Phys. sp. 820 f - 24,5

INTERNATIONALE VEREINIGUNG FÜR THEORETISCHE UND ANGEWANDTE LIMNOLOGIE

INTERNATIONAL ASSOCIATION OF THEORETICAL AND APPLIED LIMNOLOGY

ASSOCIATION INTERNATIONALE DE LIMNOLOGIE THEORIQUE ET APPLIQUEE

Verhandlungen · Proceedings · Travaux

Congress in Munich 1989

Volume 24 · Part 5

Edited for the Association by V. Sládeček and A. Sládečková

World List Abbreviation: *Verh. int. Ver. Limnol.*
DIN 1502 Abkürzung: *Verh. Internat. Verein. Limnol.*

Stuttgart 1991
E. Schweizerbart'sche Verlagsbuchhandlung
(Nägele u. Obermiller)

78 9

INTERNATIONALE VEREINIGUNG FÜR THEORETISCHE UND ANGEWANDTE LIMNOLOGIE

INTERNATIONAL ASSOCIATION OF THEORETICAL AND APPLIED LIMNOLOGY

ASSOCIATION INTERNATIONALE DE LIMNOLOGIE THEORIQUE ET APPLIQUEE

Verhandlungen · Proceedings · Travaux

Congress in Munich 1989

Volume 24 · Part 5

Edited for the Association by V. Sládeček and A. Sládečková

World List Abbreviation: *Verh. int. Ver. Limnol.*
DIN 1502 Abkürzung: *Verh. Internat. Verein. Limnol.*

Stuttgart 1991
E. Schweizerbart'sche Verlagsbuchhandlung
(Nägele u. Obermiller)

Contents of Part 5

XII. Ecology of Aquatic Organisms. 2. Algae and Macrophyta (continued)

VAN DER DOES, J. & KLINK, F. J.: Excessive growth of Lemnaceae and *Azolla* in ditches observed by false colour teledetection 2683

KOK, C. J. & VAN DE LAAR, B. J.: Influence of pH and buffering capacity on the decomposition of *Nymphaea alba* L. detritus in laboratory experiments: A possible explanation for the inhibition of decomposition at low alkalinity 2689

VAN DEN BRINK, F. W. B., MAENEN, M. M. J., VAN DER VELDE, G. & DE VAATE, A. B.: The (semi-) aquatic vegetation of still waters within the floodplains of the rivers Rhine and Meuse in The Netherlands: Historical changes and the role of inundation 2693

VAN VIERSSEN, W. & HOOTSMANS, M. J. M.: On the origin of macrophyte population dynamics during lake recovery after eutrophication 2700

HOOTSMANS, M. J. M. & VAN VIERSSEN, W.: Computer simulations of macrophyte population dynamics during lake recovery after eutrophication 2703

COOPS, H. & SMIT, H.: Effects of various water depths on *Scirpus maritimus* L.: Field and experimental observations 2706

CLEVERING, O. A. & v. GULIK, W. J. M.: The establishment of *Scirpus lacustris* ssp. *lacustris* and *S. maritimus* in the northern Delta area, The Netherlands 2711

GACIA, E. & BALLESTEROS, E.: Two methods to estimate leaf production in *Isoetes lacustris* L.: A critical assessment 2714

VIAROLI, P. & FUMAGALLI, I.: Regeneration of dissolved reactive silica during decomposition of recalcitrant plant tissues in temporary shallow-water environments 2717

BREEN, C. M. & STORMANNS, C.-H.: Observations on the growth and production of *Cyperus papyrus* L. in a sub-tropical swamp 2722

XII. Ecology of Aquatic Organisms. 3. Animals

MEISTERFELD, R.: Vertical distribution of *Difflugia hydrostatica* (Protozoa, Rhizopoda) 2726

OCAÑA, A. & PICAZO, J. S.: Study on nematode species encountered in the Monachil River (Granada, Spain): Response to organic pollution 2729

WARNER, B. G. & CHENGALATH, R.: *Habrotrocha angusticollis* (Bdelloidea, Rotifera): A new paleoecological indicator in Holocene peat deposits in Canada 2738

