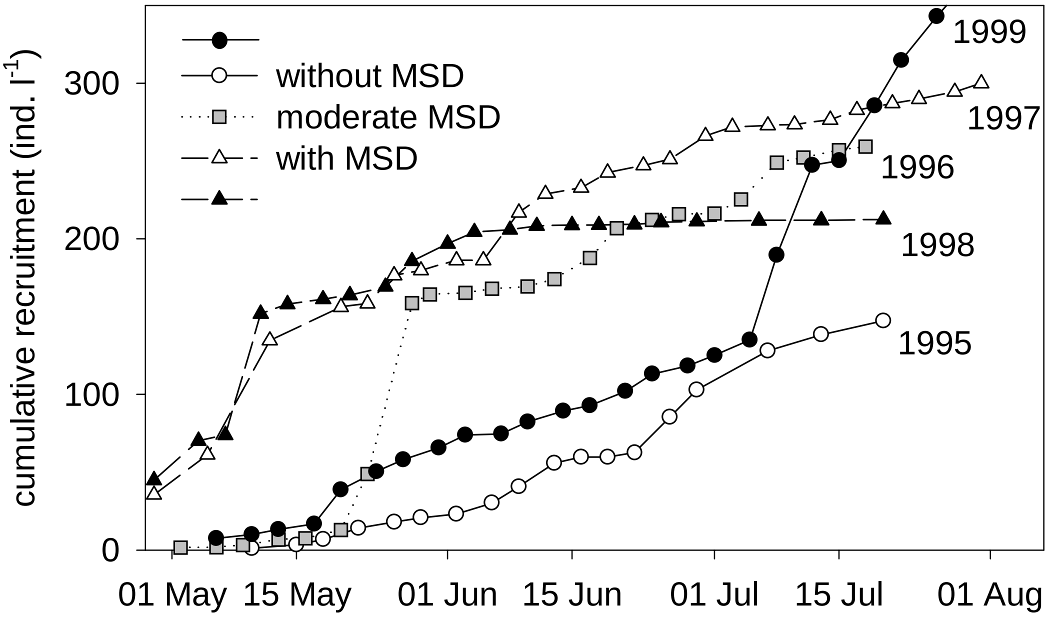

Figure 4.7. Patterns of cumulative recruitment of *D. galeata* in Bautzen Reservoir during the investigation period of 1995-1999. MSD = midsummer decline.

4.4 Discussion

The comparison of different reproductive parameters clearly suggests that fecundity of cladocerans is best described by the proportion of the actual egg number in relation to a calculated maximum egg number (realised reproductive potential). This parameter was found to be a size-corrected indicator of *Daphnia* fecundity, reflecting strong food limitation during the clear-water phase and increasing food availability at times of decreasing SAM. Cumulative recruitment instead of birth rate revealed different patterns of reproduction in years with and without a midsummer decline of *Daphnia*.

The observed relation between body size and maximum brood size certainly is a result of the size spectrum of *D. galeata* available in Bautzen Reservoir during the course of the study. Although the relation is well expressed by the linear regression, the scarcity of data for animals > 1.8 mm suggests that for a wider size range the relation might be better described by a power function (compare Hebert 1977; Vijverberg and Richter 1982; Chapman and Burns 1994). However, reasonable linear regressions were found in several studies of different *Daphnia* species (Stich and Lampert 1984; Taylor 1985; Ranta and Tjossem 1987; Duncan 1989; Macháček 1991; Gliwicz and Lampert 1994; Arbačiauskas and Gasiunaite 1996; Gliwicz and Boavida 1996) and visual inspection of other reported data revealed that the maximum brood size is linearly related to body size in many cladocerans (Hall 1964; Kerfoot 1974; Allan and Goulden 1980; Culver 1980).

The maximum brood sizes of *D. galeata* found in this study (about 25 eggs per brood at body length of 2 mm) lie within the same range as have been reported in other field studies (about 18 and 30 eggs per brood at body length of 2 mm for *D. galeata* and *D. galeata mendotae*, respectively: Vijverberg and Richter 1982; Culver 1980). Arbačiauskas and Gasiunaite (1996) found a similar relationship for parthenogenetic females of *D. galeata*. However, significantly higher brood sizes were found in daphnids which hatched from ephippia (up to 70 eggs in females of 2.5 mm length). Constructing a limiting line in Figure 6 of that study, considering parthenogenetic and exephippial generations of *D. galeata*, higher maximum clutches of a given body size are obtained than in Bautzen Reservoir (about 40 eggs in females of 2 mm length). These values are similar to data reported by Hall (1964) for *D. galeata mendotae*. From these findings, one might speculate that extremely high clutch sizes can only be found in exephippial daphnids and that the latter are of minor importance in Bautzen Reservoir. Indeed, as a result of biomanipulation, there is an overwintering population of *D. galeata* in Bautzen Reservoir (Köthe et al. 1997), contributing decisively to the formation of the spring peak. However, of course *D. galeata* regularly produces ephippia in Bautzen Reservoir (e.g. Bollenbach 1998 and Hülsmann unpubl. data) and from the analysis of mortality pattern of juvenile and adult daphnids it was concluded that recruitment from ephippia occurred during the population development in spring and early summer (Hülsmann and Weiler 2000). If it is assumed that hatchlings from ephippia in Bautzen Reservoir do not occur until a dense population has already developed, they hatch into a low-food situation and may be even more food limited than parthenogenetic females (Arbačiauskas 1998 a). This may be one reason to explain the lack of extremely high brood sizes in Bautzen Reservoir.

The maximum brood size of a given size class (under non-limiting food conditions and without predation) may further be influenced by morphologic variations (length-width relation) of the daphnids and by the egg size, both traits affecting the available space in the brood pouch. Only few studies have examined changes in body shape of *Daphnia* during the course of the season or between different clones. Ranta and Tjossem (1987) found that body length and body height of *D. longispina* both were reduced during summer and thus, their relation remained fairly constant. Egg size is strongly influenced by food levels, being high when food availability is limited (Guisande and Gliwicz 1992; Trubetskova and Lampert 1995; but see Lynch 1989). This implies that brood size and egg size should be inversely related, which indeed was shown by Guisande and Gliwicz (1992) and confirmed by field data (Chapman and Burns 1994). Although additionally genetic and maternal effects have to be considered (Glazier 1992; Ebert 1993) and egg size may also change in response to kairomones (Macháček 1991), it can be assumed that in general this inverse relation between egg size and brood size is valid (compare Chapter 6, Figure 6.4). Consequently, maximum brood sizes should always be associated with small eggs.

It should be interesting to combine data on maximum brood sizes of one species from different habitats, exposed to a wide range of environmental conditions to see whether they fit into a general model in relation to body size. If such a general model could be validated for different species, this would greatly facilitate the comparison of fecundity between different taxa (compare Vaga et al. 1985). But even without a general model, the approach describing the reproductive potential of cladocerans by using a function body size - maximum brood size may be successfully applied under the condition that this function is sufficiently validated. This was ensured in this study by using data from four years (1995-1998) with strongly diverging developments of the size structure of the population. In so doing one needs to consider SAM, as otherwise the maximum theoretical egg number might be greatly overestimated by including juvenile size classes. Periods when maximum egg numbers are attained by *Daphnia* may be very limited. It thus has to be assumed that samples have to be taken at least weekly during the course of a season to establish a maximum brood size on body length regression.

Changes in the size structure of the *Daphnia* population obviously are not only influenced by food conditions. SAM was high already before the clear-water phase and remained high at low $POC_{<30\mu m}$ values, whereas the decline of SAM in 1996, 1997 and 1998 occurred while food concentrations were rising (see Figure 3.3). Consequently, size-selective predation must be considered responsible for these drastic declines of SAM. A detailed discussion of the observed changes in size structure of the population is provided in Chapter 6. It is important to note, however, that decreases in SAM were related to a complete shift of the population´s size structure, that is, larger size classes completely vanished (compare Figures 6.1-6.3).

The high correlation of RRP with other reproductive parameters is not surprising, since all parameters rely on the same basic data (see Table 4.1). This is especially true for the correlation of RRP with CS: Both parameters depend on the number of eggs, the proportion of adults and the proportion of egg-carrying daphnids. With regard to the basic data required, BS and SBS are independent of the proportion of egg-carrying adults (Ad) in contrast to CS and SCS. It has been shown that Ad is a very sensitive parameter of food limitation (Vijverberg and Richter 1982), as under limiting conditions daphnids may require a long time to produce their first brood and may not be able to produce eggs in every adult instar (McCauley et al. 1990). Coefficients of determination of regressions with $POC_{<30\mu m}$ were higher for parameters including Ad (CS, SCS) than for Ad alone or for BS and SBS (Table 4.3). Egg ratio (ER) in comparison to CS additionally depends on the relation between juveniles and adults. As Polishchuk (1995) pointed out, this relation is more sensitive to size-selective predation, whereas the fecundity term (CS) should reflect food conditions. However, results of this study show that when applying the birth rate analysis of Polishchuk (1995), one has to consider changes in SAM, since low clutch sizes may also result from drastically reduced body size of adult daphnids.

To overcome the influence of body size on *Daphnia* fecundity estimates, SBS and SCS were introduced (Hebert 1977; Lampert 1988 b). However, these parameters may not be truly size independent (see above) and hence, results depend on the chosen standard length. To confirm this, I analysed the influence of body size on the shape of the brood size - body size regression. The slopes of these regressions were correlated with the mean body size of egg carrying females that were used to calculate the regression (using this mean body size and the corresponding regression coefficients results in BS)(Table 4.4). Significant positive relations ($p < 0.05$) between body size of ovigerous daphnids and slopes of regressions were found in 1997 and 1998 - those years when SAM declined dramatically. This also holds true for 1999, although SAM did not decline as strongly. In 1995 (constantly high SAM) no relation was found and values for 1996 (moderate decrease of SAM) were not significant. This suggests that SBS and SCS are indeed not independent of body size.

Table 4.4. Regression statistics for the relation between the slopes of the regressions egg number versus body size (used to calculate SBS and SCS) and the mean body size of egg-carrying females, which had been used to calculate the regression. Calculations were done separately for different years and only for those dates, when the regression egg number versus body size was significant ($p < 0.01$).

Year	r^2	t	p	n
1995	0.000	0.022	0.983	9
1996	0.122	1.342	0.203	15
1997	0.342	2.390	0.036	13
1998	0.517	2.925	0.019	10
1999	0.558	2.231	0.047	13

Among 27 regressions of brood size versus body size that had been calculated during the clear-water phases in 1997, 1998 and 1999 (compare Table 4.3) only 11 had slopes significantly different from zero. In all other cases BS was used instead (Lampert 1988 b). Using a standard size of 1.4 mm (smaller than the mean size of egg carrying females at that time) resulted in SBS values smaller than BS in those cases when the regressions were significant. No significant relation of SBS with $POC_{<30\mu m}$ during the clear-water phase could be found, contrary to BS (Table 4.3). Using a larger standard size (closer to the mean size of egg-carrying females during the clear-water phase) of course results in significant regressions with $POC_{<30\mu m}$, as SBS values now are essentially identical to BS. In contrast, when 1 mm is used as standard size (mean size of ovigerous females in July 1997 and 1998), spring-regressions partly result in negative SBS values. It must be concluded that SBS and SCS are either invalid or irrelevant parameters of *Daphnia* fecundity - at least in the case of Bautzen Reservoir.

The almost perfect correlation of RRP and CS (Figure 4.4, Table 4.2) and the high coefficients of determination of regressions with $POC_{<30\mu m}$ during the clear-water phase (Table 4.3) suggest that both parameters adequately describe *Daphnia* fecundity and may be used alternatively as long as SAM is high. Relating CS-values after the decline of SAM in 1997 and 1998 to the regression line between both parameters at high SAM (Figure 4.4) reveals that fecundity according to CS is up to 80% lower than according to RRP. Bearing in mind the relation between body size and maximum brood size (Figure 4.1) and the high $POC_{<30\mu m}$ values corresponding to low SAM and low size of egg-carrying females (Figure 4.2), it gets clear that CS must be low due to low body size and that food limitation is out of question in late June/July in 1997 and 1998. Thus, high RRP values do reflect increased food conditions. The same pattern, increasing RRP and decreasing body size of daphnids at high fish predation level, was found by Culver et al. (1984) and Borčić et al. (1998).

Highest RRP values in this study were found to be about 60%, except one extremely high value of 90% in 1996. As there are always some adult daphnids which carry no, or less than maximal eggs, even in non-limiting conditions (e.g. due to diseases, age, egg predation), RRP is always < 100%. Considering possible influences of predation on *Daphnia* fecundity, except Ad and RRP all reproductive parameters may be influenced by size and consequently, also by size-selective predation. The same may be suggested even for SBS and SCS (see above). However, all reproductive parameters may be influenced by egg-selective predation, performed either by fish (Gliwicz 1994) or copepods (Gliwicz and Stibor 1993). Still, as RRP takes size-specific variation in brood size into account and “includes“ Ad, it may be considered most reliable with regard to food limitation in case of variable size structure and possible predation impacts.

The regression of reproductive parameters with $POC_{<30\mu m}$ (analysed only for 1997-1999) shows that fecundity of *D. galeata* is strongly food limited during the clear-water phase in

Bautzen Reservoir. The development of $POC_{<30\mu m}$ values and reproductive parameters in 1995 and 1996 suggests that this contention is generally valid. Since low $POC_{<30\mu m}$ values and decreasing fecundity were associated with high *Daphnia* densities (see above), there might also be additional negative allelopathic effects on *Daphnia* fecundity (Seitz 1984; Matveev 1993). However, crowding effects on clutch size of *D. galeata* were either not significant (Burns 2000) or only found when exposed to media conditioned with daphnid densities > 150 ind. l^{-1} (Burns 1995). If present at all, such effects may only be conceived as a supplementary process to food limitation (Matveev 1993).

As pointed out by Boersma and Vijverberg (1994 a) it is difficult to assess the amount of food actually available for daphnids in highly eutrophic waters, as the exact food source is unknown and the feeding process itself may be influenced by many factors (e.g. Wagner 1998). So the rather clear relation between food quantity and fecundity was not to be expected when comparing $POC_{<30\mu m}$ values in this water with threshold concentrations for egg production in other systems (Lampert 1978; Gliwicz and Lampert 1990; Müller-Navarra and Lampert 1996). The high threshold and the low slope of the regression line (e.g. for the relation POC-CS) compared to those studies may be explained by low food quality. Indeed, in 1997 lowest concentrations of fatty acids were found during the clear-water stage, indicating that both low food quantity and food quality limit egg production (Weiler et al. in prep.).

As food conditions improved in summer, a saturation function of *Daphnia* fecundity should be expected (Lampert 1978; Müller-Navarra and Lampert 1996). However, this could not be found for any reproductive parameter. Values from 1999 are different in this respect, because $POC_{<30\mu m}$ values were mostly in the lower concentration range and high concentrations (in early May) were to scarce to detect a clear relation. Low CS in summer 1997 and 1998 despite high $POC_{<30\mu m}$ values are clearly related to low body size of adult daphnids after the decline of SAM. The lack of a clear pattern of RRP (assumed to be size-corrected) at that time most likely is due to (egg-) selective feeding by age-0 fish (see above). Their biomass was high in both years compared to 1995 and 1996 (Chapter 3). It has been shown that underyearling percids select larger than average-sized daphnids once their mouth-gape is big enough (Mehner et al. 1998 c). The analysis of mortality patterns of *D. galeata* further suggests that they are under control of size selective predation after the midsummer decline (compare Chapter 7; Hülsmann and Weiler 2000).

The effect of fish predation on *Daphnia* fecundity may be particularly strong, as there is evidence for egg-selective feeding (reviewed by Gliwicz 1994, confirmed by Janßen 1999). Egg predation by copepods in *Daphnia* brood cavities can be excluded in this situation (low SAM) and is supposed to be of minor importance even earlier in the season, as it was found to be restricted to daphnids larger than 2 mm (Gliwicz and Stibor 1993; Gliwicz and Lampert

1994; Gliwicz and Boavida 1996). Furthermore, copepod predation on eggs should not affect the proportion of egg-carrying adults (Ad). This parameter, however, changed drastically during the decline in fecundity, correlating significantly with $POC_{<30\mu m}$ (Table 4.3). Negative effects of excess food or inedible particles on *Daphnia* fitness could not be found (Voigt and Hülsmann in press) and food quality increased after the clear-water stage (Weiler et al. in prep.). Consequently, in summer bottom-up limitation of fecundity can be excluded as well.

Expressing reproduction of *Daphnia* by calculating potential recruitment is a more straight-forward way than calculating birth rates. Cumulative recruitment over certain periods directly reveals the reproductive capacity of the population whereas birth rates are rather abstract values since comparably low birth rates may result in high population growth in case of high *Daphnia* density (e.g. in early May 1998). Highest birth rates were always associated with low *Daphnia* abundance and resulted in low recruitment (both in early spring and in summer), whereas highest recruitment was always associated with relatively high abundance (30-40 ind. l^{-1}), but not necessarily with high birth rates. Despite the fact that negative death rates were sometimes calculated during the build-up of the population in May (see Figure 8.1), cumulative recruitment came up to the population level that was actually achieved in the field, except in 1995. This means that hatching from resting eggs was not “needed“ to achieve these high densities and one might speculate that emergence from ephippia indeed is of low importance for population dynamics of *D. galeata* in Bautzen Reservoir.

The different patterns of recruitment in years with and without a midsummer decline are in full agreement with predictions posed by Benndorf et al. (2001) concerning the initiation of a midsummer decline. Recruitment patterns in years with a midsummer decline were characterised by an early and quick increase starting from a relatively high abundance in early May. This may be attributed to a high temperature during the preceding winter and early spring (Benndorf et al. 2001). In these years, the *Daphnia* population was dominated by a strong peak cohort of about the same age during the clear water stage. Reproduction during this period was very low. If all members of this “peak-cohort“ have about the same life history, which can be expected, the simultaneous die-off of these animals should have a great impact on the *Daphnia* population and might significantly contribute to the initiation of a midsummer decline.

In summary, reproductive potential (instead of clutch size) and recruitment (instead of birth rate) are best suited to describe fecundity and reproduction of cladocera in the field. *Daphnia* fecundity was clearly food limited during the clear-water stage in Bautzen Reservoir. Different patterns of recruitment were observed in years with and without a midsummer decline. In contrast, food limitation of fecundity during the clear-water phase was essentially the same in every year, regardless whether a midsummer decline occurred or not. Consequently, low reproduction of *Daphnia* during the clear-water stage may not “cause” the midsummer decline as stated by Lampert et al. (1986) and implied by the PEG model (Sommer et al. 1986) and many others. Instead, aging of the population and the simultaneous die-off of a peak cohort of *Daphnia* may be a decisive factor for a population to decline (Hülsmann and Weiler 2000; Benndorf et al. 2001). In order to either support this hypothesis or to reject it, life table experiments were performed under approximately *in situ* conditions (Chapter 5). Additionally, a detailed demographic analysis of the population of *D. galeata* in Bautzen Reservoir was performed (Chapter 6) and mortality patterns were studied as described in Chapter 7.

5 Life history and juvenile growth of *Daphnia galeata* under natural food conditions

5.1 Introduction

In Chapter 4 bottom-up effects on *Daphnia* fecundity and reproduction were demonstrated. A severe food limitation of reproduction during the clear-water phase became obvious, in some years preceding a midsummer decline of *D. galeata* (compare Threlkeld 1985; Tessier 1986; Luecke et al. 1990; Wu and Culver 1994). However, in other years with a similarly food limited fecundity during the clear-water phase, no midsummer decline was observed. With regard to reproduction, the most striking difference between years with and without a midsummer decline were recruitment patterns (see Figure 4.7). This means that in some years (with midsummer decline) strong cohorts of daphnids born almost at the same time and under the same environmental conditions dominated the population, whereas in other years (without midsummer decline), no dominant cohort developed. In order to evaluate whether these different recruitment patterns may directly influence the initiation of a midsummer decline, one needs to have detailed demographic data of the population. Which animals reproduce when and how long do they live? Consequently, life table experiments under natural food conditions have to be performed during the period preceding a midsummer decline.

Few studies have analysed *Daphnia* life history under *in situ* conditions and most that did, focused on growth or reproductive parameters (Weglenska 1971; Threlkeld 1979; Threlkeld 1980, 1986 a; Neill 1981; Threlkeld 1985; Langeland et al. 1985; Larsson et al. 1985; Müller-Navarra and Lampert 1996) without paying attention to mortality patterns. Those *in situ* experiments that were related to a midsummer decline (Threlkeld 1979; Threlkeld 1985; Larsson et al. 1985) focused more on the actual decline phase rather than also taking the life history of those daphnids into account which were born during the build-up of the population or during the period of high *Daphnia* abundance. Recently, Gries and Güde (1999) gave evidence for a high significance of non-consumptive mortality for the dynamics of *D. galeata* in Lake Constance. High population losses due to sedimentation were attributed to an unidentified infection. However, size-frequency distributions of *D. galeata* in that study also indicate possible aging effects. That is, the animals might have died due to senescence, whereas the infection “only“ might have influenced reproduction. Even if there is direct field-evidence for non-consumptive mortality, the causes of mortality remain speculative as long as the life history of daphnids is not known.

Therefore, life table experiments were performed under approximately field conditions (but excluding predation) at different times of the spring succession of *D. galeata* in Bautzen Reservoir. Experiments were performed in two years, one (1998) with a midsummer decline and one (1999) without. Age-specific fecundity and age-specific mortality were estimated and used to calculate the intrinsic rate of increase, *r*, as a measure of fitness of cohorts born at different times during the investigation period. Additionally, juvenile growth of *D. galeata* was measured in flow-through chambers under approximately natural food conditions during the investigation period of 1997, 1998 and 1999. These values may also be used as a measure of fitness because growth rates were found to correlate with *r* (Lampert and Trubetskova 1996).

5.2 Methods

Neonates of *Daphnia* were cultured and fed on natural lake seston to measure their somatic growth during the changing food conditions in the reservoir. Each week egg carrying females of *D. galeata* were isolated from a sample of Bautzen Reservoir and neonates born within a 12 h interval were used for growth experiments in flow-through systems (Stich and Lampert 1984). A subsample of the neonates ($n \geq 3$) was taken to determine their initial length (L_i). The remaining newborn daphnids were placed in the culture vessels at a density of less than 50 animals l^{-1}. The number of experimental animals was always higher than 5 in each culture. Filtered water from Bautzen reservoir, which was sampled twice a week, was used as culture medium. In 1997 pre-filtration of reservoir water was done with 30 µm (edible size fraction) and the water supply in the experimental room (constant temperature of 18°C ± 0.5, continuous low light conditions) was replaced daily from a stock stored at 4°C in the dark. In 1998 and 1999 pre-filtration was done with 250 µm to provide a more realistic size range of particles, including both the edible and inedible fraction.

A peristaltic pump continuously provided water to the culture vessels (renewal rate > four times per day). In 1998 and 1999 the pump was directly connected to the water supply which was stored at 4°C in the dark and permanently stirred. The light regime was changed to a 16:8 h light-dark cycle in these years. After the experimental period (Δt) of 5 days (1997) or 6 days (1998, 1999) the final lengths (L_f) of the animals was measured. Growth curves of daphnids generally have a hyperbolic or sigmoid shape but as a sufficient approximation growth (in length) of *D. galeata* can be considered to be linear until maturity (e.g. Stich and Lampert 1984; Langeland et al. 1985; Hovenkamp 1991). Only some of the daphnids carried eggs at the end of the experiments. Therefore, the mean daily growth (g_L) was calculated as

$$g_L = (L_f - L_i) / \Delta t \ (\mu\mathrm{m}\ \mathrm{d}^{-1}) \qquad (5.1)$$

In order to relate growth rates to $\mathrm{POC}_{<30\mu\mathrm{m}}$ values, the mean of those two POC values that were measured during the growth experiments were used. Data for 1997 were provided by W. Weiler, IGB Berlin, partly published in Hülsmann and Weiler (2000); growth estimates of 1998 and 1999 were provided by H. Voigt (Institute of Hydrobiology, TU Dresden).

During the course of the study period of 1998 and 1999 three and six life table experiments were performed, respectively. Neonates were obtained in the same way as for growth experiments. Experimental conditions were also identical. Neonate daphnids were placed individually in glass vessels (~15 ml) with reservoir water which was changed every day (1998) or every other day (1999, but gently stirred every day). The reservoir water was prefiltered with 30 µm in 1998 and with 250 µm in 1999. Every day the experimental daphnids were checked for survival and number of offspring which was discarded. When animals were found dead during the experiments in 1999, their final length was recorded. Age at first reproduction was back-calculated from the date when the first offspring was born subtracted by the egg-development time at 18°C [3 d, calculated with the formula provided by Bottrell et al. (1976)]. The animals of each single experiment were treated as a cohort for which age-specific survival (l_x) and mean age-specific fecundity (offspring per female, m_x) was calculated. The intrinsic rate of increase, *r*, for each cohort was calculated iteratively from the Euler-equation:

$$1 = \sum_{x=\alpha}^{x=\omega} e^{-r \cdot x} l_x \cdot m_x \tag{5.2}$$

with x = age and α and ω = age at first and last reproduction, respectively.

5.3 Results

Juvenile growth

Both size and growth of neonates of *D. galeata* differed considerably during the study period in each year (Figure 5.1). The initial size of the experimental daphnids increased during the clear-water stage in every year but was continuously low later in summer. Juvenile growth was very low in the first experiment in 1997 but subsequently increased and remained on a high level throughout the study period. In 1998 growth decreased during the clear-water stage and only slightly increased after this period. The final size of the experimental animals was smaller compared to 1997, although the experimental period was longer in 1998. Similarly to 1998 growth rates declined during the clear-water stage in 1999 and were low throughout June. Animals born in July 1999 grew larger than those born in June of that year although their initial length was similarly low.

