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The role of climate in shaping zooplankton communities of shallow lakes

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Abstract

We analyzed data from 81 shallow European lakes, which were sampled with standardized methods, for combined effects of climatic, physical, and chemical features of food-web interactions, with a specific focus on zooplankton biomass and community structure. Multiple-regression analysis showed that total phosphorus (TP) generally was the most important predictor of zooplankton biomass and community structure. Climate was the next most important predictor and acted mainly through its effect on pelagic zooplankton taxa. Benthic and plant-associated taxa (typically almost half the total zooplankton biomass) were, however, affected mainly by macrophyte coverage. Neither climate nor TP affected the relation between small and large taxa, and we found only a weak trend with increasing TP of increasing mean crustacean body mass. Dividing the data set into three climate zones revealed a pronounced difference in response to lake productivity between cold lakes, with long periods of ice cover, and the two warmer lake types. These ''ice'' lakes differed from the others with respect to the effect of TP on chlorophyll *a,* the zooplankton : chlorophyll *a* ratio, the chlorophyll *a* : TP ratio, and the proportion of cyclopoids in the copepod community. Our data suggest that bottom-up forces, such as nutrient concentration, are the most important predictors of zooplankton biomass. In addition, climate contributes significantly—possibly by affecting top-down regulation by fish—and may interact with productivity in determining the zooplankton standing biomass and community composition. Hence, the present study suggests that food-web dynamics are closely linked to climatic features.

Top-down influences (predation and grazing) can be just as important as bottom-up forces (potential productivity) in structuring aquatic ecosystems (Carpenter et al. 1985). To broaden our knowledge of this issue, much effort has been directed at assessing the relative importance of top-down and bottom-up regulation of community and ecosystem structure. Many researchers have examined structure and regulation along various gradients, such as habitat productivity, food-chain length, habitat permanency, as well as size, depth, and morphometry of lakes (Hansson 1992; Keller and Conlon 1994; Post et al. 2000).

In addition to the gradient(s) under study, a climate gradient is inherent in many large-scale ecological data sets. Most nutrient-poor lakes are in high latitudes or high altitudes, whereas most nutrient-rich lakes are situated in warmer, lowland regions. Because of this and the complexities of metabolism in natural settings, it is difficult to untangle the effects of temperature from those of nutrients. Several benchmark studies concerning top-down regulation of plankton communities in temperate climates have been published (e.g., Carpenter et al. 2001), and although the reported mechanisms have been general, their importance for lakes in warmer climates is uncertain. It therefore is important to expand our knowledge of how top-down and bottom-up forces interact, not only along nutrient gradients but also along climate gradients.

Because they constitute the link between predators and primary producers, zooplankton communities play an important role, and they reflect the influence of both bottom-up and top-down processes. The relative influences of top-down and bottom-up forces on zooplankton communities can vary with nutrient availability, lake depth, and opportunities for refuge from predation (e.g., amongst macrophytes) (Schriver et al. 1995; Hessen et al. 1995; Jeppesen et al. 2003). Furthermore, changes in the composition of a zooplankton community, determined by lake productivity, also influence density-dependent impacts on phytoplankton (Pace 1984; Sarnelle 1992; Jeppesen et al. 2003).

The warmer climate at lower latitudes is associated with a shift toward omnivorous species of fish, which may exert a strong, negative effect on zooplankton, both through planktivory and through reducing algal biomass (Lazzaro et al. 2003; Blanco et al. 2004). In addition, the tendency at higher temperatures for fish to have multiple spawning opportunities, smaller size, and increased feeding intensity also points toward a higher predation pressure on zooplankton (Persson 1986). The effects on the zooplankton community from increased predation can include a lowered proportion of large, predation-sensitive species and a resulting decrease in the mean size of zooplankton (Hansson et al. 2004). A decrease in intraspecific body size may also come about through physiological mechanisms, either because of plasticity in life history or because of competitive exclusion (Moore and Folt 1993; Weetman and Atkinson 2004). Bottom-up effects caused by changes in temperature may be expected as well.

The contribution of cyanobacteria to the total phytoplankton biomass has been shown to increase with temperature. Because cyanobacteria are characterized as being less edible, their increased proportion would be expected to result in a negative impact on the zooplankton community of warmer climates. In attempting to explain among-lake differences in zooplankton communities, the problem of deciding between top-down or bottom-up influences is intractable using correlative studies; however, some information can be drawn from the ratios between trophic levels. A high ratio between planktivorous fish and zooplankton biomass should indicate a high ability of fish to control zooplankton. The ratio between zooplankton and phytoplankton biomass is sensitive to changes in top-down control—through cascading trophic interactions from fish to zooplankton and on to phytoplankton—and a low ratio may be indicative of top-down control (Jeppesen et al. 2000; Hessen et al. 2003). This ratio could also be affected, of course, by the proportion of inedible phytoplankton and by the availability of energy sources of allochthonous origin (Ghadouani et al. 2003; Pace et al. 2004). Irrespective of whether the changes result from bottom-up or top-down effects, we therefore expect a lowered zooplankton biomass, body size, and ability to control the phytoplankton community in warmer compared to colder lakes.

Our data set encompasses mainly shallow lakes, the ecology of which can be quite distinct from that of deeper lakes. The lakes we studied are shallow enough to have a potentially large fraction of their lake area invaded by macrophytes. Vegetation, when present, can affect zooplankton communities by acting as a refuge for larger, mainly pelagic

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Table 1. Physical, chemical, and biological characteristics of the 81 study lakes given as the range, mean, and median of each variable.

Variable	Range	Mean	Median
Lake size (km^2)	0.001–270	5.6	0.24
Mean depth (m)	0.4–3.9	1.7	1.5
Average air temperature during the warmest month (°C)	11.0–27.0	17.8	17.2
Duration of ice cover (months)	0–8	1.7	1
Conductivity (μS cm^{-1})	9–18,000	889	314
pH	5.0–9.8	8.1	8.2
Total phosphorus (μg L^{-1})	4.0–532	100	55
Total nitrogen (μg L^{-1})	238–11,500	1,638	1192
PVI (%)	0–100	18.7	6.1
Chlorophyll a (μg L^{-1})	0.5–378	39.6	20.8
Zooplankton biomass (μg L^{-1})	4.7–5,161	477	289
Planktibenthivorous fish CPUE (g net^{-1} night^{-1})	0–29,600	2,770	985

species, such as *Daphnia,* and also by expanding the habitat for benthic and macrophyte-associated species (Jeppesen et al. 1997*b*). Under oligotrophic and hypertrophic conditions, Plant cover is low under oligotrophic and hypertrophic conditions but can vary considerably under intermediate conditions, as can the density of plants within beds (Jeppesen et al. 1997*b*). Plant cover and density also are variable in temperate and warmer climates but typically are more sparse

Fig. 1. Distribution of the study lakes. The different symbols denote the climate zone to which the lakes were designated (filled circles, ''ice'' lakes; diamonds, ''cool'' lakes; open squares, ''warm'' lakes). Some of the symbols represent a cluster of lakes, and next to such symbols, the number of lakes in that particular cluster is denoted.

in arctic or subarctic areas. We therefore expect macrophyte cover to have effects that are, to some degree, independent of those related to the other investigated parameters (climate, productivity, and predation). Increased macrophyte cover can have positive effects on zooplankton biomass through its role as a refuge for pelagic species, but this effect is not linear. At some point, increased macrophyte cover will affect these pelagic zooplankton species negatively. This can occur through negative effects on phytoplankton biomass and increased competition for resources (within the macrophyte bed) from macrophyte-associated species that are better adapted to this environment (Jeppesen et al. 1997*b*). Thus, regarding positive effects of macrophyte cover on zooplankton biomass, we expect its clearest expression to be in the benthic or macrophyte-associated species.

