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Long-term dynamics of small-bodied and large-bodied cladocerans during the eutrophication of a shallow reservoir, with special attention for *Chydorus sphaericus* *

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Abstract

Eutrophication in Tjeukemeer involved a gradual increase in chlorophyll concentrations from ca. 30 mg m^{-3} in 1968–69 to 125 mg m^{-3} in 1976. From 1976 onwards, chlorophyll concentrations remained at a high level fluctuating between 100–225 mg m^{-3}. Hillbricht-Illkowska (1977) hypothesized that small-bodied species will become increasingly abundant and dominant over large-bodied species with increasing eutrophication. We tested this hypothesis using observations from life history experiments on *Chydorus sphaericus*, combined with data from 25 years of field observations on the population dynamics of cladocerans in Tjeukemeer.

In life history experiments with *C. sphaericus*, the fitness measure *r* in treatments with natural lake seston and laboratory cultured green algae was significantly higher on lake seston from Tjeukemeer, containing a high proportion of detritus. This suggests that detrital particles are good quality food for *C. sphaericus*. Field observations during the period 1968–1976 showed that all three categories of cladocerans: *C. sphaericus*, ‘other’ small-bodied cladocerans (predominantly *Bosmina* spp.) and large-bodied cladocerans (predominantly *Daphnia galeata*), increased in biomass with increasing chlorophyll concentration. However, of these three cladoceran categories only *C. sphaericus* showed a distinct and significant increase whereas the other two only showed a marginally significant increase. During the period 1977–1992, both ‘other’ small-bodied cladocerans and *C. sphaericus* significantly decreased in biomass with increasing chlorophyll concentration, whereas the biomass of the large-bodied cladocerans significantly increased with increasing chlorophyll content. These observations are not in agreement with the hypothesis that small-bodied zooplankton become increasingly abundant with increasing eutrophication. We suggest that the observed trends are partially caused by a food effect, and partially caused by predation pressure. *Daphnia* shows a better response to the increase in detritus and filaments of Cyanobacteria than small-bodied cladocerans, but is more vulnerable to fish predation. Densities of 0+ zooplanktivorous fish show strong annual fluctuations in Tjeukemeer, and because of hydrological conditions, 0+ fish abundance in this lake is probably negatively related to chlorophyll content.

Introduction

In the pelagic zone of eutrophic temperate lakes and reservoirs, small-bodied cladoceran species like *Bosmina* spp. and *Chydorus sphaericus* are generally more abundant than large-bodied species (i.e. *Daphnia* spp.). However, whereas the role of *Daphnia* spp. in the pelagic food web has figured in numerous studies, much less is known about the quantitative role of small-bodied cladocerans in the food web (e.g. DeMott & Kerfoot, 1982; Balseiro et al., 1992).

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It is widely accepted that the pelagic zone of lakes of low productivity tends to be dominated by large-bodied cladocerans and that the size of the dominant forms decreases with increasing trophy (Brooks, 1969; Nilsson & Pejler, 1973; Pejler, 1975; Rankin et al., 1979; Sprules & Knoechel, 1983; Ewald, 1991). Interestingly, this decrease in body size is often to a large extent the result of a niche shift by small-bodied species (e.g. *Chydorus sphaericus*, *Ceriodaphnia quadrangula*), which are originally restricted to the littoral zone, but invade the pelagic zone when the lake becomes more eutrophic (Pejler, 1975). In eutrophic lakes, detrital particles with attached bacteria are often more important than algae as food for zooplankton. These particles occur in concentrations four to six times higher than those of live algae (Mann, 1988; Meijer et al., 1990; Gons et al., 1992). Even if the detrital particles contain only 17–25% of the energetic content of living algae, they probably realise more than half of the energetic requirements of the consumers on a bulk basis (Kerfoot & Kirk, 1991).

