

The Impact of Nutrient State and Lake Depth on Top-down Control in the Pelagic Zone of Lakes: A Study of 466 Lakes from the Temperate Zone to the Arctic

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ABSTRACT

Using empirical data from 466 temperate to arctic lakes covering a total phosphorus (TP) gradient of 2–1036 $\mu\text{g L}^{-1}$, we describe how the relative contributions of resource supply, and predator control change along a nutrient gradient. We argue that (a) predator control on large-bodied zooplankton is unimodally related to TP and is highest in the most nutrient-rich and nutrient-poor lakes and generally higher in shallow than deep lakes, (b) the cascading effect of changes in predator control on phytoplankton decreases with increasing TP, and (c) these general patterns occur with significant variations—that is, the predation pressure can be low or high at all nutrient levels. A quantile regression revealed that the median share of the predator-sensitive *Daphnia* to the total cladoceran biomass was significantly related unimodally to TP, while the 10% and 90% percentiles approached 0 and 100%, respectively, at all TP levels. Moreover, deep lakes (more than 6 m) had a higher percentage of

Daphnia than shallow (less than 6 m) lakes. The median percentage of *Daphnia* peaked at 0.15 mg L^{-1} in shallow lakes and 0.09 mg L^{-1} in deep lakes. The assumption that fish are responsible for the unimodality was supported by data on the abundance of potential planktivorous fish (catch net⁻¹ night⁻¹ gill nets with the different mesh sizes [CPUE]). To elucidate the potential cascading effect on phytoplankton, we examined the zooplankton phytoplankton biomass ratio. Even though this ratio was inversely related to CPUE at all TP levels, we found an overall higher ratio in oligotrophic lakes that declined toward low values (typically below 0.2) in hypertrophic lakes. These results suggest that planktivorous fish have a more limited effect on the grazing control of phytoplankton in oligotrophic lakes than in eutrophic lakes, despite similar predator control of large-bodied zooplankton. Accordingly, the phytoplankton yield, expressed as the chlorophyll *a*–TP ratio, did not relate to CPUE at low TP, but it increased significantly with CPUE at high TP. We conclude that the chances of implementing a successful restoration program using bi-

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omanipulation as a tool to reduce phytoplankton biomass increase progressively with increasing TP, but that success in the long term is most likely achieved at intermediate TP concentrations.

Key words: top-down control; trophic cascade; arctic lakes; temperate lakes; fish; zooplankton; phytoplankton; biomanipulation.

INTRODUCTION

The debate over the factors regulating trophic structure and interactions in the pelagic zone of lakes has been ongoing for many years. Twenty to forty years ago, most scientists, with a few exceptions (example, Hrbacek and others 1961; Brooks and Dodson 1965; Brooks 1969) agreed that food webs were regulated primarily via the available resources (resource, or bottom-up, control, *sensu* McQueen and others 1986—that is, phytoplankton is regulated by nutrients and light, zooplankton by phytoplankton, etc. This view was the basis of the comprehensive worldwide International Biological Program (IBP) investigations undertaken from 1965 to 1975 to study primary production and energy flow through food webs in limnetic systems. However, it has since been shown that food web structure may be strongly regulated by consumers (predator, or top-down, control), which implies that zooplankton are regulated by fish, phytoplankton by zooplankton, etc. (Carpenter and others 1985; Gulati and others 1990; Carpenter and Kitchell 1993). Thus, regulation at the top of the food web can cascade down to the phytoplankton level (trophic cascade, *sensu* Pace and others 1999). However, there is considerable variation in the perception of how the relative influences of resource and predator control can shift along a nutrient gradient.

Based on statistical analyses of lake studies and experimental data, McQueen and others (1986, 1989) concluded that bottom-up control is strongest at the bottom of the food web (for example, between nutrients and phytoplankton) and decreases upward through the web; conversely, predator control would be strongest at the top of the web and then decreases downward. They further asserted that the cascading effect of changes in predators on phytoplankton is high in nutrient-poor lakes and low in nutrient-rich lakes, partly because nutrient-rich lakes are often dominated by bluegreen algae that are not grazed efficiently by zooplankton. A meta-analysis of data derived from food web experiments in field enclosures (Brett and Goldman 1996) appeared to confirm the hypothesis. But Leibold (1989), Sarnelle (1992), and Pace

and others (1999) argued that changes in the biomass of zooplanktivorous fish produce the greatest cascading effect on phytoplankton in nutrient-rich lakes, a contention that is supported by several food web experiments and numerous whole-lake biomanipulation experiments (Gulati and others 1990; Perrow and others 1997; Hansson and others 1998; Meijer and others 1999).