Our primary aim in the present study was to determine if and how climate affects zooplankton community biomass and composition. Second, we wanted to relate the effects of climate to those of potential productivity and predation (bottom-up and top-down influences) and see if these differ along a climate gradient. The present study was based on a large data set, with 81 lakes being sampled according to a standardized methodology. Because of the correlative nature of our data, it was not possible to draw conclusions about mechanisms through which climate could affect zooplankton communities. Nevertheless, this unique data set did provide us with the opportunity to test some of the existing predictions about how zooplankton communities will vary along a climate gradient.

Materials and methods

Lakes studied—The present study included data from 81 shallow lakes (mean depth, <4 m) across Europe. The lakes represent a wide range of sizes and nutrient concentrations (Table 1) and are spread across 10 countries (38–68°N, 9°W to 27°E)—Sweden, Finland, Estonia, Denmark, Poland, the United Kingdom, Ireland, The Netherlands, Germany, and Spain—and thus are representative of several climatic regions (Fig. 1). Most lakes were sampled twice in the year 2000 (first from late June to late July and then once between the end of July and the end of September) and once in the
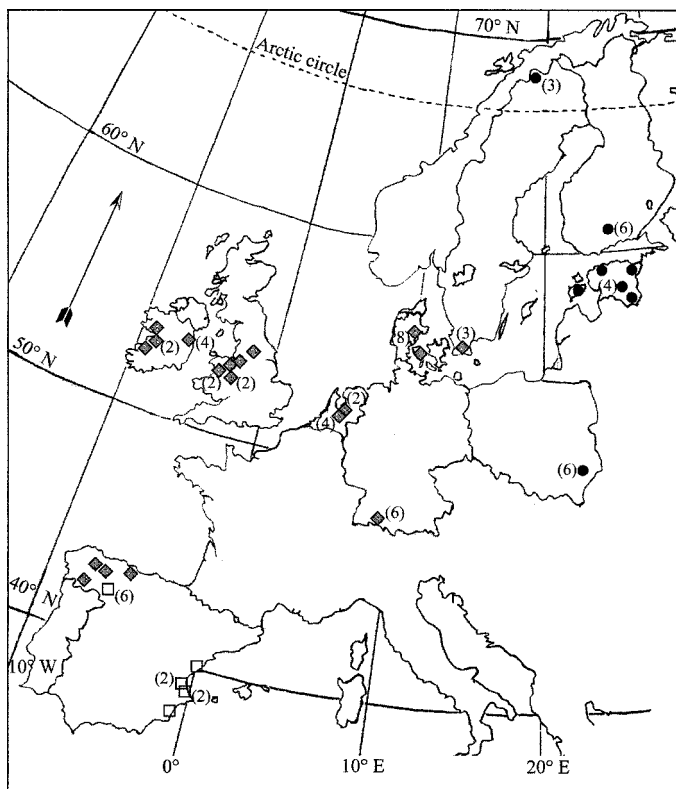
year 2001 (between the end of June and the beginning of September).

Variables sampled—All methods were standardized according to a common protocol, which has been described in detail by Moss et al. (2003). A further description of nutrient and chlorophyll analyses can be found in Nõges et al. (2003). Here, only a brief description of the methods is given.

Zooplankton samples were obtained by taking integrated tube samples (diameter, 95 mm) or combined samples from three depths at 10 (year 2000) or 5 (year 2001) locations in each lake along a transect running from the shore to the center of the lake. One (year 2000) or two (year 2001) liters from each sampling point were pooled to give a 10-liter sample. The combined samples were filtered through a 50-μm net, and the animals retained on the net were preserved with Lugol's iodine. Counting was performed at $\times$40 (cladocerans and copepods) and $\times$100 (rotifers) magnification. Biomass of rotifers was calculated using standard dry weights from Bottrell et al. (1976) and Dumont et al. (1975) or standard carbon weights from Latja and Salonen (1978), Telesh et al. (1998), and Lehtovaara and Sarvala (unpubl. data). In the year 2000, the biomass of cladocerans was calculated from length–weight relationships presented by Bottrell et al. (1976), Dumont et al. (1975), Culver et al. (1985), Luokkanen (1995), and Lehtovaara (unpubl. data). In 2001, standard weights, calculated from the previous year's results, were used to estimate biomass. Carbon weight was converted to dry weight by multiplication with a conversion factor of 2.2 (Jeppesen et al. 2002).

On all sampling occasions, water for total phosphorus (TP) and phytoplankton chlorophyll *a* (Chl *a*) analyses were taken from an integrated tube sample obtained from the center of the lake. Composition and abundance of fish were determined by test fishing with 42-m, multimeshed gill nets (mesh size, 6.25, 8, 9, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, and 75 mm). The number of nets per lake was proportional to the lake area, up to a maximum of eight nets (Moss et al. 2003). Data represent the average catch among nets, expressed as catch per unit effort (CPUE; g net^{-1} night^{-1}). Because of legal restrictions in some countries, fishing was performed in only a subset of the lakes (*see Table 4 for details*).

Macrophyte abundance, expressed as the percentage of volume infested (PVI), was measured by estimating plant coverage and height at 10-m intervals along transects from the lakeshore to the lake center. The estimate was done by inspecting the lake bottom through a water glass at each point along the transect or, if visibility was low, by taking random samples with a rake at each point. Up to 20 transects per lake were sampled, depending on the lake size (Moss et al. 2003).

Statistical analyses were performed on averaged values from up to three samplings, except for PVI and fish data, for which data from only one sampling (late summer to autumn 2000) were available. The data from the early summer 2000 sampling were combined with the data from the two late summer to autumn samplings to produce averages of all samplings; this decreased the scatter and normalized the

data. Furthermore, inclusion of the early summer data had a negligible effect on the results.

The data were analyzed in three steps. First, the responses in biomass and community composition of zooplankton were examined. To describe important changes in community structure, the relative abundances of some selected key taxa were enumerated: the percentage of *Daphnia* in the total cladoceran biomass, the percentage of rotifers in the total zooplankton biomass, and the percentage of cyclopoids in total copepod biomass. Changes in zooplankton size structure were investigated by dividing the data into functional taxonomic groups: ''large'' (advanced stages of copepods and large cladocerans), and ''small'' (nauplii, rotifers, and small cladocerans). In addition, crustacean body weight was used to examine changes in size. Second, to study the impact of vegetation on community composition, the two functional groups were divided further into two subgroups: pelagic versus benthic or plant-associated taxa (Table 2). Third, to evaluate the relative influence of top-down and bottom-up forces, the biomass of each trophic level (phytoplankton, zooplankton, and fish [the sum of planktivorous and benthivorous fish]) as well as the ratios of these were examined.