Plotting juvenile growth rates against the mean $\mathrm{POC}_{<30\mu m}$ concentration (mg l^{-1}) during the experimental period reveals considerable scattering of the data (Figure 5.2). High growth rates of about 0.15 mm d^{-1} were only obtained at POC values > 0.8 mg l^{-1}. This was the case in one experiment before the clear-water stage in 1999 and in several experiments after the clear-water stage in 1997. However, growth rates were much lower at similarly high POC concentrations in summer 1998. Lowest POC values were not associated with lowest growth rates. Whereas minimum POC concentrations were always found in the beginning of the clear-water stage (compare Figure 3.3), lowest growth rates were either obtained at the beginning (1997) or in the middle (1998) or at the end (1999) of this period.

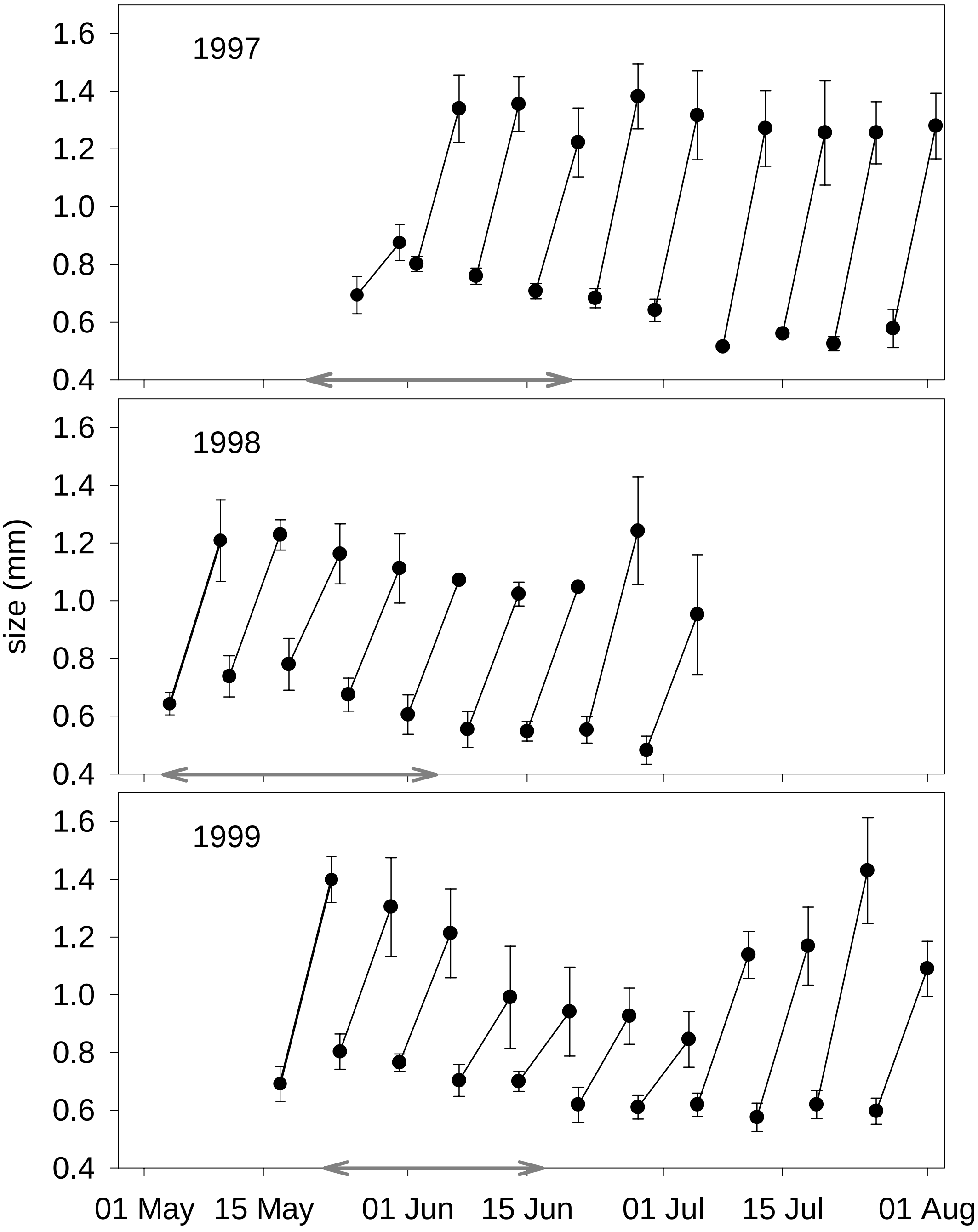

Figure 5.1. Juvenile growth of *D. galeata* in laboratory experiments during the experimental period of 1997-1999. Mean size (± SD) at the start and at the end of single experiments is shown. The experimental period was 5 days in 1997 and 6 days in 1998 and 1999. Grey arrows on the x-axis indicate the clear-water phase with a Secchi depth > 2.5 m. Data provided by W. Weiler (IGB Neuglobsow) and H. Voigt (Inst. of Hydrobiology).

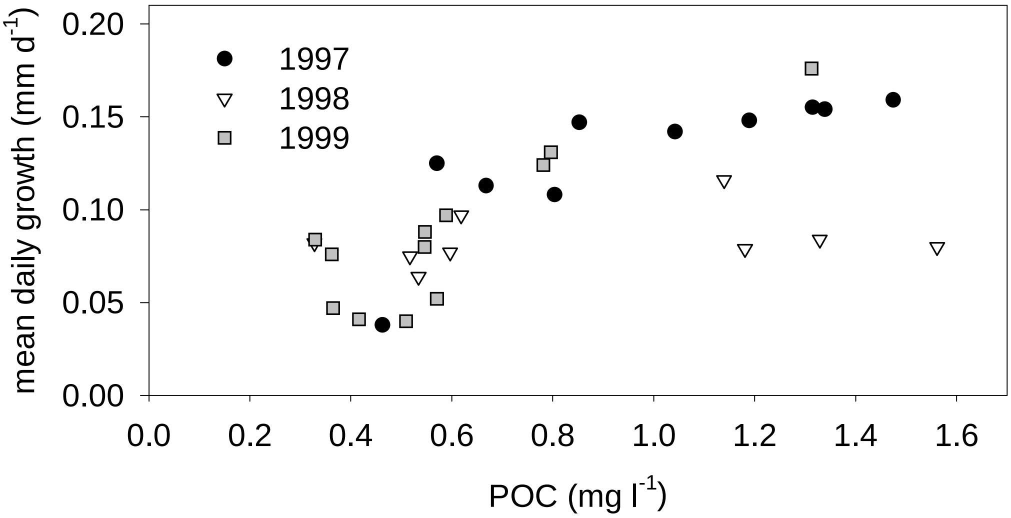

Figure 5.2. Mean daily growth (mm d^{-1}) of *D. galeata* in Bautzen Reservoir as a function of POC$_{<30\mu m}$ concentration (mg l^{-1}) during the investigation period of 1997, 1998 and 1999.

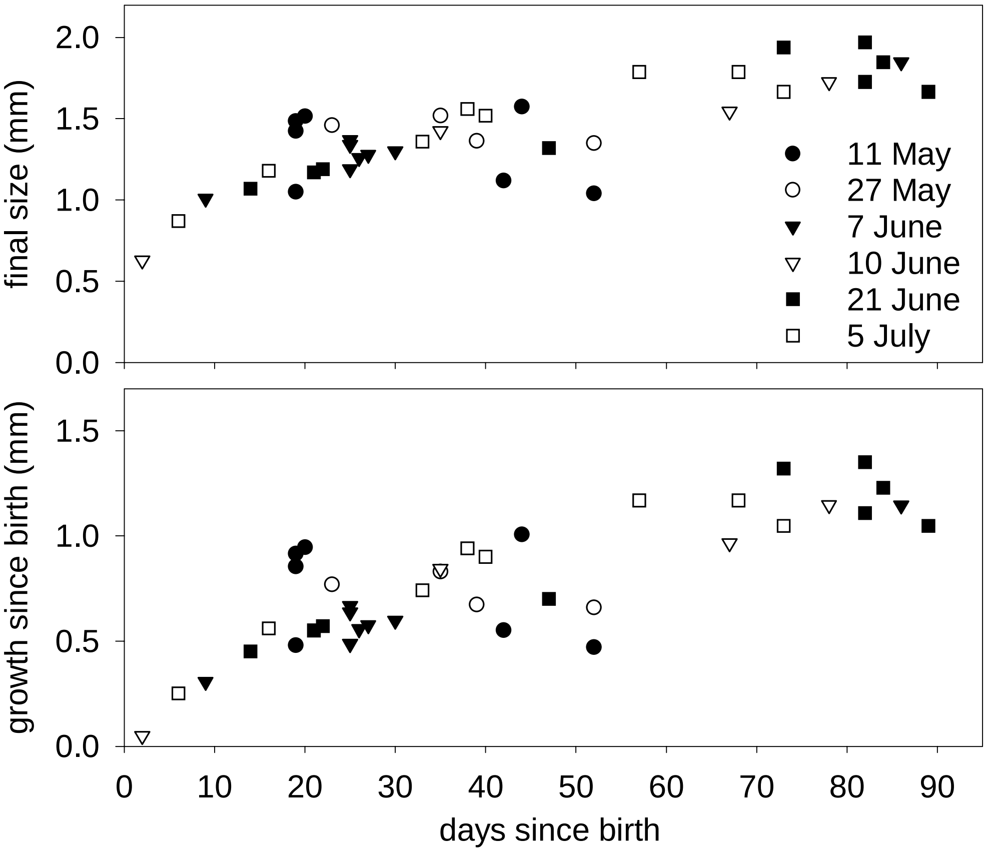

Figure 5.3. Growth of individuals of *D. galeata* in life table experiments in 1999. In the upper panel the final size (mm) of experimental animals born at different dates during the investigation period is displayed, in the lower panel growth since birth (mm) is shown. Note the different scaling of the x-axis.

In life table experiments in 1999 only the mean initial length and the final length of animals found dead were recorded. In some cohorts juvenile mortality was virtually absent, whereas some of those daphnids which had died at young age could not be measured. Hence, the shape of the growth curves is uncertain especially for the juvenile phase. Despite of this, growth of cohorts born at different times during the investigation period seemed surprisingly similar (Figure 5.3). Daphnids born on 11 May showed a strong intra-cohort variability of growth. When the first individuals of this cohort died at an age of 20 days, some of them were very large, indicating high juvenile growth rates. On the other hand, some individuals which survived twice as long remained much smaller.

Daphnia life history

In life table experiments (Figure 5.4) the reproduction of animals born during the clear-water stage in May 1998 was very low. About 50% of the individuals did not reproduce at all and among those that did, only one produced more than two broods. Moreover, the age at first reproduction was extremely retarded: Median values were about 28 (minimum value 23 d) and 20 (minimum value 13 d) days for animals born in the first or the second half of the clear-water stage, respectively. Median values of the age at death were almost identical to the age at first reproduction during this period. In June 1998, after the decline of the population and a strong increase of the food concentration, all animals reproduced, having about 8 broods (median value) and a nearly identical age at first reproduction (12-14 d). Longevity of these daphnids was much higher compared to those born during the clear-water stage.

In 1999 the first life table experiment was started before the clear-water stage emerged (Figure 5.4). All individuals of this cohort reproduced after five to six days, that is before $\mathrm{POC}_{<30\mu m}$ reached minimum values. Six out of nine animals only had one brood. Longevity of this cohort was relatively short (median value 21 days). Similarly to 1998 daphnids born during the clear-water stage produced only few broods (with some outlyers) or did not reproduce at all. Age at first reproduction was strongly delayed, but in contrast to 1998 animals born in the first half of the clear-water stage reproduced earlier (median value 15 d) than those born later (range 18-47 d). Longevity of experimental animals fluctuated strongly during the clear-water stage, but median values were low. The fitness of daphnids born in late June and July 1999 fluctuated strongly but in general, animals produced more broods, reproduced earlier and lived longer than those born during the clear-water phase.

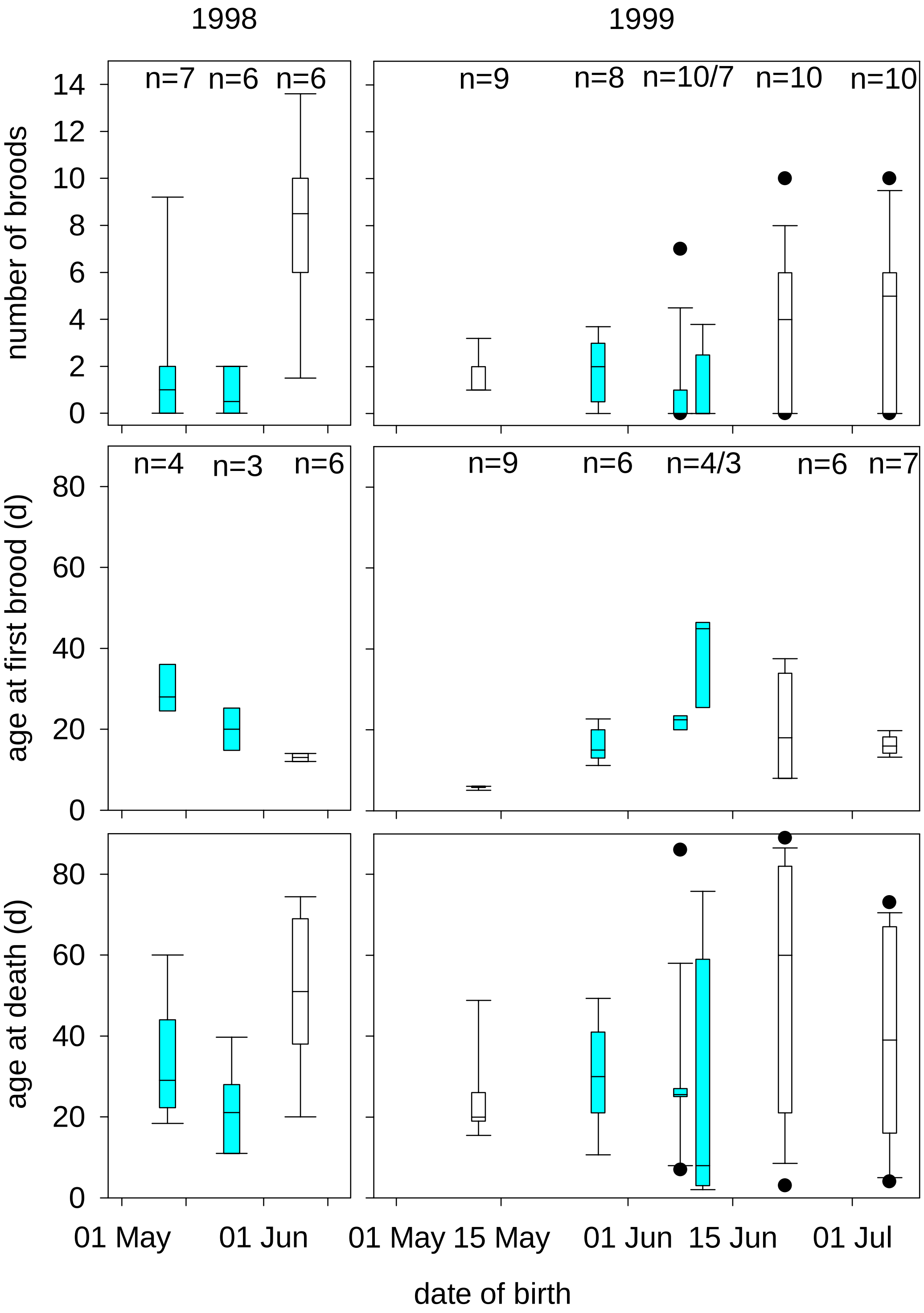

Figure 5.4. Life history characteristics of *D. galeata* from Bautzen Reservoir under approximately *in situ* conditions in 1998 (left panel) and 1999 (right panel). The number of broods, age at first brood (d) and age at death (d), are plotted against the date of birth of the experimental animals. Box plots display the median and the 10th, 25th, 75th and 90th percentiles. The numbers of the experimental animals are given in the top figures, in the middle panel the numbers of experimental daphnids which reproduced are provided. Experiments that were started during the clear-water stage are displayed with grey bars.

Regarding mean age-specific fecundity (*m_x*) in relation to the development of food quantity, a clear dependency gets obvious (Figures 5.5, 5.6). Mean brood sizes were generally low, exceptions were always based on single surviving daphnids. In 1998, animals born at the beginning of the clear-water phase (11 May) only started reproducing when food conditions increased (Figure 5.5). High *m_x* values were recorded after $POC_{<30\mu m}$ exceeded 1 mg l^{-1} and represent three successive broods of one surviving animal. This also holds true for the high fecundity of animals born on 25 May 1998. Both brood size and frequency of hatching were higher for animals born in June after the clear-water phase. Reproduction diminished after this cohort was about 40 days old.

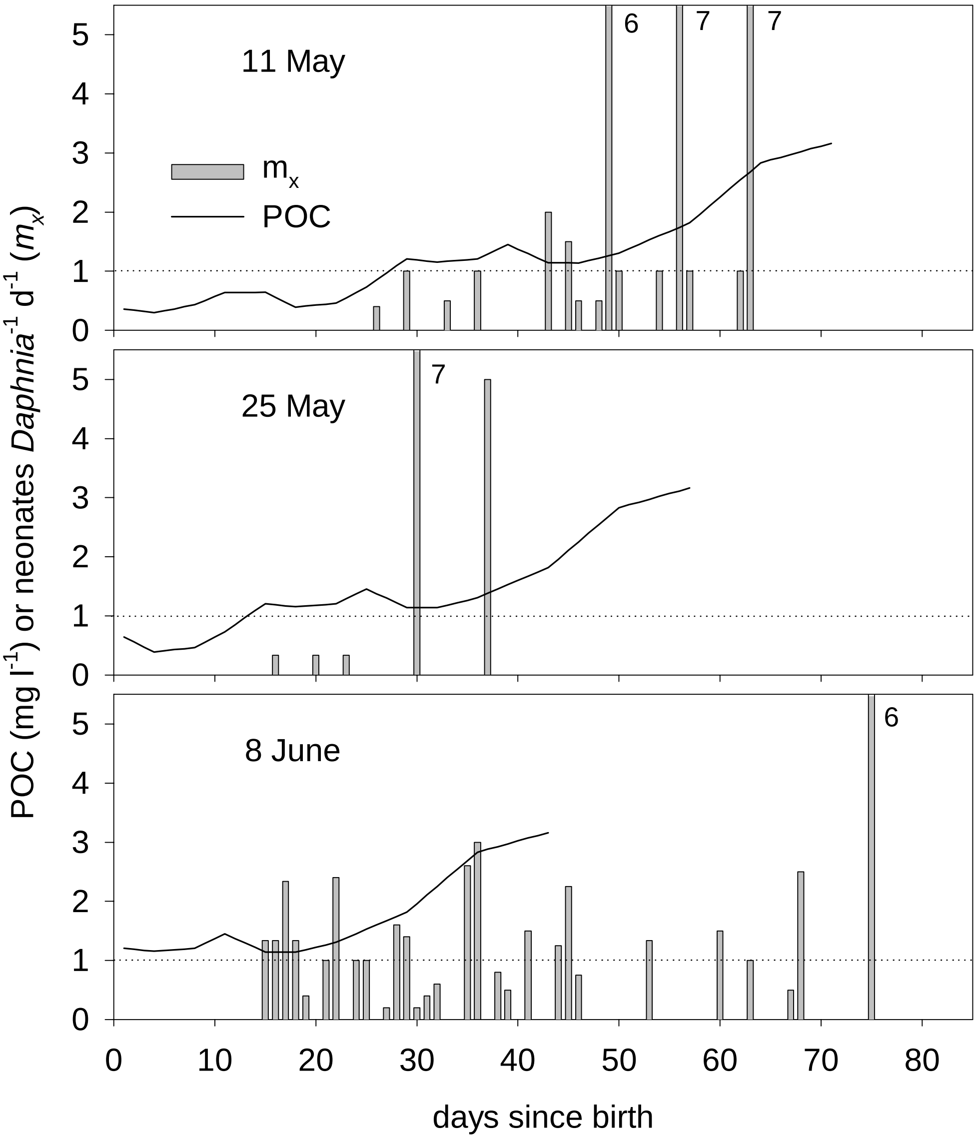

Figure 5.5. Mean age-specific fecundity (*m_x*) of *D. galeata* from Bautzen Reservoir in life table experiments started at different dates in 1998 and development of food conditions ($POC_{<30\mu m}$ mg l^{-1}) plotted against days since birth of the experimental animals.

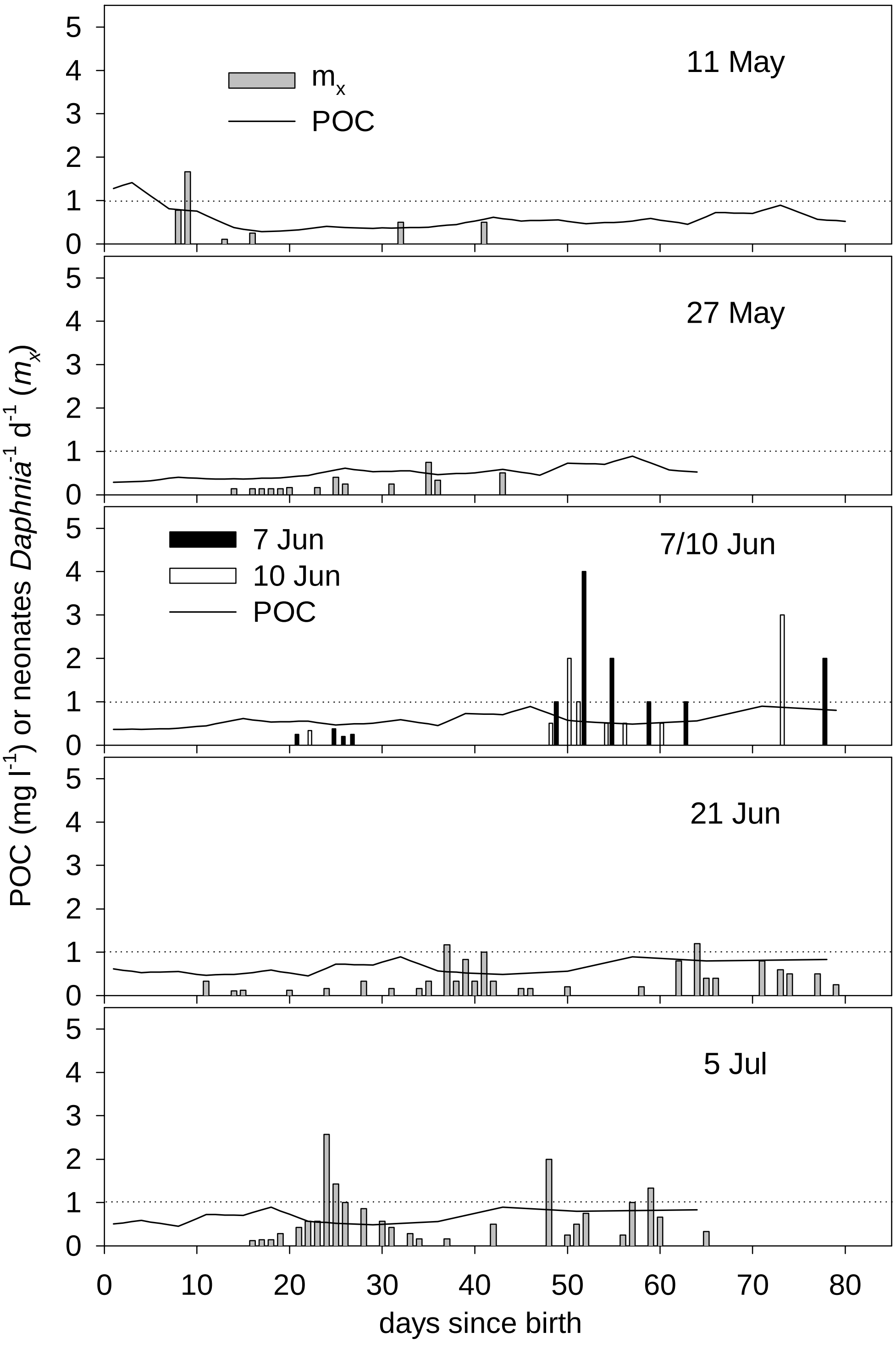

Figure 5.6. Mean age-specific fecundity (m_x) of *D. galeata* from Bautzen Reservoir in life table experiments started at different dates in 1999 and development of food conditions (POC$_{<30\mu m}$ mg l^{-1}) plotted against days since birth of the experimental animals.

Most of the animals that were born before the clear-water phase in 1999 (11 May) reproduced only once and with only one to three eggs (Figure 5.6). Reproduction almost completely ceased after the $POC_{<30\mu m}$ reached minimum values. Daphnids born during the clear-water phase (27 May and 7/10 June) had a very low fecundity (m_x values mostly < 0.5). Higher values were only found for animals born in early June after a slight increase of $POC_{<30\mu m}$ about 50 days after birth (which was mid-July). At that time only few individuals were still alive; all m_x values > 1 depend on only one reproducing daphnid. For those animals that were born later in June, this increase of food quantity came earlier. They responded with increasing fecundity. The same dependency could be observed in daphnids born on July 5.