Advocates of yet another variation on food web theory maintain that there is a stepwise shift in the balance between resource and predator control along a total phosphorus (TP) gradient. According to Persson and others (1988), the grazing pressure on phytoplankton depends on the number of food web links; in this view, it will be high in lakes with an even number of links (for example, lakes with only zooplankton and phytoplankton or lakes with predatory fish, zooplanktivorous fish, zooplankton, and phytoplankton) and low in lakes with an uneven number of links. They further suggested that there is a gradual increase in the number of food web links with increasing TP, going from one trophic level (phytoplankton) in the most nutrient-poor lakes to four levels (phytoplankton, zooplankton, planktivorous fish, and predatory fish) in mesotrophic lakes. In eutrophic lakes, the food web will be reduced to three links because few predatory fish are present. In accordance with the even-odd hypothesis, Carpenter and others (2001), using a set of experimental lakes, found that phytoplankton responded strongly to increasing nutrient loading in a three-level system, whereas comparatively minor changes occurred in a four-level system. Yet, contrary to what the hypothesis of Persson and others (1992) would predict, they found that the three- and four-level systems established at the beginning of the experiment remained stable throughout the 7-year study period, irrespective of the nutrient load of the system.

In studies focusing on zooplankton-phytoplankton interactions, Elser and Goldman (1990) and Carney and Elser (1990) developed the intermediate-state hypothesis, which holds that the grazing pressure on phytoplankton is (a) low in nutrient-poor lakes, not only as a consequence of low nutrient availability, but also because the zooplankton are dominated by copepods, which are not as efficient grazers as large-sized cladocerans; (b) high in intermediately nutrient-rich lakes in which the zooplankton are dominated by the efficient grazer *Daphnia*; and (c) low in nutrient-rich lakes, where the phytoplankton are dominated by grazing-resistant species, as also argued by McQueen and others (1986).

These hypotheses focused mainly on pelagic

Table 1. Selected Physicochemical Variables for the Study Lakes

	Maximum Depth	Total Phosphorus (mg PL ⁻¹)	Chlorophyll <i>a</i> (µg L ⁻¹)	<i>n</i>
Denmark	6.8 (1.0–37.7)	0.268 (0.010–1.458)	98.7 (10–855)	57–75
Norway	55.5 (0.7–516.0)	0.020 (0.001–0.627)	9.03 (0.5–137)	290
Greenland	10.0 (0.2–67)	0.011 (0.002–0.032)	1.26 (0.2–5.4)	74–78
New Zealand	3.6 (0.5–11)	0.029 (0.006–0.084)	3.65 (1.2–8.4)	22–23

Data given as mean (range)
n = number of lakes included in the analyses

links. Yet most planktivorous fish are also benthivorous; indeed, recent studies using stable isotopes have shown that the benthic–pelagic fish species rely to a large extent on benthic food sources in lakes (Vander Zanden and Vadeboncoeur 2002; Vadeboncoeur and others 2002), which may facilitate the trophic cascade in the pelagic (Polis and others 2000). In addition, benthic subsidies are an important factor in oligotrophic shallow lakes, because most consumer production (invertebrates) occurs in the top sediment or on plant surfaces (Jeppesen and others 1997; Vadeboncoeur and Steinman 2002). Benthic subsidies may also be important in hypertrophic shallow lakes because, due to lower zooplankton grazing, a major portion of the phytoplankton accumulates in the sediment and then becomes available as food for fish through benthic invertebrates or as detritus rather than through zooplankton (Jeppesen and others 1997). Therefore, facilitated top-down control could be high in oligotrophic and hypertrophic lakes and lower at intermediate TP concentrations.

This wide spectrum of differing opinions on the role of nutrients for predator and resource control may in part be a reflection of different study scales (time, nutrient levels, or lake depth) or limited data set. Using empirical data from 466 temperate to arctic lakes covering a 500-fold gradient in TP, we examined the changes in the relative contribution of resource supply and predator control in the pelagic zone along a broad nutrient gradient. In particular, we set out to elucidate whether fish predator control on large-bodied zooplankton is unimodally related to TP and, if so, whether the effect on zooplankton is transferred to the phytoplankton level, creating a trophic cascade.

