Differential Growth Rates of Three Cladoceran Species in Response to Mono- and Mixed-Algal Cultures

Lisa Lundstedt; Michael T. Brett

Limnology and Oceanography, Vol. 36, No. 1 (Jan., 1991), 159-165.

Stable URL:
http://links.jstor.org/sici?sici=0024-3590%28199101%2936%3A1%3C159%3ADGROTC%3E2.0.CO%3B2-Z

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Limnology and Oceanography is published by American Society of Limnology and Oceanography. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/limnoc.html.

Limnology and Oceanography
©1991 American Society of Limnology and Oceanography

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2003 JSTOR

http://www.jstor.org/
Thu Sep 4 21:33:13 2003

———, AND ———. 1987. Modeling animal guts as chemical reactors. Am. Nat. **129:** 69–96.

ROY, S., R. P. HARRIS, AND S. A. POULET. 1989. Inefficient feeding by *Calanus helgolandicus* and *Temora longicornis* on *Coscinodiscus wailesii*: Quantitative estimation using chlorophyll-type pigments and effects on dissolved free amino acids. Mar. Ecol. Prog. Ser. **52:** 145–153.

SHUMAN, F. R., AND C. J. LORENZEN. 1975. Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr. **20:** 580–586.

STEELE, J. H., AND B. W. FROST. 1977. The structure of plankton communities. Phil. Trans. R. Soc. Lond. Ser. B **280:** 485–534.

TANDE, K. S., AND D. SLAGSTAD. 1985. Assimilation efficiency in herbivorous aquatic organisms—The potential of the ratio method using ^{14}C and biogenic silica as markers. Limnol. Oceanogr. **30:** 1093–1099.

WANG, R., AND R. J. CONOVER. 1986. Dynamics of gut pigment in the copepod *Temora longicornis* and the determination of in situ grazing rates. Limnol. Oceanogr. **31:** 867–877.

Submitted: 25 January 1990
Accepted: 9 July 1990
Revised: 11 September 1990

Limnol. Oceanogr., 36(1), 1991, 159–165

Differential growth rates of three cladoceran species in response to mono- and mixed-algal cultures

Abstract—Population growth rates for *Daphnia longispina, Bosmina longispina,* and *Chydorus sphaericus* were determined in monocultures or mixtures of algae typical of the spring bloom (*Stephanodiscus, Rhodomonas,* and *Chlamydomonas*) and summer (*Scenedesmus, Chlorella,* and *Microcystis*). Algae from the spring bloom resulted in optimal population growth, whereas the green algae and cyanobacteria were of poorer quality. *Daphnia* showed the highest growth rates in all resources tested. *Chydorus* attained similar positive growth rates in most of the resources. In contrast, *Bosmina* achieved positive growth only in *Stephanodiscus* and *Rhodomonas.* For *Bosmina,* a combination of *Stephanodiscus* and *Rhodomonas* resulted in a positive synergisic effect on growth. The quality of resources depends greatly on the grazer of interest and cannot be generalized from results with *Daphnia* alone.

The most important aspect of algal-zooplankton interactions from the perspective of individual zooplankters is whether algae present can support reproduction. A common observation is that zooplankton population fecundity varies predictably with season (Gliwicz 1977; Kerfoot et al. 1988). The results of in situ life tables (Threlkeld 1985; Hovenkamp 1990) suggest that the midsummer decline of the cladoceran community could be explained by qualitative changes in the algal community, whereas it had previously been ascribed to predation. The importance of predation in summer has probably been overestimated, which suggests that the availability of suitable resources may be more important in determining population dynamics and interactions between species than previously thought.

Field studies suggest that green algae are of higher nutritional quality than cyanobacteria for cladocerans, but differences between species in response can be very large (Gliwicz 1977; Threlkeld 1985). Kerfoot et al. (1988) suggested that naked flagellates of the spring bloom (particularly cryptophyceans) are the most nutritious algal species, but Sarnelle (1986) indicated that cryptophyceans were of very low nutritional quality. Field studies are handicapped by the fact that it is impossible to determine which algae, of the many present in the plankton, determine the rate of egg production for a particular species or how strongly reproduction is influenced by factors such as temperature and interactions with filamentous and toxic algae.