All dependent variables were investigated using multiple regression (stepwise procedure, variables entered the analysis if $p \leq 0.1$) to determine the possible effect of the independent variables: morphometry (lake size), potential productivity (TP), plant abundance (PVI), and climate. Residuals were checked for normality and homogeneity of variance. If neither criterion was met, the variables were transformed ($\log_{10}$, $\log_{10} + 1$, or arcsine of square root) before analysis. As mentioned, fish and PVI data were available for only a subset of the lakes; when these were not significant as predictors, regressions were rerun that omitted them from the model to increase the power of the test.

Selecting variables that will give a reasonable description of the climate regime is important. Experiments and time-series analyses have shown that both winter and summer temperatures have effects on zooplankton community development and succession in European lakes, but the effects of winter temperature usually do not last longer than through early summer (Gerten and Adrian 2000; Mckee et al. 2002). In these studies, however, temperature differences found during the winter were small, and the lakes did not have long periods of ice cover, which may affect the fish fauna. We used the average of the mean air temperature during the warmest month of summer (for as many years as we could find for each local region) as a proxy for the summer climate, and we used the duration of ice cover to describe the winter climate. In our data set, two rather distinct groups of lakes were identified with respect to the duration of ice cover (Fig. 2): one with short or no ice cover ($<$2 months), and one with long periods of ice cover ($>$4 months). A between-group check of lakes lying within a comparable range of summer temperatures showed effects of ice-cover duration on small zooplankton taxa (one-way ANOVA; $F_1 = 4.8$, $p = 0.03$ and $F_1 = 6.7$, $p = 0.01$ for pelagic and benthic or plant-associated taxa, respectively) and on fish (one-way ANOVA; $F_1 = 4.4$, $p = 0.047$). Hence, we judged winter conditions to be important for the description of lake climate and, thus, integrated summer temperature and duration of ice

Table 2. The genera found in the present study, of which most species were considered to be either pelagic or plant-associated/benthic in their habitat choice. Many genera include species of both types, and we assigned a genus to a specific group only when we thought it fit to say that a majority of the species were similar in habitat choice. Hence, some rotifer genera were included in both groups in all statistical procedures (*Bipalpus, Collotheca, Hexarthra, Lepadella, Anureopsis, Colurella, Conochilus, Eosphora, Epiphanes, Euchlanis, Floscularia, Macrochaetus, Monommata, Mytilinia, Platyias, Ploesoma, Pompholyx, Proalides, Sinantheria, Testudinella, Trichotria,* and *Tripleuchlanis* sp.). Calanoid and cyclopoid copepods include both copepodites and adults.

Large	Small	
"Pelagic"		
Crustaceans:	Crustaceans:	Rotifers:
Bythotrepes	*Bosmina*	*Ascomorpha*
Daphnia	*Ceriodaphnia*	*Asplanchna*
Diaphanosoma	*Chydorus sphaericus*	*Brachionus*
Holopedium	Nauplii	*Filinia*
Limnosida		*Gastropus*
Leptodora		*Kellicottia*
Polyphemus		*Keratella*
Cyclopoid copepods		*Polyarthra*
Calanoid copepods		*Synchaeta*
"Plant-associated or benthic"		
Crustaceans:	Crustaceans:	Rotifers:
Eurycercus	*Chydorus**	*Cephalodella*
Camptocercus	*Graptoleberis*	*Dicranophorus*
Acroperus	*Pleuroxus*	*Elosa*
Alonopsis	*Rhynchotalona*	*Lecane*
Simocephalus	*Disparalona*	*Rotatoria*
Scapholeberis	*Alonella*	*Trichocerca*
Sida	*Alona*	
Ophryoxus	*Biapertura*	
Leydigia	*Oxyurella*	
Latona	*Moina*	
Iliocryptus	*Streblocerus*	
	Drepanothrix	
	Pseudochydorus	
	Anchistropus	
	Macrothrix	

* Except *C. sphaericus.*

cover into a single parameter using a principal component analysis (PCA) approach. A PCA using the unrotated factor solution produced one component explaining 72% of the variation in the two variables. The scores from the PCA were used as an independent variable in the multiple-regression analysis. Summer temperature was positively correlated ($r = 0.85$), and duration of ice cover was negatively correlated ($r = -0.85$), with this PCA component; hence, a higher score represents a warmer climate. This approach has the advantage of integrating factors, such as the differences in altitude, latitude and that between coastal and inland climates, into a single variable.

A main purpose of the present study was to investigate the effects of climate. To do so more closely, and to study the possible interactions with other independent variables, the lakes were divided into three climate zones. First, lakes with mean temperatures below and above 20°C during the
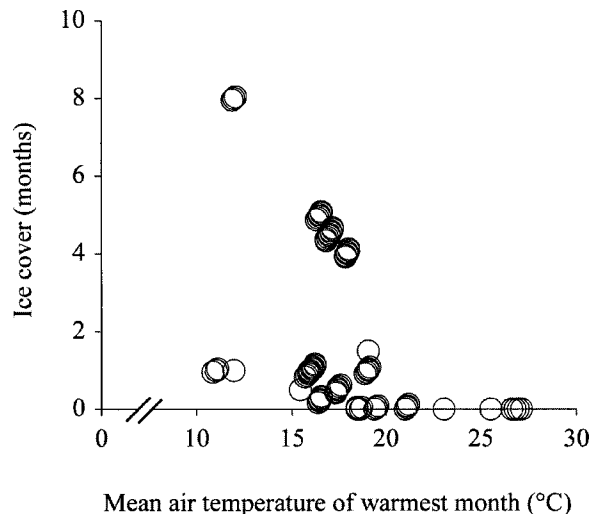

Fig. 2. Distribution of the two variables used to describe climate: number of months with ice cover during winter, and mean air temperature during the warmest month of summer. To allow viewing of all data, the data points were slightly scattered diagonally when they overlapped.

warmest summer month were separated. Lakes with temperatures exceeding 20°C are hereafter referred to as "warm." Second, lakes with temperatures below 20°C were divided according to the duration of ice cover. Lakes with 4 months or more of ice cover were termed "ice" lakes, and lakes with <4 months of ice cover were called "cool" lakes. The data for each climate zone were then examined separately using stepwise multiple regression. Fish were not used as an independent variable in this part of the analysis, because the sample size from two of the climate zones was too small.

Results

Zooplankton community effects—Multiple-regression analysis showed that total zooplankton biomass was positively related to TP and PVI and was negatively related to climate, with TP being the most important predictor, climate the second, and PVI the third (Table 3). The contribution of *Daphnia* sp. to cladoceran biomass and of cyclopoids to total copepod biomass both increased with increasing TP, but the relation was not so clear for the copepods. The positive relation between TP and the contribution of *Daphnia* sp. to cladoceran biomass was a consistent pattern across all three zones (Fig. 3), but it was not statistically significant in the warm zone, where *Daphnia* sp. were rare (Table 4). The increase in the proportion of cyclopoids with increased TP that was recorded for the total data set was driven mainly by the results from the ice zone (Fig. 3). The multiple-regression analysis, however, showed that the share of cyclopoids was more closely related to lake area in this zone (Table 4). No clear trend with TP was found for the percentage of rotifers relative to the total zooplankton biomass in the total data set and in any of the climate zones (Fig. 3; Tables 3, 4). Rotifers did decrease, however, with PVI in the cool zone (Table 4).