MATERIALS AND METHODS

Study Areas

The study includes data collected in Greenland, Denmark, New Zealand, and Norway. The Green-

land (G) lakes are located near the coast in the Zackenberg and Lake Store Sø valleys (74°N) in northeast Greenland and west Greenland on a transect from near the ice cap at Kangerlussuaq (67°N) to the coast. Sampling in New Zealand (NZ) was conducted on South Island (44°S) from Christchurch to Dunedin. Sampling in Denmark (DK) (55°–57°N) and Norway (N) (65°–77°N) was done throughout the countries. The DK lakes were mainly eutrophic, whereas the lakes in N, NZ, and G ranged from oligotrophic to mesotrophic (Table 1).

The methods of sampling and analyses used for the DK lakes have been described in detail by Jeppesen and others (2000a); for N lakes, by Faafeng and others (1990) and Hessen and others (1995a, 1995b); for NZ lakes, by Jeppesen and others (2000b); and for G lakes by Jeppesen and others (2002a) and Lauridsen and others (2001). A brief summary is given here. In all lakes, sampling was conducted during mid to late summer (July–August in DK, July–August and in a few lakes in early September in N, January–early February in NZ); thus, it was done outside the season when temporary clearwater phases occur in lakes and during the season of maximum predation effects by young-of-year (YOY) fish (Jeppesen and others 1997).

In N, chlorophyll *a*, TP, and zooplankton (10 L, more than 45 µm) were analyzed from depth-integrated samples over the trophogenic zone (twice the Secchi depth; maximum 0–10 m, minimum 0–2 m for chlorophyll *a*, TP, and phytoplankton; maximum 0–20 m for zooplankton). In DK, depth-integrated samples for chlorophyll *a* and water chemistry were taken with a 3.31 Patalas sampler in the photic zone; in NZ and G, samples were taken from the surface to the bottom. Densities of selected zooplankton species in DK lakes were determined on depth-integrated (surface to bottom) water samples taken at one to three stations. Depending on the trophic state, 4.5 or 9 L of the pooled sample were filtered onto an 80-µm mesh net and fixed in acid Lugol's iodine. NZ and G lakes were sampled

once during midsummer using a similar device and similar sampling techniques (depth-integrated from top to bottom). In these lakes, zooplankton were sampled at one to five stations placed along a transect running parallel to the shore in the deepest part. A 12–20-L subsample (depending on the trophic state) of the pooled sample was filtered onto a 20- μm mesh net. Length–weight relationships, according to Dumont and others (1975) and Bottrell and others (1976), were used to estimate biomass. The various mesh sizes (20–80- μm) used for zooplankton in the different countries have no effects on the cladoceran counts, because all are cladocerans retained; they have little effect on total zooplankton biomass because only a few rotifers and nauplii are able to pass through the most coarse filter used.

Lake water TP was determined as molybdate-reactive phosphorus (Murphy and Riley 1972) after persulphate digestion (Koroleff 1970). Chlorophyll *a* was determined spectrophotometrically after ethanol (DK, G, NZ) or acetone (N) extraction. To convert chlorophyll *a* ($\mu\text{g L}^{-1}$) to dry weight (μg), we multiplied by 67 (Jeppesen and others 1997).

The composition and relative abundance of the pelagic fish stock were determined in some of the lakes from DK, NZ, and G with multiple mesh-sized gill nets (6.25, 8, 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, 75 mm); the length and depth of each section were 3 and 1.5 m, respectively. In DK, fish surveys were conducted according to a standardized test-fishing program (Mortensen and others 1990). Between six and 66 nets were used, depending on lake size and depth. The nets were set in late afternoon and left in place until the next morning (approximately 18 h) in both the littoral zone and at the bottom in the pelagic zone. Pelagic nets were also used in deep lakes. Fishing was conducted between 15 August and 15 September because previous test-fishing had indicated that the distribution of the fish population was most even during that period (Mortensen and others 1990). In NZ and G, four to 10 nets were used, depending on lake size and depth. In most of these lakes, the nets were placed in the littoral zone at a depth of 2 m and at the bottom in the pelagic zone. In deep lakes, pelagic nets were also used; and in a few lakes, the fishing was restricted to the littoral zone. In all lakes, the nets were set in the late afternoon and retrieved the next morning. Average catch per unit effort (CPUE) in terms of number of fish net^{-1} night^{-1} was calculated.