Threlkeld (1985) indicated that increased temperature enhanced resource stress or in-

---

Acknowledgments

We thank Steven Schoenberg and Lars Bern for comments on the manuscript.

dividual energy requirements. Changes in individual growth, juvenile survivorship, and egg viability were often not related to detectable changes in algal cell counts or chlorophyll determinations (Threlkeld 1985). Thus the only way that the nutritional quality of individual algal species can be determined is in the laboratory with experimentally structured phytoplankton assemblages.

Laboratory studies suggest that small diatoms and *Cryptomonas* are higher quality resources than are large diatoms and green algae (Infante and Litt 1985), and green algae are higher quality resources than are cyanobacteria (Arnold 1971; deBernardi 1981). These results were all obtained with *Daphnia* as a bioassay. Generalization of these results to other crustacean zooplankters assumes that other species have similar responses to algal resources, which assumption may not be true. Crustacean zooplankton are known to differ dramatically in their abilities to select specific algae (Bern 1990). Large *Daphnia* may, in fact, be the least selective of crustacean zooplankters. Different species might have divergent responses to their resources—less selective species might be broader in resource use. In any case, there is a lack of comparative studies on the nutritional quality of phytoplankton and the resource utilization of different zooplankton species (particularly genera other than *Daphnia*).

We propose that patterns of phytoplankton seasonal succession common to meso- and eutrophic lakes can explain patterns in cladoceran species dynamics (i.e. population growth rates, fecundities, and succession) noted in field studies. To test this hypothesis, we examined growth at the population level for three cladocerans (*Daphnia longispina, Bosmina longispina,* and *Chydorus sphaericus*) in response to algal resources in monoculture and in combination. *Bosmina* and *Daphnia* represent dominant genera during the so-called clear-water phase—the transitional period between spring phytoplankton dominance by diatoms (Bacillariophyceae) and naked flagellates (a taxonomically diverse group) to summer dominance by greens (Chlorophyceae) and cyanobacteria (Cyanophyceae) (Lampert et al. 1986; Sommer et al. 1986; Kerfoot et al. 1988). *C. sphaericus* can be a major component of the zooplankton during summer, especially in lakes dominated by cyanobacteria (George and Edwards 1974; Gliwicz 1977).

The algae we tested can be divided into two seasonal and ecological categories (Sommer et al. 1986): a small diatom and naked flagellates of the spring bloom, *Stephanodiscus hantzschii, Rhodomonas minuta,* and *Chlamydomonas* sp.; and green algae and cyanobacteria of summer, *Scenedesmus acutus, Chlorella homosphaera,* and *Microcystis aeruginosa.* The algal combinations *Stephanodiscus* plus *Rhodomonas* and *Rhodomonas* plus *Scenedesmus* were also examined. These combinations represent the middle of the spring bloom and the transition between spring bloom and summer plankton, respectively.

Stephanodiscus and *Microcystis,* usually colonial in lake plankton, were largely single-celled in the monocultures used. *D. longispina* was obtained from Lake Vallentuna, *B. longispina* from Lake Erken, and *C. sphaericus* from a laboratory monoculture. The synthetic medium L16 (Lindström 1984), modified with B vitamins and earth extract, was chosen because its ionic composition resembles that of temperate mesotrophic lakes, and it does not adversely affect zooplankton. All experiments were carried out at 13.5°±0.4°C with a 14:10 L/D cycle.

In order to assure that all growth results obtained were due to the food items tested and not to algae consumed before the start of the experiment, we conditioned 100 zooplankters to each alga for 10 d before we began experiments. Egg development time for the clone of *Daphnia* used at 15.1°±0.2°C was 3.9±0.1 d (±1 SD) ($n = 12$); hence the complete cycle from initiation of ovarian development to neonate release at this temperature is <8 d. Bottrell (1975) found an egg development time for *C. sphaericus* at 15°C of 3.8 d, while Kerfoot (1974) found an egg development time of 3 d for *Bosmina* at this temperature. Thus the preconditioning period used was sufficient to assure that all results were due to the algae tested, if we

Table 1. Morphological characteristics and concentrations of the test algae. Values expressed as mean ±1 SD. Algal concentrations given are averaged across all replicates and days 0, 5, and 10 of the experiment.