The small-bodied *C. sphaericus* often appears as a common plankter in eutrophic waters where extensive Cyanobacteria blooms are prevalent (Gannon, 1972). *C. sphaericus* belongs to the Chydoridae, which are adapted to creeping along submerged surfaces, either macrophytes or bottom substrates, and are poor swimmers (Fryer, 1968), although some species occasionally leave their substrate (Whiteside, 1974). As most Chydoridae remain in close contact with a substrate, they belong to the microbenthos rather than to the zooplankton. *C. sphaericus* is an exception, as it has two alternative ways of life. It can be found in the littoral zones of lakes among macrophyte vegetation and on bottom substrates that are rich in organic material (Goulden, 1971; Keen, 1973; Daggett & Davis, 1974; Whiteside, 1974; Williams, 1982), as well as in the water column in the open water zone of eutrophic lakes and ponds (Cummins et al., 1969; Franken & Franken, 1978; Pedros-Alio & Brock, 1985; Rognerud & Kjellberg, 1990; Vijverberg et al., 1990; Ewald, 1991).

The foodweb dynamics of Tjeukemeer have been studied intensively from 1968 to 1992 (Vijverberg et al., 1993). During the first ten years of the study, the lake progressively became more eutrophic (Moed & Hoogveld, 1982). Floating macrophyte fields, which up to 1970 occupied approximately 10% of the lake's surface area, disappeared in the late summer of 1971 and did not reappear since (pers. obs. J. Vijverberg). At the same time filamentous Cyanobacteria increased. Total algal biomass, measured as chlorophyll concentration, progressively increased, and the relative abundance of Cyanobacteria (dominated by *Oscillatoria* spp.) increased from ca. 1000 filaments ml^{-1} in 1968–69 to around 5000 filaments ml^{-1} in 1971, and reached a maximum level of around 50 000 filaments ml^{-1} in 1976–1978 (Moed & Hoogveld, 1982). Since 1972 *Oscillatoria* spp. have dominated the phytoplankton community in the lake, both in numbers and in biovolume.

Because most small-bodied cladoceran species inhabiting the pelagic zone of lakes and reservoirs are of littoral origin, they are probably better adapted to detrital food than large-bodied pelagic cladocerans. Furthermore, because of their narrower carapace gape, the feeding process in small-bodied cladocerans is less inhibited by the presence of large filamentous Cyanobacteria than the feeding process in large-bodied cladocerans, because there is a lower risk of filaments entering the food chamber and entangling the thoracic appendages (Gliwicz & Siedlar, 1980). Largely based on these two arguments, Hillbricht-Illkowska (1977) hypothesized that small-bodied zooplankton species will become increasingly abundant and dominant over large-bodied species as lakes become more eutrophic. We tested this hypothesis by addressing three questions: (1) is the intrinsic rate of population increase (*r*) of *C. sphaericus* on a medium of natural seston from Tjeukemeer with algae and a high detritus content higher than on algal food alone?, (2) does the biomass of small-bodied cladocerans increase at a faster rate than that of large-bodied cladocerans under conditions of progressive eutrophication?, and (3) does *C. sphaericus*, belonging to a taxonomic group of benthic organisms, which is supposed to be preconditioned to detrital food, increase faster in biomass than other small-bodied cladocerans such as *Bosmina* spp.?

Material and methods

Study area

Tjeukemeer, situated in the North of the Netherlands, is a shallow (mean depth = 1.5 m), eutrophic freshwater lake with a surface area of 2150 ha. The lake is part of an interconnected system of waterbodies, which act as a reservoir for the surrounding polders. The system receives water from the nearby IJsselmeer (120 000 ha) during the growing season (April to September) and polderwater, which is rich in humic compounds, during the winter. The littoral zone of the lake is poorly developed, covering only 1% of the lake's surface area.

Laboratory experiments

C. sphaericus was cultured on two different types of food: (1) natural seston from lake Tjeukemeer, and (2) a 1:1 (by Carbon mass) mixture of the green algae *Chlamydomonas globosa* and *Scenedesmus obliquus*, supplied at a total food level of 1 mg C l^{-1}, a concentration which is well above the incipient limiting level of a small-bodied cladoceran (Duncan, 1989). For the medium with natural seston, lake water from Tjeukemeer (1990, April–May) was collected fresh every day and sieved over a 76 μm mesh plankton gauze in order to remove crustacean zooplankton. *C. globosa* and *S. obliquus* were cultured axenically in 2 litre flow-through systems (Boersma & Vijverberg, 1994). The algae were harvested daily from the overflow bottles of these continuous cultures. The culture medium of the algae was removed by centrifuging twice for 20 min at 3000 r.p.m., followed by rinsing with distilled water. The algae were resuspended in 0.45 μm-filtered lake water from Tjeukemeer. The algal density was measured using a haemacytometer, counting a minimum of 500 cells. The carbon content of *C. globosa* was 2.52×10^{-11} g C cell^{-1}, and that of *S. obliquus* was 2.30 x 10^{-11} g C cell^{-1}, resulting in carbon: dry weight ratios of 0.53 and 0.50, respectively. *S. obliquus* was usually unicellular. Both algal species had a maximum length of around 15 μm. Fresh media were prepared daily.