We divided the lakes into two size classes, shallow and deep, defined as lakes with a maximum depth of less than 6 m or 6 m or more. Maximum

depth was chosen because mean depth was known only for a subset of lakes. Before analysis, we first averaged the data from the different stations for each sampling date, then averaged the data per lake (one to three samplings per lake), to arrive at one data set per lake. Ratios were calculated after averaging the numerators and denominators for the different sampling dates. To avoid interference by acidification effects on zooplankton, only lakes with a pH higher than 6.5 were included in the analysis. Biomanipulated lakes were also excluded.

Statistics

For the statistical analyses, we performed a multiple regression with forward selection of variables. In addition, we performed quantile regressions (Cade and others 1999), using the 10th, 50th, and 90th quantiles. Quantile regression is based on the minimizing of least absolute deviations. Regression quantiles extend the usual univariate concept of quantiles to the linear model by defining a sequence of lines that are above a proportion of observations for different quantiles, R_1 , ranging from 0.00 to 1.00. Estimates of regression quantiles were obtained from a simplex linear programming solution by minimizing an asymmetric loss function of absolute values of residuals, where positive residuals are given weights equal to τ and negative residuals are given weights equal to $1-\tau$. Computer routines written in S-Plus (Koenker and d'Orey 1987, 1994) were used to estimate regression quantiles, test hypotheses about parameters, and compute confidence intervals. We used the regression quantile rank-score test procedure implemented in S-Plus (Cade and others 1999). Coefficients of determination for regression quantiles, R_1 , were computed by subtracting from 1 the weighted absolute deviations from the original model divided by the weighted absolute deviations from a null model (regression model without independent variables). R_1 is interpreted as the proportionate reduction in variation between the simple quantile estimate of the dependent variable and the estimate conditioned on the independent variables. We used the following quadratic model:

$$Y = \mu + \beta_1 \cdot D + \beta_2 \cdot \text{LTP} + \beta_3 \cdot D \cdot \text{LTP} + \beta_4 \text{LTP}^2 + \beta_5 \cdot D \cdot \text{LTP}^2$$

where D is equal to 0 if the maximum depth is less than 6 m, else 1, LTP is \log_e -transformed TP, and $D \cdot \text{LTP}$ is the interaction between D and LTP , allowing for different phosphorus slopes in shallow and deep lakes.