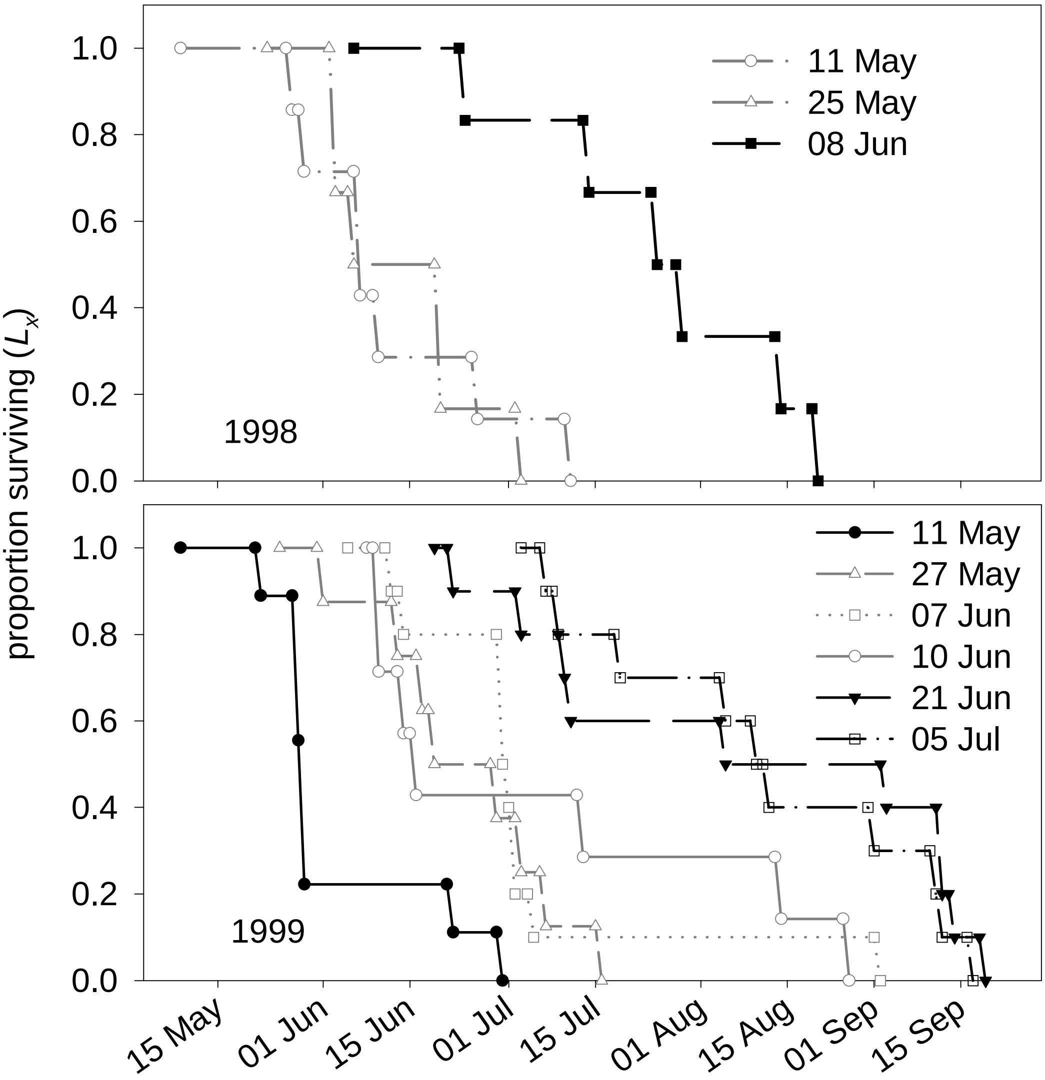

Figure 5.7. Mean age-specific survival (l_x) of *D. galeata* from Bautzen Reservoir in life table experiments started at different dates in 1998 (above) and 1999 (below). Each line represents one life table experiment, starting on the date of birth of the experimental animals. Experiments which were started during the clear-water phase are displayed with open symbols and in grey.

The survivorship over time also strongly depended on food conditions and revealed distinct patterns when plotted against the actual dates during the course of the study (Figure 5.7). In 1998 daphnids born during the clear-water stage died synchronously (and steadily), although their age differed by two weeks. Survival probability decreased exactly at the end of the clear-water phase. The survivorship of daphnids born in June 1998 was considerably longer but also decreased steadily throughout life. Daphnids born before the clear-water phase in 1999 (11 May) had a low mortality until an abrupt die-off about 20 days after birth. Some individuals survived for another 30 days, but the majority of this cohort had vanished at the end of the clear-water phase. Survivorship-curves of daphnids born during the clear-water stage in 1999 are more erratic, still, similar to 1998, also these curves intersect and are largely parallel, declining especially in mid-June, when Secchi depth decreased. “Delays“ during the die-off correspond to temporal increases of the $POC_{<30\mu m}$ concentration. Some specimens survived until the age of about 90 days. As in 1998, survivorship was highest for daphnids born after the clear-water stage in 1999, those born at the end of June lived even longer than those born in early July.

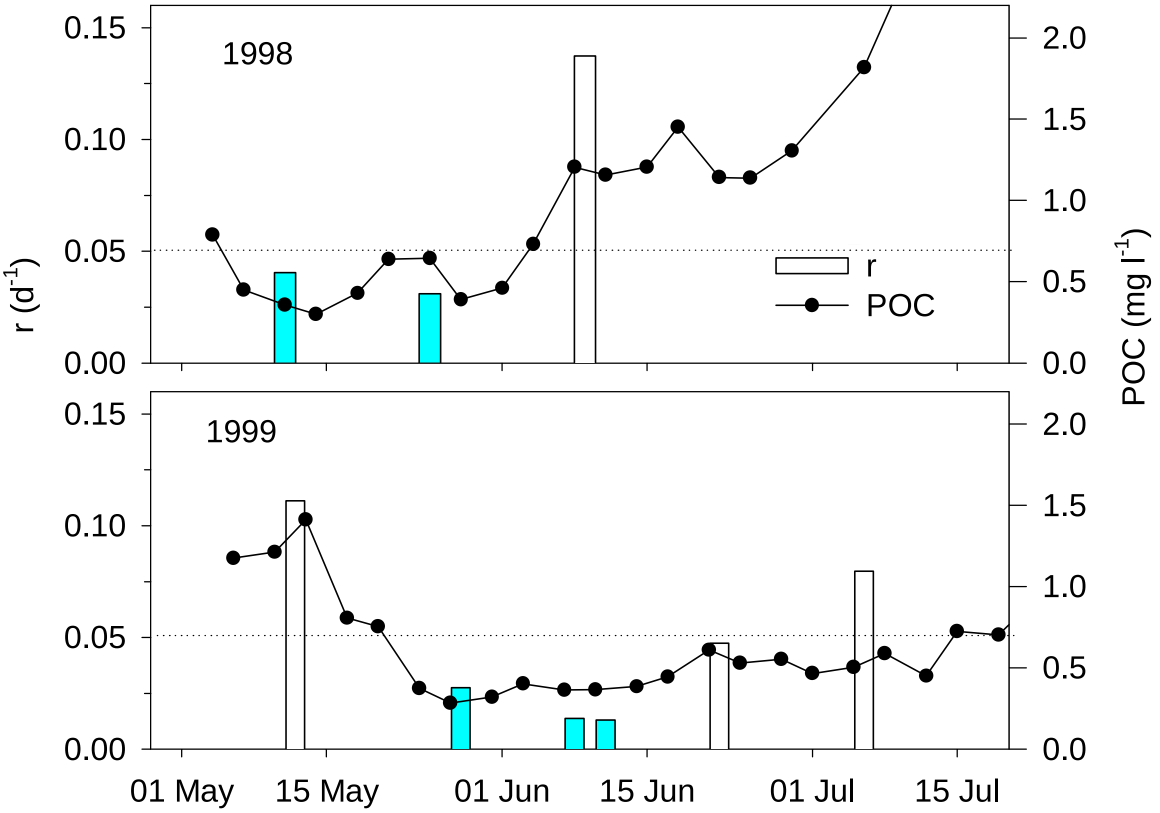

Figure 5.8. Intrinsic rate of increase *r* (d^{-1}) of *D. galeata* in life table experiments under approximately *in situ* conditions in 1998 and 1999 plotted against the date of birth of the experimental animals. Experiments that were started during the clear-water stage are displayed with grey bars. $POC_{<30\mu m}$ values (mg l^{-1}) from Fig. 3.3 are provided for orientation.

According to fecundity and mortality patterns in life table experiments the intrinsic rate of increase was low during the clear-water stage in both years (Figure 5.8). Moreover, it was the lower, the later the experimental animals were born during this period. A much higher fitness was achieved by animals born after the clear-water stage. This was most obvious in 1998 but was also to be seen in 1999 although food concentrations increased only slightly. A high intrinsic rate of increase was also observed in daphnids born shortly before the clear-water stage. This was mainly an effect of their short juvenile development time, whereas the number of broods and longevity was lower compared to summer-individuals (Figure 5.4).

Only a weak correlation between juvenile growth, *g*, and the intrinsic rate of increase, *r*, could be found. It is described by the function r (d^{-1}) = 0.0002 + 0.696 g (mm d^{-1}), $r^2 = 0.387$, DF = 8, p = 0.074.

5.4 Discussion

Confirming the results on fecundity (Chapter 4), influences of food limitation on life history parameters of *D. galeata* during the clear-water phase were very similar in the years with and without a midsummer decline. Especially the age at first reproduction was extremely prolonged compared to laboratory studies with even lower food concentrations (Lynch 1989; Vanni and Lampert 1992; Boersma and Vijverberg 1994 b). Obviously, only the interplay of all bottom-up forces (food quantity, food quality, maternal effects, dissolved substances) results in such strong effects concerning e.g. the age at first reproduction or mean age at death which could not be expected from laboratory studies with defined food, media and culture animals. The strong effect of different bottom-up conditions on survival probability clearly suggest that non-consumptive mortality might be a significant factor in *Daphnia* population dynamics.

Estimates of juvenile growth suggest that this parameter is food limited during the clear-water phase ($POC_{<30\mu m}$ < 0.8 mg l^{-1}). However, other factors also have an influence, above all maternal effects. Relatively high growth rates at low $POC_{<30\mu m}$ concentrations were found in 1998 and 1999 at the beginning of the clear-water phase shortly before maximum water transparency was attained. In 1997 this period was missed because growth experiments started too late during the clear-water phase. At the beginning of this period neonate size increased. This must be rearded as a consequence of increasing egg size (compare Figure 6.3) and hence, offspring fitness should be high (Gliwicz and Guisande 1992). The longer the period of low food conditions lasted, the lower offspring fitness was, although egg volumes remained high. Probably, this was also an effect of aging of the cohort of adults (see Chapter 6). Correlations between juvenile growth and *r* could not be expected to be as high as in laboratory experiments conducted by Lampert and Trubetskova (1996) because food conditions changed during experiments performed in this study (approximately *in situ* conditions). Accordingly, only a weak correlation between both parameters was found.

The comparison of juvenile growth rates and growth curves of animals from life table experiments in 1999 suggests that growth in life table experiments was somewhat lower, but still comparable to growth experiments, despite of the different experimental design (flow-through versus static system). Animal born before the clear-water phase (11 May) reached a final size of about 1.5 mm in growth experiments which lasted six days. Exactly at an age of six days all daphnids in life table experiments (and also those from growth experiments) produced their first brood. When the first members of this cohort died at an age of 20 days, they still had a similar size. But since this cohort was extremely food limited after the onset of the clear-water stage (see below), it is very likely that not only reproduction but also growth more or less stopped. Those few daphnids which were measured after an early death in life table experiments also suggest that growth was slightly lower but still comparable to growth experiments.

The life history patterns of *D. galeata* during spring and early summer in Bautzen Reservoir can be generalised in the following way: Animals born during the build-up of the population due to excellent food conditions reproduce early, but have low survival rates when food conditions deteriorate. Reproduction almost completely ceases in this situation and maximum longevity is about 50 days. Virtually all individuals of this cohort die during the clear-water stage. Although only data of this period in 1999 are available, I suppose that conditions were similar in other years. Animals spending most of their juvenile stages under good food conditions may adapt their feeding appendages only with considerable time-lags to decreasing food concentrations (Voigt and Benndorf 2000) and consequently, are more vulnerable to starvation.

During this early phase of the clear-water stage changes in food conditions are severe and occur quickly. Therefore, life history of animals born during these changes can be expected to change accordingly strong. In this sense, unfortunately there is a gap in life table data because no experiment was started during the decline of $POC_{<30\mu m}$ concentrations. It can be expected that daphnids born in this situation are able to enlarge their filter screens during their juvenile development and thus, should be able to withstand low food conditions. Accordingly, their longevity should be higher compared to those individuals, who matured before food decreased. It is exactly this cohort of daphnids born during the decline of $POC_{<30\mu m}$ concentrations, which should form the greatest part of the peak-cohort observed in years with a midsummer decline. Since they mature and reproduce at low food conditions lasting for several weeks, it is very likely that their mean life-span matches the end of the clear-water phase.

Animals born after the initiation of the clear-water phase both have a shortened longevity and an extremely retarded age at first reproduction, resulting in very low intrinsic rates of increase. Mostly, they only reproduce once there has been an increase of food (that is at the end of the clear-water phase). Survival to maturity is only about 50%. The effects of starvation get worse, the later neonates are born during the clear-water phase, such that all daphnids born during this period die simultaneously. Daphnids born after the clear-water phase (at increasing food levels and declining density in the case of 1998) have a longer live-span, produce more offspring and reproduce earlier compared to those born during the clear-water phase.

Results of life table experiments in different periods of the seasonal succession (if available) were consistent in both years, but unfortunately a comparison of the results with other studies is hampered because age-specific mortality under *in situ* conditions has hardly been investigated. Threlkeld (1980) conducted life table experiments with cohorts of *Daphnia* being exposed in the epilimnion or the hypolimnion of Wintergreen Lake, respectively. The mean longevity of *D. pulicaria* was 20 and 38 days, respectively, values for *D. galeata mendotae* were 24 and 36 days, respectively. Lei and Armitage (1980) estimated the mean longevity of *D. ambigua* cultured in the field and found values from 14 to 9 days when temperature ranged between 17° and 25°C. These figures are within the range of the results found in the present study, however, they are much shorter than the values found in laboratory experiments (Vijverberg 1976; Lei and Armitage 1980; Lynch 1980; Orcutt and Porter 1984). Probably, longevity is generally shortened under fluctuating *in situ* conditions compared to constant conditions in the laboratory. This conclusion has also been drawn by Lei and Armitage (1980) and is confirmed by results of Threlkeld (1986 b) who found longevity of *D. parvula* to be reduced to 1-12 days during a reservoir flood.

Moreover, apart from food quantity and quality, further factors may influence survival, first of all maternal effects (Lynch and Ennis 1983; Cowgill et al. 1984) or e.g. cyanobacterial toxins (Lampert 1981; DeMott et al. 1991; Jungmann 1992; Hietala et al. 1997). However, *D. galeata* has been shown to be able to thrive during massive blooms of *Microcystis* spec. (Ritter 1997) which developed in many previous years in Bautzen Reservoir (Benndorf and Henning 1989; Böing et al. 1998; Deppe et al. 1999). Microcystin production is not related to cyanobacteria biomass but to growth rates though (Jähnichen et al. 2001) and consequently toxic effects on *Daphnia* should mainly be expected before dense blooms developed. Since the substance is mostly found inside the cells, it may only impair daphnids after ingestion. This, however, may be avoided by daphnids (Kurmayer and Jüttner 1999) possibly by chemosensory mechanisms (Wagner 1998).

The mean life-span of daphnids born during the clear-water stage was almost identical to the mean age at first reproduction which is a key factor for *Daphnia* fitness (Vanni and Lampert

1992). A strong influence of low longevity on overall mortality can be expected in this situation (Dorazio 1984). Although it has long been recognised that the postembryonic development is prolonged at decreasing food levels (Weglenska 1971; Hrbáčkova and Hrbáček 1978; Vanni and Lampert 1992), values obtained in this study seem to be rather extreme. However, similarly high values were also found by Orcutt and Porter (1984) at low food availability and at a temperature of 15°C. Using natural food conditions, Neill (1981) and Arbačiauskas (1998 b) also reported juvenile development times of > 20 days at temperatures > 15°C. Temperature and food conditions may strongly interact in their impact on juvenile development (Neill 1981; Orcutt and Porter 1984). The present results suggest that food-limited reproduction and survival during the clear-water stage is essentially the same in every year, whether a midsummer decline develops or not. This is also corroborated by the analysis of fecundity parameters in different years (see Figure 4.3).

The concordance of field observations of fecundity and results obtained in life table experiments suggests that the latter indeed do reflect the field situation. A detailed discussion on the problem of extrapolating laboratory data to field situations is provided in Chapter 8. Direct effects of predation were excluded in the experimental set up, but an indirect of predators on *Daphnia* life history via kairomones, which were present in the water taken from Bautzen Reservoir cannot be excluded. However, laboratory experiments which demonstrated kairomone effects were usually performed with unrealistically high densities of predators. Moreover, changes of SAM may effectively be induced by indirect demographic effects of predation without kairomone effects (Lampert 1993). Since the water used in the experiments was only collected twice a week from the reservoir, it can be suggested that kairomone concentrations were decreasing and therefore, their effects are considered to be small compared to the food effects. From a *Daphnia* perspective, both a quick release by fish and an easy degradation of the kairomone guarantee the reliability of the signal (Loose et al. 1993). A detailed discussion of direct and indirect predation effects on life history parameters is provided in Chapter 6.

It has to be concluded that the recruitment pattern prior to the clear-water phase is a major determinant for the initiation of the midsummer decline. In 1997 and 1998 (with midsummer decline) the population increased threefold during one week in early May. The strong decline in June in both years (end of clear-water phase) can partly be attributed to the die-off of this peak cohort. This conclusion is a bit speculative at this point because no life table experiment was started during the decrease of $POC_{<30\mu m}$ at the beginning of the clear-water phase. Daphnids born during this period should make the greatest part of the peak cohort. Their longevity probably is higher compared to animals which were born a bit earlier and mostly died after they had released their first brood. It is very likely that survival probability of the peak cohort declined at the end of the clear-water phase. Additionally, according to life table experiments, a high mortality of animals born during the clear-water stage occurred at the same time. The situation was similar in 1996, however, neither the increase in May nor the decline at the end of June were as strong as in 1997 and 1998. By contrast, in 1995 and 1999 (no midsummer decline) the population increased slowly and continuously and no dominant cohort developed. When those daphnids that were born at the same time during the build-up of the population died simultaneously, this had only minor effects, since only a small part of the population was affected. These conclusions are corroborated by a long-term study of *Daphnia* dynamics in Bautzen Reservoir (Benndorf et al. 2001). In that study a long lasting midsummer decline of *D. galeata* was always associated with a high biomass of this species in April/May. If the interpretation of the data that were presented up to now holds true, it should be able to be confirmed by changes in the size-distribution of the *Daphnia* population in the field. This is examined in Chapter 6. Additionally, mortality patterns and sedimentation in field samples should support the expected high significance of non-consumptive mortality in years with a midsummer decline. This is analysed in Chapter 7.

6 Demography and life history characteristics of *Daphnia galeata* as related to food conditions and age-0 fish predation

6.1 Introduction

In Chapter 5 the effects of changing food conditions on *Daphnia* life history characteristics were shown, as analysed in life table experiments. Emphasis has been laid on the determination of age-specific fecundity and survival. In field samples of *Daphnia*, however, it is not possible to determine the exact age of the animals and thus only size-related life history parameters may be analysed. Strong seasonal changes in the size structure of *Daphnia* populations have frequently been reported (Threlkeld 1979; Brambilla 1980; Vijverberg and Richter 1982; Lampert 1993) and were either attributed to food conditions (Threlkeld 1976; Lampert 1988 b) or size selective predation (Vijverberg and Richter 1982, Černý and Bytel 1991). Effects of food limitation on *Daphnia* life history are discussed in Chapters 4 and 5. Age at maturity is delayed and size at maturity (SAM) is reduced at low food conditions (Vanni and Lampert 1992; Boersma and Vijverberg 1994 b). However, when food limitation is strong, SAM may also increase (McCauley et al. 1990) or it may be overestimated methodically (Stibor and Lampert 1993). Food deficiency also induces a decrease in brood size, whereas the size of the eggs increases (Guisande and Gliwicz 1992; Trubetskova and Lampert 1995; but see Lynch, 1989). On the other hand, direct and indirect effects of size selective predation by fish, as well as kairomone effects, induce a reduction of age and size at maturity and egg size (Macháček 1991; Stibor 1992; Lampert 1993; Reede 1995; Sakwinska 1998). All these variables are strongly related: Small neonates hatch from small eggs and mature at a smaller size (Lampert 1993).

The succession of bottom-up and top-down influences in Bautzen Reservoir is described in Chapter 3. A clear-water stage with low food conditions regularly develops in May, lasting for about 4 to 6 weeks. Juvenile fish (mainly perch and zander) hatch in late April or the beginning of May. Depending on their growth, fish start feeding on daphnids some weeks later when their gape-size is big enough (Mehner et al. 1998 b, c). At that time daphnids might face a conflict between a food-deficiency-strategy (delayed maturity, large eggs) and a predation-avoidance-strategy (young age and small size at maturity). How does *D. galeata* react to this combination of bottom-up and top-down factors and how fast do the reactions take place? In this Chapter I try to relate demographic and life history changes in the population of *D. galeata* to food conditions and predation by juvenile fish. With regard to the key mechanism of biomanipulation, the maintenance of a high *Daphnia* abundance, I finally ask how successful the adaptations have been.

6.2 Methods

Field sampling and calculation of life history parameters (SAM, brood size) of *D. galeata* are explained in Chapter 3 and 4. Size frequency distributions were analysed from tube-samples from 1997 through 1999 (1997 and 1998 with midsummer decline, 1999 without midsummer decline). Compared to net samples taken in 1995 and 1996 they were considered to be less biased in size distribution (Hülsmann unpubl. data). The egg size was measured during the course of the study period from 1997 to 1999 for all clutches with eggs in developmental stage I (egg membrane intact, compare Threlkeld 1979). Height (h) and width (b) of one egg per clutch was measured and egg volume was calculated according to its geometric shape (rotated ellipsoid)

$$V = 1/6 \pi h b^2 \qquad (6.1)$$

Intra-clutch variability in egg size is small (McKee 1997) and was checked regularly during the measurements.

6.3 Results

Seasonal changes in the size-structure of the population

At the beginning of the population development size frequency distributions of *D. galeata* (Figures 6.1-6.3) were similar in every year (1997-1999). Shortly before or right at the beginning of the clear-water stage, the population had a strong cohort of adults, most of which carried eggs. Thereafter, the proportion of ovigerous females drastically declined and the population was dominated by small juvenile size classes (< 1 mm) in 1997 and 1998, whereas in 1999 the size distribution was more even at the beginning of the clear-water phase. In all years the proportion of egg-carrying adults increased again towards the end of the clear-water phase, concerning almost exclusively the biggest size classes. Due to this increased recruitment, the population showed a kind of bimodal size distribution at the end of the clear-water stage in every year. After this period of high water transparency and low food, the biggest size classes (> 1.5 mm) of the *Daphnia* population vanished in all years within about 10 days. But whereas in July 1997 and 1998 virtually no animals > 1 mm could be found, adult size classes mostly ranged between 1.0 and 1.5 mm in July 1999. Changes in the size structure of the population were analysed using the data on mean size of egg-carrying daphnids presented in Figure 4.2. An increase of the size of egg-carrying daphnids during the clear-water stage could be seen (Figure 6.4) Although the slope of the regression against time was similar in 1997 and 1999, the relation was less clear in the latter year (Table 6.1). In every year, mean summer values of the size of ovigerous daphnids were significantly smaller than mean values during the clear-water phase.

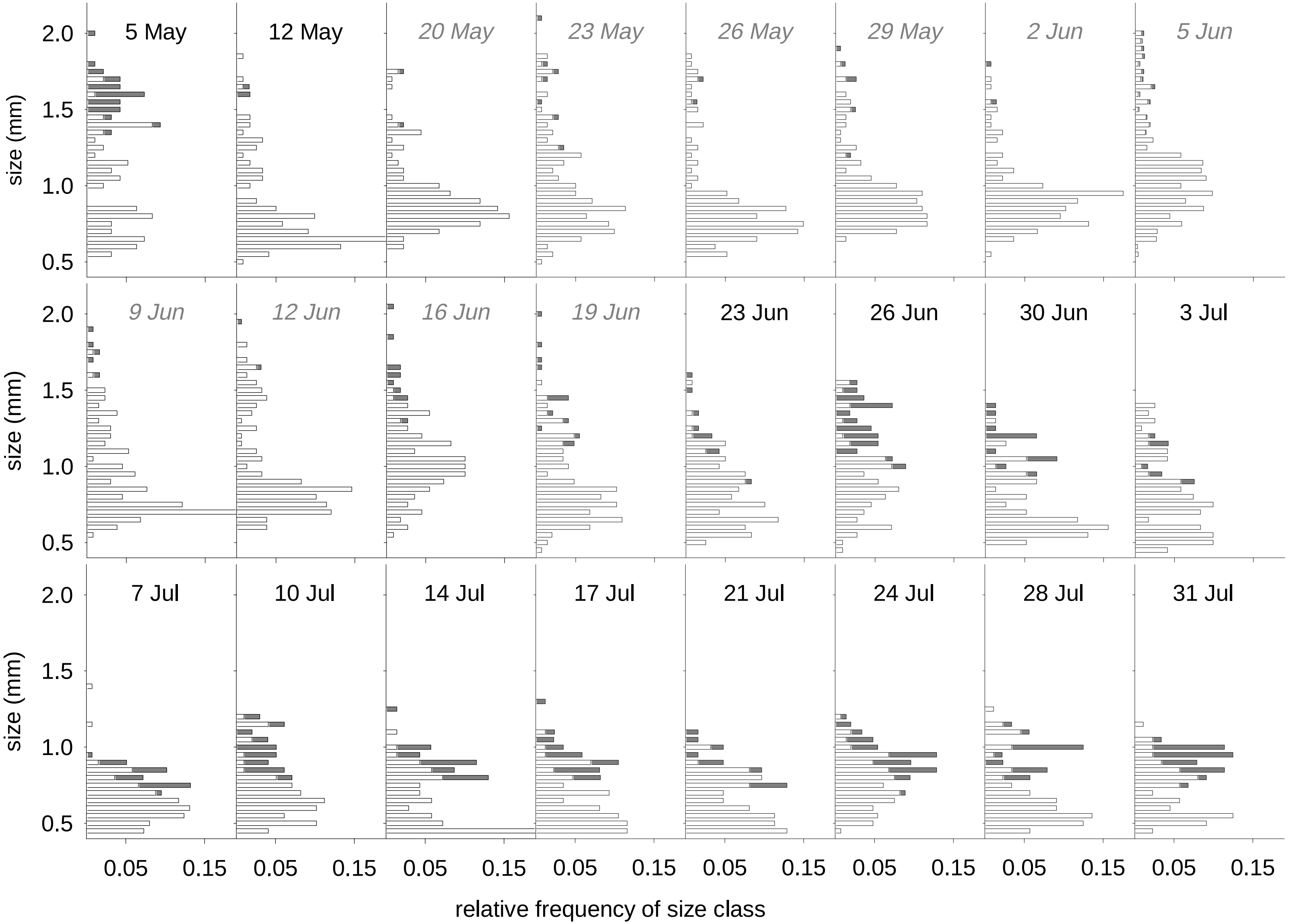

Figure 6.1. Size-frequency distribution of *D. galeata* in Bautzen Reservoir during the investigation period of 1997. The shaded bars represent egg-carrying daphnids. Dates representing the clear-water stage are displayed in grey and italics.