Experimental animals were kept at 17.5 °C and a light: dark regime of 16:8 h. Parthenogenetic females of *C. sphaericus* were randomly collected from the field about 4 weeks before the start of the experiment and kept on 76 μm mesh filtered lake water. As soon as the field caught females produced their second batch of newborns, the mothers were removed. The first and second generation animals were reared on filtered lake water to maturity. The offspring produced by the animals of the second generation were transferred individually to 100 ml tubes for acclimation to the two food types. The animals were selected in such a way that the clonal composition for the two food treatments was the same. Newborns produced in these cultures were used for the experiments.

For each treatment, thirty neonates were collected within 12 h of birth and placed individually in 100-ml test tubes. The animals were inspected and transferred to clean tubes with fresh medium every other day. We recorded the time needed to reach maturity as the first day on which there were eggs present in the brood chamber. Once the animals reached maturity, we measured the number of eggs per brood and the duration of the adult instars, which is equal to the development time of the eggs. The life table experiment was continued until the animals reached the fourth adult instar. The intrinsic rate of population increase (*r*) was estimated using the Euler equation, and the standard error of *r* was computed using the jackknife method (Meyer et al., 1986). *r* was taken as a measure for fitness (Stearns, 1992).

Table 1. Model parameters for regressions of $\log_{10}$-transformed annual mean cladoceran biomass of large-bodied cladocerans (Clad. Large), *C. sphaericus* (*Chydorus*), and 'other' small-bodied cladocerans (Clad. Small) as dependent variables and time (year) as the independent variable. Regressions are calculated for two periods: (1) period 1968–1976, the period of increasing eutrophication, and (2) period 1977–1992, the period of hypertrophic state. See also Figure 4.

Period	Group	Slope	Intercept	r^2	*P*
1968–1976	Clad. Large	0.04	2.34	0.23	0.19
	Clad. Small	0.05	1.95	0.46	0.045
	Chydorus	0.21	0.50	0.49	0.035
1977–1992	Clad. Large	−0.03	2.98	0.12	0.19
	Clad. Small	0.02	2.24	0.07	0.32
	Chydorus	0.01	1.71	0.01	0.72

Field work

Zooplankton was sampled from 1968 to 1992 with a 5-litre Friedinger closing sampler at five fixed stations, generally at fortnightly intervals during April–September. Samples were taken at two depths, one just below the surface and the other just above the bottom. The samples were pooled, concentrated by filtering through a 120-μm mesh plankton gauze and preserved in 4% formaldehyde. Densities of animals per species and length-frequency distributions were established based on a one-tenth subsample. Mean annual biomass was calculated over the growing season (April–September) using the length/weight relationship for each species given in Table 1 of Vijverberg et al. (1990).

Chlorophyll-*a* was taken as a measure for total phytoplankton biomass, and was estimated from spectrophotometer readings after extraction of the pigments in 80% ethanol at 75 °C for 5 min (Moed & Hallegraeff, 1978).

Data analysis

For a detailed analyses of the changes in the cladoceran community structure we distinguished three categories of cladocerans: (1) large-bodied species (mainly *D. galeata*), (2) *C. sphaericus*, and (3) 'other' small-bodied cladocerans (mainly *Bosmina* spp.). The changes in population density of these categories were investigated for two trends: (1) changes in cladoceran biomass with time (years), and (2) changes in cladoceran biomass with phytoplankton biomass (chlorophyll content). The field data were analysed by linear regression. Although time series are generally dependent, we believe that this is not the case with the present field data. In our data set every data point (year) represents a mean value for the growing season (April–September) of a specific year, based upon approximately 11 samples collected during that period. Slopes of regression lines were compared and tested for parallelism using a sub-routine of the ANOVA-MANOVA routine of Statistica (Statsoft, 1992). In the analysis we used species or zooplankton size category as the independent variable, zooplankton biomass as the dependent variable, and phytoplankton biomass as the co-variable.