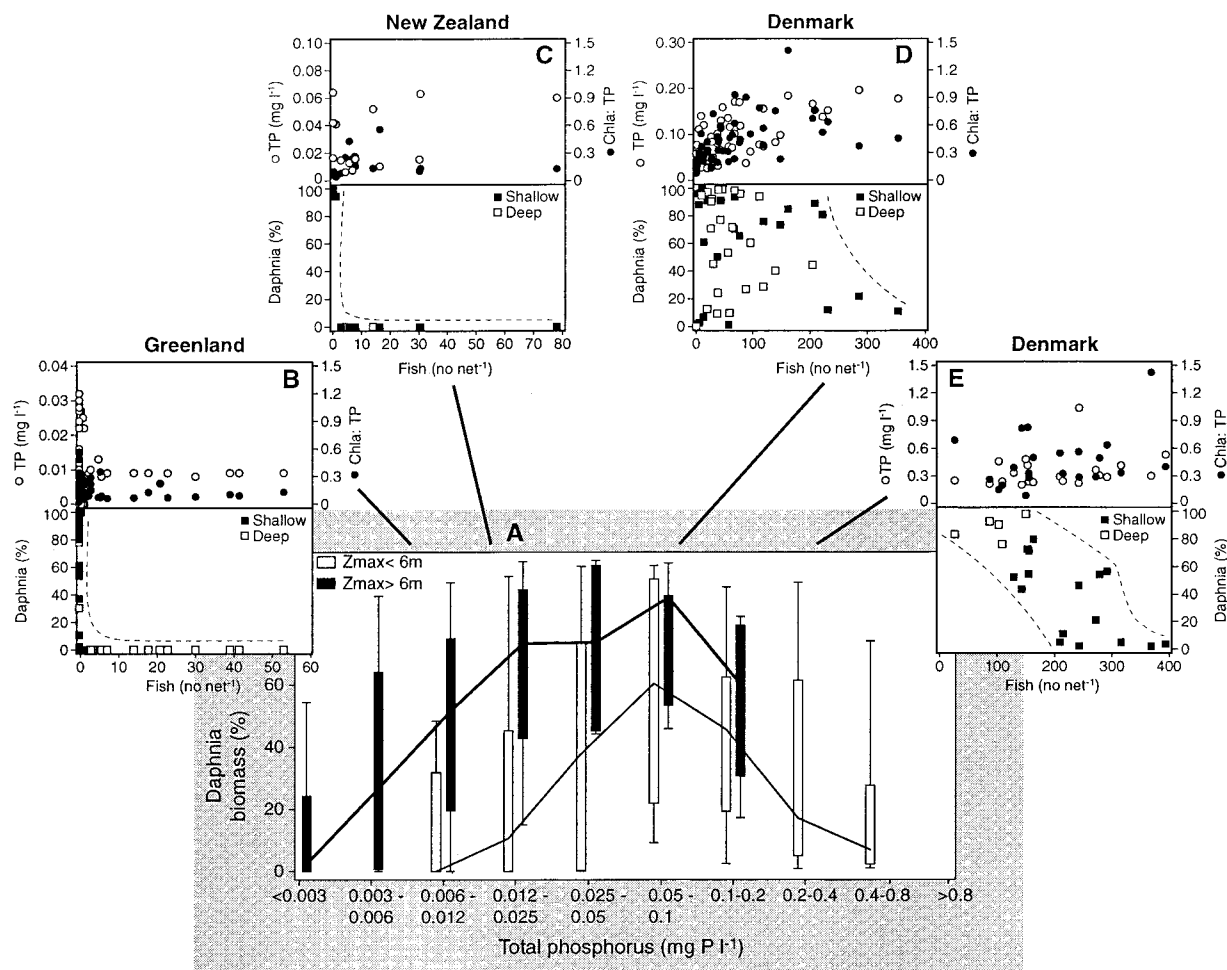


Figure 1. (A) Boxplot showing percentage of *Daphnia* for the total biomass of cladocerans along a gradient of total phosphorus (TP) (all averages are for July–August) in 365 deep (more than 6 m) and shallow (less than 6 m) Danish and Norwegian lakes. Mean 25%, 75%, 10%, and 90% percentiles are shown. (B) (C) (D) (E) TP concentrations in the lake water, chlorophylla–TP ratio (Chla:TP), and percentage of *Daphnia* versus total catch of planktivorous fish (CPUE, no. net⁻¹ night⁻¹) in multiple mesh-sized gill nets in Greenland, New Zealand, and Danish lakes with contrasting nutrient concentrations. The lines connecting subplots B,C,D,E with subplot A point to the median TP levels of the lakes 10 to presented in each individual graph.

First, we tested the hypotheses of no interaction between depth and TP, which is $H_1: \beta_3 = \beta_5 = 0$. If H_1 could not be rejected, we tested for no difference in the level of Y between the shallow and the deep lakes, $H_2: \beta_1 = 0$, and for no effect of TP, $H_3: \beta_2 = \beta_4 = 0$. All tests were conducted at a significance level of 5%. Prior to the statistical analyses, the response variables were transformed to achieve a suitable linear model (natural logarithmic, $z = \log_e(y)$, or the logistic $z = \log_e \frac{y}{1-y}$). Back-transformation to the original data scale was done by $Exp(z)$ or $\frac{1}{1 + Exp(-z)}$.

RESULTS AND DISCUSSION

Data from the N and DK lakes showed that the proportion of *Daphnia* in total cladoceran biomass was unimodally related to TP and generally higher in deep lakes (Figures 1, 2 and Table 2). The contribution of *Daphnia* peaked at 0.15 mg P L⁻¹ in shallow lakes and at 0.09 mg P L⁻¹ in deep lakes (Figure 2 and Table 2). The decreasing percentage from medium to high TP has often been observed. Most frequently, it is attributed to the increase in abundance and the proportion of planktivorous fish in nutrient-rich lakes (Persson and others 1988; Jeppesen and others 2000a; Carpenter and others 2001); this view has been confirmed by numerous