DE MANUEL, J.: Distribution of Brachionidae (Rotifera: Monogononta) in Spanish reservoirs 2741

ESPARCIA, A., ARMENGOL, J., VICENTE, E. & MIRACLE, M. R.: Vertical distribution of *Anuraeopsis* species as related to oxygen depletion in two stratified lakes 2745

WALZ, N. & ROTHBUCHER, F.: Effect of food concentration on body size, egg size, and population dynamics of *Brachionus angularis* (Rotatoria) 2750

CARMONA, M. J. & SERRA, M.: Comparative total protein and demographic patterns of mictic and amictic female rotifers 2754

ROTHHAUPT, K. O.: The influence of toxic and filamentous blue-green algae on feeding and population growth of the rotifer *Brachionus rubens* (Abstract) 2760

MATVEEVA, L. K.: Can pelagic rotifers be used as indicators of lake trophic state? 2761

BONACINA, C., BONOMI, G., DI COLA, G. & MONTI, C.: An improved model for the study of population dynamics in *Tubifex tubifex* (Oligochaeta, Tubificidae) 2764

VIJVERBERG, J. & KOELEWIJN, H. P.: Size dependent mortality and production of *Diaphanosoma brachyurum* (LIEVEN) in an eutrophic lake 2768

HERZIG, A. & AUER, B.: The feeding behaviour of *Leptodora kindti* and its impact on the zooplankton community of Neusiedler See (Austria) (Abstract) 2772

SIEBECK, O. & BÖHM, U.: UV-B effects on aquatic animals 2773

DUNCAN, A. & DOS SANTOS, L. C.: Cohort analysis in three species of *Daphnia* in the London reservoirs 2778

GERRITSEN, J. J.: The influence of phosphorus-limited grown algae on grazing of *Daphnia magna* (Abstract) 2783

GABRIEL, W. & TAYLOR, B. E.: Optimal resource allocation in cladocerans 2784

GIANI, A.: The nutritive value of different algae as food for two *Daphnia* species 2788