Results

Laboratory experiments

In the life history experiments with *C. sphaericus*, we always observed two eggs per brood. The fitness measure r calculated for *C. sphaericus* on lake seston and algae-medium is presented in Figure 1. Lake seston resulted in a significantly higher r compared with cultured green algae by t-test ($t = 4.20$; df = 20; $P < 0.001$).

Field observations

From the start of the study, chlorophyll concentrations tended to increase annually. Starting at ca. 30 mg m^{-3} in 1968–69, chlorophyll-*a* concentrations reached a maximum annual mean of ca. 225 mg m^{-3} in 1979 (Figure 2). Between 1979 and 1992 the chlorophyll-*a* concentrations remained at a high level, and fluctuated between 100 and 225 mg m^{-3} (mean ca. 160 mg m^{-3}). The total cladoceran biomass roughly followed the same trend, with an increase in biomass up to 1976, followed by fluctuations around a high biomass level of ca. 1200 mg dry wt m^{-3} (Figure 3). The cladoceran biomass fluctuations during 1977–1992 are very large (range: 400–2400 mg dry wt m^{-3}), much larger than the observed fluctuations in chlorophyll concentrations (range: 100–220 mg m^{-3}).

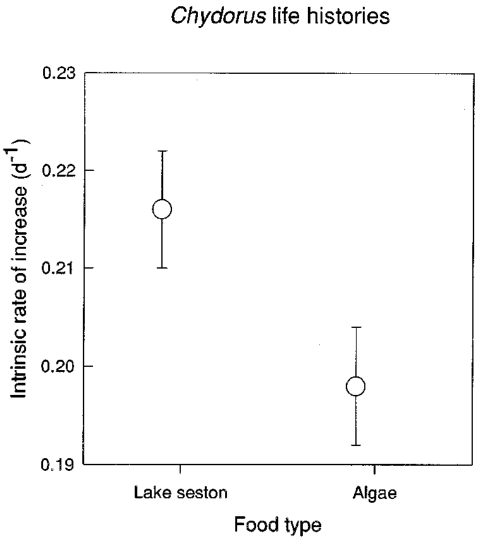

Figure 1. The intrinsic rate of population increase (r, d^{-1}) of *Chydorus sphaericus* in different food treatments. Two food types were used: (1) lake seston from Tjeukemeer (Lake seston), and (2) a 1:1 mixture of *Chlamydomonas globosa* and *Scenedesmus obliquus* at a total concentration of 1.0 mg C l^{-1} (Algae). Error bars indicate 95% confidence limits of the means.

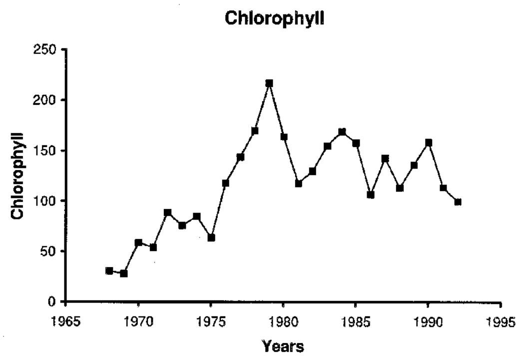

Figure 2. Change of annual mean chlorophyll content (April–September, mg m^{-3}) over time in Tjeukemeer (1968–1992).

During the whole study period, both small-bodied cladocerans and large-bodied cladocerans were present in substantial numbers. The group of small-bodied cladocerans was dominated by three species, *C. sphaericus*, *Bosmina coregoni*, and *B. longirostris*,

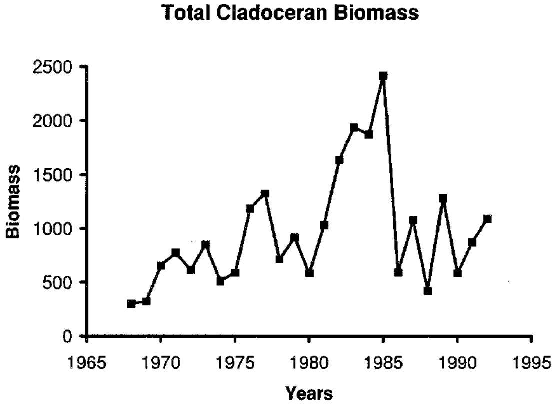

Figure 3. Change of annual mean cladoceran biomass (April–September, mg dry wt m^{-3}) over time in Tjeukemeer (1968–1992).