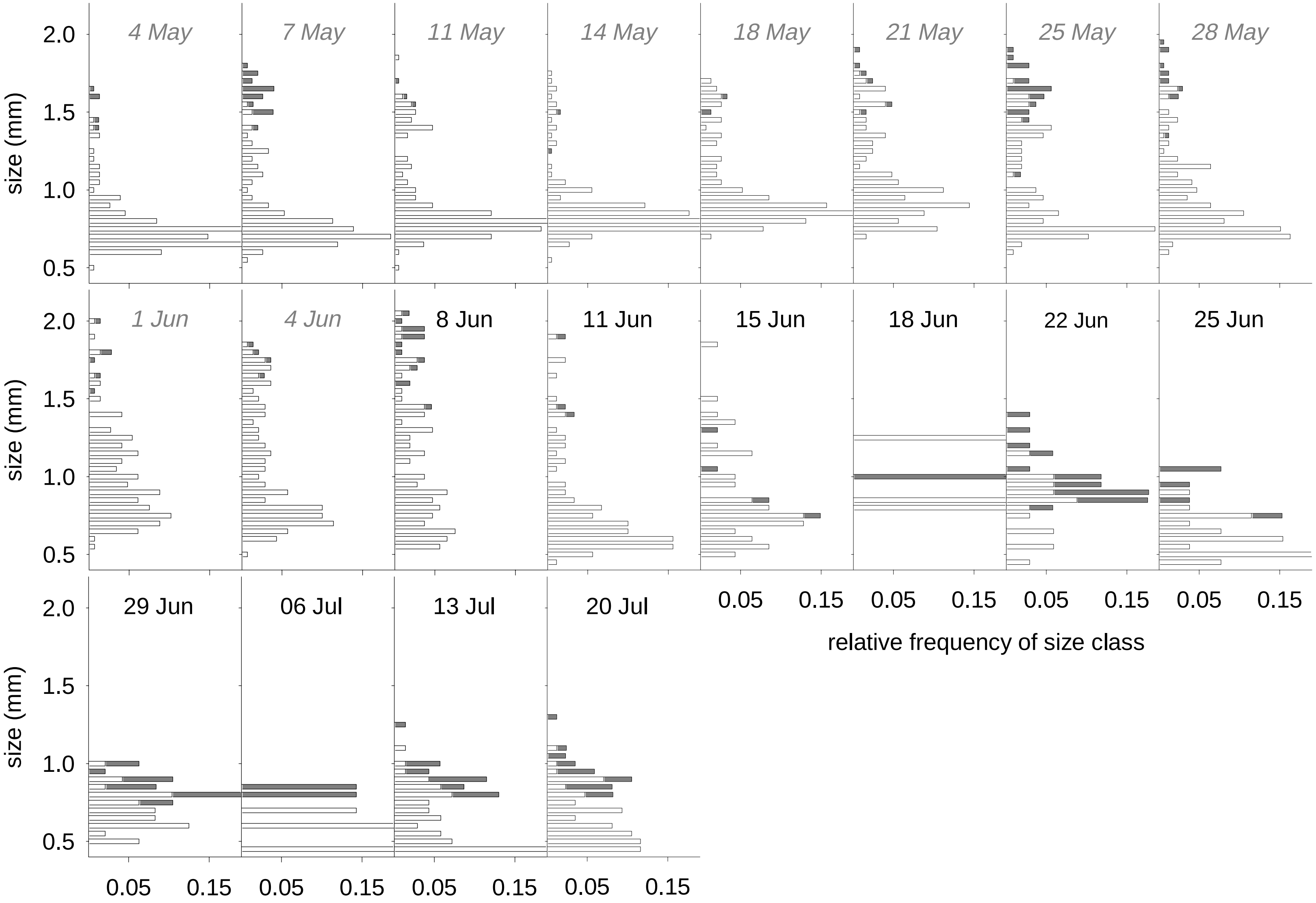

Figure 6.2. Size-frequency distribution of *D. galeata* in Bautzen Reservoir during the investigation period of 1998. Symbols as in Fig. 6.1.

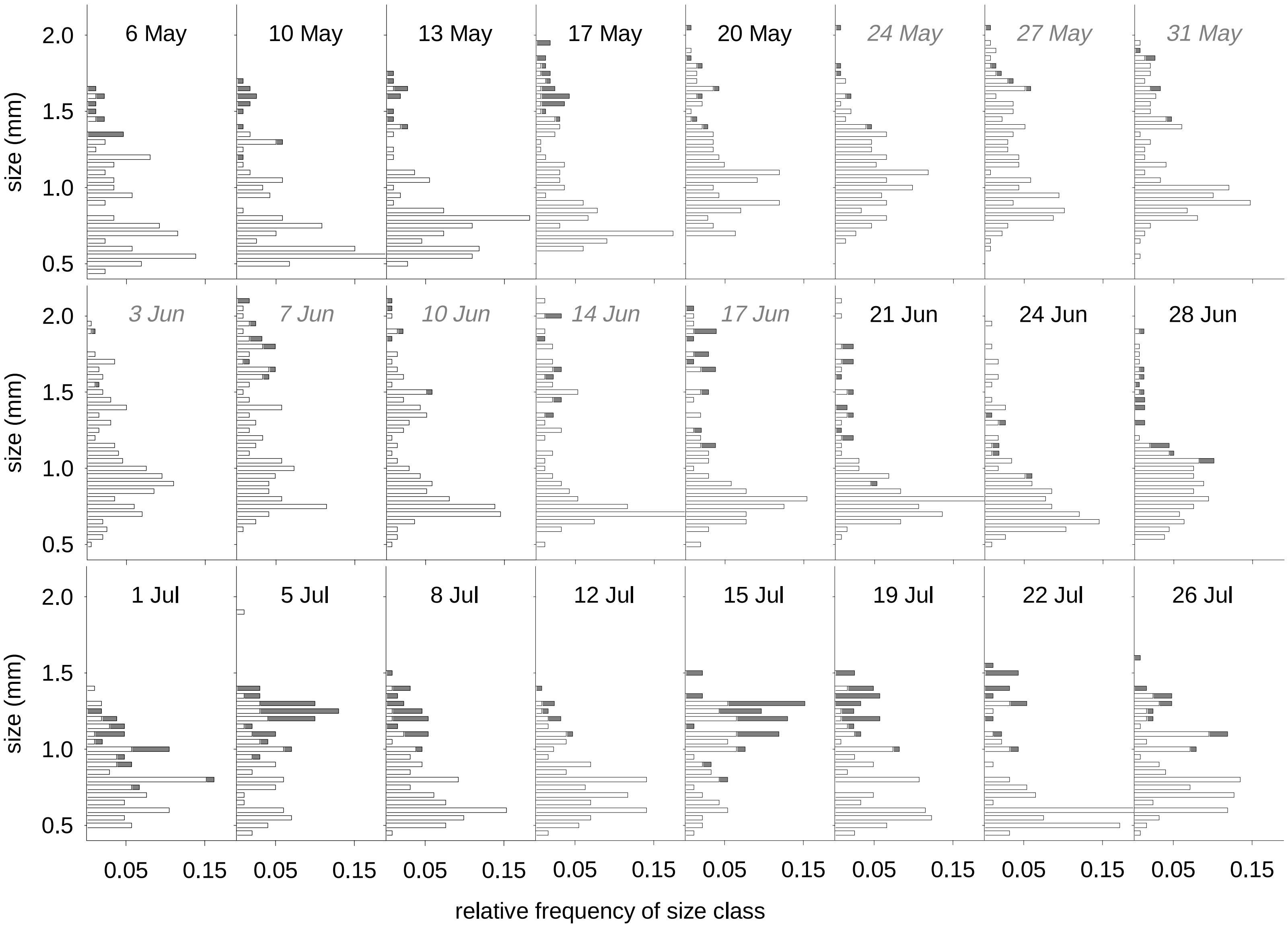

Figure 6.3. Size-frequency distribution of *D. galeata* in Bautzen Reservoir during the investigation period of 1999. Symbols as in Fig. 6.1.

Table 6.1 Changes in the size structure of the population of *D. galeata* in Bautzen Reservoir during the summer of 1997, 1998 and 1999 as shown in Figure 6.4. A linear regression between the development of the mean size of egg-carrying females during the clear-water phase and time was calculated using the following periods: 20 May-12 June 1997, 14 May-8 June 1998, 20 May-10 June 1999. Mean values of these periods were compared with mean summer values, considering the periods 7-31 July 1997, 18 June-20 July 1998 and 1-29 July 1999, when size of egg-carrying females was stable on a low level. Transitional phases with declining sizes were not considered.

Year	Slope (increase per day in µm)	r^2	p	n	Mean size clear-water (µm)±SD	Mean size summer (µm) ±SD
1997	5.19	0.82	0.0019	8	1699±175	925±110
1998	14.61	0.81	0.0024	8	1691±190	974±137
1999	6.52	0.58	0.048	7	1789±182	1237±148

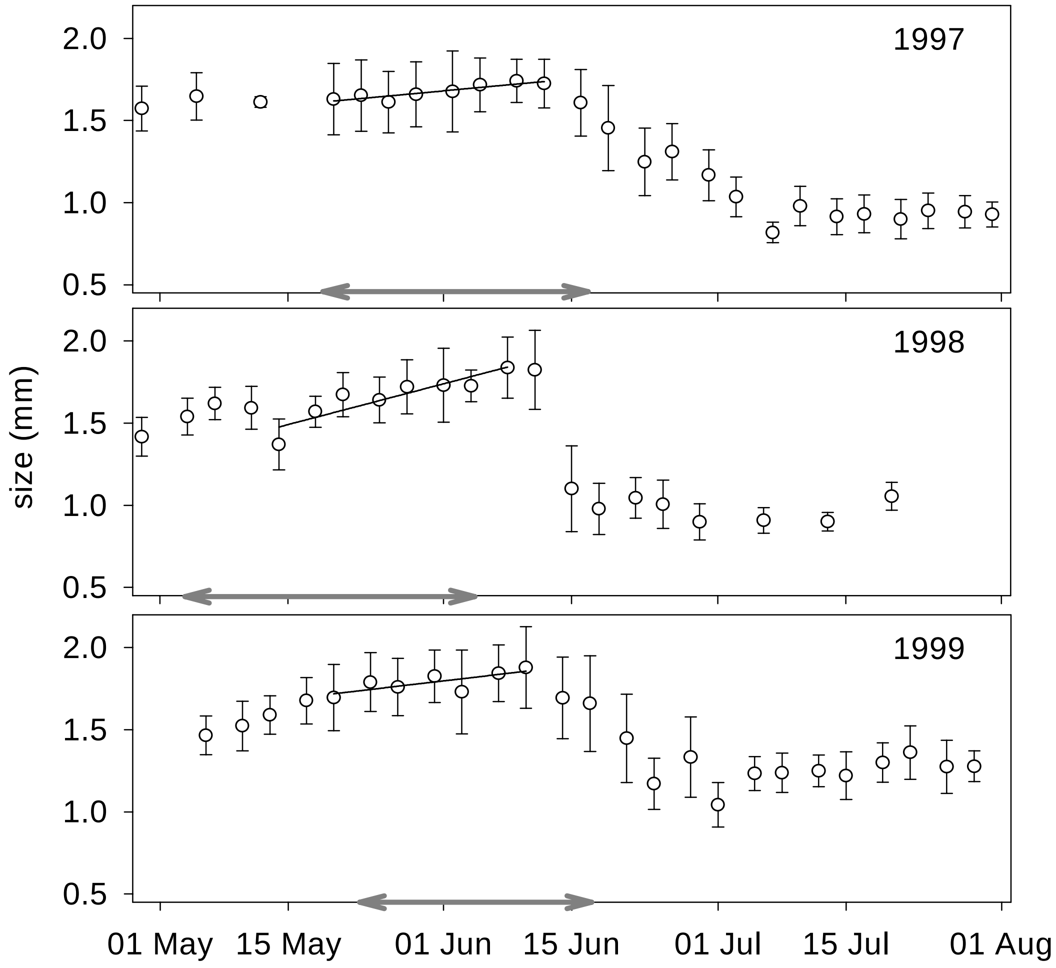

Figure 6.4. Temporal pattern of mean size (± SD) of egg-carrying females (mm) of the *Daphnia* population in Bautzen Reservoir during the investigation period of 1997, 1998 and 1999 (taken from Figure 4.2). A linear regression of mean size of egg-carrying daphnids versus time was calculated for periods approximately representing the clear-water stage (indicated by grey arrows on the x-axis) in each year. See Table 6.1 for more details.

Seasonal changes in reproductive parameters

When the brood size decreased (compare Figure 4.3) the mean egg volume increased at the same time (Figure 6.5). The egg volume remained high during the first phase of the clear-water stage and declined at the end of this period. Eggs were small during the rest of the summer. Declining egg volumes were not reflected by increasing brood sizes. Plotting egg volume against different parameters possibly affecting it (Figure 6.6), reveals that eggs were always small when (1) the size off egg-carrying daphnids was small, (2) food concentration was high and (3) biomass of juvenile fish was high.

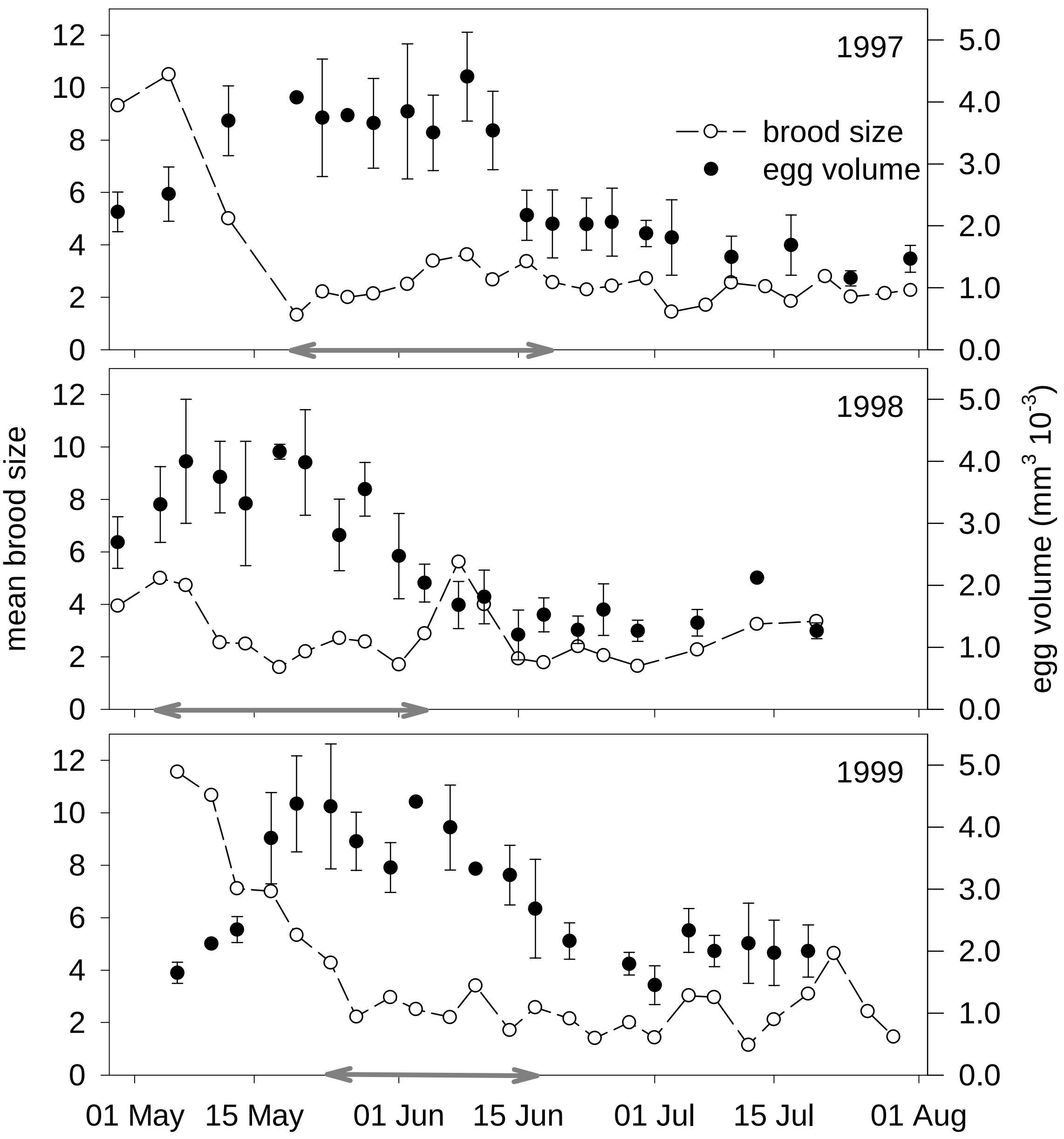

Figure 6.5. Temporal development of mean brood size (mean number of eggs per clutch) and mean egg volume (mm^3 10^{-3}) ± SD of *D. galeata* during the investigation period of 1997, 1998 and 1999. Grey arrows on the x-axis indicate the clear-water stage with Secchi depth > 2.5 m.

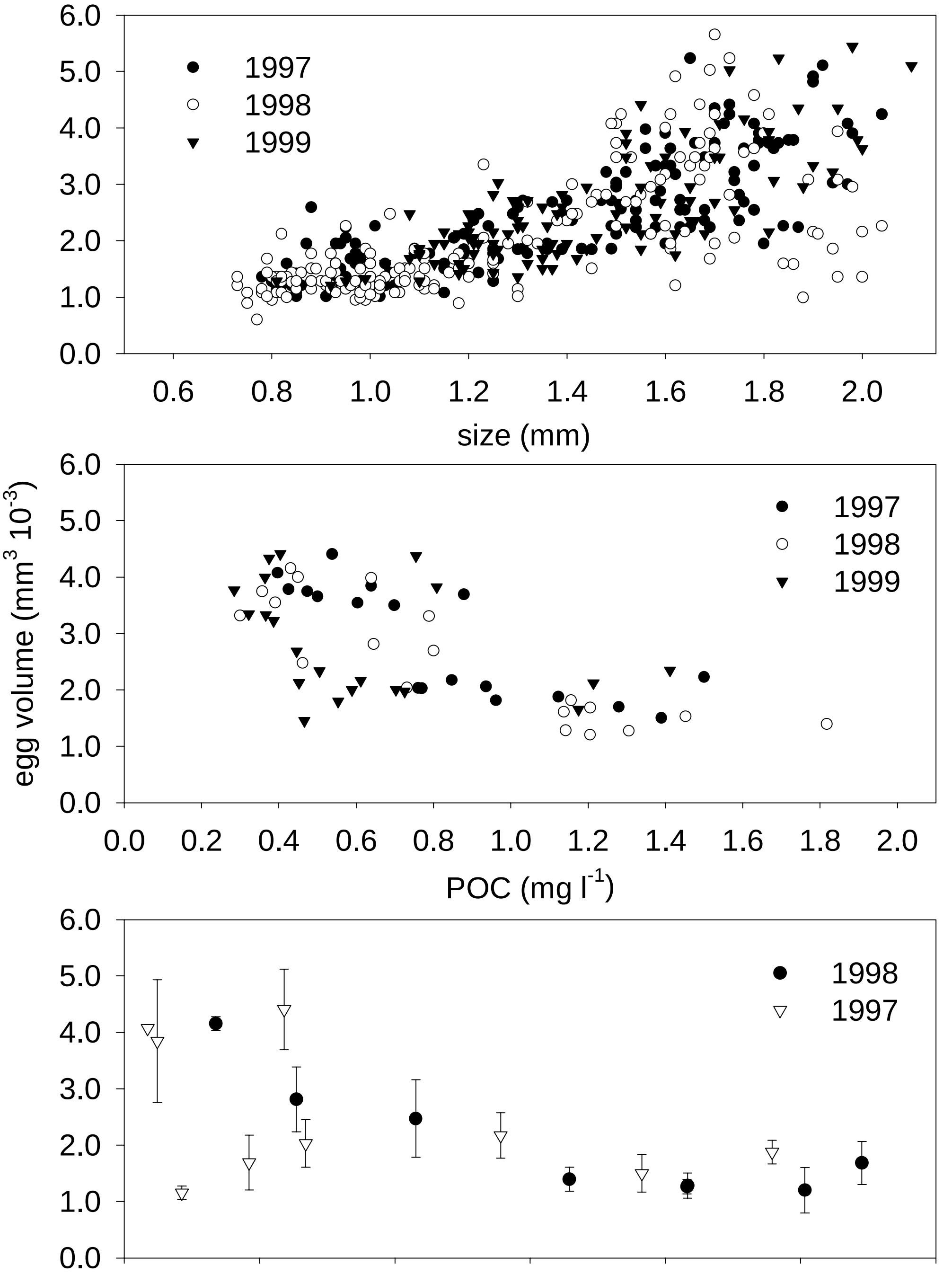

Figure 6.6. Dependency of egg volume (mm^3 10^{-3}) on the body size of egg-carrying individuals of *D. galeata* (mm; top panel), on food concentration (POC$_{<30\mu m}$, mg l^{-1}; middle panel) and on age-0 fish biomass (mg ww m^{-3}; lower panel). In the top panel egg volume of single broods is shown whereas in the middle and lower panel mean egg volume of the population is provided. SD is shown only in the lower panel but is omitted in the middle panel for clarity.

On the other hand, big eggs were only found when large daphnids were present and when food concentration and biomass of juvenile fish was low. However, eggs may also be small under these conditions. Consequently, these parameters only determine the maximum possible egg volume. For a more detailed analysis, Figure 6.7 provides the body size-egg volume relations for single dates at the end of the clear-water stage and for one date later in summer. There was a decrease both of egg volume and body size of egg-carrying females during that period in every year. However, the relation between both parameters differed. In 1997 and 1999 both values gradually declined at the end of the clear-water phase (simultaneously to the decline of abundance in the case of 1997). By contrast, in 1998 egg volume also strongly decreased, but body size of egg-carrying females did not. On 8 June eggs carried by 2 mm daphnids were as small as those carried by 0.8 mm daphnids later that summer.

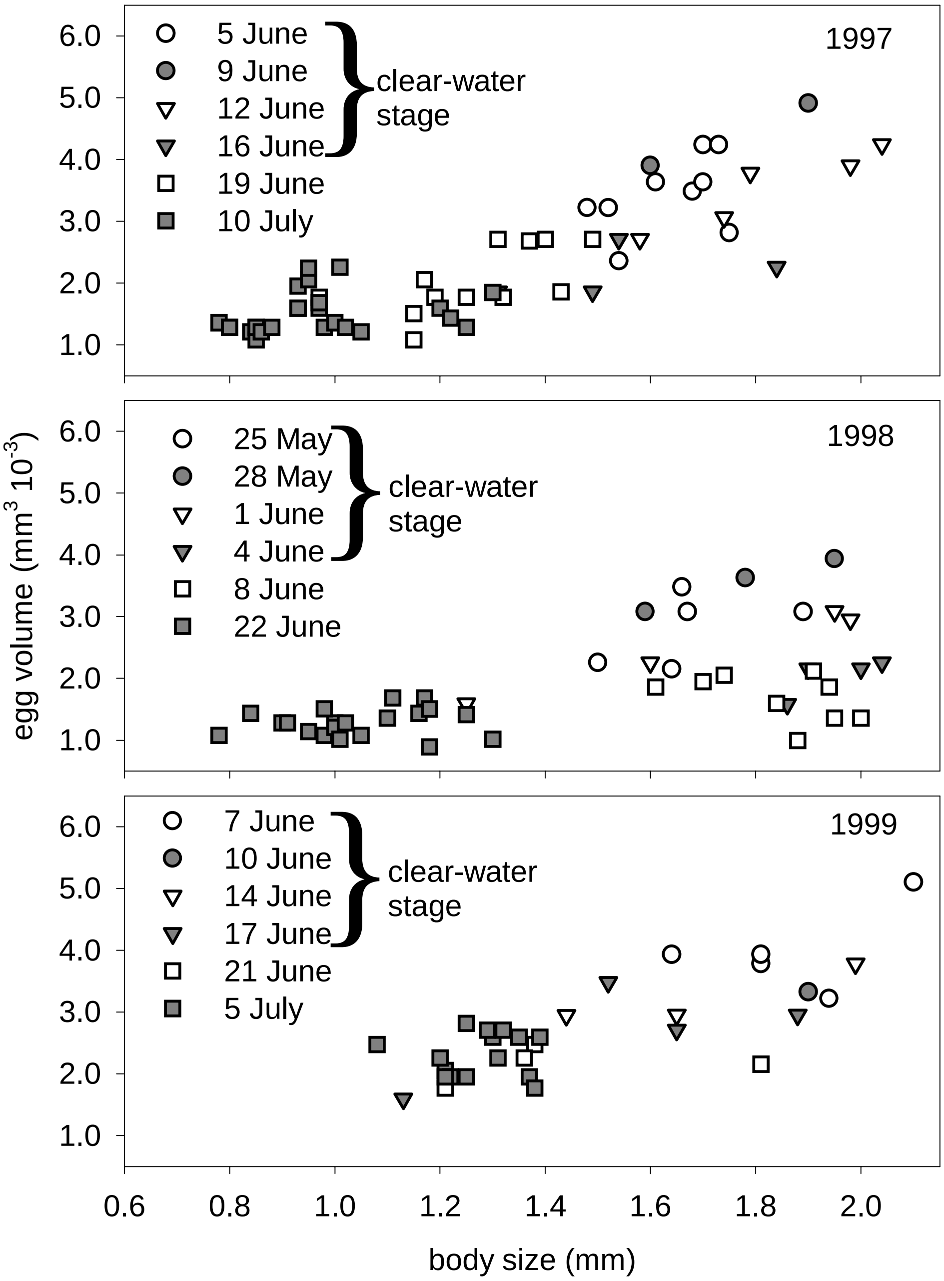

Figure 6.7. Relation between body size of egg-carrying daphnids and egg volume (of single broods) at the end of the clear-water stage and later in summer in three successive years in Bautzen Reservoir.