FUHLENDORF, D. C.: Measuring seasonal patterns of food limitation in *Daphnia* – an experimental study 2792
BERBEROVIĆ-JUNGE, R.: Starvation resistance of two coexisting *Daphnia* species under temperature conditions simulating vertical migration behaviour (Abstract) 2794
GLIWICZ, M. Z.: Food thresholds, resistance to starvation, and cladoceran body size 2795
WOLF, H. G. & WEIDER, L. J.: Do life-history parameters of *Daphnia* as determined in the laboratory correctly predict species successions in the field? 2799
TOLLRIAN, R.: Some aspects in the costs of cyclomorphosis in *Daphnia cucullata* 2802
RINGELBERG, J.: The relation between ultimate and proximate aspects of diel vertical migration in *Daphnia hyalina* 2804
LEHTOVAARA, A. & SALONEN, K.: Diel vertical migration of *Daphnia longispina* in a humic lake with steep thermal and oxygen stratification (Abstract) 2808
GORBI, G., PARIS, G. M., MORONI, F. & BACHIORRI, A.: Differences in population dynamics of *Daphnia magna* clones 2809
BACHIORRI, A., ROSSI, V., BONACINA, C. & MENOZZI, P.: Enzymatic variability of a colonizing population of *Daphnia obtusa* KURZ (Crustacea, Cladocera) in Lake Orta (Italy) 2813
ROSSI, V., ROZZI, M. C. & MENOZZI, P.: Life strategy differences among electrophoretic clones of *Heterocypris incongruens* (Crustacea, Ostracoda) 2816
CHAPMAN, M. A., GREEN, J. D. & NORTHCOTE, T. G.: The enigma of *Diaptomus connexus* (Copepoda) in Mahoney Lake: One or two populations? (Abstract) 2820
HARTMANN, H. J.: In situ predation on planktonic ciliates by copepods, measured with diffusion exclosures (Abstract) 2821
FERRARI, I., FARABEGOLI, A., PUGNETTI, A. & STELLA, E.: The occurrence of a calanoid Australasian species, *Boeckella triarticulata* (THOMSON), in fish ponds of Northern Italy 2822
MALY, E. J.: Dispersal ability and its relation to incidence and geographic distribution of Australian centropagid copepods 2828
BURNS, C. W. & XU, Z.: Utilization of cyanobacteria (blue-green algae) as food by freshwater calanoid copepods (Abstract) 2833
VILLALOBOS, L. & ZUNIGA, L.: Latitudinal gradient and morphological variability of copepods in Chile: *Boeckella gracilipes* DADAY 2834
WYNGAARD, G. A.: Evidence of food limitation in a subtropical copepod population 2839
ELGMORK, K.: Winter reproduction strategies in freshwater cyclopoids 2844
HALVORSEN, G.: The ecology of *Cyclops abyssorum tatricus* KOZMINSKI in Norway (Abstract) 2847
VAN DEN BOSCH, F. & GABRIEL, W.: The impact of cannibalism on the population dynamics of cyclopoid copepods 2848
SANTER, B.: The role of food limitation in summer diapause of cyclopoid copepods (Abstract) 2851
ADRIAN, R.: The feeding behaviour of *Cyclops kolensis* and *C. vicinus* (Crustacea, Copepoda) 2852
GROSSNICKLE, N. E.: Comparative feeding study of the opossum shrimp, *Mysis relicta*, in Trout Lake, Wisconsin, USA, Lake Pääjärvi, Finland, and Lake Jonsvatn, Norway 2864
YOUNG, L. B. & HARVEY, H. H.: The influence of lake pH and crayfish size on carapace elemental composition in *Orconectes* spp. and *Cambarus* spp. 2869
CHAISEMARTIN, C.: Respiratory rates and adenylate energy charge in healthy and parasitized muscles of crayfish (*Austropotamobius pallipes*) 2873
SCHMIDT-HALEWICZ, S. & BAUER, J.: Response of the macroinvertebrate community in NTA-, phosphate- and copper-charged freshwater ponds 2877
ALLAN, J. D., FLECKER, A. S. & KOHLER, S. L.: Diel changes in epibenthic activity and gut fullness of some mayfly nymphs 2881
ZWICK, P.: Growth and emergence of *Leuctra prima* (Plecoptera): Habitat – species interactions 2886
NEUMANN, P.: The egg development of *Brachyptera seticornis* (Insecta, Plec.) (Abstract) 2891
RUPPRECHT, R. & FRISCH, S.: The sensitivity of *Nemurella pictetii* (Insecta: Plecoptera) to acidity 2892
MALMQVIST, B.: Stonefly functional responses: Influence of substrate heterogeneity and predator interaction 2895
AURICH, M., WAGNER, R., REDER, E. & VEITH, R.: Defensive behaviour of the larva of *Apatania fimbriata* (PICTET) (Abstract) 2901
MUOTKA, T.: Life history patterns of *Rhyacophila obliterata* in northern Finland (Abstract) 2902
JACKSON, J. K. & RESH, V. H.: Use of cellulose acetate electrophoresis to examine population genetics of the caddisfly *Helicopsyche borealis* 2903
ERLANDSSON, A.: Group dynamics in the water cricket *Velia caprai* (Hemiptera) 2908
GÍSLASON, G. M. & JÓHANNSSON, V.: Effects of food and temperature on the life cycle of *Simulium vittatum* ZETT. (Diptera: Simuliidae) in the River Laxá, N-Iceland 2912