Table 2. Model parameters for regressions of $\log_{10}$-transformed annual mean cladoceran biomass of large-bodied cladocerans (Clad. Large), *C. sphaericus* (*Chydorus*), and 'other' small-bodied cladocerans (Clad. Small) as dependent variables and $\log_{10}$-transformed mean chlorophyll-*a* content as the independent variable. Regressions are calculated for two periods: (1) period 1968–1976, the period of increasing eutrophication, and (2) period 1977–1992, the period of hypertrophic state. See also Figure 5.

Period	Group	Slope	Intercept	r^2	P
1968–1976	Clad. Large	0.71	1.27	0.41	0.07
	Clad. Small	0.59	1.15	0.37	0.08
	Chydorus	2.98	−3.77	0.59	0.02
1977–1992	Clad. Large	2.20	−1.97	0.32	0.03
	Clad. Small	−2.15	7.02	0.36	0.01
	Chydorus	−2.61	7.39	0.40	0.01

whereas the group of large-bodied cladocerans was dominated by one species only, *Daphnia galeata*. The changes in population density of three categories, *C. sphaericus*, 'other' small-bodied and large-bodied cladocerans, were investigated for two trends: (1) changes in cladoceran biomass with time (years), and (2) changes in cladoceran biomass with phytoplankton biomass (chlorophyll content). The results of the regression analyses are shown in Tables 1 and 2, and Figures 4 and 5. During the first period (1968–1976), biomass of both *C. sphaericus* and 'other' small-bodied cladocerans increased with time, but large-bodied cladocerans did not significantly increase (Figure 4a, Table 1). During the period 1977–1992, biomass of all three categories did not significantly change with time (Figure 4b, Table 1). When we compare the changes in biomass of cladocerans in relation to the chlorophyll concentration during the period 1968–1976, all three categories of cladocerans increased in biomass with increasing chlorophyll concentration. However, of these three cladoceran categories only *C. sphaericus* showed a distinct and significant increase whereas the other two only showed a marginally significant increase (Figure 5a, Table 2). Therefore, *C. sphaericus* does clearly increase with a higher rate with increasing chlorophyll concentration than 'other' small-bodied cladocerans and large-bodied cladocerans (pairwise comparison of slopes; $P = 0.03$ and $P = 0.04$, respectively). In the period 1977–1992, both *C. sphaericus* and 'other' small-bodied cladocerans and *C. sphaericus* significantly decreased in biomass with increasing chlorophyll concentration, whereas the biomass of large-bodied cladocerans showed a significant positive relationship with chlorophyll concentration (Figure 5b, Table 2). Therefore, large-bodied cladocerans differ significantly in their response to increasing algal biomass from *C. sphaericus* and 'other' small-bodied cladocerans ($P < 0.01$ for both comparisons).

Discussion

We observed that *C. sphaericus* adults in the life table experiments always carried two eggs per brood. This agrees with Robertson (1988) who states that the Chydoridae, with the exception of two sub-families, produce a maximum of two eggs per brood, and only rarely less than two. In life history experiments with *C. sphaericus* the fitness measure *r* was sigificantly higher on natural lake seston from Tjeukemeer, containing ca. 80% detritus versus 20% algae (Gons et al., 1992), than on laboratory cultured green algae. This suggests that detrital particles are good quality food for *C. sphaericus*, even better than a mixed medium of two different green algae (*Chlamydomonas* sp. and *Scenedesmus* sp.) which is generally a good quality food for *Daphnia* (Vijverberg, 1989).