No impact of climate on zooplankton size was apparent

Table 3. Multiple regression (stepwise procedure) with the following dependent variables: CHLA, $\log_{10}$(chlorophyll *a*); ZOO, $\log_{10}$(total zooplankton biomass) CPUE, $\log_{10}$((catch per unit effort of planktibenthivorous fish) + 1)); LPEL, $\log_{10}$(biomass of large pelagic zooplankton); SPEL, $\log_{10}$(biomass of small pelagic zooplankton); LBEN, $\log_{10}$(biomass of large benthic zooplankton); SBEN, $\log_{10}$(biomass of small benthic zooplankton); CYC, arcsine(square root[percentage of cyclopoids of the total copepod biomass/100]); DAP, arcsine(square root[percentage *Daphnia* of the total cladoceran biomass/100]); ROT, arcsine(square root[percentage rotifers of the total zooplankton biomass/100]); PLA:ZOO, fish:zooplankton ratio; ZOO:CHLA, zooplankton:chlorophyll *a* ratio; CHLA:TP, chlorophyll *a*:total phosphorus ratio. Independent variables were: TP, $\log_{10}$(total phosphorus); AREA, $\log_{10}$(lake area); PVI, arcsine(square root[percentage volume of the lake infested by macrophytes/100]); CLIM, (PCA score, where positive values correspond to "warmer" climate); CPUE (not used when it was examined as dependent variable). Zooplankton variables are expressed as μg L^{-1} (dry weight), and all percentages are calculated from biomass data. Both CHLA and TP are expressed as μg L^{-1}. Fish CPUE is expressed as g net^{-1} night^{-1} (wet weight) and lake area as km^2. Probability levels of *t*-values for coefficients are denoted as follows: † $0.10 > p > 0.05$, * $0.05 \geq p > 0.01$, ** $0.01 \geq p > 0.001$, and *** $p \leq 0.0001$.

	Coefficients						Regression statistics			
Variable	Intercept	TP	CLIM	PVI	AREA	CPUE		p	r^2	n
Zooplankton community variables										
ZOO	0.71**	0.88***	−0.20***	0.38*			$F_3 = 19.7$	<0.001	0.49	65
CYC	0.65**	0.26*					$F_1 = 5.4$	0.023	0.06	81
DAP	0.06	0.30***		−0.31*			$F_2 = 10.6$	<0.001	0.26	64
ROT								NS		
Size and habitat										
LPEL	0.63*	0.78***	−0.15*		0.12†		$F_3 = 13.2$	<0.001	0.34	81
SPEL	0.39	0.83***	−0.21*	0.36†			$F_3 = 10.7$	<0.001	0.34	65
LBEN	−0.20*			0.65***			$F_1 = 12.2$	0.001	0.16	65
SBEN	−0.24	0.60***		0.74***			$F_2 = 11.9$	<0.001	0.28	64
Trophic structure										
CHLA	−0.50**	1.0***			0.15***		$F_2 = 72.0$	<0.001	0.65	80
CPUE	1.5**	0.90**	0.25†				$F_2 = 9.2$	0.001	0.37	34
PLA:ZOO	0.67***		0.44***				$F_1 = 14.0$	0.001	0.31	33
ZOO:CHLA	0.96***		−0.29***	0.65**			$F_2 = 9.8$	<0.001	0.24	64
CHLA:TP	−0.48***				0.15***		$F_1 = 12.6$	0.001	0.14	80

in the analysis of taxonomic composition; that is, no effects of climate on large taxa, such as *Daphnia* sp., or on small taxa, such as rotifers, were found (Table 3). *Daphnia* sp. were scarce, however, in the warm zone (Fig. 3). Changes in the size distribution within taxa may have been overlooked by our analysis, because standard weights were used to calculate rotifer biomass. Use of this procedure meant that only crustaceans could be tested for changes in body mass. Multiple stepwise regression using mean body mass ($\log_{10}$ transformed) as the dependent variable showed only a weak, nonsignificant trend of increasing mean crustacean biomass with TP ($F_1 = 3.5$, $p = 0.07$, $r^2 = 0.05$, $n = 65$). Mean body mass of cyclopoid copepods and *Daphnia* sp. showed a positive relation with TP and a negative one with fish ($F_2 = 9.1$, $p = 0.001$, $r^2 = 0.36$, $n = 36$ and $F_2 = 8.9$, $p = 0.002$, $r^2 = 0.49$, $n = 22$, respectively). Calanoid body mass showed a negative relation with fish ($F_1 = 6.5$, $p = 0.02$, $r^2 = 0.19$ $n = 29$).

The importance of habitat—The increase in total zooplankton biomass with increasing TP was mainly caused by the response of pelagic taxa (Table 3). Benthic or plant-associated taxa were best predicted by PVI, although TP significantly improved the regression for small taxa (Table 3; Fig. 4). No difference in response to TP was found between large and small pelagic taxa (ANCOVA; $F_1 = 0.002$, NS for slope and $F_1 = 0.06$, NS for intercept). The increase

in pelagic taxa with higher TP was similar in all climate zones. The positive effect of PVI on the biomass of benthic taxa was visible for large taxa only when the material was divided into zones, and then only in the ice and cold zone (Table 4).

Trophic structure—Stepwise multiple regression showed that TP was the most important predictor for all three trophic levels: phytoplankton, zooplankton, and fish (Fig. 5). Chlorophyll *a* was positively related to TP and lake area, and fish biomass was positively related to TP and climate (Table 3). With respect to the slope of the response to TP, no difference was found between phytoplankton, zooplankton, and fish (ANCOVA; $F_2 = 1.8$, NS for the interaction term). Accordingly, the fish:zooplankton ratio and the zooplankton:Chl *a* ratio were not related to TP, but they were related to climate, either positively (fish:zooplankton ratio) and negatively (zooplankton:Chl *a* ratio) (Fig. 6; Table 3).