	Mean length (μm)	Mean width μm)	Volume (μm³)	Concentration tested (μg C ml⁻¹)		
				Daphnia	*Bosmina*	*Chydorus*
Chlorella homosphaera	4.6±0.81	—	55	2.1±0.24	4.7±0.44	6.0±0.31
Microcystis aeruginosa	4.8±1.4	—	73	1.6±0.14	1.7±0.26	1.0±0.04
Stephanodiscus hantzschii	3.9±0.30	5.1±0.16	80	1.7±0.03	1.1±0.14	1.0±0.03
Scenedesmus acutus	13.0±1.3	5.0±0.80	150	4.1±0.08	*	7.7±0.39
Rhodomonas minuta	11.0±1.6	6.4±1.0	165	1.6±0.18	1.8±0.64	2.4±0.27
Chlamydomonas sp.	10.0±2.2	7.8±1.9	375	2.5±0.21	3.0±0.32	4.0±0.19
R. minuta + *S. acutus*				2.1±0.22	4.8±0.48	5.8±0.18
R. minuta + *S. hantzschii*				1.7±0.13	1.5±0.24	2.0±0.45

* No individuals survived the preconditioning period in this treatment.

assume that the egg development time was always <5 d.

Experiments were carried out at average algal concentrations of >1 μg C ml⁻¹ (Table 1). Algal concentrations were always >0.5 μg C ml⁻¹. These concentrations assured that all responses were due to algal quality and not quantity (Gliwicz 1990). The bioassays with *Daphnia* were carried out in 300-ml flasks and those for *Bosmina* and *Chydorus* in 75-ml flasks. Algal concentrations were measured individually for each replicate on days 0, 5, and 10.

Algal concentrations were estimated via fluorescence to algal biovolume regressions—the regression coefficients of all these relations being >0.95. Algal biovolumes can be approximately converted to μg C ml⁻¹ by considering that algal dry weight is usually 20% of wet weight and that the C content is usually 50% of dry weight. Thus C ml⁻¹ is equal to ~10% of wet weight. Algal concentrations varied among permutations because the algal species tested have different growth characteristics, because the experiments were started on three successive days (one for each zooplankton species) and the algae used were therefore in different growth phases, and because the individual zooplankters differed in capacity to influence the growth rates of the algae. Our experience indicates that zooplankton can be very negatively affected by excessive handling, so we elected to have inequities in algal concentration as opposed to overly stressed animals.

Four replicates of 20 individuals each were used. The individuals tested were chosen at random from the conditioning populations. In cases where <80 individuals survived the conditioning period, we used fewer than four replicates. The experiment lasted 10 d, and the change in population size during this period was considered a measure of algal quality. During sample processing, the clutch size of all egg-bearing individuals was noted. All results were converted to (N_t/N_0), where N_0 and N_t denote the number of individuals present at the beginning and at the end of the experiment. All statistical analyses were performed on untransformed data. The influence of zooplankton and algal species and interactions among them in treatment response were assessed with a two-way ANOVA.

Population growth rates varied considerably, depending on zooplankton species and algal resource (Fig. 1, Table 2). *Daphnia* achieved the highest rate of increase on all resources tested, and *Bosmina* had the second highest maximum rate of increase. This result is probably because all three species have a similar juvenile development period and length of adult instar (Bottrell 1975), while *Daphnia* had much larger clutch sizes (maximal observed clutch, 32 eggs) than either *Bosmina* (maximal observed clutch, 8 eggs) or *Chydorus* (maximal observed clutch, 2 eggs). These findings are consistent with clutch sizes observed in the field and have far-reaching ecological significance. Thus, given high-quality resources and little selective predation—a condition common to the spring algal bloom—*Daphnia* will grow much faster and achieve a much larger population size and exert a greater influence on the phytoplankton community than will either *Bosmina* or *Chydorus*. This dominance