We studied the changes in cladoceran abundance in terms of biomass. However, production would have been a better indicator than biomass of the functional role of these organisms in an ecosystem. Production is a measure of flow of energy or organic matter within a community, thus also of the success of a species or functional group (guild) in a given ecosystem (Benke, 1993). We chose biomass because it is

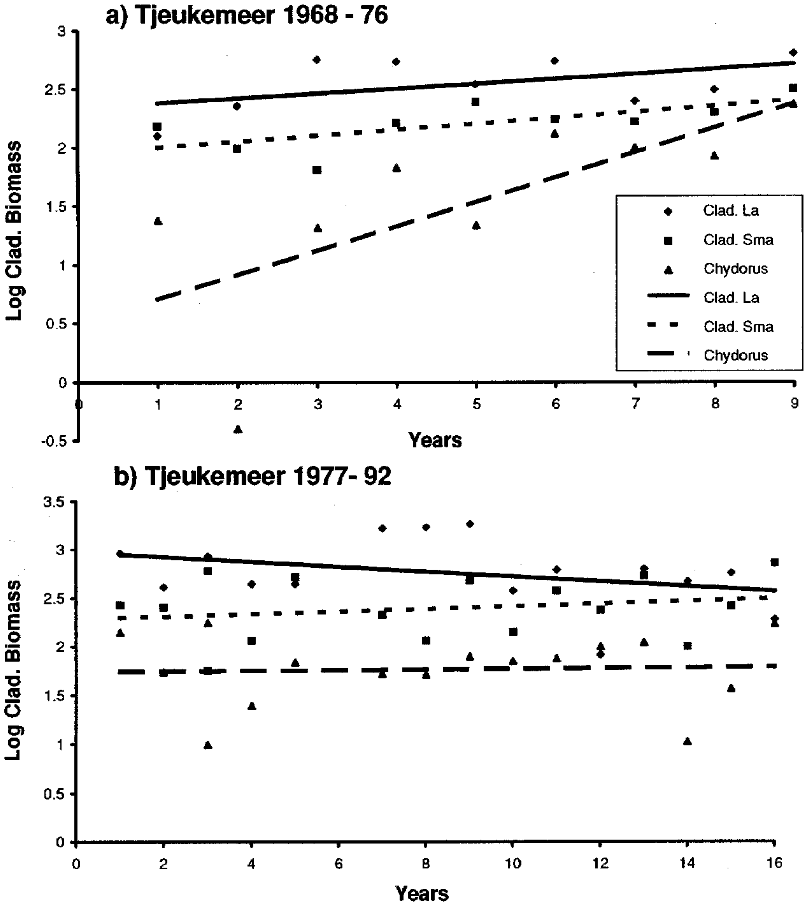

Figure 4. Relation between $\log_{10}$-transformed annual mean cladoceran biomass of large-bodied cladocerans (Clad. La), *C. sphaericus* (Chydorus), and 'other' small-bodied cladocerans (Clad. Sma) as dependent variables and time (year) as the independent variable. Regressions are given for two periods: (a) period 1968–1976, the period of increasing eutrophication, and (b) period 1977–1992, the period of hypertrophic state. For summary statistics see Table 1.

relatively easy to measure, whereas production studies imply the quantification of dynamical parameters such as growth and development, for which we did not have data for the whole study period. However, using species specific P/B ratios we can roughly calculate production. Species specific P/B ratios are based on field observations in Tjeukemeer during the years 1969–1971 and on laboratory observations on growth and development using fresh Tjeukemeer lake seston, carried out during 1970–1973 and in 1982 (Vijverberg 1980; Vijverberg & Richter, 1982; Vijverberg & Koelewijn, 1991; Vijverberg, unpubl.). We observed that the P/B ratios of small-bodied species were about two times higher than those of large-bodied species. Thus, using biomass as a variable we underestimated the impact of the small-bodied species in the system. Taking the P/B ratio's into account, approximately two thirds of the total cladoceran production was realised by small-bodied species and only one third by large-bodied species (mainly *D. galeata*) during the study period.

We tested the hypothesis of Hillbricht-Illkowska (1977) that smaller species will become increasingly more abundant and more dominant over larger species during eutrophication, because small cladoceran species such as *C. sphaericus* are better adapted to detrital food than larger ones, and because filter feeding efficiency of small-bodied cladocerans is less