When the data were divided into the three climate zones, TP remained the most important predictor for all three trophic levels in all zones, except among warm lakes, where fish CPUE was positively related to lake area (Table 4). This result is very dependent, however, on one lake (Albufera, Spain), which has a surface area two to three orders of magnitude larger than those of the other lakes. Both slope and intercept of the Chl *a* regression differed significantly among climate zones (ANCOVA; $F_2 = 4.9$, $p < 0.05$ and $F_2 = 4.0$,
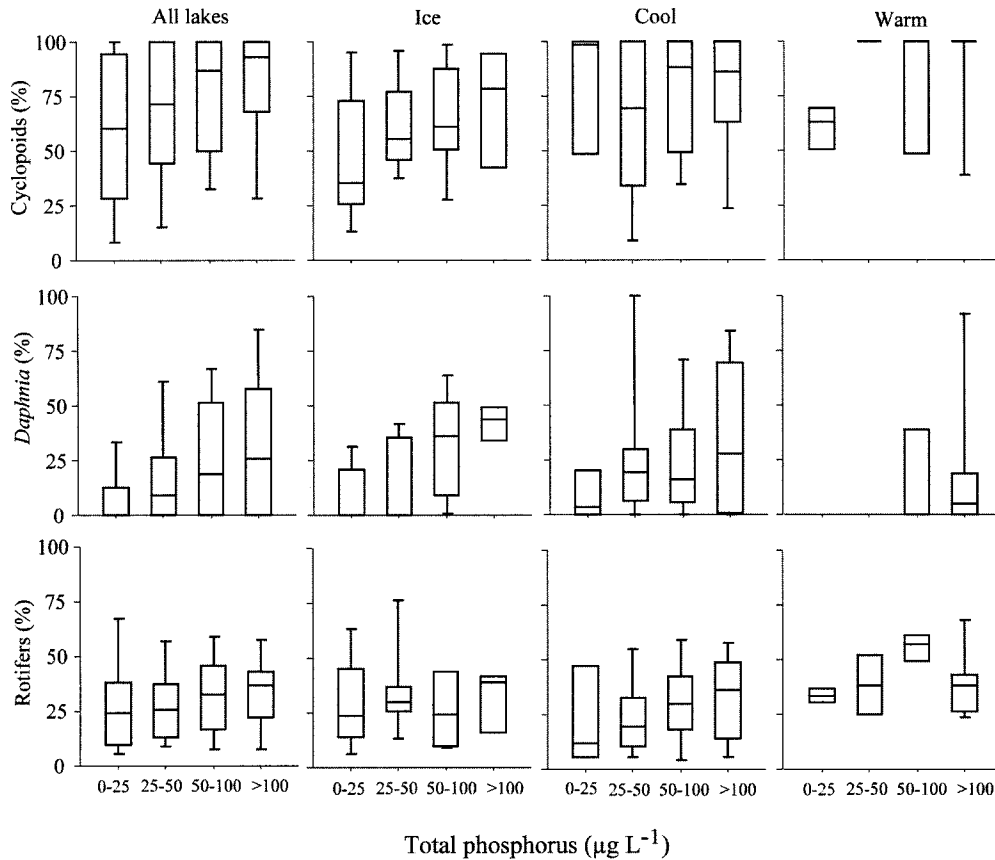
Fig. 3. The relation between TP and the relative biomass of some key taxonomic groupings in the zooplankton community. To aid interpretation of the data, the data are presented as boxplots showing the 10%, 25%, 50%, 75%, and 90% percentiles for four TP classes.

$p < 0.05$, respectively), with the ice lakes showing the steepest slope (Fig. 5). For zooplankton, however, no difference in intercept or slope among zones was found (ANCOVA; $F_2 = 1.9$, NS for intercept and $F_2 = 1.4$, NS for slope). Although the slope of the TP versus fish regression seemed to be less steep in the warm zone, the low number of samples from the warm zone reduced the power of the test, and the slopes and intercepts among climate zones did not differ (ANCOVA; $F_2 = 0.5$, NS for intercept and $F_2 = 0.3$, NS for slope). In the ice zone, the slope of the relation between TP and Chl a was steeper than that for zooplankton and fish (Fig. 5). A significant negative relation in the ice zone between TP and the zooplankton : Chl a ratio was found, as well as a positive relation between TP and the Chl a : TP ratio (Table 4). No similar relations were found in the two other climate zones. In the warm zone, fish biomass varied only negligibly over a wide range of TP concentrations, but no significant relation between TP and the fish : zooplankton ratio was found in any climate zone.

The analyses of the different climate groups may have been affected by the differences in lake area and PVI found between climate zones (Table 5). A trend toward higher TP and fish CPUE also was observed in the warmer climate zones (one-way ANOVA; $F_1 = 2.7$, $p = 0.07$ for TP and $F_1 = 2.7$ $p = 0.09$ for CPUE).

Discussion

In our study lakes, the concentration of TP, a classic bottom-up variable, explained most of the variation in zooplankton biomass and much of the variation in community composition. Not all taxa were affected to the same extent, however, and the strength of the relationship with TP sometimes differed across climate zones. The most important finding in the present study was that inclusion of a climatic parameter significantly improved prediction of the total zooplankton biomass—mainly through climate's effect on pelagic taxa. As expected, prediction of the total zooplankton biomass was improved by including PVI in the model—that is, the vegetation had a positive effect on the biomass of benthic and macrophyte-associated species.

Jeppesen et al. (2003) found a unimodal relationship, along a TP gradient, for the contribution of *Daphnia* sp. to cladoceran biomass, peaking at 500 μg P L^{-1} for shallow lakes. In apparent contrast, we found a monotonic increase in the share of *Daphnia* sp. with increasing TP. These results may not be contradictory, however, because we covered a narrower range of TP than did the previous study. Jeppesen et al. (2003) attributed the decline in the share of *Daphnia* sp. toward low TP to three factors: increased predation risk because of higher water clarity, longer exposure to predators

Table 4. Multiple regression (stepwise procedure) performed on data divided into three climate zones. Variable names and probability level of *t*-values are as denoted in Table 3. In this analysis only, however, TP, PVI, and AREA were used as independent variables.

Variable	Climate zone	Coefficients				Regression statistics			
		Intercept	TP	PVI	AREA		p	r^2	n
Zooplankton community variables									
ZOO	Ice	0.93***	0.92***	0.40*		$F_2 = 34.1$	<0.001	0.80	21
	Cool	1.2**	0.68***			$F_1 = 26.3$	<0.001	0.39	43
	Warm	0.25	1.1**			$F_1 = 14.2$	0.003	0.54	14
CYC	Ice	1.0***			0.36***	$F_1 = 34.9$	<0.001	0.61	24
	Cool						NS		
	Warm						NS		
DAP	Ice	−0.11	0.40**	0.55*		$F_2 = 6.3$	0.009	0.41	21
	Cool	−0.12	0.31*			$F_1 = 4.1$	0.05	0.09	43
	Warm	−0.57	0.42†			$F_1 = 3.3$	0.099	0.23	13
ROT	Ice						NS		
	Cool	0.55***		−0.36*		$F_1 = 4.2$	0.05	0.12	34
	Warm						NS		
Size and habitat									
LPEL	Ice	0.76*	0.86***			$F_1 = 21.8$	<0.001	0.50	24
	Cool	0.58	0.73***			$F_1 = 14.1$	0.001	0.26	43
	Warm	−0.18	1.0**			$F_1 = 9.6$	0.009	0.44	14
SPEL	Ice	0.51†	0.95***	0.52†		$F_2 = 22.2$	<0.001	0.71	21
	Cool	0.76*	0.65***			$F_1 = 11.5$	0.002	0.22	43
	Warm	0.06	1.0**			$F_1 = 15.5$	0.002	0.56	14
LBEN	Ice	0.11		1.4***		$F_1 = 14.7$	0.001	0.43	21
	Cool	0.09		1.2***		$F_1 = 14.5$	0.001	0.31	34
	Warm						NS		
SBEN	Ice	−0.53*	1.1***		0.21***	$F_2 = 43.0$	<0.001	0.80	24
	Cool	−0.02	0.48*			$F_1 = 6.3$	0.02	0.13	43
	Warm						NS		
Trophic structure									
CHLA	Ice	−1.1***	1.4***		0.14*	$F_2 = 77.0$	<0.001	0.90	21
	Cool	0.25	0.64***	−0.46†		$F_2 = 14.4$	<0.001	0.49	33
	Warm	−0.84	1.1**			$F_1 = 16.5$	0.002	0.58	14
CPUE	Ice	1.2	0.90†			$F_1 = 3.2$	0.09	0.17	18
	Cool	0.80	1.3*			$F_1 = 6.4$	0.04	0.44	10
	Warm	3.9***			0.34†	$F_1 = 5.0$	0.09	0.56	6
ZOO:CHLA	Ice	2.3***	−0.58**			$F_1 = 10.4$	0.004	0.32	24
	Cool	0.91***		0.61†		$F_1 = 3.6$	0.07	0.10	33
	Warm						NS		
CHLA:TP	Ice	−1.1***	0.41***		0.14*	$F_2 = 13.7$	<0.001	0.57	24
	Cool	0.25	−0.36*	−0.46†		$F_2 = 3.6$	0.04	0.19	33
	Warm						NS		