Reidelbach, J.: Studies on population dynamics of blackflies (Diptera: Simuliidae) in a grassland stream (Abstract) 2917
Smit, H., Klaren, P. & Snoek, W.: *Lipiniella arenicola* Shilova (Diptera: Chironomidae) on a sandy flat in the Rhine-Meuse estuary: Distribution, population structure, biomass and production of larvae in relation to periodical drainage 2918
Heinis, F.: The relation between oxygen regimes and distribution patterns of the larvae of Chironomidae (Abstract) 2924
Cure, V.: Structure and ecological role of phytophilous chironomids from some Danubian ecosystems in Romania 2925
Savage, H. M., Rejmánková, E., Arredondo-Jimenez, J. I., Roberts, D. R. & Rodriguez, M. H.: Preliminary limnological and botanical characterization of larval habitats for two primary malarial vectors, *Anopheles albimanus* and *An. pseudopunctipennis*, in coastal areas of Chiapas State, Mexico (Abstract) 2930
Wolf, B. A. M.: Some aspects of the nutritional ecology of a detritus-feeding Diptera larva: *Ptychoptera paludosa* (Abstract) 2931
Yaméogo, L., Calamari, D., Grunewald, J. & Fairhurst, C. P.: The aquatic monitoring and bioassay component of the WHO Onchocerciasis Control Programme in West Africa 2932
Aloi, J. E. & Brönmark, C.: Effects of snail density on snail growth and periphyton 2936
Jokinen, E. H.: The malacofauna of the acid and non-acid lakes and rivers of the Adirondack Mountains and surrounding lowlands, New York State, USA 2940
Dorgelo, J.: Growth, food and respiration in the prosobranch snail *Potamopyrgus jenkinsi* (E. A. Smith) (Hydrobiidae, Mollusca) 2947
Yipp, M. W.: The relationship between hydrological factors and distribution of freshwater gastropods in Hong Kong 2954
Riccardi, N., Mangoni, M. & Piva, A.: The elemental (C, H, N, O, S) and biochemical composition of *Unio mancus* (Pfeiffer) and *Anodonta cygnea* L. 2960
Tokeshi, M.: Aggregation, habitat characteristics and species coexistence (Abstract) 2964
France, R. L. & Welbourn, P. M.: Abundance of *Rana clamitans* tadpoles in Canadian Shield lakes 2965
Meili, M.: In situ assessment of trophic levels and transfer rates in aquatic food webs, using chronic (Hg) and pulsed (Chernobyl ^{137}Cs) contaminants 2970

XIII. Sediments

Curtis, P. J.: P and Fe release from anoxic Precambrian Shield lake sediments mediated by addition of Fe(II)-insoluble and Fe(II)-soluble bases 2976
Rowan, D. J. & Kalff, J.: The limnological implications of catchment sediment load 2980
Caraco, N. F., Cole, J. J. & Likens, G. E.: Phosphorus release from anoxic sediments: Lakes that break the rules 2985
Norton, S. A., Verta, M. & Kahl, J. S.: Relative contributions to lake sediment chemistry by atmospheric deposition 2989
Ekholm, P., Yli-Halla, M. & Kylmälä, P.: Availability of phosphorus in suspended sediments estimated by chemical extraction and bioassay 2994
Hupfer, M. & Uhlmann, D.: Microbially mediated phosphorus exchange across the mud-water interface ... 2999
Kjensmo, J.: Bio-geochemical composition of recent sediments from the mixo- and the monimolimnion of Lake Svinsjøen 3004
Hori, R., Hj. Ikhsan, S. bin, Wood, Abd. K. bin & Abu Bakar, Md. Y. bin: Neutron activation analysis of the sediment of Kelang River, Malaysia 3009
Sager, M.: Detection of environmental mobilities of nutrients and heavy metals in sediments 3012
Osborne, P. L. & Totome, R. G.: Sediment deposition in Lake Kutubu, Papua New Guinea 3018
Tatur, A., del Valle, R. & Pazdur, M.: Lake sediments in maritime Antarctic zone: A record of landscape and biota evolution: preliminary report 3022
Golterman, H. L.: Influence of FeS on denitrification in shallow waters 3025
De Groot, C.-J.: The influence of FeS on the inorganic phosphate system in sediments 3029
Koyama, T.: Biochemical reduction process in the lake sediment-water interface. On the basis of laboratory experiments 3036
Marxsen, J. & Fiebig, D.: Measurement of bacterial production in stream-bed sediments (Abstract) 3044
Tomaszek, J.: Oxygen consumption by bottom sediments 3045
Wasmund, N.: Microautoradiographic determination of the viability of algae in deep sediment layers (Abstract) 3050
Andersen, F. Ø. & Jensen, H. S.: The influence of chironomids on decomposition of organic matter and nutrient exchange in a lake sediment 3051