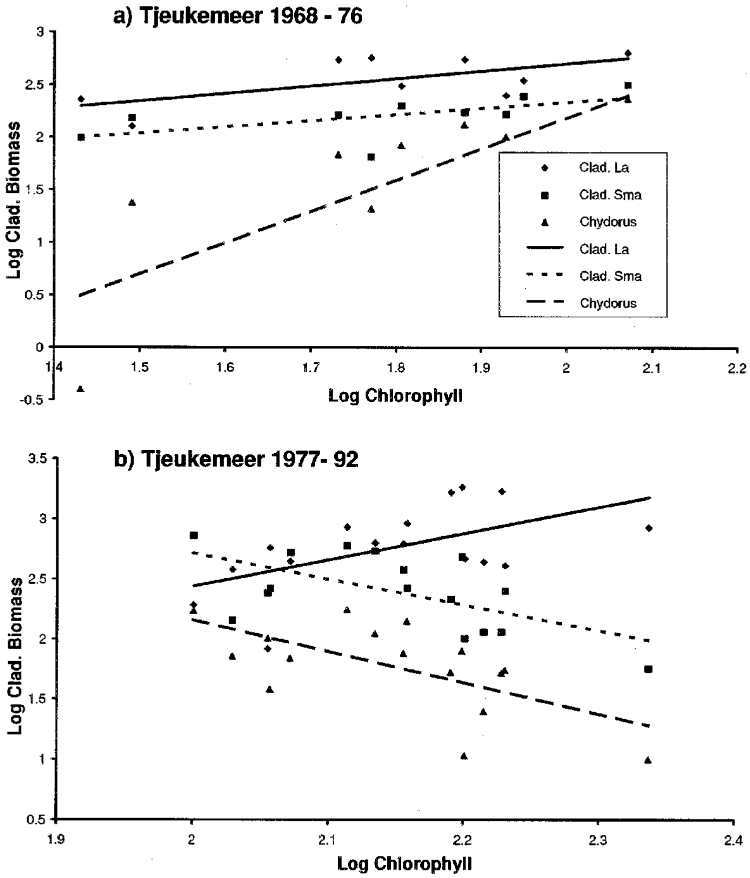

Figure 5. Relation between $\log_{10}$-transformed annual mean cladoceran biomass of large-bodied cladocerans (Clad. La), *C. sphaericus* (Chydorus), and 'other' small-bodied cladocerans (Clad. Sma) as dependent variables and $\log_{10}$-transformed mean annual chlorophyll concentrations the independent variable. Regressions are given for two periods: (a) period 1968–1976, the period of increasing eutrophication, and (b) period 1977–1987, the period of hypertrophic state. For summary statistics see Table 2.

hampered by the presence of large colonial Cyanobacteria than that of large-bodied cladocerans. The results of the first period of our study (1968–1976), the period of increasing phytoplankton biomass, supports the hypothesis of Hillbricht-Illkowska (1977): biomass of all small-bodied cladocerans increased with time, but biomass of large-bodied cladocerans did not. Although all three categories of cladocerans increased in biomass with increasing chlorophyll concentration. Only *C. sphaericus* showed a distinctly significant increase whereas the other two only showed a marginally significant increase with increasing chlorophyll concentration. Therefore, *C. sphaericus* does clearly increase with a higher rate with increasing chlorophyll concentration than 'other' small-bodied and large-bodied cladocerans. The results of our life history experiments also support the idea that *C. sphaericus* is able to utilize detritus efficiently as a resource for growth and production. Our hypothesis that *C. sphaericus,* given its phylogeny, is better adapted to eutrophic conditions than the other small-bodied species, is also supported by the observations during this period of increasing chlorophyll concentration, as *C. sphaericus* then performs better than the other cladocerans. However, the observations during the second period (1977–1992), the period of hypertrophic state, do not support the hypothesis of Hillbricht-Illkowska (1977) nor our '*Chydorus* preadaptation' hypothesis. During this period, we observed a decrease rather than a further increase in the biomass of small-bodied species with increasing chlorophyll concentrations, with both *C. sphaericus* and ‘other’ small-bodied cladocerans showing the same relationship. Furthermore, instead of a decrease of large-bodied cladocerans with increasing phytoplankton biomass, we observed a significant increase. Such an increase in *Daphnia* biomass with increasing phytoplankton biomass, which was dominated by filamentous *Oscillatoria* spp., was not expected. In environments with high concentrations of filamentous Cyanobacteria, small-bodied cladocerans are expected to perform better than large-bodied cladocerans (Webster & Peters, 1978; Hawkins & Lampert, 1989). This has been explained by differences in the carapace gape width. The narrow carapace width in small-bodied cladocerans decreases the probability that filaments are taken in and may become entangled in the filtering limbs to obstruct the feeding process. Rejection movements with the terminal claw remove the filaments, but also the particles already collected, thus reducing the efficiency of feeding and resulting in an increased energetic cost (Burns, 1968; Gliwicz & Siedlar, 1980; Porter & McDonough, 1984). However, inhibition of *Daphnia* feeding by filamentous Cyanobacteria is not a general phenomenon. In several cases high densities of filamentous Cyanobacteria did not inhibit consumption of filaments or other algae present in the phytoplankton assemblage (Holm et al., 1983; Knisely & Geller, 1986; Schaffner et al., 1994; Epp, 1996). Furthermore, life history experiments show that *Daphnia* is growing and reproducing well on a diet of pure cultured *Oscillatoria limnetica*, although not as good as on a high quality diet with *Scenedesmus* as food (Repka, 1996). *Daphnia* also grows and reproduces well on natural seston from Tjeukemeer, which contains a high proportion of *Oscillatoria* filaments: Boersma (1995) observed that growth rate and fecundity for *Daphnia* fed natural seston were only a small fraction lower than for *Daphnia* fed a high quality diet (*Scenedesmus).* Under natural conditions, *Daphnia* often persists during blooms of filamentous Cyanobacteria (Mills & Forney, 1988; present study), most likely by a combination of selectively avoiding some filamentous species and successfully consuming others.