because of a longer development time mediated by low food, and a higher degree of benthic facilitation of the potentially zooplanktivorous fish. In the warm lakes of the present study, the share of *Daphnia* sp. generally was low, most likely because of higher predation risk in these lakes, where small fish that have several cohorts per year (e.g., *Gambusia*) are important (Blanco et al. 2004).

Rotifers made up slightly <30% of the total zooplankton biomass in the overall data set and did not respond to changes in TP. This concurs with the results of Hessen et al. (1995) and Jeppesen et al. (2000), although the share of rotifers generally was lower in their studies compared to the present.

In a study on subtropical lakes, Bays and Crisman (1983) found an increase in rotifer biomass with increased lake productivity, suggesting that climate differences may be involved in the response of rotifers to productivity. This suggestion was not corroborated, however, by the present study.

A common pattern found in field studies and experiments with copepods is an increase in cyclopoid relative to calanoid copepods under the conditions of either an increase in productivity (Jeppesen et al. 2000; Hansson et al. 2004) or an increase in fish predation (Hurlbert et al. 1986; Hessen et al. 1995). The relative abundance of calanoids and cyclopoids is regulated by competitive effects of calanoids on
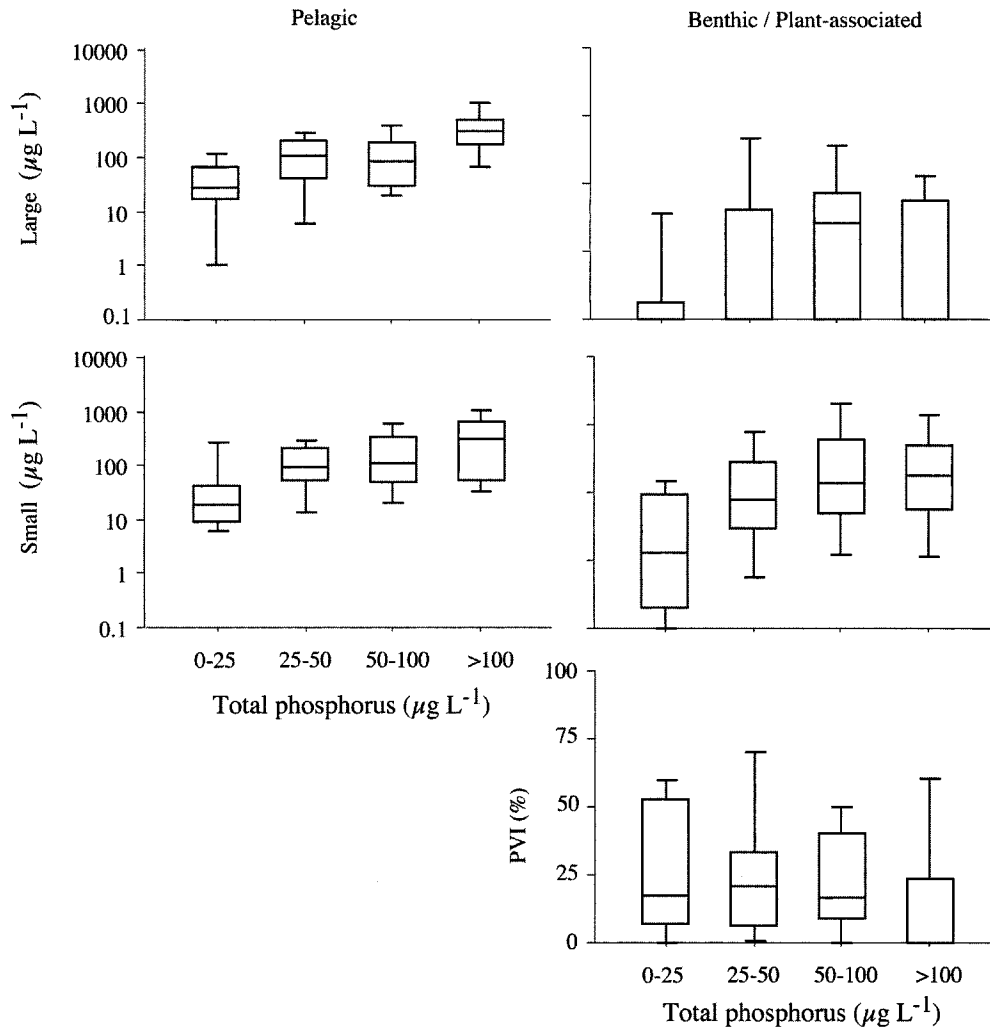
Fig. 4. The relation between TP and the dry weight biomass of large (top) and small taxa (bottom), divided into pelagic (left) and benthic or plant-associated taxa (right). The relation of PVI with TP is added for comparison. Boxplots show the 10%, 25%, 50%, 75%, and 90% percentiles for four TP classes.

cyclopoid nauplii, which are mediated both by effects in the phytoplankton community and by effects of cyclopoid predation on calanoid juveniles (Soto and Hurlbert 1991). The effect of an increasing nutrient concentration on this balance is to increase the survival of cyclopoid juveniles, which are inferior competitors for food (Neill and Peacock 1980). The effect of planktivorous fish on the relative abundance of copepods can be both direct, such as through predation, and indirect, such as through grazers (e.g., *Daphnia* sp.) that compete with copepods for phytoplankton and depress rotifer populations, a potentially important food source for omnivorous cyclopoids (Hurlbert and Mulla 1981; MacIsaac and Gilbert 1989). Although it is unclear what mechanisms are involved in our set of lakes, the significant increase in cyclopoids, relative to calanoids, with increasing productivity supports the hypothesis that the balance between calanoids and cyclopoids is influenced by a food bottleneck affecting cyclopoid copepods.