Iwakuma, T. & Otsuki, A.: Role of chironomid larvae in reducing rate of nutrient release from lake sediment: Evaluation by a mathematical model 3056
Schroeder, F., Klages, D. & Knauth, H.-D.: Contributions of sediments to the nitrogen budget of the Elbe estuary 3063
Kerner, M.: The coupling of microbial respiration processes within the two-dimensional spatial structure of an intertidal mud flat sediment of the Elbe Estuary 3067
Wiltshire, K. H.: Experimental procedures for the fractionation of phosphorus in sediments with emphasis on anaerobic techniques 3073

XIV. Received too late for classification

Herrmann, J.: Bioindication of nutrient and organic pollution by benthic stream invertebrates – pitfalls and problems (Abstract) 3079
Munawar, M., Leppard, G. G. & Munawar, I. F.: Ecotoxicology of stressed environments: Structural and functional strategy 3080
Ward, J. V. & Stanford, J.: Benthic faunal patterns along the longitudinal gradient of a Rocky Mountain river system 3087

Overbeck, J.: Plenary lecture: Initial, present and future aim of limnology 3095

Societas Internationalis Limnologiae: Twenty-Fourth Congress, Munich/Federal Republic of Germany, 1989 3102
Officers and list of members 3137
Contents of volume 24 (completely) ..... (1)

Verh. Internat. Verein. Limnol.	24	2784–2787	Stuttgart, Dezember 1991

Optimal resource allocation in cladocerans

Wilfried Gabriel and Barbara E. Taylor

Introduction

The natural pattern for growth and reproduction of cladocerans results in continued growth during most or all of adult life. This reproductive strategy is not well understood because optimal control theory predicts simultaneous growth and reproduction only under very special conditions (SIBLY et al. 1985) which are unlikely to obtain for cladocerans. Theoretically preferred is the "bang-bang" strategy: no investment into reproduction until an optimal switching point is reached, then no further growth. TAYLOR & GABRIEL (1985) showed that indeterminate growth of *Daphnia pulex* and *D. pulicaria* is suboptimal under the assumption of constant mortality. To explain why *Simocephalus vetulus* (MÜLLER), another daphniid cladoceran, is not a "bang-bang strategist", PERRIN et al. (1987) proposed that structural constraints such as size of the brood chamber could require continued growth after first reproduction.

Because reproductive output is among the most important components of fitness, one can expect that the resource allocation pattern has been shaped by strong selection pressure during evolution. But there are many plausible excuses for disagreements between theory and nature. Genetic, developmental, physiological, or other factors that could constrain an organism from achieving optimal allocation are poorly known and thus difficult to include in a model. Before invoking such constraints to reconcile nature to theory in the case of resource allocation for *Daphnia*, we decided to analyse the problem further. From laboratory data for *Daphnia pulex*, we constructed a model in which adult growth and reproduction are functions of resource allocation. We numerically solved the model for optimal resource allocation patterns under various conditions. These optimal patterns are more similar to natural patterns than previous analyses led us to expect, and they indicate how selection may have shaped the life histories of cladocerans.

Methods and model

To describe growth and reproduction of cladocerans we used laboratory data for *Daphnia pulex* (TAYLOR 1985). From these measurements we estimated the various functions and parameters of the model, including net production as a function of body size and food concentration. Production is modelled as a continuous process during the intermolt; reproduction and change in body size are implemented as discrete events at instar transitions. For each adult instar A the allocation α_A of net production P_A to reproduction determines growth and reproduction: the number of eggs produced is proportional to $\alpha_A P_A$ and the weight increment is proportional to $(1-\alpha_A)P_A$. Measured values of α_A were used in this model to describe the natural allocation pattern. To find the optimal resource allocation patterns, we chose intrinsic growth rate r as our measure of fitness. For any specified size dependent mortality scheme, the life history parameters l_x (survival probability) and m_x (reproduction) are constants or functions of the α_A's. Therefore, the discrete form of the renewal equation

$$1 = \Sigma\, l_x\, m_x \exp(-rx)$$

can be used to calculate numerically those α_A-values which maximize r. We assume three simple cases of mortality: i) size-independent, ii) survivorship linearly decreasing with body length to model a fish-like predation, and iii) survivorship linearly increasing with body length to represent invertebrate predation. For the results presented, the size-independent mortality is assumed to be 10 % per adult instar and the size-dependent mortality is calculated as increasing or decreasing linearly with body length so that at 0.75 mm or 3.5 mm the mortality becomes 10 % or 60 %. A more detailed description of the model will be given elsewhere (TAYLOR & GABRIEL 1992).