6.4 Discussion

In this Chapter, changes in the size structure and in selected life history parameters (SAM, egg volume, brood size) of the *Daphnia* population during spring and early summer were demonstrated. These changes may be interpreted as reactions to complex interactions between bottom-up and top-down factors.

At the beginning of the clear-water stage, the observed life history changes of the *Daphnia* population may be attributed exclusively to declining food conditions (juvenile fish biomass at that time is low in any case). This is most obvious for the decrease of fecundity (shown here as mean brood size), which was already discussed in Chapter 4. The simultaneous increase of egg volume may be interpreted as a change of reproductive allocation from high quantity offspring production to high quality offspring production, indicating a trade-off between offspring size and number (Ebert 1993). Guisande and Gliwicz (1992) found that an increase of egg size at decreasing food conditions was associated with increasing lipid content, carbon and mass of the egg. Egg size is positively correlated with neonate size (Guisande and Gliwicz 1992; Lampert 1993; compare also Figure 5.1) and larger neonates have a higher survival probability at low food conditions (Tessier and Consolatti 1989; Gliwicz and Guisande 1992). However, increasing egg size may also result from increasing size of the mothers (Glazier 1992; Lampert 1993). This effect should be of minor importance at the beginning of the clear-water stage, despite the fact that body size of egg-carrying females increased during this period. However, this was most pronounced towards the end of this period. At that time, egg volume actually decreased (Figure 6.5), although food conditions were still bad. Moreover, the relation between body size and egg volume was different in 1998 compared to 1997 and 1999 (Figure 6.7).

Taking the results of the life table experiments (Chapter 5) and the development of juvenile fish (Figure 3.5) into consideration, it is possible to interpret the reproductive patterns which can be seen in the size-frequency distributions and in patterns of reproductive allocation. Daphnids which mature shortly before food conditions decline mostly die after having released their first brood (with small eggs). This was obvious in the first life table experiment in 1999 and can clearly be seen in size-frequency distributions at the beginning of the clear-water phase of each year. Those daphnids that become adult at the beginning of the clear-water stage have a low fecundity and long time lags between successive broods. These adults continue to reproduce at a low level (that is, few, but large eggs) throughout the clear-water stage and increase in size. Recruitment of adults from juvenile stages is very low during this period, since only few neonates are produced, juvenile growth is reduced and age at maturity is extremely retarded. Daphnids born during this period of low food conditions have their first brood at the end of the clear-water stage, their fecundity responding to any slight and short-term increase in food availability. First-brood eggs are generally smaller than those from later broods (Glazier 1992; Lampert 1993). Consequently, this mechanism may explain the decrease in egg size at the end of the clear-water stage in 1997 and 1999. The size of egg-carrying daphnids also declined at that time, indicating that indeed these younger daphnids produced those small eggs (Figure.6.7). However, in 1998 egg size declined while body size of ovigerous females remained high and it is very unlikely that individuals of *D. galeata* mature at a size of 1.8-2 mm. Probably, at that time fish kairomones were more important than in other years due to the very high biomass of juvenile fish, because adult daphnids, when exposed to fish kairomones, reduce egg size (Macháček 1995). Afterwards, the different factors influencing egg size (body size, food conditions, fish kairomones) strongly interact: High biomass of juvenile fish (among other factors, see Chapter 7) causes low densities of small-bodied daphnids, unable to control phytoplankton biomass, which results in high POC concentrations. All these factors promote small eggs.

Towards the end of the clear-water stage the size structure of the population of *D. galeata* showed distinct signs of aging. The size of the adult cohort and the minimum size of juveniles increased, whereas the recruitment to adult stages seemed to be low. Although not very clearly, a bimodal size distribution could be seen at the end of the clear-water stage in 1997 to 1999 (e.g. 12 June 1997, 28 May 1998, 10 June 1999, see Figures 6.1-6.3). From simulations with an individual-based model Koh et al. (1997) concluded that *Daphnia* populations near to extinction (due to environmental and chemical stressors) show a bimodal size and age distribution and increasing average age. The regressions of the size of egg-carrying daphnids versus time suggest that only <u>one</u> cohort of adults dominates the population during the clear-water stage (Figure 6.4, Table 6.1). This was most clearly in 1997 and 1998, less so in 1999. This interpretation is in line with conclusions drawn from different recruitment patterns in single years (compare discussion in Chapter 5). In 1997 and 1998 (with midsummer decline) adult daphnids dominating the population during the clear-water stage really represent a cohort because they were born during a short time interval of about one week. By contrast, in 1999 (no midsummer decline) recruitment per unit time was continuously low. Consequently, the range in age of the adult daphnids during the clear-water phase should be larger, although in principal the same mechanisms work during this period as in years with midsummer decline.

At the end of the clear-water stage changes in the size structure of the *Daphnia* population obviously are not only influenced by food conditions. SAM was high already before the clear-water phase and remained high at low POC values, whereas the decline of SAM in 1997, 1998 and 1999 (and also in 1996, compare Figures 3.3 and 4.2) occurred while food concentrations were increasing. Lampert (1988 b) suggested that food availability rather than predation was responsible for similar size changes, as daphnids mature earlier in high-food conditions (Tilmann and Lampert 1984; Lynch 1989; Brett 1993). However, in Bautzen Reservoir SAM was also high when food concentration was high in early spring. Instead, predation is more likely to be responsible for the observed size changes in summer (compare Gliwicz and Boavida 1996). Biomass and consumption of age-0 fish in Bautzen Reservoir was higher in July 1996 (when SAM declined) than in July 1995 (stable SAM). In 1997 and 1998 (strong decrease of SAM) age-0 fish biomass was even higher than in 1996 and increased at the same time as $POC_{<30\mu m}$ (compare Figures 3.3, 3.5). Thus, it can be concluded that a strong reduction of SAM only occurs at high biomasses of juvenile fish in Bautzen Reservoir, which means that only a moderate fish biomass must be assumed for 1999. However, moderate reductions of SAM may also be due to demographic mechanisms (see below).

SAM may be adjusted by daphnids phenotypically either in response to chemical cues released by fish (Macháček 1991; Stibor 1992) or as a demographic effect combined with shifts in relative abundance of small first-brood eggs, which hatch to smaller neonates, maturing at a smaller size (Lampert 1993). In field situations, probably both effects act together and may even amplify each other, as small neonates may further reduce SAM under the influence of fish kairomones. Effects of clonal replacement may also play a role (Tessier et al. 1992). Stibor and Lampert (2000) found different responsiveness of clones isolated at different times of the season to kairomones and attributed this to changes in the clonal composition. The assumed shift in clonal composition during the study period could not be verified by allozyme analysis though. Investigations of the genetic structure of *D. galeata* in Bautzen Reservoir suggest that only few clones dominate (Voigt 1996; Ritter 1997). Only moderate seasonal changes in clone frequencies were observed and no clear evidence for an influence on life history characteristics could be found. Still, it can be assumed that clones differ e.g. in SAM. Determining SAM according to Stibor and Lampert (1993), however, prevents this value to be severely underestimated with regard to the whole population. It may be over- or underestimated for single clones though. Normally however, the size of egg-carrying females at any single date was very similar (Figure 6.4, compare Figure 4.1). Thus, clonal differences in SAM may be more important on a seasonal scale than at particular dates (compare Pace et al. 1984; Stibor and Lampert 2000).

The timing of population dynamics, life history adaptations and bottom-up and top-down factors at the end of the clear-water stage in different years (1997-1999) can be summarised in the following way:

- Increasing $POC_{<30\mu m}$ values were recorded at the same time as the decline of *Daphnia* density, always preceding the end of the clear-water stage.
- Egg volume and *Daphnia* abundance decreased simultaneously.

- SAM decreased with a short (3-4 days) delay in 1997 and 1999, whereas in 1998 SAM declined one week after the decline of *Daphnia* density.
- The decline of *Daphnia* density in 1997 and 1998 started after the biomass of juvenile fish exceeded 200 mg ww m^{-3}.

If it is assumed that small egg sizes are a prerequisite for small SAM (Lampert 1993), SAM should be reduced with a time lag corresponding to juvenile development time. Bearing in mind the juvenile development times from the life table experiments (minimum age at maturity 11 d even after the clear-water phase), it gets clear that the decrease in egg size may not explain the fast decrease of SAM. Instead, results from life table experiments suggest that the initiation of this decrease was due to an alternation in generations. Daphnids born during the clear-water stage had their first (very retarded) brood exactly at the end of this period. Only at that time (when food conditions eventually already increased) had they accumulated enough energy to produce their first clutch. Compared to the cohort of adults, which was present during the clear-water stage, these animals were significantly smaller (about 1.3 mm). This may similarly be seen in size-frequency distributions (Figures 6.1–6.3) and in growth curves of daphnids from life table experiments (Figure 5.3). Their broods consisted of small eggs, which hatched to small neonates, which (at least in 1997 and 1998) were exposed to high food conditions and high kairomone concentrations. All these factors favour small SAM, explaining the further decrease.

The changes in primiparous size found in this study (decrease by about 0.7 mm in two weeks in 1998) seem to be rather extreme. Related to the maximum SAM (about 1.6 mm) it represents a reduction in size of 44%, which is in the same (relative) order of magnitude as Lampert (1993) reported for *D. magna* in Großer Binnensee (range in SAM 1.8-3.2 mm), however, it happened much faster. SAM < 0.8 mm until now has only been reported for *D. galeata* by Arbačiauskas (1998 b). Lynch (1980) in his review gave a value of about 1 mm, which was also found by Boersma (1995) in Tjeukemeer. In earlier studies in this water, Vijverberg and Richter (1982) found a minimum SAM of 0.9 mm in late summer (note that *D. hyalina* is in fact *D. galeata*). Lake Tjeukemeer, similarly to Bautzen Reservoir, is highly eutrophic and age-0 fish play a key role in its food web (Vijverberg et al. 1990).

Concerning the timing of life history adaptations, the reduction of SAM in 1998 was delayed compared to 1997 and 1999, when it declined simultaneously with *Daphnia* density. In 1998 SAM decreased only when the density was already very low, however, the reduction occurred even faster than in other years. This may be explained by the feeding strategies of juvenile fish. While fish grow during their early development, they subsequently feed on larger prey as their mouth gape becomes bigger (Hansen and Wahl 1981; Mills et al. 1984; Mehner et al. 1998 c). Investigations of food selection of perch and zander in Bautzen Reservoir showed that they feed on smaller than average-sized daphnids as long as they are smaller than 25 mm in total length (TL) which can be expected during the clear-water stage (Mehner et al. 1998 c; Wagner et al. 1999). Laboratory experiments with juvenile perch feeding on *Daphnia* showed the same results (Janßen 1999). Perch smaller than 25 mm TL selected small and medium sized daphnids (< 1.5 mm) whereas larger fish strongly selected larger prey sizes.

However, even more than *Daphnia* size, the presence of eggs influenced prey selection. Perch ≥ 21 mm TL started selecting egg-carrying daphnids of medium size and fed on such individuals although they could not be found in zooplankton samples (with more than 100 daphnids measured). When perch grew larger (29 mm TL), they strongly selected egg-carrying daphnids from all size classes. Both in 1997 and in 1998 the mean length of juvenile perch reached 25 mm TL exactly at that date when SAM was high for the last time (Wagner et al. 1999; Janßen 1999). This means that before this date, daphnids that matured at a smaller size were strongly selected by perch. There might have been some daphnids that became mature at a smaller size at the end of the clear-water stage in 1998, similar to 1997 and 1999, but they did not show up because fish were smarter in finding them. Consequently, a decrease of SAM can only be observed once juvenile percids change their size selection towards larger size classes. When they do so, however, they may accelerate the process of reducing SAM by indirect demographic effects as described by Lampert (1993).

Biomass of juvenile fish was very high in 1998 compared to 1995 and 1996 and it can be assumed that the proposed mechanism of preventing a reduction of SAM only works when feeding pressure of gape-limited fish on daphnids is strong. The combination of food limitation during the clear-water stage and predation (concerning timing, intensity and selectivity) in 1998 seems to represent the worst case for *D. galeata* in Bautzen Reservoir because the population almost vanished in summer (< 1 ind. l^{-1}). By contrast, in 1997, with similarly high biomass of juvenile fish, *D. galeata* stabilised at a low level (~10 ind. l^{-1}) in summer. In that year the timing of size-selection of juvenile fish was slightly different. SAM (observably) decreased simultaneously with *Daphnia* density and thus, medium-sized daphnids, which were now below the preferred size range of juvenile fish, benefited from increasing food levels during the decline and had a high chance to reproduce successfully (at least once). As can be seen in the size-frequency distribution on 8 June 1998 (Figure 6.2), those large daphnids that were still beyond the ingestible prey size for juvenile fish also responded with increased egg production to increasing food levels. But because fish grew fast and changed their feeding behaviour, it must be assumed that most of these daphnids were eaten before the eggs hatched.

Due to the morphometric and physical characteristics of Bautzen Reservoir, daphnids may neither hide from predation in a hypolimnetic refuge (Wright and Shapiro 1990) nor do macrophytes provide protection (Lauridsen and Lodge 1996). Consequently, life history adaptations must be regarded as key strategies to minimise predation effects. Reducing the size at maturity and reducing offspring size may allow cladocerans to coexist with high densities of planktivorous fish (Vanni 1987, Lampert 1991). However, if this strategy is counteracted by a changing feeding selectivity of juvenile fish, such catastrophic crashes as in 1998 cannot be prevented.

In summary, life history adaptations of *D. galeata* strongly respond to changing bottom-up and top-down factors. At the beginning of the clear-water phase, changing food conditions are most important, inducing a change from high quantity (many small eggs) to high quality (few big eggs) reproduction. The population structure during the clear-water phase is dominated by a single cohort of adults, which continue to grow and to reproduce at a low level. The end of the clear-water stage is marked by an alteration of generations. Animals born during this period have their first, very retarded brood with small eggs and at a smaller size compared to the “old” cohort of adults. SAM may be further reduced by direct and indirect effects of predation, interacting with increasing food levels. The *Daphnia* population is most vulnerable to predation at the time when the new generation takes over. Consequently, predation impact depends on timing of both age-0 fish consumption and feeding selectivity.

7 Mortality pattern of *Daphnia galeata* in Bautzen Reservoir: The importance of non-consumptive mortality

7.1 Introduction

A midsummer decline of large-bodied cladocerans, in particular daphnids, is a common phenomenon in temperate lakes and reservoirs (Sommer et al. 1986). This decline has been attributed to poor food conditions (Lampert et al. 1986; Sommer et al. 1986), predation by fish, especially age-0 fish (Mills and Forney 1983), or a combination of low food and invertebrate predators (Luecke et al. 1990; De Stasio et al. 1995). Neither the bottom-up nor the top-down view has been supported consistently though. Concerning bottom-up effects, declining fecundity due to food limitation is mainly considered to be the reason for the decrease of *Daphnia* densities (e.g. Lampert et al. 1986; Luecke et al. 1990). However, reduced fecundity itself obviously is not the reason for a population to decline. The question remains: Which part of the population dies during the decline and why?

Direct effects of starvation on *Daphnia* mortality are generally considered to be more important for juvenile stages, as starvation resistance increases with body size (Threlkeld 1976; Tessier and Consolatti 1989). Typically, *Daphnia* densities decrease rapidly during the decline phase (see references in Table 8.3). When fecundity prior to the decline is reduced (clear-water phase) and thus, recruitment is low, it seems unlikely that the drop in *Daphnia* density is due to massive mortality of juveniles, all dying at the same time. Another possible bottom-up effect on *Daphnia* mortality is increased adult mortality due to aging of the population (Hülsmann and Weiler 2000; Benndorf et al. 2001). However, as pointed out above (Chapter 5), surprisingly few studies have dealt with non-consumptive mortality under *in situ* conditions and generally, predation is considered to be the most important source of adult mortality in *Daphnia* populations (e.g. Gliwicz and Pijanowska 1989; Lampert and Sommer 1993).

Concerning top down effects on the initiation of a midsummer decline, only few studies have quantified fish consumption to evaluate its impact on *Daphnia* populations and among those results were contradictory. Mills and Forney (1983) found that consumption of age-0 perch exceeded production of *D. pulex* in years with a midsummer decline. By contrast, other studies found that *Daphnia* mortality during the decline could not be explained by age-0 fish consumption alone (Wu and Culver 1994; Boersma et al. 1996; Mehner et al. 1998 b). There is, however, strong evidence that effects of size-selective predation may be important. As concluded from demographic changes in *Daphnia* populations, a disproportionate loss of adult daphnids, especially when combined with low fecundity, may enhance direct predation effects (Gliwicz et al. 1981; Hülsmann and Mehner 1997; Mehner et al. 1998 b, c). On the other hand, several studies reported high juvenile death rates causing a decline (e.g. De Bernardi 1974; Boersma et al. 1996).

Different sources of mortality should have different effects on demography of a *Daphnia* population. Planktivorous fish selectively feed on large prey (Gliwicz and Pijanowska 1989), though size-selection of age-0 fish depends very much on their gape-size (Mehner et al. 1998 c). Contrary to fish, invertebrate predators are generally considered to preferentially prey on smaller species and instars, yet, this cannot be generalised, but depends on the size of different zooplanktivorous invertebrates (Benndorf et al. 2000). Moreover, results concerning e.g. size selection of *L. kindtii* are contradictory (compare Herzig and Auer 1990; Lunte and Luecke 1990). Effects of non-predatory sources of mortality (starvation, disease, inability to adapt to changing environmental conditions) also might differ in strength during the life history of an individual *Daphnia*, probably interacting with age-specific mortality (Threlkeld 1976). Summarising, since in natural environments it is virtually impossible to quantify all these mortality factors simultaneously, size-specific mortality of *Daphnia* may hardly be determined by looking at its sources. This is why the explanations of observed (total-) mortality patterns remained rather speculative and contradictory in many studies of *Daphnia* population dynamics during midsummer declines (e.g. Hall 1964; Threlkeld 1979; De Stasio et al. 1995).

To overcome this problem, several approaches have been developed to estimate size-specific mortality of cladocerans from population parameters and growth data (Argentesi et al. 1974; Vijverberg and Richter 1982; Lynch 1983). However, the application of existing population dynamics models (De Bernardi 1974; Hovenkamp 1989; Boersma et al. 1996) to field data is problematic, because model parameters have to be adjusted to the specific population of interest (see below). Lynch´s (1983) approach requires considerable computational effort and is difficult to apply. From a *Daphnia* perspective, however, it is not important to know the exact instar- or size-specific mortality, but to distinguish between juvenile (pre-reproductive) and adult (potentially reproductive) mortality. This was done in this study by combining data derived from field samples (abundance, size-structure, fecundity) with estimates of juvenile growth rates obtained under approximately *in situ* conditions. This is a first step to gain insight into the mechanisms leading to a midsummer decline. However, death rates calculated from field data of course incorporate all sources of mortality and additionally are confounded by errors (Taylor and Slatkin 1981; Taylor 1988).

Therefore, an attempt has been made to determine non-consumptive mortality of *D. galeata* during the population development in spring and early summer. Two approaches were combined. First, non-consumptive mortality was estimated in the field using sediment traps (Gries and Güde 1999) and second, age-specific mortality patterns estimated in life table experiments (Chapter 5) were used to model population dynamics of *D. galeata*. These model results were compared with cumulative recruitment (population dynamics without mortality) and actual population dynamics observed in the field (including consumptive and non-consumptive mortality).

7.2 Methods

Field sampling of *D. galeata* and further processing of samples is described in Chapter 3. Formula for the calculation of recruitment are provided in Chapter 4. Laboratory experiments to determine juvenile growth rates are explained in Chapter 5. Mortality of juvenile and adult daphnids was calculated separately for the periods May-July of 1997, 1998 and 1999. *Daphnia* sedimentation and age-specific mortality patterns were analysed in 1998 and 1999.

The general approach, which was used to separately calculate juvenile and adult mortality, is similar to the discrete event model INSTAR (Vijverberg and Richter 1982), used also by Hovenkamp (1989, 1990) and Boersma et al. (1996), except that (1) I only discriminated between juvenile and adult *Daphnia*, (2) juvenile growth rates were estimated weekly in the laboratory under approximately field conditions (Chapter 5) and (3) hatching frequency of *D. galeata* was estimated according to Johnsen (1983) as explained in Chapter 4. The number of individuals that die during one sampling interval is estimated by comparing computed densities of juvenile and adult *Daphnia* with the estimated abundance in the field.

From growth rate estimates and the population structure at sampling date t_i the hypothetical proportion of adults at the next sampling date (t_{i+1}) was calculated by applying the following stepwise procedure to all measured animals:

	if	then	else
(I)	$L_{ti} < SAM_{ti}$	$L_{ti+1} = L_{ti} + (g_L\ \Delta t)$	adult at t_{i+1} (and at t_i)
(II)	$L_{ti+1} < SAM_{ti+1}$	juvenile at t_{i+1}	adult at t_{i+1}

with L_{ti} = measured size at time t_i, L_{ti+1} = calculated size at time t_{i+1}, SAM_{ti} = size at maturity at t_i, SAM_{ti+1} = size at maturity at t_{i+1}, Δt = time between t_i and t_{i+1} in days, g_{Li} = mean daily growth from the culture experiments at t_i.

Weekly growth rates were linearly interpolated for the second sampling date in that week. The influence of changing temperatures on juvenile growth was neglected in this approach, because in some earlier studies only minor differences were found within a temperature range of 15°C to 20°C (Vijverberg 1980; Hanazato and Yasuno 1985; Langeland et al. 1985; Hovenkamp 1991). This was similar to the situation in Bautzen reservoir during the greatest part of the investigation periods (compare Figure 3.1).

From the calculated proportions of juveniles and adults and the estimated number of newborn daphnids since the last sampling date, a hypothetical (or potential) abundance of juvenile and adult daphnids at time t_{i+1} was calculated. The absolute mortality (ind. l^{-1}) during the sampling intervals was estimated as the difference between the hypothetical and the actual abundance of juvenile and adult specimen of *D. galeata* at time t_{i+1}. Juvenile mortality also includes egg mortality. Densities of *D. galeata* observed in the field at successive sampling dates and calculated potential densities were used to compute the rate of population change r and the 'potential' rate of population change r':

$$r = (\ln N_{ti+1,obs.} - \ln N_{ti,obs.}) / \Delta t \ \ (\mathrm{d}^{-1}) \tag{7.1}$$

$$r' = (\ln N_{ti+1,calc.} - \ln N_{ti,obs.}) / \Delta t \ \ (\mathrm{d}^{-1}) \tag{7.2}$$

$N_{ti+1,obs.}$, $N_{ti,obs.}$ = observed abundance at t_{i+1} and t_i, respectively and $N_{ti+1,calc.}$ = calculated abundance at t_{i+1}. A mortality rate m (d^{-1}) of juvenile, adult and total mortality was calculated by subtracting r from r' which results in:

$$m = (\ln N_{ti+1,calc.} - \ln N_{ti+1,obs.}) / \Delta t \ \ (\mathrm{d}^{-1}) \tag{7.3}$$

For comparison, the death rate d of *D. galeata* was also calculated as the difference between birth rate b and rate of population change r according to the egg ratio method (Paloheimo 1974). Total mortality rate m and d were found to be virtually identical (Hülsmann and Weiler 2000).

In order to measure the non-consumptive mortality of *D. galeata* directly in the field, sedimentation was determined in May and June 1998/1999 using sediment traps (Gries and Güde 1999). The traps consisted of four cylindrical tubes (with a length of 1 m and a diameter of 10 cm) attached to a frame and were suspended about 1 m above the ground near the deepest part of the reservoir (corresponding to a depth of about 10 m) using the method of Horn and Horn (1990). This type of trap is assumed to have an efficiency of 100% in deep standing waters (Bloesch and Burns 1980; Gardner 1980). Sampling design differed in several aspects in 1998 and 1999. Exposure time and sampling frequency was one week in 1998 but was each shortened to three to four days in 1999. To avoid a possible overestimation of sedimentation due to vertical migration of zooplankton, traps were recovered at night in 1998. The overlying water was gently removed and the settled material was preserved in 3% sucrose-formalin solution (Haney and Hall 1973). In 1999 the traps were recovered during the day. The overlying water was not completely removed, but the trap content was suspended and brought to the laboratory, where it was allowed to settle for about three hours. When live animals were found in the sample, they were now gently removed by siphon and the remaining material was preserved. In order to get a rough idea of horizontal differences in sedimentation and to avoid missing values due to lost traps, a second sediment trap was exposed in the pelagic zone in 1999, about 100 m closer to the shore but at a similar depth. Before counting all samples were filtered through 100 µm gauze and the filtrate was discarded. Only whole organisms or fragments with eye-spots were counted. Exuviae were disregarded and could easily be distinguished from dead organisms due to their transparency. If available, at least 100 individuals were counted and measured from the anterior margin of the head to the base of the spine. The size-frequency distributions of daphnids obtained from pelagic samples and from trap samples were compared introducing a time shift of 3-4 days (pooled samples from both traps were used in 1999).