The expected decrease in zooplankton body size in warm-er climates was not evident in the present study. We found a weak trend of decrease in body size for certain predation-sensitive taxa (against increased fish CPUE), but we did not see an effect of climate on crustacean body size or a shift toward smaller taxa. Our results thus seem to contradict those of other studies that present a negative relationship between temperature and body size of ectotherms in general and of zooplankton in particular (Atkinson 1994; Gillooly and Dodson 2000). Theoretical studies showing that life-history trade-offs may lead to lower body size at high temperature mention abundant food resources as a prerequisite for their models (Atkinson and Sibly 1997). In field studies such as the present, food abundance varies because of a number of factors that may conceal climate effects. In its approach, the present study also differs from the study of New World water bodies by Gillooly and Dodson (2000). They found an increased body size at higher latitudes, but they included only pelagic, herbivorous zooplankton in their study. Our inclusion of benthic and macrophyte-associated species
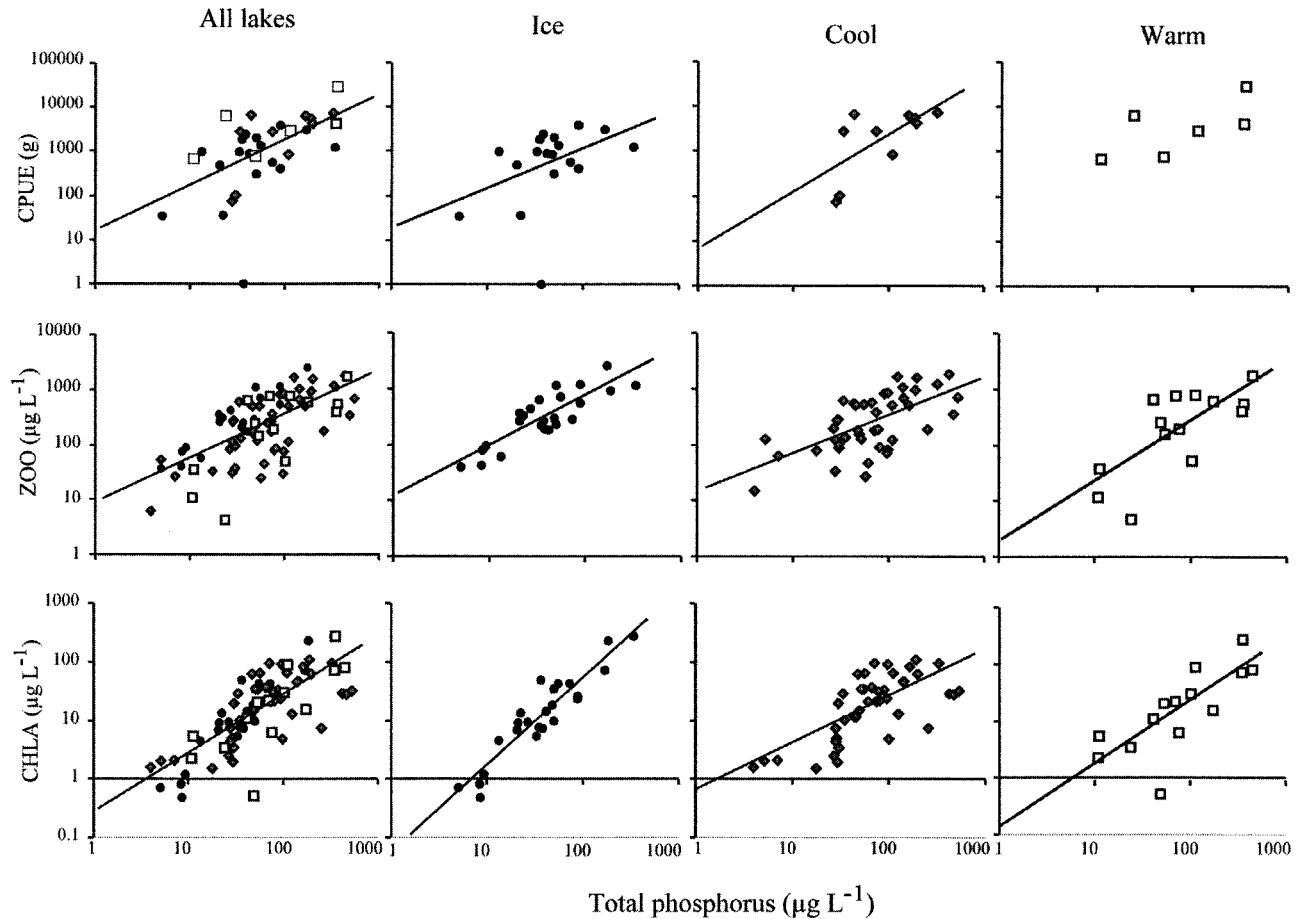
Fig. 5. The relation between TP and fish biomass (wet weight), total zooplankton biomass (dry weight), and Chl *a*. Lines indicate significant regressions (*see Table 2*).

might thus be one possible explanation for the lack of a clear trend, especially because the average size of these species often is larger than that of pelagic species (Jeppesen et al. 1997*b*) and because vegetation density was higher in warmer climate in our data set.

Our data set encompasses shallow lakes, and given comparable trophy, fish predation on zooplankton has a greater impact in these lakes compared with deeper one (Keller and Conlon 1994; Jeppesen et al. 1997*a*, 2003). This stems from the depth-independence of fish biomass that leads to higher abundance of fish per unit volume and a presumed higher encounter rate between planktivorous fish and their prey (Hairston 1988; Downing et al. 1990). Additionally, a relatively large abundance of benthic prey can subsidize a consistently high predation pressure on zooplankton (Jeppesen et al. 1997*a*). Aquatic vegetation, because it functions as refuge from planktivory, has direct effects on zooplankton (Lauridsen et al. 1997), but it also has an indirect importance, which is effected through phytoplankton, periphyton, suspension–resuspension dynamics, and fish community interactions (Persson and Crowder 1997; Romare and Hansson 2003). With regard to zooplankton biomass and community composition in the shallow lakes that we studied, macrophytes (measured as PVI) proved to be an important predictor, mainly of the biomass and relative abundance of benthic

or plant-associated taxa. On the other hand, the strong positive relationship between TP and total zooplankton biomass was almost entirely the result of an influence on pelagic taxa (Table 3). The lack of a climate effect on benthic or plant-associated taxa may have been caused by the higher PVI found in warmer lakes. Thus, had the data set been more balanced with respect to PVI, it is possible that a climate effect would have been recorded for benthic or plant-associated taxa as well.

The effect of climate on zooplankton biomass in the present study may be either direct, such as from temperature-related stress, or indirect, such as via increased predation or lowered quality of food. In field studies and experiments in tropical and subtropical lakes, it has been shown that predation from fish or invertebrates is an important factor regulating zooplankton communities and their consequent grazing impact on phytoplankton (Arcifa et al. 1992; Nagdali and Gupta 2002; Pagano et al. 2003). In the present study, the fish community likely was the route through which the climate effect was mediated, and although TP exerted a positive influence on all three trophic levels (phytoplankton, zooplankton, and fish), additional effects were exerted by climate. Climate was positively related to fish biomass and the fish : zooplankton ratio, and it had a negative effect on the zooplankton : Chl *a* ratio (Fig. 6; Table 3). These effects
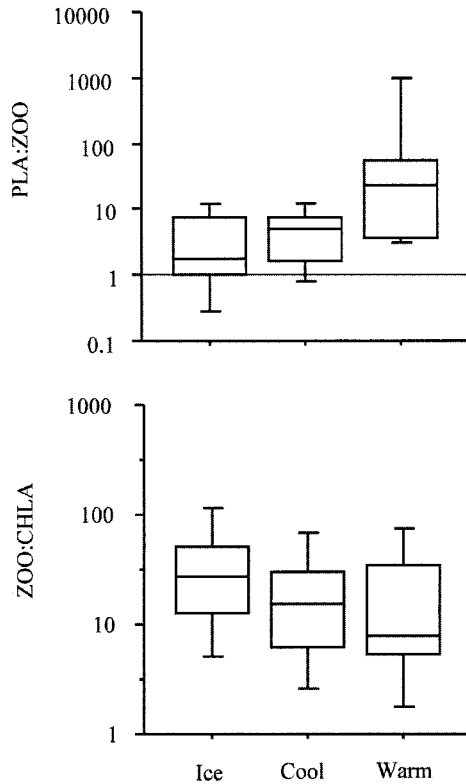
Fig. 6.   The relation to climate of the planktivorous and benthivorous fish : zooplankton ratio and the zooplankton : Chl *a* ratio. Boxplots show the 10%, 25%, 50%, 75%, and 90% percentiles for the three climate zones.