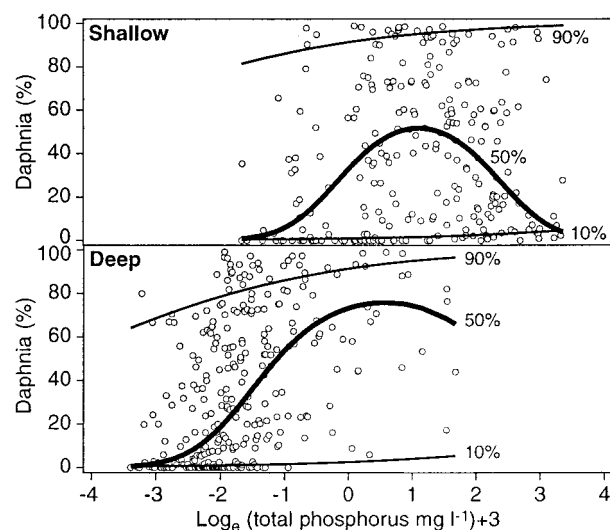


Figure 2. Percentage of *Daphnia* in the total population of cladocerans in 365 Danish and Norwegian lakes divided into two size classes, maximum depth of less than 6 m and greater than or equal to 6 m. Also shown are 10%, 50%, and 90% quantiles obtained by quantile regression. The 50% quantile peaks at 0.09 mg P L⁻¹ in deep lakes and 0.15 mg P L⁻¹ in shallow lakes. For the 50% model, see Table 2.

biomanipulation experiments (Hansson and others 1998; Meijer and others 1999). Accordingly, an inverse relationship was found between the proportion of *Daphnia* and the abundance of planktivorous fish, expressed as CPUE in multimesh-sized gill nets for DK lakes covering a TP gradient from 0.2 to 1.1 mg P L⁻¹ (Figure 1E). Unfortunately, only qualitative fish data, based on interviews and catch data, are available for N lakes. However, similar to the data from DK lakes, the proportion of *Daphnia* in N lakes declined in the more eutrophic, cyprinid-dominated lakes, whereas the pattern was less clear in the more oligotrophic lakes (Hessen and others 1995b). The dominant planktivorous fish in eutrophic European lakes, such as roach and particularly bream, are strongly benthivorous as well, which may allow strong, benthic-subsidized predator control on zooplankton. This process is cumulative, because high predation on zooplankton translates into low grazing on phytoplankton and therefore, especially in shallow lakes, a high rate of phytoplankton settling which in turn becomes a food resource for benthic invertebrates and ultimately for fish (Jeppesen and others 1997) (Table 3). At intermediate TP, the control by piscivores on planktivorous fish is higher (Persson and others 1992; Carpenter and others 1997), thereby releasing predation on zooplankton, which in turn leads to

higher grazing on phytoplankton and less fueling of benthic invertebrates by phytoplankton sedimentation (Table 3).

The observed decrease in the percentage of *Daphnia* with shifts from medium to low TP (Figures 1, 2 and Table 2) has previously been observed in N lakes and attributed to low calcium (Ca) and high carbon-phosphorus (C:P) ratios (Hessen and others 1995a, 1995b), because these parameters correlated positively with TP. The negative influence of low Ca on *Daphnia* growth has been confirmed experimentally (Hessen and others 2000); and to the extent that ambient TP is also positively correlated with food C:P (that is, low P yields high C:P), this condition could also result in reduced growth in P-demanding species such as *Daphnia* (Hessen 1992; Sterner and Hessen 1994; Elser and others 2000). The extent to which such quality constraints may be superimposed on food quantity constraints for *Daphnia* in nutrient-poor lakes is not yet clear. Although factors such as Ca concentration and elemental ratios of food and food quality may influence the growth and survival of *Daphnia* in a dilute environment, several studies conducted in ultraoligotrophic lakes have shown that *Daphnia* are abundant in most fishless lakes and absent or restricted to low densities or small *Daphnia* species in most lakes with fish (Anderson 1982; Paul and others 1995; Gliwicz and others 2001; Jeppesen and others 2001; Lauridsen and others 2001). When fish predation is low, *Daphnia* populations manage to overcome the growth constraints of the dilute environment.