Recruitment of neonates (Chapter 4) and age-specific mortality patterns from life table experiments (Chapter 5) were used to model *Daphnia* dynamics under the following assumptions:

- Non-consumptive mortality in the field is represented by life table experiments irrespective of differences in physical conditions (temperature, wave action etc.).
- Conditions at the beginning of the clear-water stage were comparable in 1998 and 1999. Accordingly, results of the first life table experiment in 1999 were also applied to daphnids born shortly before this period in 1998.
- Daphnids that were already present when investigations started in early May (age unknown) show the same age-specific mortality patterns as those born shortly before the clear-water stage.
- Daphnids born after the clear-water stage all have the same age-specific mortality, such that l_x values from the last life table experiment of each year were applied to all neonates born after the start of this experiment.
- Daphnids born during an interval of approximately one week are considered to face very similar bottom-up conditions and thus, the same set of l_x values was applied to them.

Recruitment of neonates was calculated on a daily basis according to Formulas 4.2–4.7 by replacing Δt by 1, 2, … Δt. Age-specific survival of neonates was calculated by applying l_x values from Chapter 5 to these newborns. Generally, the time interval for which the same set of l_x values was applied, was one week. If life table experiments were not performed in this temporal resolution, l_x values were linearly interpolated from two successive experiments. Detailed information about which l_x values have been used for which animals is provided in Table 7.1.

Table 7.1. Data basis for computing age-specific survival of neonates born during certain time intervals in 1998 and 1999. Interpolated l_x values were derived from two successive life table experiments.

period	data basis of l_x values
29 April-10 May 1998	experiment from 11 May 1999
11 May-17 May 1998	experiment from 11 May 1998
18 May-24 May 1998	interpolated from experiments from 11 May 1998 and 25 May 1998
25 May-31 May 1998	experiment from 25 May 1998
1 June-7 June 1998	interpolated from experiments from 25 May 1998 and 8 June 1998
8 June-20 July 1998	experiment from 8 June 1998
6 May-16 May 1999	experiment from 11 May 1999
17 May-26 May 1999	interpolated from experiments from 11 May 1999 and 27 May 1999
27 May-6 June 1999	experiment from 27 May 1999
7 June-9 June 1999	experiment from 7 June 1999
10 June-16 June 1999	experiment from 10 June 1999
17 June-20 June 1999	interpolated from experiments from 10 June1999 and 21 June 1999
21 June-27 June 1999	experiment from 21 June 1999
28 June-4 July 1999	interpolated from experiments from 21 June1999 and 5 July 1999
5 July-29 July 1999	experiment from 5 July 1999

The calculated abundance of neonates born on successive days was added up for the whole period and compared to the actual abundance and cumulative recruitment.

7.3 Results

Mortality patterns clearly differed from year to year (Figure 7.1). With few exceptions adult mortality rates were always higher than juvenile mortality rates in 1997. The latter were consistently low and often had negative values. By contrast, adult mortality strongly increased at the time of declining *Daphnia* density in mid-June and remained high throughout summer. In 1998 juvenile, adult and total mortality rates developed mostly similar, being either equally high or low. Only at two dates during the clear-water stage a significant adult mortality was calculated despite of juvenile and total mortality being virtually non-existent. Mortality increased dramatically during the decline of the population (at the beginning of June) and remained high thereafter. Due to the very low abundance after the decline, strong fluctuations of mortality are likely to result from errors. Adult mortality rates in 1999 were mostly higher than juvenile mortality rates, but apart from that, no consistent trend was visible. The short-term drop in abundance in mid-June (end of clear-water phase) occurred when juvenile and adult mortality rates were equally high.

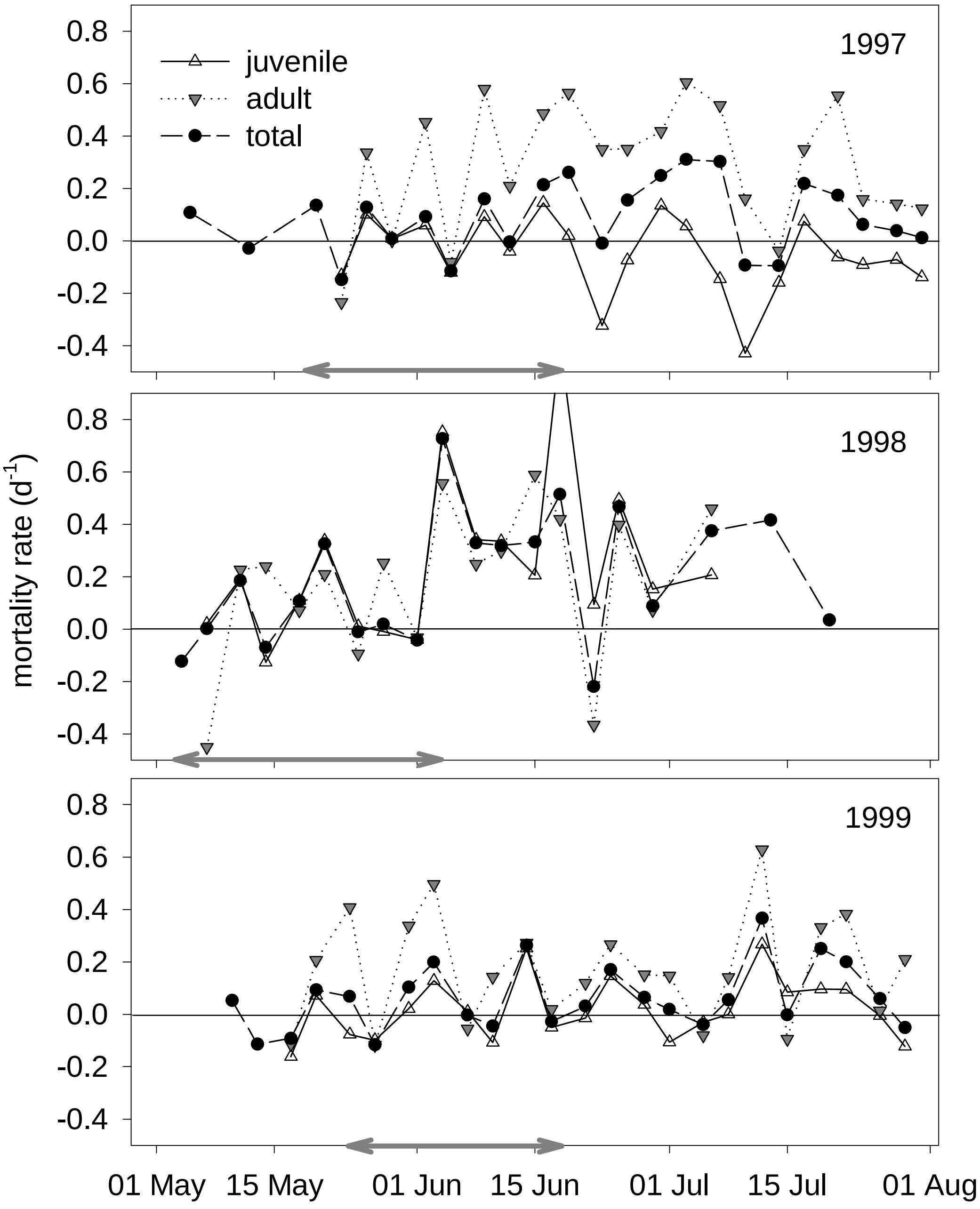

Figure 7.1. Mortality rate (d^{-1}) calculated separately for juvenile and adult daphnids, as well as considering the whole population of *D. galeata* in Bautzen Reservoir during the investigation period of 1997-1999. Due to the lack of growth data no stage-specific mortality was calculated in early May 1997. Grey arrows on the x-axis indicate the clear-water stage with a Secchi depth > 2.5 m.

Sedimentation of daphnids was generally very low, the daily losses were mostly far below 1% of the population (by number, Table 7.2). Whereas the highest sedimentation in 1998 was recorded in May shortly after the beginning of the clear-water phase, maximum values in 1999 were estimated in June at the end of the clear-water stage. With few exception, values obtained from trap 2 were always higher than those found in trap 1. The increase of *Daphnia* sedimentation in June 1999 was reflected in both traps though.

Table 7.2. Sedimentation (ind. l^{-1} d^{-1}) of *D. galeata* in Bautzen Reservoir during the investigation period in 1998 and 1999. Daily losses (% d^{-1}) were calculated considering the whole population (total losses) or only adult daphnids (adult losses). For 1999 separate sedimentation values for the two traps are provided. The losses of that year were calculated using the maximum value of both traps. n.d. = no data available.

Date	Sedimentation (ind. l^{-1} d^{-1}) Trap 1	Trap 2	Total losses (% d^{-1})	Adult losses (% d^{-1})
18 May 98	1.83		1.4	0.91
25 May 98	0.07	n.d.	0.2	0.39
8 June 98	0.01		0.08	0.09
24 May 99	0.012	0.005	0.03	0.14
27 May 99	0.013	0.089	0.2	0.7
31 May 99	0.005	0.003	0.01	0.02
3 June 99	n.d.	0.002	0.00	0.03
7 June 99	0.001	0.003	0.01	0.09
10 June 99	0.008	0.033	0.09	0.28
14 June 99	0.014	0.049	0.1	0.56
17 June 99	0.010	0.060	0.29	0.8
21 June 99	n.d.	0.006	0.02	0.04
24 June 99	0.001	0.023	0.07	0.23
28 June 99	n.d.	0.008	0.03	0.11

Size-frequency distributions of field- and trap samples did not strongly differ in 1998 (Figure 7.2). On May 18 and June 8 small size classes were present in higher proportions in trap samples than in the zooplankton samples, whereas samples of 25 May showed the opposite. No trap sample was available on 1 June, the date immediately before the decline. Similar to the situation in 1998, pelagic samples were always dominated by small size classes in 1999 (Figure 7.3). In contrast to 1998, however, a clear pattern of size distributions in sediment samples emerged in 1999. At the beginning of the clear-water phase, the dominance of large individuals in the traps changed to unspecific distribution. From the beginning of June until the end of the clear-water stage (17 June) again almost exclusively large size classes were found in the traps. Thereafter, the size distribution was more or less homogenous.

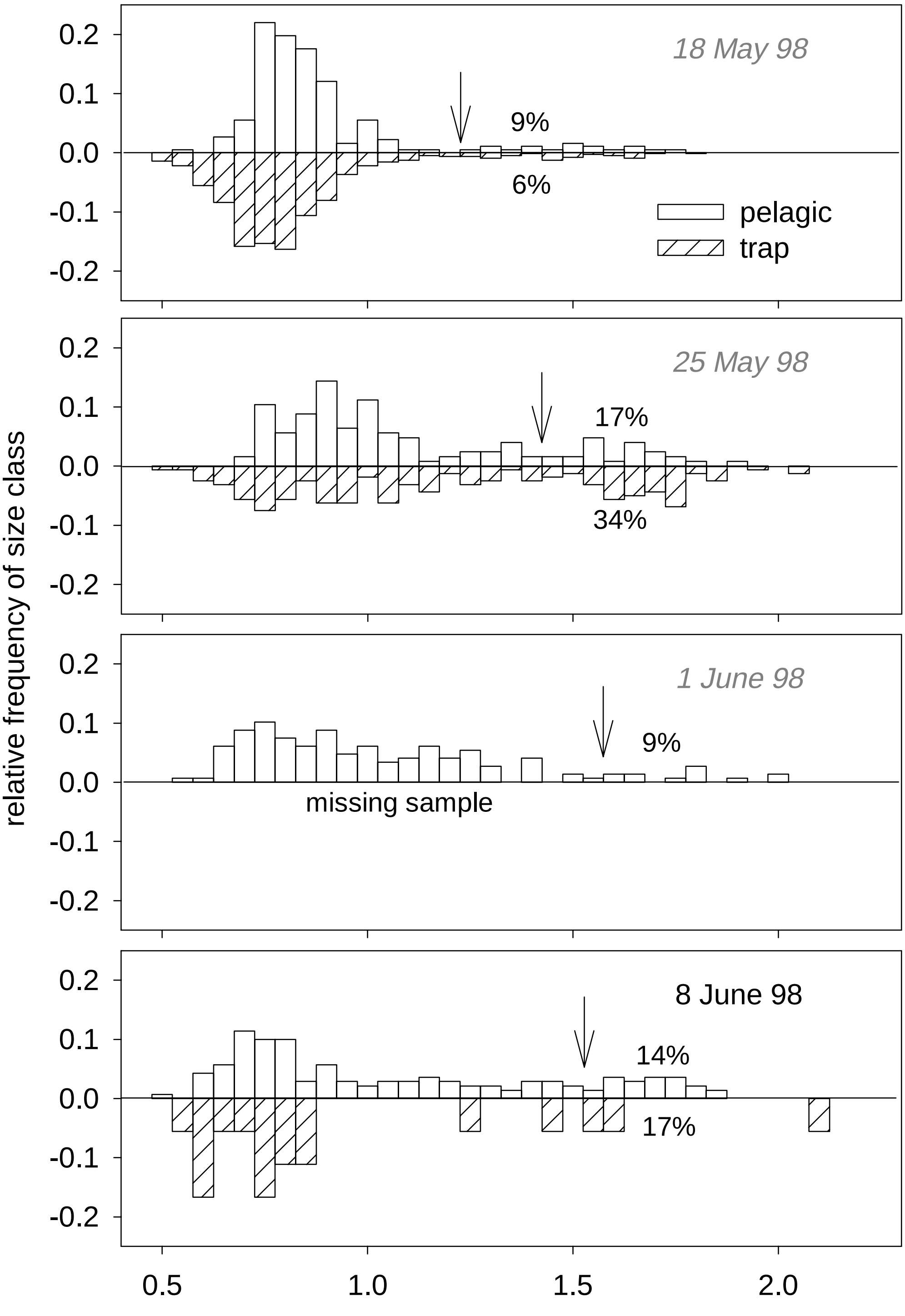

Figure.7.2. Size frequency distribution of *D. galeata* in pelagic samples and in sediment traps in Bautzen Reservoir in 1998. The date refers to the time of trap recovery. Pelagic samples were taken three to four days earlier. Size at maturity is indicated by vertical arrows, numbers give the proportion of adults in the pelagic and in trap samples. Dates representing the clear-water stage are displayed in grey and italics.

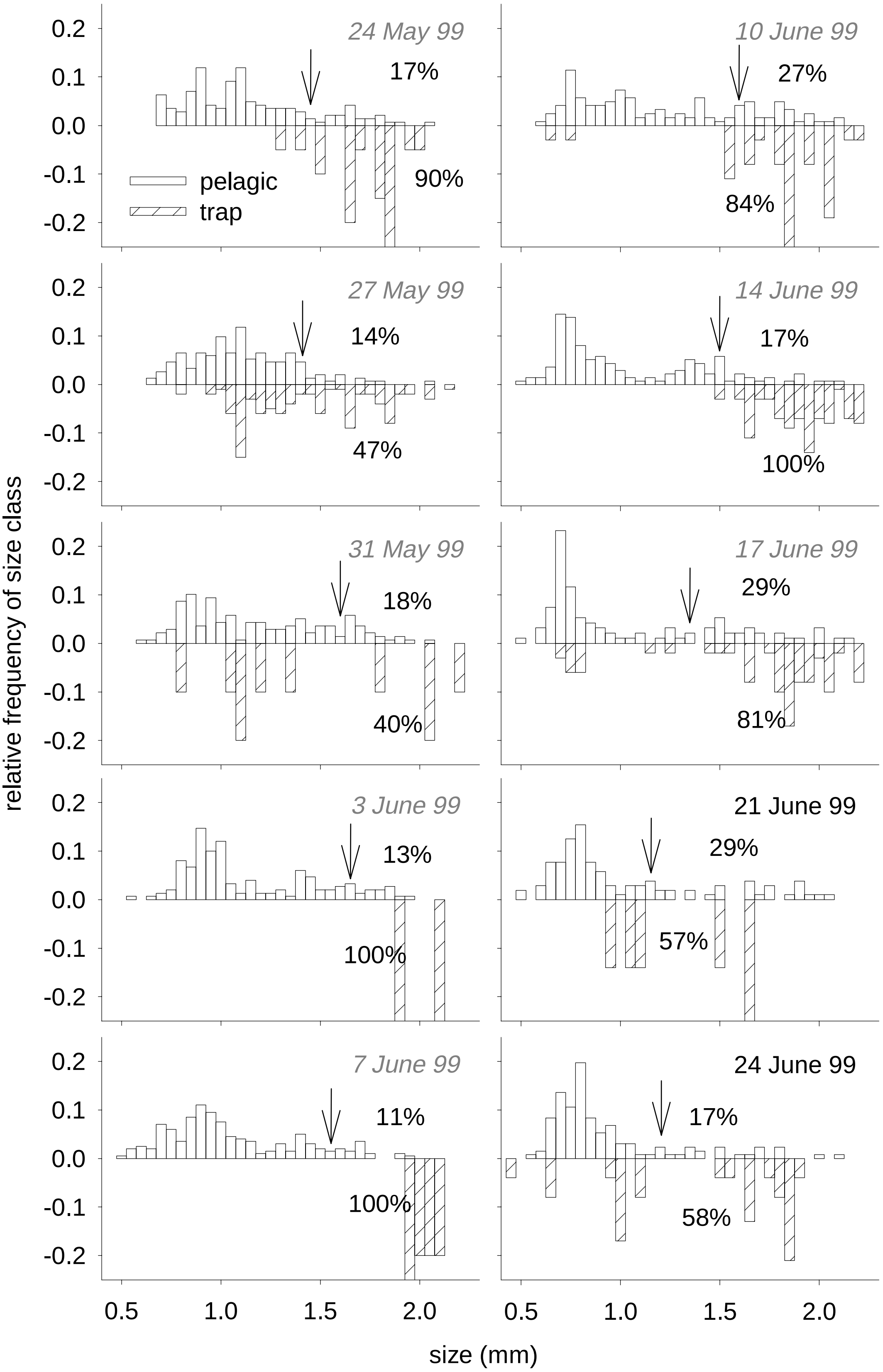

Figure.7.3. Size frequency distribution of *D. galeata* in pelagic samples and in sediment traps in Bautzen Reservoir in 1999. Symbols and explanations as in Fig. 7.2.

When age-specific mortality patterns as determined in life table experiments were incorporated into recruitment estimates, the development of computed *Daphnia* densities more or less resembles the actual population dynamics (Figure 7.4). The computed peak abundance of *D. galeata* was found to be higher and to occur a bit later than the actual densities in 1998. After a plateau-phase of about 1 week, computed densities decline in two distinct steps from 160 ind. l^{-1} to 88 ind. l^{-1} at the end of May and then, after a slight increase, gradually decrease during the rest of the investigation period. Neglecting the first short-term decrease of actual *Daphnia* densities in Bautzen Reservoir in May 1998 (which was only represented by one sampling date), the actual decline also took place in two distinct steps. However, each of the steps was steeper than the model values. During the decline phase in early June, which marked the beginning of the midsummer decline, the population decreased by 88% in four days. The corresponding decline of model values, which occurred a few days earlier, is characterised by a population loss of 33% in four days. In any case mortality is extremely high at this time because according to recruitment estimates the population should increase.

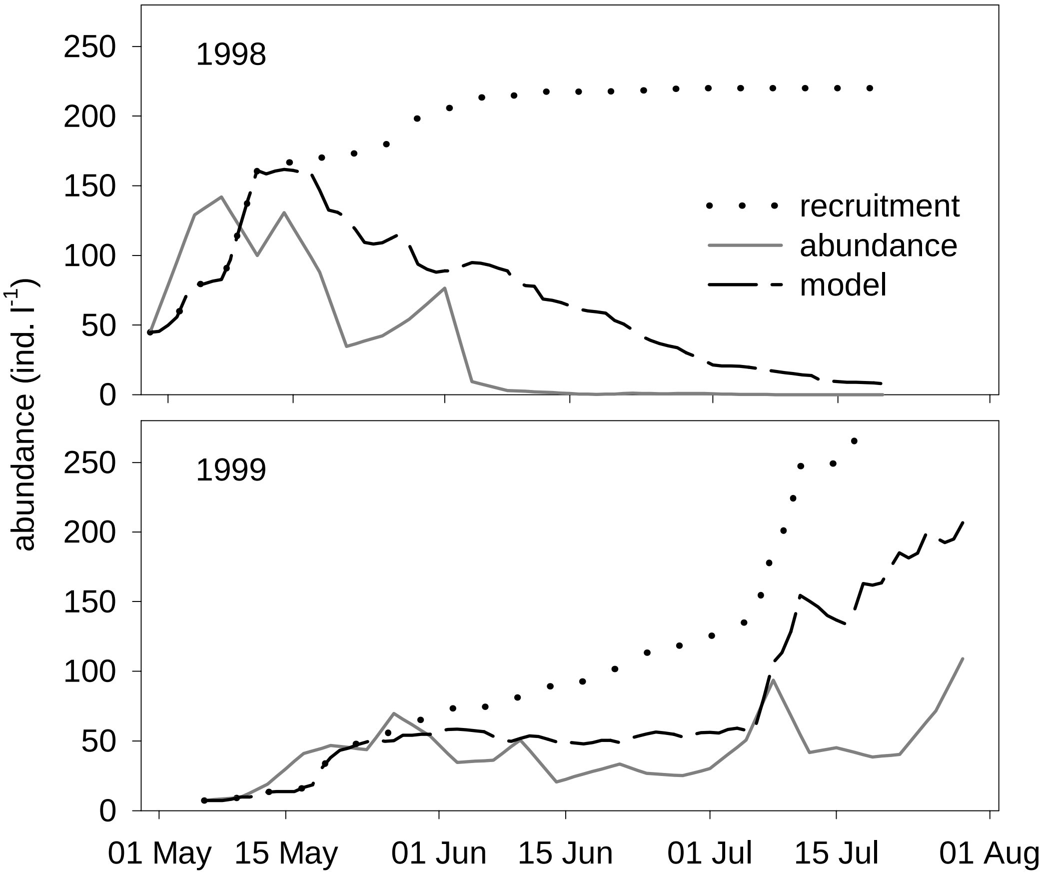

Figure 7.4. Model values, cumulative recruitment and actual abundance of *D. galeata* in Bautzen Reservoir during the investigation period of 1998 and 1999. Model values were calculated from daily recruitment and age-specific mortality patterns. Cumulative recruitment describes population dynamics under the assumption of no mortality. See text for further explanations.

As in 1998, computed densities of *D. galeata* in 1999 increase with a time lag compared to actual densities, but apart from that, the situation was completely different in the latter year. Computed densities increase slowly and level off and stabilise at about 50 ind. l^{-1} without showing a peak abundance. For July 1999 a strong increase of *Daphnia* abundance was calculated. The actual abundance of *D. galeata* also increased slowly in May 1999 but reached a peak abundance (69 ind. l^{-1}) at the end this month. After some fluctuations *Daphnia* density stabilised at about 30 ind. l^{-1} in June and only slightly increased in July.

7.4 Discussion

Mortality patterns of *D. galeata* in different years suggest considerable differences both of bottom-up and top-down factors. However, in all years investigated there was evidence for high adult mortality at the end of the clear-water stage, in some years contributing to a midsummer decline of *Daphnia*.

Mortality patterns in the field were estimated from the abundance of eggs, juvenile and adult daphnids and of course incorporate all sources of mortality and all sources of errors. Thus, they cannot be directly compared to life table data and sedimentation. On condition that juvenile fish are the main predators in May and June and that they forage on juvenile daphnids during the clear-water stage due to gape-limitation (Mehner et al. 1998 c; Wagner et al. 1999) and further assuming that their density was higher in 1997 and 1998 than in 1999, it is possible to interpret the observed mortality pattern. During the clear-water phase adult mortality was mainly non-consumptive and can be attributed to a combination of age-specific and starvation-induced mortality (see below). Juvenile mortality was mainly caused by juvenile fish and differed from year to year according to varying predation pressure.

Some of the differences between mortality patterns in different years may be explained by specific conditions in single years, e.g. even higher biomass of juvenile fish (foraging on juvenile daphnids) during the clear-water stage in 1998 compared to 1997 and presumably also 1999 and differences in *Daphnia* population structure (absolute and relative density of juveniles). With regard to the latter point, uncertainties in determining SAM (Stibor and Lampert 1993) and the significance of pre-reproductive mortality (but not of smallest juvenile instars) found in life table experiments are important. To a certain degree, adult mortality estimated from field samples may thus actually be mortality of late juvenile instars (Hülsmann and Weiler 2000). However, despite these differences and uncertainties in mortality patterns as determined from field samples, the fact remains that adult mortality contributed substantially to total mortality during *Daphnia* declines at the end of the clear-water stage, irrespective of the magnitude of the decline in different years. Thus, the results presented in this study confirm the aging-hypothesis proposed by Benndorf et al. (2001).

According to life table experiments, the following (non-consumptive) mortality pattern should be expected: After the onset of food limitation adult mortality should be high, then decline and increase again towards the end of the clear-water stage. At that time “old“ adults that survived throughout the clear-water phase and “young“ adults that were born during this period and are just about to become mature die simultaneously. Juvenile mortality should first be low or moderate and then eventually increase during the clear-water phase, due to mortality of animals that were about to become adult. These predicted patterns, however, did not show up clearly in sediment samples. The first sample in 1998 (18 May) was taken too late to represent the beginning of the clear-water phase (4 May). Mainly juveniles were found. Later, as predicted, adults were slightly over-represented in trap samples compared to the pelagic. However, right at the end of the clear-water phase a sample got lost. Contrary to 1998, in 1999 mostly - and towards the end of the clear-water phase exclusively - adult daphnids were found in sediment samples. So in this year, juvenile mortality of medium-sized daphnids which was found in life table experiments was not reflected in the field samples. Since size-frequency distributions from trap samples definitely indicate adult size-classes, this discrepancy may not be explained by an uncertain determination of SAM. It is also unlikely that juvenile size classes were overlooked in trap samples because they were also found at some dates in 1999.