Results and discussion

The natural pattern of growth and reproduction at abundant food is given in Fig. 1 a. The frequency histogram below the figure represents the part α_A of net production that is allocated to reproduction. We count the last juvenile instar where allocation to reproduction can start as A = 1. (The eggs resulting from this allocation are laid at the beginning of instar 2 and hatch at end of instar 2.) At this instar already 76 % of net production is devoted to reproduction. This allocation increases to over 95 % at adult instar 10, resulting in small but continuous growth after first egg production. This natural pattern is contrasted by the model results in Fig. 1 b–d. With size-independent mortality

0368-0770/91/0024-2784 $ 1.00
© 1991 E. Schweizerbart'sche Verlagsbuchhandlung, D-7000 Stuttgart 1

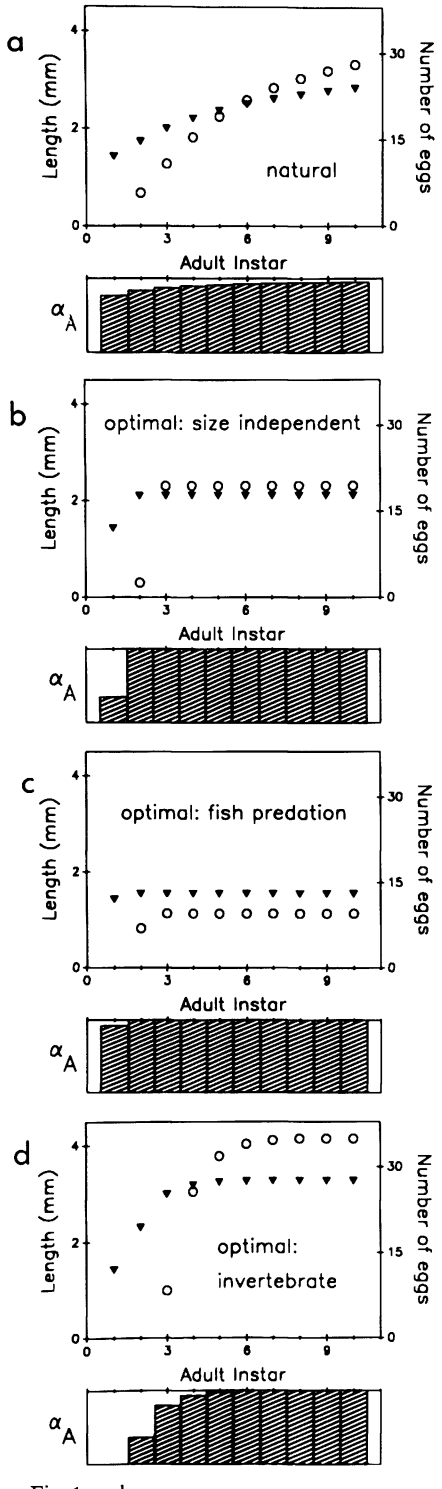

Fig. 1 a–d.

(Legends of Figs. 1 + 2 see next page)