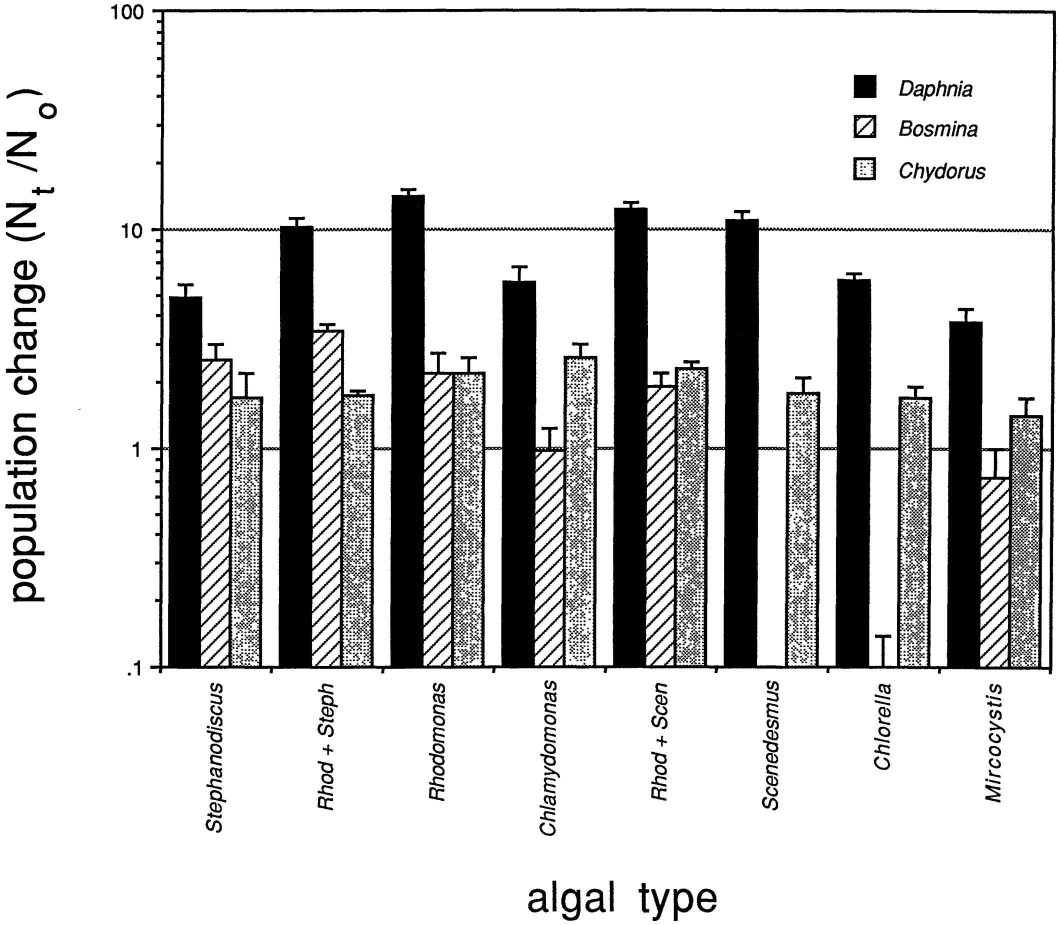

Fig. 1. Population growth responses (expressed as N_t/N_0) for the individual zooplankton-algae permutations. Values expressed as mean ±1 SD. Note the logarithmic ordinate.

is commonly observed during the spring bloom (Sommer et al. 1986; Lampert et al. 1986; Kerfoot et al. 1988) and is the presumed cause of the subsequent clear-water phase (Sommer et al. 1986; Lampert et al. 1986).

Both *Daphnia* and *Chydorus* achieved positive population growth rates on all the resource types tested. *Chydorus* showed the smallest differences in growth among resource types. The generalist nature of *Chydorus* may explain why this species often attains its annual maximum in summer and is particularly important in lakes dominated by cyanobacteria, when large cladocerans are adversely affected by selective predation and other small species (*Bosmina*) are affected by the low quality of the phytoplank-

Table 2. Two-way ANOVA summary for the experiment.