The strong influence exerted by fish in nutrient-poor lakes, despite low fish density, can be attributed to several factors. First, zooplankton are exposed to these predators for a longer period of time prior to reproduction because growth rates are low due to limited food availability (Dahl-Hansen 1995); C:P ratios are frequently high and, for many of the oligotrophic lakes, Ca concentrations are low. Second, the increasing clarity of the water at lower TP enhances the risk of predation by visually hunting fish in the pelagic zone. Third, the higher clarity also enhances the proportion of benthic to pelagic primary production and thus the share of benthos to the total production of consumers (Jeppesen and others 1997; Vander Zanden and Vadebonceur 2002; Vadebonceur and others 2002). Therefore, as lakes are transformed from mesotrophic to oligotrophic, opportunistically feeding fish are increasingly sustained by benthos, which in turn may facilitate predation on large-bodied zooplankton. Thus, the benthic facilitation of predation on large-bodied zooplankton may be high in both oligotrophic and

Table 2. Results of the Quantile Regression for the 50% quantile (Median) relating the Percentage of *Daphnia* in the Total Biomass of Cladocerans (*Daphnia* (%), model A) and the Biomass Ratio of Zooplankton to Phytoplankton (zoo:phyt, model B) to Total Phosphorus (TP) and Depth (Two Size Classes)

	β_0	β_1	β_2	β_3	β_4	β_5	R^1	P
(A) <i>Daphnia</i> (%) Estimate (95% CL)	0.06 (−0.22,0.50)	1.14 (0.34,1.65)	0.47 (0.28,0.61)	ns.	−0.40 (−0.46,0.34)	ns.	0.13	<0.01
(B) zoo:phyt Estimate (95% CL)	−1.10 (−1.27,−0.98)	−0.70 (−0.88,−0.30)	−0.47 (−0.57,−0.36)	0.19 (0.04,0.36)	NS	NS	0.11	<0.01
Final model (median):								
(A) < 6 m, <i>Daphnia</i> (%) = 100/(1 + exp [0.06 + 0.47 LTP −0.40 (LTP ²)] −0.01) (B) < 6 m, zoo:phyt = exp [−1.10−0.47 LTP]								
(A) ≥6 m, <i>Daphnia</i> (%) = 100/(1 + exp [1.2 + 0.47 LTP −0.40 (LTP ²)] −0.01) (B) ≥6 m, zoo:phyt = exp [−1.80− 0.28 LTP]								

CL, confidence limit; NS, not significant
Model $\log_e(Z) = \beta_0 + \beta_1 \cdot D + \beta_2 LTP + \beta_3 D \cdot LTP^2 + \beta_5 D \cdot LTP^2$, where $Z = y'/(1 - y')$, $y' = \text{Daphnia (\%)/100} + 0.01$ in model A and $Z = \text{zoo:phyt in model B}$. $LTP = \log_e(TP) + 3$, which means that the x-axis reaches 0 at a TP of approximately 0.05 mg PL^{-1} . $D = 0$ if maximum depth is less than 6 m, otherwise, $D = 1$.

Table 3. Suggested Changes in Top-down Control in the Pelagic of Lakes and Implications for the Use of Biomanipulation as a Restoration Technique Based on the Present Study and Some Earlier Studies

		Mesotrophic–Slightly			Shallow Relative to Deep
		Oligotrophic	Eutrophic	Eutrophic	
A	Piscivory	Low-medium ¹	High ^{1,2}	Low	?
B	Proportion of benthic food resources (invertebrates, algae, or detritus) in the diet of planktivorous fish	High because of high benthic primary production relative to phytoplankton ^{1,2}	Medium, because higher piscivorous control (A) of planktivorous fish means higher densities of large-bodied zooplankton, shifting in part the focus of the remaining fish toward zooplankton	High, because of low zooplankton grazing and proportionately high sedimentation of phytoplankton, which directly or indirectly via consumers becomes available as a food resource for fish	Higher in shallow lakes, because of proportionally higher production of benthic invertebrates than zooplankton ^{1,2}
C	Top-down control of large-bodied zooplankton	High ⁴ , because of high water clarity and high benthic facilitation (B)	Medium ⁴ , because of high piscivorous control (A, B) and in shallow lakes because of high biomass of submerged plants	High ² , because of high abundance of planktivorous fish and high benthic facilitation (B), despite low water clarity	Higher, because a higher biomass of planktivorous fish can be maintained due to higher ^{2,3} benthic invertebrate production ^{2,3} because of higher fish abundance per unit volume ² Higher per unit of m ^{2,3}
D	Zooplankton–phytoplankton biomass ratio	High ⁴	Medium ⁴	Low ⁴	
E	Cascading top-down effects of fish on phytoplankton	Low, because of high D and resource control of phytoplankton	Medium, because of medium D and medium resource control of phytoplankton	High, because of low D and low resource control of phytoplankton	Higher, because of C, D, and lower resource control of phytoplankton (higher internal loading during summer) Higher, because of higher E
F	Short-term success of biomanipulation	Low, because of low E	Medium, because of medium E	High, because of high E	
G	Long-term success of biomanipulation	Low, because of low E	High, because of high A	Low, because of low A	Most likely higher when chances for success are high