Only speculations are possible concerning the influences of predation on sedimentation (an eaten daphnid can no longer settle). Juvenile fish prefer small or medium sized daphnids as long as they are gape-limited which should be the case during the clear-water phase (Mehner et al. 1998 c; Wagner et al. 1999). The same kind of size-selection can be expected for invertebrate predators such as *L. kindtii*. However, *Leptodora* only reached higher densities after the clear-water phase (Figure 3.6) and concerning juvenile fish, no data are available for 1999. However, as can be concluded from the development of the *Daphnia* population, it is very likely that fish density was lower in 1999 than in 1998. During the period 1995-1998 this was the year with highest juvenile fish biomass (Figure 3.5). Size-distribution of settled daphnids was rather homogenous during the clear-water phase in 1998 but it remains unclear whether this was due to or despite size-selective feeding. In addition to these qualitative aspects, a major problem in comparing mortality patterns and sedimentation is a quantitative one: Whereas life table experiments suggest a strong impact of non-consumptive mortality, sedimentation was insignificant for *Daphnia* dynamics. Estimated daily losses were always $< 1\%$ of the population and even when related to mortality, sedimentation remained negligible.

The inconsistency of results obtained by life table experiments and by sediment traps poses the question: How reliable are these methods? For measures of sedimentation the type of trap used was recommended by Bloesch and Burns (1980). In their review, they assumed sampling efficiency to be near 100% and concluded that an exposure time of one week is sufficiently short. However, this was concluded from chemical parameters only. Sedimentation in this investigation was even lower in 1999 than in 1998. Possibly, this resulted from shortening the exposure time from one week in 1998 to three to four days in 1999 (similar to Gries and Güde 1999). If non-consumptive mortality was significant for the drastic decline in 1998 (after 1 June), a high sedimentation should have been estimated for the period 1 June-8 June. However, this was not the case. Since the main decline occurred until 4 June, the exposure time (1 week) might have been too long, such that post-mortal decay was so fast that these corps could no longer be distinguished from exuviae. Krause (1961) gave evidence that the main losses during the decay process occur immediately after the death of zooplankton organisms. Predation of course may not only influence the size distribution of settled daphnids (see above) but also sedimentation estimates. Settling daphnids in a weak condition should be easy to prey on. This might be of importance because traps were used by water mites as spawning site and refuge (personal observation). Since water mites suck out their prey, these *Daphnia* corps may also be indistinguishable from exuviae.

Additionally, considerable differences in sedimentation between two traps exposed at different locations but similar depth in 1999 suggest that quantitative results are doubtful and strongly depend on trap position. Kozerski (1994) emphasised the importance of currents, diffusion and bottom shear stress on sedimentation and suggested to use the term “trapping“ instead of “sedimentation“ when talking about trap collections. The higher importance of these mechanisms in shallow compared to deep lakes led to the development of new trap designs for shallow lakes (Kozerski and Leuschner 1999). Bautzen Reservoir, although not particularly shallow, with regard to currents and turbulence may resemble shallow waters due to high wind exposure, which prevents stable stratification (compare Benndorf and Henning 1989; Köhler 1992). In contrast to Kozerski (1994), however, who suggested particles to be “overtrapped“ with usual trap designs in shallow lakes, I suppose sedimentation to be too low in this study.

Probably, the depth of the trap in relation to turbulence and currents in different strata is an important factor for trap efficiency. Additionally, the position on a longitudinal axis of Langmuir circulations, which are common in this wind-exposed water, may be important. The traps were positioned in the north-eastern region of the reservoir. Prevailing wind direction is west-southwest. Consequently, zooplankton organisms which tend to stay away from the surface may be concentrated at the up-wind side of the reservoir which is west (George and Edwards 1976; George and Winfield 2000). This can in particular be expected for daphnids in a weak condition. Summarising, the attempt to quantify *Daphnia* sedimentation in Bautzen Reservoir seems to have failed. Proper investigations of sedimentation in this water probably would require a much higher number of samples and a combination of methods. Still, concerning qualitative aspects, size-frequency distributions indicate that non-consumptive mortality of *D. galeata* is mainly directed to adult size classes, at least towards the end of the clear-water phase.

The model approach to determine effects of non-consumptive mortality on population dynamics did not discriminate between juvenile and adult daphnids. It is possible, however, to understand the patterns of mortality by having a closer look at the data. The "two-step-pattern" of the decline of computed density in 1998 can be attributed to adult mortality. The first step of the decline is mainly due to the die-off of those daphnids, that were already present at the beginning of May and those born until 4 May. The second phase of the decline mainly results from mortality of high numbers of animals born between 7 May and 11 May 1998.

As explained above, these daphnids should form the cohort of adults, which dominates the population during the clear-water stage. Since no life table experiment was started at the date of their birth, l_x values from the first experiment in 1999 were used to model their survival. These data suggest an early maturation and a drastic decrease of survival at the age of about 3 weeks. The use of these data is reasonable, but nevertheless remains speculative. However, the consistency of general trends in "real" population dynamics and model estimates renders the explanation given above very plausible. In any case, the combination of steep increases of recruitment and subsequent mortality patterns with equally steep decreases of survival probability may result in drastic declines of the population even without predation effects. By contrast, the same set of l_x values resulted in a stabilisation of computed abundance on a medium level in 1999 because recruitment increased slowly and constantly.

Model estimates imply that under specific conditions *Daphnia* density may decrease to about 50% of the peak density until the end of the clear-water phase without predation effects. Moreover, these calculations indicate that even abrupt declines may partly be attributed to non-consumptive mortality. Such drastic declines of *Daphnia* as observed in 1997 and 1998, however, may not be explained without predation. For both years detailed consumption estimates of age-0 fish and invertebrate predators are available (A. Wagner, pers. comm.). Drawing up a balance sheet of all mortality factors of *D. galeata* in Bautzen Reservoir for these years reveals that up to about 70% (in 1997) and 80% (in1998) of *Daphnia* mortality during the decline phase are due to predation by age-0 fish and invertebrates. The remaining non-predatory mortality can be explained by the model approach combining recruitment patterns with survivorship curves from life table experiments.

Results of this study also suggest that the general statement that food shortage causes the decline of *Daphnia*, whereas predation keeps density low (Sommer et al. 1986; Luecke et al.

1990; Wu and Culver 1994) is not strictly correct. As explained in Chapter 6 and predicted by Benndorf et al. (2001), timing of predation pressure and feeding selectivity in relation to non-consumptive mortality (mainly due to aging effects) is an important factor for determining the extent of the decline. Once the *Daphnia* population has declined below a critical level, it may of course easily be controlled by predation. Invertebrate predators in this situation may also contribute to the suppression of daphnids (De Stasio et al. 1995; Bollenbach 1998).

The continuous decrease of model estimates of *Daphnia* abundance in summer 1998, contrary to the situation at the end of the clear-water phase, may not be interpreted only as bottom-up effect because fecundity was high at that time (compare Figure 4.3) and a high intrinsic rate of increase was calculated for daphnids born during this period (compare Figure 5.8). Instead, extremely low recruitment can be explained by a low abundance and a low proportion of adults, which was a result of size-selective predation by fish. Low recruitment results in a population decrease even at a low non-consumptive mortality.

Without predation, the mechanisms presented here probably would result in cycling of the population in those years when a strong peak cohort develops (compare Kwik and Carter 1975; McCauley and Murdoch 1987). In the case of Bautzen Reservoir, high predation by juvenile fish can be expected in years with high temperatures in spring, favouring early spawning and high growth rates of fish (Mehner 2000). High temperature of course also promotes high birth rates in *Daphnia* (especially in early spring when food is still abundant). Thus, different scenarios of bottom-up and top-down interactions can be expected depending on the temperature regime which indeed explained about 80% of the observed patterns of *Daphnia* dynamics in a long-term study of Bautzen Reservoir (Benndorf et al. 2001).

In summary, the mortality of *D. galeata* in Bautzen Reservoir cannot be explained by non-consumptive mortality alone. Still, non-consumptive mortality, mainly directed to adult daphnids, may significantly contribute to population declines at the end of the clear-water stage. To which degree this contributes to the population decline depends on recruitment patterns before this period, whereas the extent of the decline mainly depends on timing between non-consumptive mortality and predation.

8 General discussion and conclusions

This study on population dynamics and life history characteristics of *D. galeata* in Bautzen Reservoir provides some new aspects to population dynamics and life history of cladocerans in general which are important topics in aquatic ecology. Some of these aspects, concerning both results and methods of this investigation are not particularly new, but were just not as well recognised or partly forgotten. Results of this study also draw attention to some unsolved problems in cladoceran population dynamics with major implications to evolutionary ecology on the one hand and to practical aspects of food web management on the other hand.

Daphnia population dynamics and life history

Concerning bottom-up effects on *Daphnia* populations, results of this study support previous findings that food limitation of zooplankton may be significant also in highly eutrophic waters (e.g. Boersma and Vijverberg 1994 a). Low food availability (involving both quantity and quality) during the clear-water stage leads to reduced fecundity and hence, recruitment of the population. Juvenile growth is reduced, age at maturity is delayed and longevity of daphnids is strongly shortened during this period. The strength of the latter effect depends on the timing of food shortage and life history of animals born at different times of the spring succession. Up to this point, the situation of food limitation during the clear-water stage does not differ between years with or without a midsummer decline. However, this does not mean that bottom-up conditions have low importance for the initiation of a midsummer decline. Instead, timing aspects between *Daphnia* population dynamics and bottom-up conditions, mediated by temperature and stratification (see below) determine the significance of food conditions for the occurrence of a midsummer decline.

In Table 8.1 some main characteristics of the *Daphnia* population are compared for years with and without a midsummer decline. The only clear difference between both types of population development (until the end of the clear-water stage) is the recruitment pattern during the build-up of the population. A strong increase of recruitment (in years with midsummer decline) always started from relatively high *Daphnia* densities (> 30 ind. l^{-1}, compare Figure 4.7). This density was reached already at the beginning of May in both years with a drastic decline of *D. galeata* in summer (1997, 1998). In 1996 this density was reached in the middle of May. Benndorf et al. (2001) predicted that the temperature in winter and early spring (cumulative day degrees from 1 January to 30 April, TWSP) was responsible for an early and strong increase of *Daphnia* abundance and subsequent aging effects at the end of the clear-water stage. The authors found a threshold temperature distinguishing between years with and without a midsummer decline. In 1996 this threshold (440 day degrees) was not reached and Benndorf et al. (2001) concluded that aging effects had low influence in this year. However, the temperature threshold is exceeded when day degrees are summed until the middle of May when *Daphnia* reached a density of about 30 ind. l^{-1} and subsequently increased strongly. Thus, the concept of a temperature threshold seems to be valid, but it may be delayed into May in some years. The first spring-peak of *D. galeata* in May 1996 was missed by the fortnightly sampling interval of Benndorf et al. (2001) and consequently, aging effects were not recognised in that study.

Table 8.1. Summary of population dynamics and development of life history parameters of *D. galeata* during the investigation period in years with and without a midsummer decline in Bautzen Reservoir.

	With midsummer decline (1996, 1997, 1998)	Without midsummer decline (1995, 1999)
Start-abundance in May	high (> 30 ind. l^{-1}) in 1997, 1998, low in 1996	low (< 10 ind. l^{-1})
Recruitment	quick increase, then low	slowly and continuously
SAM during clear-water stage	high	high (1999) or medium-high (1995)
Food limitation during clear-water stage	yes	yes
SAM in summer	low (1996) or extremely low (1997, 1998)	medium-high (1995) or medium (1999)
Fecundity in summer	medium (1996) or high (1997, 1998)	low (1995) or medium (1999)

Benndorf et al. (2001) suggested that high TWSP favours the occurrence of a midsummer decline via aging effects due to the development of a strong peak cohort of daphnids. This proposed mechanism indeed could be confirmed by this study. However, one may ask why the population does not increase that strong in every year once a density of about 30 ind. l^{-1} is reached. In this situation direct temperature effects can be considered to be small. As pointed out above, timing aspects between the *Daphnia* development and the phytoplankton succession are important and these may depend on temperature and stratification stability. As shown in Chapter 3 and summarised in Table 8.2, *Daphnia* reached its maximum densities already before or exactly at that date when the Secchi depth exceeded 2.5 m for the first time in years with a midsummer decline. By contrast, in years without a decline, the onset of the clear-water phase occurred at medium *Daphnia* densities during the build-up of the population. This means that in years without a midsummer decline even relatively low *Daphnia* densities were able to exert such a strong grazing pressure on phytoplankton that water transparency increased strongly and low food availability limited further growth of the population. In years with a midsummer decline this negative feed-back of food limitation on population growth came a bit “too late“, obviously because even higher *Daphnia* densities were not able to reduce their food resources as quickly as observed in years without a midsummer decline.

Table 8.2. Physical conditions and timing of bottom-up and top-down factors in relation to *Daphnia* dynamics. TWSP and TESU = cumulative water temperature during winter and early spring and during early summer, respectively, according to Benndorf et al. (2001). See text for further explanations. * marks the peak abundance of *D. galeata* in spring.

	With midsummer decline			Without midsummer decline	
	1996	1997	1998	1995	1999
TWSP	cold	warm	warm	warm	warm
TESU	cold	warm	warm	cold	warm
Stratification stability	medium	low	very low	high	high
Onset of clear-water stage	23 May	20 May	4 May	22 May	24 May
Daphnia abundance at that date (and 3 days before) (ind. l^{-1})	61 (81*)	56 (130*)	129* (45)	30 (16)	44 (46)
Duration of clear-water stage	35 d	30 d	31 d	38 d	24 d
Max. biomass of age-0 fish (mg m^{-3})	161	478	545	128	probably low
Fish biomass at moment of *Daphnia* decline (mg m^{-3})	< 50	> 200	> 200		
Max. abundance of *L. kindtii* (ind. l^{-1})	2.6	4.1	0.8	0.8	1.9
Leptodora density at moment of *Daphnia* decline (ind. l^{-1})	1.1	0.6	0.8		

A detailed analysis of interactions between particle concentrations and phytoplankton composition on the one hand and *Daphnia* filtering rates, appendage beat rates and filter morphology during the spring succession in Bautzen Reservoir is performed at present (Voigt in prep.) and may provide new insights into this particular problem. Abiotic factors may, however, also have a direct effect. Years without a midsummer decline were characterised by a high stratification stability of the water body which developed at that time when water transparency increased. This may have led to increased sedimentation of algae, reinforcing grazing effects and leading to an earlier onset of food limitation of *Daphnia*. By contrast, in years with a midsummer decline the water body was still well mixed at the time when the *Daphnia* population increased strongly (Figure 3.2).

Additional grazing pressure of other zooplankton species, e.g. *Asplanchna priodonta* (Köthe 1995), might influence food conditions for *D. galeata* in Bautzen Reservoir. Indeed, population biomass of this rotifers species was high in early May 1995, a year without a midsummer decline of *Daphnia* (Hülsmann et al. 1997). However, this species reached similarly high or even higher densities in spring 1997 and 1998 (Bollenbach 1998), whereas in 1999 lower values were recorded (Hülsmann unpubl. data). In any case, the strong and quick increase of *Daphnia* abundance in years with a midsummer decline seems to represent a kind of “overshoot“, which is beyond the carrying capacity of the system. Peak densities > 100 ind. l^{-1} could always be maintained for a few days only. High mortality, in particular of old daphnids, adapted to high food conditions and unable to withstand low food availability most probably is the reason for this shuttle back to lower densities immediately after the increase. This interpretation is corroborated by the model approach (Figure 7.4). Although it could not be shown in this study (because no life table experiment was performed in that particular situation), results presented here strongly suggest that animals which mature at the beginning of the clear-water stage make the peak cohort, dominate the population during this period and die off after about four weeks. How much this effects the population depends on the strength of this cohort. If recruitment increased strongly before the clear-water phase, mortality at the end of this period will also be high (e.g. population loss of 33% in four days in 1998 in the model approach). It seems that the importance of this demographic effect on *Daphnia* population dynamics has been largely overlooked during the last decades.

There are two other examples that TWSP as defined by Benndorf et al. (2001) is not always sufficient to explain *Daphnia* dynamics. TWSP was high in 1995 and 1999 and accordingly, a midsummer decline due to aging effects should be expected. By contrast, the temperature in early summer (Mai-June, TESU) of 1995 was low and therefore, predation by age-0 fish should be low, which indeed was shown by Mehner et al. (1997). Combining TWSP and TESU, a short midsummer decline was predicted for 1995. Indeed, Benndorf et al. (2001) stated that a short midsummer decline had occurred. However, this classification was due to only one out of three sampling dates in August 1995 when the *Daphnia* biomass was below 1 mg ww l^{-1}. Aging effects due to TWSP are impossible at that time and they did not occur in spring either, despite of high TWSP. This parameter had no influence in that year because there was virtually no winter population of *D. galeata* due to the extreme midsummer decline in 1994 which lasted until late fall (Ritter 1997). In this study 1995 is considered as “without midsummer decline“ and the discrepancy to the classification of Benndorf et al. (2001) is due to different data sets and different definitions of a midsummer decline (compare Chapter 3). But even when it is accepted that 1995 had a midsummer decline, the parameters TWSP and TESU offer no explanation for the phenomenon.

This also holds true for the population development of *D. galeata* in 1999. According to predictions posed by Benndorf et al. (2001) a long midsummer decline should be expected whereas no midsummer decline was observed. It can be suggest that even more than cumulative temperatures or monthly means the dynamics of the temperature development are important for both the effects on *Daphnia* and on fish. This is because the responses to temperature increases are non-linear. Temperature dynamics also determine stratification stability which may have a great influence on food conditions for *Daphnia* as explained above. Concerning temperature effects on growth and survival of age-0 fish, it can be suggested that fast growth is important in particular right after hatching (Mooij 1996). From catches of age-0 percids in Bautzen Reservoir in different years it appears that hatching always takes place until the beginning of May (Mehner et al. 1998 b; A. Wagner pers. comm.). In this sense, 1999 was not as warm as 1997 and 1998 because surface temperatures remained below 15°C until the end of May, whereas in both other years this value was exceeded already in the middle of May.

Results of this study indicate that the duration of the clear-water stage may be related to mean life-span of a peak cohort of *Daphnia* in most cases. Thus, I suggest that seston concentration increases due to decreased grazing at the end of this period. By contrast, Voigt and Benndorf (2000) suggested that density of adult daphnids may decline because they are not able to cope with increasing particle concentrations after the clear-water stage. Being adapted to low food conditions, their large and dense filters may actually decrease fitness due to clogging and increased furca movements. However, the proposed mechanism could not be confirmed by laboratory experiments with adult daphnids, which were offered different concentrations of lake seston (Voigt and Hülsmann in press). Moreover, this mechanism should only work with some time lag and only at significantly increased seston concentrations. Timing of planktonic events, however, indicate the opposite: $POC_{<30\mu m}$ concentrations (slightly) increased during the first sampling interval when abundance of *D. galeata* (largely due to adult mortality) decreased (Figures 3.3, 3.7). Strong increases of $POC_{<30\mu m}$ were only recorded when *Daphnia* densities were already very low. This also holds true for the inedible POC fraction (Voigt and Benndorf 2000 and Voigt unpubl. data). Probably, energy allocation during the clear-water phase is a more important determinant of *Daphnia* longevity than food conditions during the population decline. The relatively low longevity of *D. galeata* under approximately *in situ* conditions when compared to results from laboratory studies do not seem to be particularly low when compared to other *in situ* investigations (see Chapter 5).

To evaluate whether the findings of this study are unique to the situation in Bautzen Reservoir or if they represent a more general mechanism also to be found in other systems, an extensive literature search was conducted (Table 8.3). For the literature survey, only those studies were considered, where sampling frequency was at least once per week and population development was recorded from the increase in density until the midsummer decline. “Special cases“, such as declines related to a reservoir flood (Threlkeld 1986 b) were disregarded. A midsummer decline was defined as a period of at least two weeks of strongly reduced abundance (< 20% of maximum abundance) during June through August. A dominant peak-cohort was declared existent when about 50% (ore more) of the population at the moment of maximum abundance (or shortly before) were born during the preceding week. Aging effects were considered to be of importance if (1) a dominant peak cohort did exist, (2) the duration of high *Daphnia* density was up to 7 weeks and (3) low reproduction was recorded during this period. The threshold of 7 weeks was chosen as maximum life-span of *Daphnia* under low food conditions according to Vijverberg (1976).

From the literature survey (Table 8.3) the conclusion can be drawn that aging effects may have been significant in most reported cases of midsummer declines of *Daphnia*. In three studies (No. 10, 13, 27) aging effects are likely to have occurred but no clear decision is possible due to the lack of data on *Daphnia* fecundity. Only in three out of 27 reported cases (No. 4, 9, 15) did a midsummer decline occur when a peak cohort was present but aging effects were considered to be unlikely due to the long duration of periods of high *Daphnia* densities. Their duration probably exceeded mean life-span of the peak cohort. However, in each of these three cases did considerable fluctuations of *Daphnia* abundance occur before the decline. It can be suggested that these fluctuations at least partly were due to aging effects which did not coincide with additional mortality factors and therefore only resulted in short-termed and moderate decreases of *Daphnia* abundance.

This interpretation hints at the conclusion drawn before (Chapter 7) that a midsummer decline with extended periods of low *Daphnia* density only occurs when additional mortality factors besides aging effects act at the same time (see Table 8.2). This is corroborated by the fact that fecundity of *D. galeata* strongly increased during the decline phases in Bautzen Reservoir (Figure 4.3) and that this response to increasing food conditions occurred almost immediately (Figures 5.6, 5.7). Increasing fecundity during the decline phase seems to be “normal“ (compare references in Table 8.3) and points to the common phenomenon of cycling of populations (Kwik and Carter 1975; McCauley and Murdoch 1987). The results of a model approach by Scheffer et al. (2000) support the view that effects of food limitation and predation interact in causing a midsummer decline. This is in line with predictions derived from a long-term data analysis by Benndorf et al. (2001) concerning a “long midsummer decline“.

Table 8.3. Reported cases of midsummer declines of cladocera, ordered by maximum abundance. In studies No. 25-27 population biomass (dry weight) is provided. If studies included several years and/or lakes, they are given separately. Aging was considered to be possible (✔) if a peak cohort was present and high *Daphnia* densities and low reproduction were found for up to 7 weeks. Further details of chosen criteria are given in the text; n.d. means not determined.

Study No.	Species	Study size, year	Maximum density	Peak cohort	Duration of high density	Reproduction at high density	Timing of decline	Reproduction at moment of decline	Proposed reason for decline	Aging possible	Source
1	*D. catawba*	Lake Lacawac 1979/1980	3-6 ind. l^{-1}	+	4 weeks	low	June	increasing	size-selective predation (fish)	✔	Tessier (1986)
2	*D. pulicaria*	Roi Lake 1982	7 ind. l^{-1}	-	2-3 weeks	low	July	increasing	size-selective predation (fish)	-	Murtaugh (1985)
3	*D. hyalina*	Lago Maggiore 1973	10 ind. l^{-1}	+	6-7 weeks	decreasing	July	increasing	size-selective predation (invertebrates)	✔	De Bernardi (1974)
4	*D. rosea*	Sunfish Lake 1969	15 ind. l^{-1}	+	7-8 weeks	decreasing	June	low	low fecundity	-	Clark and Carter (1974)
5	*D. rosea*	Vermont Lake 1979	22 ind. l^{-1}	-	5 weeks	decreasing	July	increasing	low fecundity + competition	-	DeMott (1983)
6	*D. pulicaria*	Lake Mendota (1991)	25 ind. l^{-1}	+	6-7 weeks	decreasing	July	low	low fecundity + predation	✔	De Stasio et al. (1995)
7	*D. galeata*	Lake Esrom 1974	30 ind. l^{-1}	+	4-5 weeks	decreasing	July	increasing	low fecundity	✔	Petersen (1983)
8	*D. hyalina*	Lake Vechten 1986	31 ind. l^{-1}	-	6-7 weeks	moderate	July	decreasing	size-selective predation (invertebrates)	-	Hovenkamp (1989)
9	*D. galeata mendotae*	McCarrons Lake 1985	40 ind. l^{-1}	+	8 weeks	low	July	increasing	size-selective predation (fish)	-	Wright and Shapiro (1990)
10	*D. galeata, D. cucullata* and hybrids	Tjeukemeer 1990	80 ind. l^{-1}	+	4-5 weeks	n.d.	June	n.d.	starvation (+ fish predation)	✔?	Boersma et al. (1996)

Table 8.3 continued

Study No.	Species	Study size, year	Maximum density	Peak cohort	Duration of high density	Reproduction at high density	Timing of decline	Reproduction at moment of decline	Proposed reason for decline	Aging possible	Source
11	*D. hyalina*	Tjeukemeer 1969	80 ind. l^{-1}	+	5-6 weeks	decreasing	August	increasing	size-selective predation (fish)	✔	Vijverberg and Richter (1982)
12	*D. galeata*	Bautzen Reservoir 1996	81 ind. l^{-1}	+	6 weeks	low	June	increasing	aging +size selective predation	✔	This study
13	*D. hyalina*	Alderfen Broad 1982	100 ind. l^{-1}	+	5 weeks	n.d.	August	n.d.	unknown	✔?	Cryer et al. (1986)
14	*D. hyalina*	Ardleigh Reservoir 1982	110 ind. l^{-1}	-	14 weeks	decreasing	August	increasing	size-selective predation (fish)	-	Mason and Abdul-Hussein (1991)
15	*D. hyalina*	Alderfen Broad 1981	120 ind. l^{-1}	+	12 weeks	n.d.	July	n.d.	size-selective predation (fish)	-	Cryer et al. (1986)
16	*D. galeata mendotae*	Wintergreen Lake 1976	110 ind. l^{-1}	+	2-3 weeks	decreasing	July	n.d.	size-selective predation (fish)	✔	Threlkeld (1979)
17	*D. pulicaria*	Wintergreen Lake 1976	120 ind. l^{-1}	+	6-7 weeks	low	June	increasing	size-selective predation (fish)	✔	Threlkeld (1979)
18	*D. galeata*	Bautzen Reservoir 1997	130 ind. l^{-1}	+	5 weeks	low	June	increasing	aging +size selective predation	✔	This study
19	*D. galeata*	Bautzen Reservoir 1998	140 ind. l^{-1}	+	4-5 weeks	low	June	increasing	aging +size selective predation	✔	This study
20	*D. galeata*	Lake Mendota 1987	140 ind. l^{-1}	+	3 weeks	low	June	increasing	low fecundity (+ fish predation)	✔	Luecke et al. (1990)
21	*D. rosea*	Tsukuba Pond 1987	150 ind. l^{-1}	+	4-5 weeks	low	May	low	low fecundity	✔	Shei et al. 1988
22	*D. hyalina*	Tjeukemeer 1970	140 ind. l^{-1}	+	6-7 weeks	decreasing	August	low	size-selective predation (fish)	✔	Vijverberg and Richter (1982)

Table 8.3 continued

Study No.	Species	Study size, year	Maximum density	Peak cohort	Duration of high density	Reproduction at high density	Timing of decline	Reproduction at moment of decline	Proposed reason for decline	Aging possible	Source
23	*D. longispina*	Lake Maly Okenenok 1987	180 ind. l^{-1}	+	4 weeks	low	June	increasing	low fecundity + invertebrate predation	✔	Krylov and Arbačiauskas 1994
24	*D. hyalina*	Tjeukemeer 1971	320 ind. l^{-1}	+	6-7 weeks	high	July	high	size-selective predation (fish)	✔	Vijverberg and Richter (1982)
25	*D. pulex*	Oneida Lake 1977	220 µg l^{-1}	-	8 weeks	n.d.	July	n.d.	size-selective predation (fish)	-	Mills and Forney (1983)
26	*D. galeata mendotae*	Lake Erie 1989	380 µg l^{-1}	+	3-4 weeks	low	July	increasing	low fecundity (+ fish predation)	✔	Wu and Culver (1994)
27	*D. pulex*	Oneida Lake 1975	400 µg l^{-1}	+	4-5 weeks	n.d.	June	n.d.	size-selective predation (fish)	✔?	Mills and Forney (1983)

In five reported cases of midsummer declines provided in Table 8.3 (No. 2, 5, 8, 14, 25) a decline of *Daphnia* abundance was observed when no peak cohort was present and thus, aging effects should be of low importance. In study No. 2 *Daphnia* density was so low that the supposed suppression by fish seems very plausible. The decline of *Daphnia* abundance in the studies 5 and 8 occurred relatively slowly and simultaneously to the increase of a competing *Daphnia* species. It can be suggested that systems with alternations in dominance of closely related species with similar competitive abilities differ from systems such as Bautzen Reservoir where only one *Daphnia* species (potentially) dominates the zooplankton community during the whole season. In studies No. 14 and 25 strong evidence is provided for high predation pressure of planktivorous fish on *Daphnia*.