Since it is generally accepted that a high abundance of large-bodied cladocerans is dependent upon a low predation pressure by zooplanktivorous fish (e.g. Hrbacek et al., 1961), we checked for a negative correlation between the mean chlorophyll concentration during the growing season of a specific year and the biomass of 0+ fish in September of the same year, using 12 years of observations on 0+ fish of Tjeukemeer over the period 1976-1987 (W. L. T. van Densen, unpublished). Within the group of zooplanktivorous fish, the 0+ fish are the most important group of vertebrate predators in terms of predation pressure on the zooplankton (Vijverberg et al., 1990). The biomass stock estimate of 0+ fish in September is a reliable measure for the mean biomass of 0+ fish during the growing season (Lammens et al., 1985). There appeared to be a negative relationship between the mean chlorophyll content as the independent variable, and 0+ fish biomass as the dependent variable (slope $= -3.5$, $r^2 = 0.27$, $P = 0.083$, $N = 12$). Although this relationship is only marginally significant, it suggests that fish predation pressure was higher when chlorophyll content was lower. Such a relationship between 0+ fish abundance and chlorophyll content is not unexpected since 0+ fish stocks in Tjeukmeer are unstable due to fisheries management measures affecting the stocks of the main piscivore, pikeperch (*Stizostedion lucioperca*), and hydrological conditions. Until the autumn of 1976, the biomass stock of the pikeperch was kept at a moderate level by an intensive and effective commercial fisheries with gill-nets. This fisheries was abruptly stopped during the winter of 1976/77 when the commercial fisheries in the Frisian Lake District sold their fishing rights for ’scale fish’ to the sport fisheries (Lammens, 1988). Since legal regulations forbid sport fisheries to use gill-nets and angling is much less effective, this resulted in a ca. four times higher biomass stock of piscivorous pikeperch, which in turn resulted in an increased predation pressure upon the 0+ fish and a reduction of the local recruitment of smelt, the dominant fish species in the 0+ age group (Lammens et al., 1985). Therefore, since 1977 passive migration of fish larvae from the nearby IJsselmeer became much more important for the recruitment of young fish in Tjeukemeer (Densen & Vijverberg, 1982). Generally, during spring and summer, waterflow is from the IJsselmeer into the Frisian Lakes System, whereas the direction of waterflow is reversed during autumn and winter. Much depends, however, on weather conditions, with a higher rain fall resulting in less inflow of IJsselmeer water in the Frisian Lakes. Most fish larvae enter the lake during spring. Since IJsselmeer water contains less algae than Tjeukemeer water it is not surprising that 0+ fish abundance and chorophyll content are negatively correlated. We also hypothesize that under hypertrophic conditions with a relatively high chlorophyll content, a high abundance of filamentous Cyanobacteria, and a large proportion of detrital particles in the seston, large daphnids may be competitive dominant over the small-bodied cladocerans. To fully understand the observed trends in zooplankton biomass, experimental research is necessary to investigate the competitive interactions among large-bodied and small bodied-cladocerans under hypertrophic conditions.

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