Source	df	MS	*F*-test	*P*	Variance (%)
Zooplankton	2	485	1,004	0.0001	66.3
Algae	7	28	57	0.0001	13.2
Interaction (Z × A)	14	19	39	0.0001	18.2
Error	70	0.48			2.3

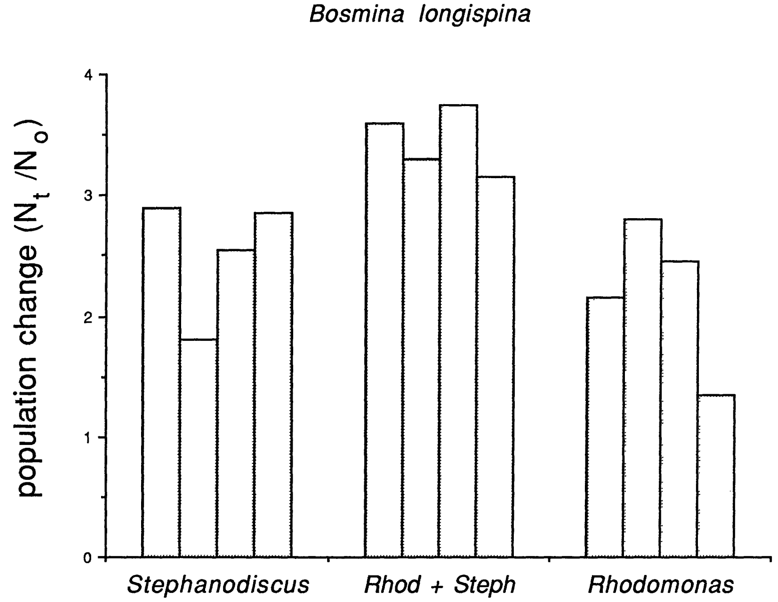

Fig. 2. The influence of resource synergy on *Bosmina* growth rates. The values shown are of individual replicates. The results obtained for *Rhodomonas* plus *Stephanodiscus* were significantly greater (one-tailed *t*-test) than those for *Rhodomonas* ($P < 0.005$) and *Stephanodiscus* ($P < 0.01$) individually.

ton present (George and Edwards 1974; Gliwicz 1977).

Bosmina achieved positive growth rates on only two of the algae tested singly, *Stephanodiscus* and *Rhodomonas*. *Bosmina* achieved its highest growth rate (13.2% increase d^{-1}) on the combination of *Stephanodiscus* plus *Rhodomonas* (Fig. 2); the rates in monocultures of *Stephanodiscus* and *Rhodomonas* were 9.7 and 8.2%. The combination of *Stephanodiscus* plus *Rhodomonas* corresponds to the early to middle period of the spring algal bloom. Field data (Kerfoot et al. 1988) indicate that *Bosmina* can have its spring peak in standing stock at this time, i.e. before *Daphnia* has its spring peak. *Bosmina* is also much more selective than either *Daphnia* or *Chydorus* (Bern 1990). Thus the ecological strategy of *Bosmina* may be to glean the highest quality particles from the phytoplankton while *Daphnia* and *Chydorus* may both be dependent on the nutritional quality of the dominant species in the algal community. This mixed diet suggests that further attention should be paid to mixtures of algae when assessing the ecological responses of zooplankton to their resources, particularly since natural zooplankton populations are almost always confronted with diverse algal assemblages.

The large amount of variation explained by zooplankton species (Table 2) indicates that they had different responses to the resources. The large amount of variation explained by the interaction between zooplankton and algae indicates that the relative quality of the algae depends on the particular zooplankter tested. Both of these results strongly argue against using only one species or group of zooplankton to characterize the nutritional quality of algae. Unfortunately most previous freshwater studies of algal quality for crustacean zooplankters have used only daphnids. Our results suggest the importance of tests with zooplankters other than *Daphnia*. The very characteristic that makes *Daphnia* a popular animal for laboratory studies, i.e. the ease with which it can be cultured, suggests that other zooplankters, particularly those which are more difficult to culture, differ in their nutritional requirements.