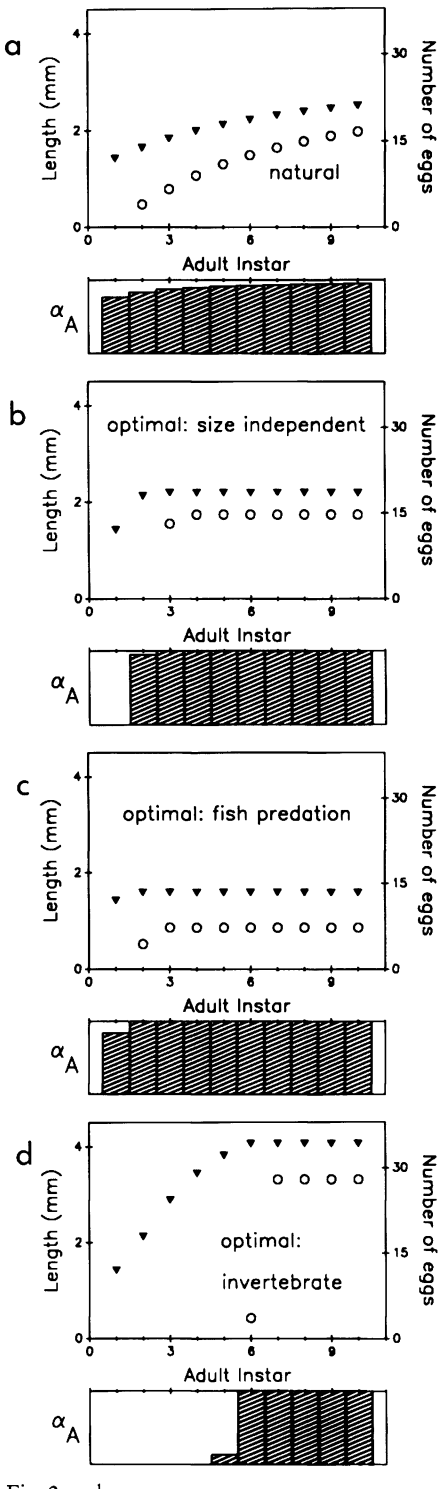

Fig. 2 a–d.

(Legends of Figs. 1 + 2 see next page)

Table 1. Intrinsic growth rates r for the best "bang-bang strategy" and comparison of r under natural resource allocation with the optimal values achievable for assumed size-independent mortality, fish-like and invertebrate-like predation risks under abundant and limited food conditions.

food	predation	optimal	natural	difference		bang-bang
		r [d^{-1}]	r [d^{-1}]	abs.	rel. [%]	r [d^{-1}]
high	independent	0.3412	0.3368	0.0044	1.3	0.3389
	fish	0.2710	0.2592	0.0118	4.3	0.2702
	invertebrate	0.1909	0.1460	0.0449	23.5	0.1897
low	independent	0.2314	0.2247	0.0067	2.9	0.2313
	fish	0.1665	0.1607	0.0058	3.5	0.1648
	invertebrate	0.0873	0.0183	0.0690	79.0	0.0864

(Fig. 1 b) the optimal strategy is to cease growing after one intermediate allocation to reproduction. Qualitatively the same is predicted if the mortality increases with body length (Fig. 1 c), but the first intermediate allocation to reproduction is higher and consequently the final body size is smaller than for size-independent mortality. Under invertebrate predation (Fig. 1 d) it is optimal to postpone the first reproduction by one instar and to have four intermediate allocations before investing all into reproduction. The largest final body size would be attained with this allocation pattern.

The natural allocation pattern seems to be quite independent of food level (Taylor 1985, Lynch 1989), and it seems to be mainly a function of weight and/or age. At least for the *Daphnia pulex* clone used in the experiments by Taylor, the natural α_A values are a function only of the instar number. Therefore, limited food implies retarded growth and fewer eggs without any qualitative change in the natural allocation pattern (Fig. 2 a). The optimal strategy under size-independent mortality delays reproduction by one instar (Fig. 2 b), as compared to the high food situation. Food shortage does not change the optimal strategy under fish predation very much (Fig. 2 c), but the intermediate α_A is lower, i.e. allocation gives a higher proportion to growth, so that the final body size is similar. Under invertebrate predation the optimal strategy strongly depends on the food level. Optimization with limited food postpones the first reproduction further, and there is only one intermediate allocation before reaching the final body size, which is larger than under abundant food.

Table 1 compares the intrinsic growth rates for natural and optimal allocations and the best "bang-bang" allocation for various predation schedules and food levels. The simple optimal control model obviously does not predict intermediate allocations and its "bang-bang strategy" can result in higher r values than natural allocation. The fitness under this strategy is very close but always below the optimum which our model reaches with intermediate allocations. The natural resource allocation seems to be suboptimal under all conditions tested. Invertebrate predation produces the largest deviations from the optimal values. In most cases, however, the realized fitness is very close to its maximum, so that indeterminate growth seems not to be very expensive. Similar results are obtained with more complicated predation schedules, such as arctangent or parabolic functions. A weak point of any such optimization is the underlying assumption of constant environmental conditions within and between generations.