Table 5.   The minimum, maximum, and mean value (backtransformed from log or arcsine square-root transformed data) of the independent variables used in the multiple regression analyses. See Table 3 for abbreviations. The statistics show significant differences between climate groups for each variable (Tukey post-hoc test performed if significant differences were detected, with a univariate ANOVA at $p < 0.05$; * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, and *** $p < 0.001$).

	Minimum	Maximum	Mean		
Area (km²)					
Ice	0.0140	270	0.48	]*	]*
Cool	0.0150	32	0.42	]*	]*
Warm	0.0012	22	0.04	]*	
PVI (%)					
Ice	0	59	6.6	]*	]*
Cool	0	85	7.7	]*	]***
Warm	0	100	49.0	]*	
TP (μg L⁻¹)					
Ice	5.1	339	37		
Cool	4.0	532	65		
Warm	11.0	446	75		
CPUE (g)					
Ice	33	3,853	731		
Cool	75	7,433	1,811		
Warm	681	29,575	3,280		

may be interpreted as an increase in predation from fish in warmer lakes relative to colder ones, resulting in cascading effects on the potential of zooplankton to control the phytoplankton community. Our estimate of fish biomass probably underestimates the actual increase in fish predation pressure on zooplankton in warmer climates, because it does not fully include the effects of changes in species composition within the fish community. On the other hand, the effect of fish in warm lakes may have been overestimated, because the sampling was conducted at the end of summer, when water levels in the high-temperature Spanish lakes normally decrease, resulting in intensified risk of predation. The decrease in the zooplankton : Chl *a* ratio, from ice to warm lakes (Fig. 6), could also be explained by bottom-up effects, such as an increase in the share of inedible phytoplankton or, perhaps, decreased subsidy from allochthonous carbon. A pan-European experimental study (Van de Bund et al. 2004) showed no consistent pattern in the share of inedible algae when size was used as a criterion. A tendency was observed, however, toward an increase in the contribution of cyanobacteria at warmer sites, but a clearer relationship was seen when comparing within sites, namely a higher contribution of cyanobacteria during warmer times. In spite of this, zooplankton were able to control phytoplankton and maintain a high zooplankton : Chl *a* ratio over a wide range of productivity and temperatures as long as large crustaceans were not removed by fish. Because zooplankton were not able to control phytoplankton biomass at the warmest site,

however, even in the absence of fish, bottom-up effects on the zooplankton : Chl *a* ratio were probably also of importance (Vakkilainen et al. 2004). In relation to the present results, however, it is not clear why the effect of inedible algae should lead, in turn, to a relatively higher fish : zooplankton ratio in warmer lakes.

According to food-web theory, the slope of the biomass development along a productivity gradient should differ between phytoplankton, zooplankton, and fish (Oksanen et al. 1981). In our data set, however, all trophic levels increased with increasing TP concentration, which is in accordance with later, theoretical studies suggesting that the increase in all trophic levels may be caused by density-dependent interactions in the fish community (Sarnelle 1994) or adaptations, such as shifts in species composition or inducible defenses, within the primary-producer community or herbivore community (Leibold 1989; Abrams and Vos 2003).

In comparing arctic lakes with temperate, subtropical, or tropical lakes and ponds, an increasingly steep slope of Chl *a* with TP, with warmer climate, has been found (Mazumder and Havens 1998; Sarnelle et al. 1998; Flanagan et al. 2003). Contrary to these results, we found a much steeper slope between TP and Chl *a* in the ice zone compared to the warmer lakes.

A range of between 0.5 and 1.5 in the slope of the regression of zooplankton biomass against TP has been reported previously (Hanson and Peters 1986; Pace 1986; Shortreed and Stockner 1986; Hessen et al. 1995; Jeppesen et al. 1997*a*; Sarnelle et al. 1998). The slope found in the present study is comparable to the mean of these studies (0.88 vs. 0.81, respectively). The slope of the published study from subarctic lakes (1.5) was higher than the mean

slope of three temperate studies (0.6) and higher than that found for tropical ponds (0.8). Judging whether this was actually an effect of climate is troublesome, because the studies differed in, for instance, methods, morphology of the studied lakes, and range of productivity over which the study was performed. In the present study, no difference in the slope against TP was found for zooplankton biomass among climate zones despite the inclusion of lakes from a broad geographical range.

Fish biomass increased with TP in the ice and cold zones but not in the warm zone (Table 4). In the warm zone, fish biomass was high even at low TP. This may be expected if, as often is the case in warm lakes, fish species are free to reproduce during winter and have a higher degree of omnivory—the subsidy from other food sources may result in a relatively high predation pressure on zooplankton even in lakes of lower productivity.

Our results indicate differences in the response in biomass of trophic levels to increased productivity among climate zones. Considering the regressions (against TP) of Chl *a*, total zooplankton biomass, and biomass of planktivorous and benthivorous fish, the amount of variation explained by TP was highest in the ice zone and lowest in the intermediate, cool zone (with the exception of the fish regression, which had a low r^2 value in the ice zone, probably because of one extreme outlier). Furthermore, algal and zooplankton biomass were roughly similar in the high-productivity lakes in all climate zones, but biomass and trophic structure tended to differ among climate zones in the low-productivity end of the TP gradient (Fig. 5). At low TP, the fish biomass was relatively high in the warm zone, and zooplankton biomass was slightly higher in the two colder zones, as indicated by the fact that the intercept of the zooplankton was significantly higher than zero in these two zones but not in the warm zone. The most obvious difference among zones was between the ice zone and the warmer lakes. Low-productivity lakes in the ice zone were characterized by low Chl *a* concentration, a high zooplankton : Chl *a* ratio, and a low Chl *a* : TP ratio compared to warmer lakes at comparable TP concentrations (Table 4; Figs. 5, 6).

The effects of climate are not necessarily independent of biotic interactions, and studies of freshwater ecosystems provide examples of both density-independent effects and, as suggested by the present results, density-dependent effects on biotic interactions in lakes (Schindler et al. 1990; Carpenter et al. 1992). Although the present study is purely correlative and cannot assess the mechanisms involved, our data suggest that bottom-up effects are the most important predictors of zooplankton biomass. Climate—possibly through top-down regulation by fish—is also a significant contributory factor and may interact with productivity in governing the zooplankton biomass level and community composition. Hence, the present study provides an incentive for a continued merging of research efforts on food-web dynamics and climate effects.

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