The algae tested could be ranked as to overall quality (in decreasing order)—*Rhodomonas, Chlamydomonas, Scenedesmus,* *Stephanodiscus, Chlorella,* and *Microcystis.* It should be kept in mind, however, that the three zooplankters all had different optimal resources. *Daphnia* grew best in *Rhodomonas, Bosmina* grew best in *Stephanodiscus* plus *Rhodomonas,* and *Chydorus* grew best in *Chlamydomonas.* A pilot study showed that a small *Cryptomonas* sp. (770 μm^3) provided growth responses almost identical to those for *Rhodomonas* (Brett unpubl. data).

As previously mentioned, some green algae have been shown to be of higher quality than cyanobacteria for daphnids (Arnold 1971; deBernardi et al. 1981). Recent research indicates that resource quality influences not only the total number of eggs produced but also their fitness (Brett unpubl. data). Neonates produced by individuals consuming high-quality resources reached maturity sooner at a larger size and produced more eggs relative to neonates produced by individuals that consumed low-quality resources despite the fact that both types of neonates consumed the same resources. The maternal effect was particularly pronounced if the neonates ended up in low-quality resources (Brett unpubl. data). The present study did not consider an important aspect of algal-zooplankton interactions. Namely, it has been shown that filamentous algae can significantly interfere with the feeding of some zooplankters (Gliwicz and Lampert 1990)

Burns and Xu (1990) looked at egg production of adult females of the calanoid *Boeckella* spp. offered monocultures of several filamentous cyanobacteria, the small diatom *Cyclotella,* and *Cryptomonas.* They found the highest rates of egg production in *Cryptomonas* and *Cyclotella* for two of the three species tested. In the third species, total egg production rates were virtually independent of resource type. In fact, the starved controls produced quite a few eggs, suggesting that maternal algal consumption immediately before egg production was of only limited importance. Their results are not directly comparable to ours, since Burns and Xu did not follow a complete generation; in fact they followed only a portion of the adult instar. This distinction is very important as it is much easier to induce copepods to produce eggs than it is to foster growth, survival, and production of viable eggs through more than one generation. The only study of which we are aware that has succeeded in culturing freshwater calanoids through several generations did so with a combination of *Cryptomonas* and *Chlamydomonas* (Williamson and Butler 1987).

The results of our study are in close agreement with field observations from temperate meso- and eutrophic lakes, suggesting that algae of the spring bloom, especially cryptophyceans, are highly nutritious and that the green algae and cyanobacteria of summer are less so. A marked synergistic effect of *Stephanodiscus* plus *Rhodomonas* was noted for *Bosmina.* Future attention should be paid to synergistic relations when assessing algal-zooplankton interactions.

The relative abilities of the different cladocerans to utilize various substrates could provide valuable insights into the seasonal and competitive dynamics of these zooplankters. For example *Daphnia,* because of its higher maximum growth potential, would be expected to dominate during periods of high concentrations of high-quality resources and little selective predation. *Chydorus* could be expected to dominate when selective predation is intense, thus favoring small species, and resource quality is low. *Bosmina* is more selective than either *Daphnia* or *Chydorus* and may specialize in collecting high-quality particles from algal assemblages of mixed quality. Thus, results obtained for *Daphnia* should not be used uncritically to characterize other zooplankters.

Shifts in resource quality probably exert a strong influence on zooplankton populations and communities. These influences occur simultaneously with shifts in intensity and orientation of selective predation, shifts in resource quantity, changes in temperature, and interference with feeding from filamentous and toxic algae.

Lisa Lundstedt
Michael T. Brett[1,2]

---

[1] To whom correspondence should be sent.

[2] Present address: Div. Environ. Stud., Univ. Calif., Davis 95616.

Institute of Limnology
Uppsala University
Box 557
751 22 Uppsala, Sweden

References

ARNOLD, D. E. 1971. Ingestion, assimilation, survival, and reproduction by *Daphnia pulex* fed seven species of blue-green algae. Limnol. Oceanogr. **16:** 906–920.

BERN, L. 1990. Food choice in some freshwater, crustacean zooplankters. Acta Univ. Upps. Compr. Summar. Uppsala Diss. Fac. Sci. 245.