But ponds and lakes are temporally variable, and thus cladocerans perceive a variety of environments even during one growing season. One can question whether the intrinsic growth rate is the appropriate fitness measure under variable environmental conditions. Optimizing the total reproductive output can lead to indeterminate growth as shown by Gabriel (1982) in a different model approach. Other measures of fitness will be discussed elsewhere in detail; e.g. for non-overwintering cladocerans the number of adults able to produce resting eggs at the end of the season might be a better fitness measure.

If the environment changes from generation to generation one has to maximize the geometric mean fitness over successive generations. The re-

Fig. 1. Body size (= triangles) and fecundity (= circles) at abundant food resulting from allocation α_A of net production to reproduction (histogram below figure) for adult instars A starting with A = 1 as the last juvenile instar where first allocation to reproduction can occur. a) Natural allocation. b – d) Model results under the assumption of size-independent mortality (b), fish (c), and invertebrate predation (d).

Fig. 2. Same as Fig. 1 but for limited food (30 % below the incipient limiting level).

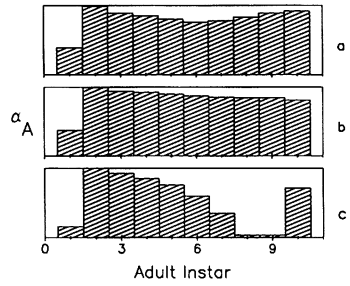

Fig. 3. Optimal resource allocation α_A of net production to reproduction if mortality varies between generations. a) Equal probability is assumed for fish and invertebrate predation at abundant food. b) As a) but with size-independent mortality as a third equal probable predation schedule. c) As b) but for limited food (30% below the incipient limiting level).

sulting optimal resource allocation is then not just a superposition of the results under constant conditions. This is demonstrated in Fig. 3 for the simple case that food is always constant but predation changes between generations. In reality we must of course consider that food conditions and kind and intensity of predation may change between generations and as well within generations. Depending on the frequency of the various environments this probably can result in almost any optimal resource allocation pattern.

More detailed measurements on resource allocations and its correlation with other life history parameters of different clones and species would be helpful to gain more insight into the selective forces shaping the observed growth and reproduction patterns. From our model we conclude: The natural resource allocation pattern with its consequences of indeterminate growth is suboptimal for any constant environment, but it can be understood as adaptive to variable environments which change between generations in food availability and predation risk.

Acknowledgements

BET was supported in part by contract DE-AC-09-76SROO819 between the U. S. Dept. of Energy and the Research Foundation of the University of Georgia and in part by a research fellowship from the Max-Planck-Gesellschaft.

References

GABRIEL, W., 1982: Modelling reproductive strategies of *Daphnia*. – *Arch. Hydrobiol.* **95:** 69–80.

LYNCH, M., 1989: The life history consequences of resource depression in *Daphnia pulex*. – *Ecology* **70:** 246–256.

PERRIN, N., RUEDI, M. & SAIAH, H., 1987: Why is the cladoceran *Simocephalus vetulus* (MÜLLER) not a 'bang-bang strategist'? A critique of the optimal-body-size model. – *Functional Ecology* **1:** 223–228.

SIBLY, R., CALOW, P. & NICHOLS, N., 1985: Are patterns of growth adaptive? – *J. theor. Biol.* **112:** 553–574.

TAYLOR, B. E., 1985: Effects of food limitation on growth and reproduction of *Daphnia*. – *Arch. Hydrobiol. Ergebn. Limnol.* **21:** 285–296.

TAYLOR, B. E. & GABRIEL, W., 1985: Reproductive strategies of two similar *Daphnia* species. – *Verh. Internat. Verein. Limnol.* **22:** 3047–3050.

– – 1992: To grow or not to grow: optimal resource allocation for *Daphnia*. – *Amer. Nat.* (in press).

Authors' address:

Max Planck Institute for Limnology, Department of Physiological Ecology, Postfach 165, D-2320 Plön, FRG.

Present address of B. E. TAYLOR: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801, U.S.A.