The finding that non-consumptive adult mortality was significant for the initiation of a midsummer decline of *D. galeata* in Bautzen Reservoir contrasts several studies, where juvenile mortality was found to be decisive for the decline of *Daphnia* populations e.g. in Lago Maggiore (De Bernardi 1974), Lake Vechten (Hovenkamp 1989) and Lake Tjeukemeer (Boersma et al. 1996). In Lago Maggiore and Lake Vechten, invertebrate predators were considered to be responsible for the enhanced mortality of juvenile daphnids. Hovenkamp (1990) indeed could show that predation by *Chaoborus* and *Leptodora* accounted for total juvenile mortality of *Daphnia* in Lake Vechten for most of the sampling season, confirming results of Dodson (1972), who estimated a proportion of > 90% of *Chaoborus* predation on the mortality of *D. rosea*. However, in these studies *Daphnia* densities were distinctly lower than in Bautzen Reservoir (see Table 8.3) and in the case of Lake Vechten, a species replacement from *D. hyalina* to *D. cucullata* took place. In Lake Tjeukemeer, *Daphnia* abundance was comparable or even higher than in Bautzen Reservoir and - another similarity – age-0 fish are the main vertebrate zooplanktivores (Boersma et al. 1996). However, contrary to results presented in this study, Boersma et al. (1996) computed the highest mortality for daphnids < 1 mm. As this could not be explained by age-0 fish consumption, they concluded that non-predatory sources of mortality, especially starvation accounted for this high juvenile mortality.

Boersma and Vijverberg (1994 a) indeed showed that *Daphnia* in Lake Tjeukemeer was food limited during most of the season, however, the significance of increasing mortality of *D. galeata* at decreasing food levels found in life table experiments (Boersma and Vijverberg 1994 b) cannot be judged for the field situation. Fecundity and birth rates of *D. galeata* and the hybrid *D. galeata* x *cucullata* in Tjeukemeer were low prior to and during the midsummer decline (Boersma 1995; Boersma and Vijverberg 1995). This pattern, and also the phytoplankton succession in spring (dominance of diatoms) and summer (dominance of blue-greens) were similar in Tjeukemeer and in Bautzen Reservoir (Boersma and Vijverberg 1995;

Böing et al. 1998). Hence, the contradictory results of Boersma et al. (1996) and this study concerning size-selective mortality are unlikely to be caused by bottom-up factors.

They might however - at least in part - be explained by different computation of *Daphnia* growth. Obviously, this is crucial for the estimates. Boersma et al. (1996) used laboratory derived data on juvenile growth, established a ratio between SAM and the maximum size of daphnids and computed growth of animals in the field using a von Bertalanffy equation. In their model, small SAM (determined in field samples) reduced somatic growth. In contrast, high growth rates of *D. galeata* were found after the decline in SAM in this study. Arbačiauskas (1998 b) also found high juvenile growth rates of *Daphnia* related to small SAM. The relation between juvenile growth and SAM seems to depend on many factors and may not be as clear as assumed by Boersma et al. (1996) for several reasons: (1) the number of juvenile instars is not fixed, but depends on food availability (Boersma and Vijverberg 1994 b), (2) juvenile growth is retarded at low food conditions (Neill 1981; Lynch 1989; Gliwicz and Lampert 1990) and (3) high SAM can result from both good or bad food conditions (McCauley et al. 1990). If it is supposed that Boersma et al. (1996) underestimated growth, mortality of small size classes would be overestimated in their study and vice versa for large size classes.

To sum up the discussion on midsummer declines of *Daphnia*, the following types of declines can be differentiated:

- Type I: aging effects and predation coincide in most cases, leading to a quick and strong decrease.
- Type II: moderate declines are possible without aging effects when they are related to an alternation of species with comparable competitive abilities.
- Type III: in some cases predation pressure is strong enough to cause a decline without initiation by aging.

Concerning type I the type of predator does not seem to be of great importance, but mostly fish were considered to be responsible. It can be supposed that in those cases described in Table 8.3 where no predation was supposed to be significant for the decline by the authors, it has either been overlooked or severe competition (as in the case of No. 5) was involved. As explained above, aging effects alone should not cause a midsummer decline, at least according to the definition used in this study.

Finally, the extent of a midsummer decline may be influenced by different factors related to predator avoidance strategies. Comparing the situation in two years with a midsummer decline in Bautzen Reservoir, 1997 and 1998, aging effects were possible and biomass of juvenile fish was similarly high. The even stronger decrease of *Daphnia* density in 1998 compared to 1997 may be explained by timing effects of feeding selectivity of fish, probably resulting in a “retarded“ decrease of SAM. Additionally, the low stratification stability in 1998 did not allow the daphnids to take refuge in hypolimnetic water layers with reduced oxygen concentrations (Wright and Shapiro 1990; Tessier and Welser 1991). Such a distribution pattern could be seen in vertically stratified zooplankton samples taken at daytime in July of 1996 and 1997 shortly after the decline of *Daphnia* abundance (J. Kranich and M. Bollenbach, Inst. of Hydrobiology, unpubl. data). In these years a hypolimnetic refuge at least partly was present (Figure 3.2) and in particular adult daphnids were found in deep water layers. This may be an additional factor leading to a stabilisation of the *Daphnia* population at a low level in 1996 and 1997 in contrast to the almost complete elimination of *D. galeata* in summer 1998.

Unsolved problems and new questions

All methods, calculations and considerations concerning population dynamics of *Daphnia* presented in this study (and numerous others) strongly rely on the assumption that reproduction mainly takes place via parthenogenetic eggs. It can be expected though that hatching from resting eggs contributes to the population development in spring to a certain extent (e.g. De Stasio 1990). In Bautzen Reservoir the density of the overwintering population of *D. galeata* is fairly high, which can be regarded as an effect of biomanipulation (Benndorf 1997). Results from a long-term data analysis (Benndorf et al. 2001) and recruitment calculations presented in this study (Figure 4.7) suggest that hatching from ephippia (with the exception of 1995, see Figure 8.1) is not “needed“ to explain spring densities of *D. galeata* in Bautzen Reservoir. However, comparing the timing of cumulative recruitment and *Daphnia* abundance reveals that the spring increase in *Daphnia* density can be fully explained by parthenogenetic reproduction only in 1997 during the study period 1995-1999 (Figure 8.1). In all other years the population increase should have occurred up to one week later according to parthenogenetic reproduction. Consequently, negative mortality was calculated in particular during these short periods. *In situ* observations on emergence of daphnids from resting eggs indicate that the hatching period is restricted to 3-4 weeks in spring (Wolf and Carvalho1989; Cáceres 1998, but see De Stasio 1990 for other cladoerans). Although ephippia accumulate in the deepest part of a lake (Herzig 1985; Carvalho and Wolf 1989; Cáceres 1998), this is not necessarily the place where most daphnids emerge. Since light (and daylength) seems to be the most important stimulus to induce hatching (Stross and Hill 1968; Carvalho and Wolf 1989), hatching success from ephippia can be expected to be higher in shallow regions (Moritz 1987), although their density is lower there compared to the profundal.

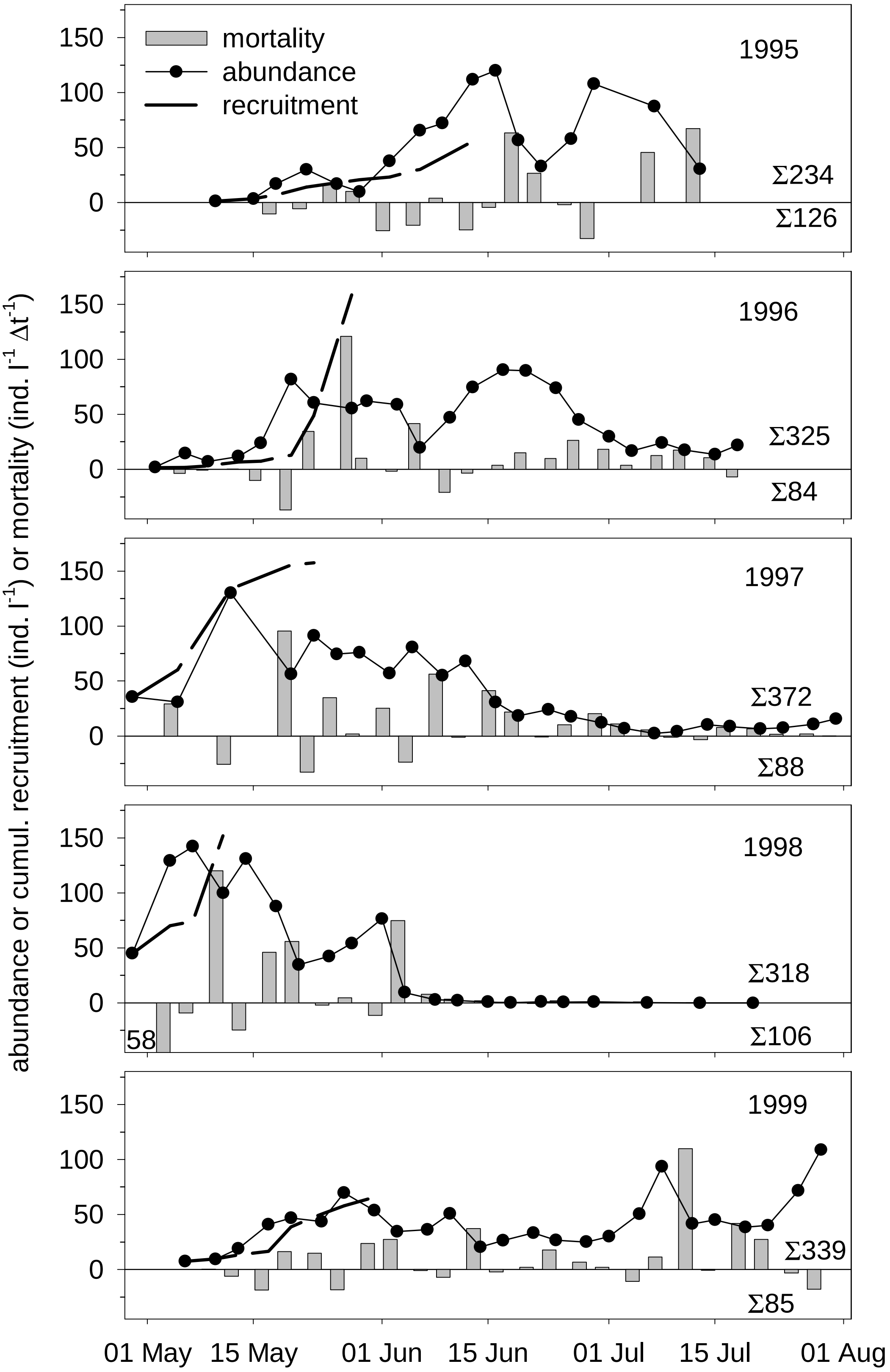

Figure 8.1. Comparison of the abundance of *D. galeata* and cumulative recruitment (ind. l^{-1}) during the early population development during the investigation period of 1995-1999. Additionally, absolute mortality (ind. l^{-1}) during each sampling interval (Δt) is shown. Numbers represent the sum of positive and negative mortality values, respectively, for the whole investigation period of each year.

Negative mortality values may indicate hatching from ephippia but may also result from accumulated errors in estimates of birth rate *b* and the rate of population change *r*. It is virtually impossible that negative mortality estimates presented in this study (Figure 8.1) are completely due to hatching from ephippia. Assuming a mean depth of the pelagic zone of 10 m, $1.26\ 10^{6}$ ind. m^{-2} should have emerged during the investigation period of e.g. 1995 to explain negative mortality estimates. Even if ephippia density in the sediment in some places might be as high as that (e.g. maximum densities in Mondsee $8.2\ 10^{5}$ m^{-2}; Herzig 1985), such a high hatching rate must be considered to be unrealistic (Wolf and Carvalho 1989; Cáceres 1998). However, there may be a mechanism which can explain a certain contribution of emergence from resting eggs to negative mortality estimates. As explained above, hatching may occur mainly in shallow regions of the reservoir which were not sampled. Exephippial daphnids grow faster and have a much higher fecundity compared to parthenogenetically derived females (Arbačiauskas and Gasiunaite 1996). Thus, even relatively low hatching rates may have an effect on population growth provided the hatchlings find favourable conditions and reproduce. However, no evidence for this mechanism was found in a study on differences in population dynamics of *D. galeata* in the littoral and the pelagic zone of Bautzen Reservoir (Hülsmann et al. 1999). The littoral sampling station was situated in a shallow bay in the western part of the reservoir in that study. It is likely though that ephippia concentrate in the eastern part of the water due to (west-) wind action. In that case, hatchlings from resting eggs in littoral areas may have been overlooked by Hülsmann et al. (1999) but no conclusion is possible at the present state of knowledge.

In case hatching from ephippia contributes significantly to the population increase in spring, this may actually increase the probability of a midsummer decline to occur. From an evolutionary point of view daphnids probably are not “used“ to high population biomasses in winter promoting an early and strong population growth in spring. If they were, they should have evolved mechanisms to prevent hatching from ephippia in situations when *Daphnia* density is already high or growing. On the other hand, emergence from resting eggs may enhance clonal diversity (Müller and Seitz 1994) which may be advantageous for the persistence of the population during the course of the season.

The timing of size-selective predation of age-0 fish on daphnids in relation to food limitation may be of particular importance for the initiation of a midsummer decline of *Daphnia*. Recruitment to adult stages is strongly (food) limited during the clear-water stage. Predation on small size classes will thus strongly reinforce effects of food limitation. For the case of Bautzen Reservoir evidence was found that juvenile perch change their size selection towards larger prey sizes (that is, adult daphnids) exactly at the end of the clear-water stage when the population declined (Mehner et al. 1998 c, Janßen 1999). In this situation non-predation mortality of adult daphnids due to aging was supposed to be high (Benndorf et al. 2001, this study) and thus, predation on adults will reinforce the indirect bottom-up effects on *Daphnia* mortality.

There is an additional mechanism which may enhance gape-limited predation effects on *Daphnia* populations. Daphnids reduce SAM in response to chemical cues released by fish (e.g. Macháček 1991; Stibor 1992). Reducing size makes them less vulnerable to predation and enhances their chance to reproduce successfully. However, if the daphnids react to kairomones produced e.g. by juvenile perch by reducing SAM (Reede 1995, 1997), they might run into a trap, because these smaller adult size classes are strongly selected by gape limited juvenile fish (Janßen 1999). This is an interesting problem from an evolutionary point of view: Timing will determine whether reduced SAM will decrease or increase the risk of mortality due to predation by age-0 fish. It is possible though that biomass of gape-limited juvenile fish usually is too low to induce life history adaptations in *Daphnia*.

No life table experiments have been performed thus far using gape-limited perch producing kairomones. Since the chemical nature of the fish cue is not known, the possibility remains that fish only start producing it during their ontogeny. Possibly, small fish have no or different effects on *Daphnia* life history compared to larger fish. If this should be true, it would shed a new light on the chemical nature of fish kairomones. Further, no experiments have been performed which explicitly consider both kairomone effects and effects of size-selection of juvenile fish and how they interact in influencing *Daphnia* life history and population dynamics.

Some of the conclusions drawn in this study concerning the effects of timing of food limitation and predation for the initiation of a midsummer decline are still speculative to a certain extent. Since many factors are involved, laboratory experiments to confirm the proposed mechanisms are difficult to perform. Therefore, the most promising strategy to further address this problem is the use of individual-based models. Such models allow to use data typically available from field studies (Mooij and DeAngelis 1999). Different scenarios of food limitation and predation may help to predict under which conditions a midsummer decline is likely to occur.

Methodical aspects

Reproductive potential and cumulative recruitment provide better insight into relevant mechanisms than clutch size and birth rate calculated the traditional way. Whereas clutch size may underestimate fecundity due to interactions with body size, birth rate is not necessarily a good predictor of recruitment. Performing laboratory experiments under approximately *in situ* conditions (but excluding predation and temperature effects) is a powerful tool for examining the importance of bottom-up factors for *Daphnia* population dynamics. It is impossible though, to weight the relative importance of food quantity, food quality and maternal effects. However, only the combination of detailed field investigations and laboratory experiments enables one to gain insight into relevant mechanisms.

Results of this study stress the importance of long-term investigations on the one hand and of short sampling intervals on the other hand. Both demands probably can only be met by concentrating on particular periods of interest, because otherwise the working expense would be immense. The long-term approach allows the detection of seasonal patterns despite interannual differences, whereas short sampling intervals are a prerequisite for the proper determination of rates, making it possible to detect the importance of timing of different processes. In this study the calculation of recruitment was of particular importance, which inevitably requires sampling intervals shorter than or equal to the egg development time. This calculation, based on the approach of Johnsen (1983), was first developed by Dorazio (1986) but has virtually never been applied in further studies, most probably because requirements (short sampling intervals and determination of egg age distribution) were considered too high. In a similar approach with even shorter sampling intervals Razlutskij (in press) estimated death rates of ovigerous females and eggs in separate size classes and showed that the precision of birth rate estimates can be improved by 3.5 to 5.5 times if these death rates are incorporated into calculations.

Calculations of recruitment also were the basis of the approach of separately calculating juvenile and adult mortality and modelling effects of non-consumptive mortality. An underestimation of recruitment (due to sampling intervals > D) will lead to wrong estimates of total mortality and juvenile mortality will be negative. Short sampling intervals also ensure that hatched daphnids will not become adult during this period and hence, their growth does not need to be considered in this approach. However, analysis of population dynamics based on the egg ratio technique in any case will only give reliable results if the sampling interval is more or less equal to the egg development time (Keen and Nassar 1981; Gabriel et al. 1987), which implies that the sampling interval has to be adjusted to prevailing temperatures in the water under study.

Another requirement to obtain reliable population dynamics estimates is the accurate determination of population densities. This point has been stressed in many studies (e.g. Lynch 1982, 1983; Taylor 1988) and was considered in this investigation by using pooled samples, both horizontally and vertically. Doing so however, makes it impossible to consider the influence of vertical differences in temperature and distribution of *Daphnia* on egg development time and growth. But as temperature gradients were low according to own measurements (see also Benndorf and Henning 1989; Köhler 1992), only marginal effects can be expected.

The method of determining juvenile growth rate and life history characteristics of *D. galeata* did not consider the influence of temperature. This might be acceptable, as in former studies only minor effects on *Daphnia* growth were found in the temperature range present during this investigation (Vijverberg 1980; Hanazato and Yasuno 1985; Hovenkamp 1991), though uncertainties remain. But since food shortage and temperature may strongly interact in influencing juvenile development of *Daphnia* (Neill 1981), no attempt to correct growth data to actual temperatures in Bautzen reservoir was made. If this approach should be applied to *Daphnia* populations exposed to a much wider temperature-range in the environment or under conditions of vertical migration (compare Loose and Dawidowicz 1994), experimental expense in *Daphnia* cultures would have to be enhanced, at best similar to the design of Stich and Lampert (1984).

Another possible source of error is the elimination of inedible particles by filtering the lake seston with a 30 µm mesh gauze in 1997. Filtration of daphnids in the field might be hindered by the inedible seston fraction resulting in energy loss and lower energy intake and consequently decreased growth compared to cultured animals. Furthermore, as the lake water was only sampled twice per week, the lake seston was aging before being offered to the daphnids. Therefore, food conditions might have been better than in the field. On the other hand, food limitation in life table experiments may have been stronger than in the field because water was only changed every other day in 1999, and with high individual filtering rates daphnids may have depleted food resources during this time interval (Wagner 1998). However, the general patterns of juvenile growth and life history characteristics were very similar in different years, despite slight modifications of the methods. More importantly, field data and laboratory experiments are consistent and when combined provide a “complete“ picture.

Conclusions concerning biomanipulation

For biomanipulation experiments it would be highly desirable to prevent midsummer declines of large cladocerans, namely daphnids. The occurrence of aging effects probably can only be influenced by management measures to a limited extent because they largely depend on timing between bottom-up factors and the population development of *Daphnia*. Since the water temperature in winter and early spring was found to be important, Benndorf et al. (2001) concluded that climate warming is a potential threat for successful biomanipulation. Consequently, measures aiming at preventing or reducing global warming also stabilise biomanipulation. But of course this is not a case for lake and reservoir management. The literature survey presented in Table 8.3 suggests that aging effects occur in waters of quite different trophic states and food web structures. It is possible, however, that moderate feeding pressure of planktivorous fish prevents *Daphnia* populations to increase in such a way that aging becomes important. Indeed, Benndorf and Kamjunke (1999) concluded that the probability of a midsummer decline to occur had increased in Bautzen Reservoir since the proportion of pisciviorous fish on the total adult fish biomass exceeded 40%. Consequently, they recommended this value to be achieved by food web manipulations, representing a fish community with an optimal (rather than minimal) biomass of zooplanktivorous fish.

It was concluded from field studies (Mills et al. 1987), enclosure experiments (McQueen and Post 1988; Hülsmann and Mehner 1997) and theoretical analysis (Scheffer et al. 2000) that daphnids decline once a critical fish density is exceeded. In this sense, it is unfavourable when the main predators are juvenile fish because their predation pressure is highly unpredictable due to different breeding success and different growth rates in successive years. The growth of age-0 fish should largely depend on temperature (Mooij et al. 1994). Thus, the temperature devlopment after hatching determines age-0 fish predation (compare Mehner 2000) and this cannot be directly influenced. Food web management therefore should aim at establishing an optimal stock of planktivorous fish keeping invertebrate predators low and eventually preventing *Daphnia* populations to increase beyond the carrying capacity of the system. Second, management measures should stimulate mechanisms which prevent cohorts of juvenile fish to become too large and promote the fast reduction of age-0 fish.

Since timing aspects were found to be of great importance, it would be advisable when those species would be favoured which spawn either earlier or later than e.g. pikeperch and perch. Therefore, pike should be well suited. In case pike successfully may spawn in the biomanipulated water, age-0 pike could effectively reduce juvenile fish of other species. This probably can be achieved by enhancing spawning conditions by proper water level management (Benndorf and Kamjunke 1999) and creating favourable (eventually artificial) habitats e.g. by introducing spruce trees (Skov and Berg 1999). This could also enhance the probability that the 1+ year-class of perch survives through the winter and may exert an early feeding pressure on the new cohort in spring (Dörner et al. 1999). Recruitment to larger size classes of perch may be essential for the stability of biomanipulation because large perch are key predators of juvenile size classes of e.g. roach and bream (Dörner et al. in prep.). It remains doubtful, however, if these measures would have a sustained effect in the case of Bautzen Reservoir where fluctuating water levels and high nutrient levels prevent macrophyte growth. By contrast, in natural waters (in particular in shallow ones) increasing macrophyte cover may promote such a shift in the piscivorous fish community from zander to pike after biomanipulation measures (Meijer et al. 1995).

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