BOTTRELL, H. H. 1975. Generation time, length of life, instar duration and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the River Thames, Reading. Oecologia **19:** 129–140.

BURNS, C. W., AND Z. XU. 1990. Utilization of colonial cyanobacteria and algae by freshwater calanoid copepods: Survivorship and reproduction of adult *Boeckella* spp. Arch. Hydrobiol. **117:** 257–270.

DEBERNARDI, R., G. GIUSSANI, AND E. L. PEDRETTI. 1981. The significance of blue-green algae as food for filtering zooplankton: Experimental studies on *Daphnia* spp. fed by *Microcystis aeruginosa.* Int. Ver. Theor. Angew. Limnol. Verh. **21:** 477–483.

GEORGE, D. G., AND R. W. EDWARDS. 1974. Population dynamics and production of *Daphnia hyalina* in a eutrophic reservoir. Freshwater Biol. **4:** 445–465.

GLIWICZ, Z. M. 1977. Food size selection and seasonal succession of filter-feeding zooplankton in a eutrophic lake. Ekol. Pol. **25:** 179–225.

———. 1990. Food thresholds and body size in cladocerans. Nature **343:** 638–640.

———, AND W. LAMPERT. 1990. Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. Ecology **71:** 691–702.

HOVENKAMP, W. 1990. Instar-specific mortalities of coexisting *Daphnia* species in relation to food and invertebrate predation. J. Plankton Res. **12:** 483–495.

INFANTE, A., AND A. H. LITT. 1985. Differences between two species of *Daphnia* in the use of species of algae in Lake Washington. Limnol. Oceanogr. **30:** 1053–1059.

KERFOOT, W. C. 1974. Egg-size cycle of cladoceran. Ecology **55:** 1259–1270.

———, C. LEVITAN, AND W. R. DEMOTT. 1988. *Daphnia*-phytoplankton interactions: Density-dependent shifts in resource quality. Ecology **69:** 1806–1825.

LAMPERT, W., W. FLECKNER, H. RAI, AND B. E. TAYLOR. 1986. Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. Limnol. Oceanogr. **31:** 478–490.

LINDSTRÖM, K. 1984. Selenium as a growth factor for plankton algae in laboratory experiments and some Swedish lakes. Hydrobiologia **101:** 35–48.

SARNELLE, O. 1986. Field assessment of the quality of phytoplanktonic food available to *Daphnia* and *Bosmina.* Hydrobiologia **131:** 47–56.

SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG*-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. **106:** 433–471.

THRELKELD, S. T. 1985. Resource variation and initiation of midsummer declines of cladoceran populations. Ergeb. Limnol. **21:** 333–340.

WILLIAMSON, C. E., AND N. M. BUTLER. 1987. Temperature, food and mate limitation of copepod reproductive rates: Separating the effects of multiple hypothesis. J. Plankton Res. **9:** 821–831.

Submitted: 27 June 1989
Accepted: 30 May 1990
Revised: 27 September 1990

Limnol. Oceanogr., 36(1), 1991, 165–171

Effects of a *Chaoborus*-released chemical on *Daphnia ambigua*: Reduction in the tolerance of the *Daphnia* to summer water temperature

Abstract—Daphnia ambigua was reared at eight different temperatures (5°, 10°, 15°, 20°, 23°, 25°, 28°, and 30°C) in water conditioned by a predator, *Chaoborus flavicans. D. ambigua* developed spikelike helmets in juvenile stages probably in response to a chemical released from the *Chaoborus* larvae. Helmet size was affected by water temperature (max size at 23°C) and decreased with decreasing temperature from 23° to 10°C. At high temperatures (28° and 30°C), survival rate of juveniles exposed to the *Chaoborus*-released chemical decreased greatly. Molting to the high-helmeted morph might increase the risk of mortality at those temperatures. Results suggest that the predator releases a chemical that reduces the tolerance of cyclomorphic *Daphnia* to high tem-

---

Acknowledgments

I am grateful to Ken'ichi Satake for financial support and Toshio Iwakuma for suggestions. I also thank two anonymous reviewers for criticisms.