¹Carpenter and others 1997²Jeppesen and others 1997³Vadeboncoeur and others 2002⁴Present study

Table 4. Relationships between Percentage Contribution of *Daphnia* to the Total Biomass of Cladocerans, Ratio of Chlorophyll *a* (Chla) ($\mu\text{g L}^{-1}$) to Total Phosphorus (TP) ($\mu\text{g PL}^{-1}$), and biomass ratio of Zooplankton to Phytoplankton (zoo:phyt) ($\mu\text{g DW } \mu\text{g DW}^{-1}$) versus Catch per Unit Effort of Potentially Planktivorous Fish (CPUE) (no. net $^{-1}$ night $^{-1}$) and TP ($\mu\text{g L}^{-1}$) in Lakes from Greenland, Denmark, and New Zealand

$$\begin{aligned} \text{Daphnia (\%)} &= 100 / (1 + \exp [1.64 \pm 1.14 - 0.60 \pm 0.14 \log_e (\text{CPUE} + 1) + 0.67 \pm 0.09 (\log_e (\text{CPUE} + 1))^2 - 0.10 \pm \\ &\quad 0.02 (\log_e (\text{CPUE} + 1))^3 + 1.22 \pm 0.22 \log_e (\text{TP})] - 0.01), r^2 = 0.46, P < 0.0001, n = 156 \\ \text{Chla:TP} &= \exp [-1.91 \pm 0.06 + 0.19 \pm 0.02 \log_e (\text{CPUE} + 1)], r^2 = 0.42, P < 0.0001, n = 156 \\ \text{zoo:phyt} &= \exp [-0.86 \pm 0.10 - 0.23 \pm 0.03 \log_e (\text{CPUE} + 1)], r^2 = 0.28, P < 0.0001, n = 156 \end{aligned}$$

Multiple regression (forward procedure) including $\log_e (\text{CPUE})$, $(\log_e (\text{CPUE}))^2$, $(\log_e (\text{CPUE}))^3$, $\log_e (\text{TP})$, $(\log_e (\text{TP}))^2$, and $\log_e (\text{maximum depth})$ as independent variables

hypertrophic lakes, although the C sources fueling the benthos are different (Table 3).

The idea that fish have a strong influence on large-bodied zooplankton in nutrient-poor lakes is apparently supported by corresponding data on fish CPUE and the percentage of *Daphnia* from oligomesotrophic NZ and G lakes and from oligo-ultraoligotrophic G lakes, which we used because of the lack of quantitative fish data from N lakes (Figures 1B, C). In both areas, the proportion of *Daphnia* decreased substantially with increasing CPUE, but the CPUE threshold for the loss of *Daphnia* varied. With only one exception, *Daphnia* were completely absent from all lakes with fish when CPUE per night exceeded 0.3 fish net $^{-1}$ in G lakes (Figure 1B) and 1–2.7 net $^{-1}$ in NZ lakes (Figure 1C), whereas the threshold was as high as approximately 200 net $^{-1}$ in mesotrophic to eutrophic DK lakes (Figure 1D) and approximately 300 net $^{-1}$ in highly eutrophic DK lakes (Figure 1E). Higher CPUE values are, of course, needed in eutrophic lakes to sustain a predation pressure comparable to that of oligotrophic lakes, due to the faster zooplankton growth rate. Yet multiple regressions revealed that the percentage of *Daphnia* was significantly inversely related to CPUE and positively related to lake water TP, suggesting a higher predation risk at a given CPUE in oligotrophic lakes (Table 4). This relationship should, however, be interpreted with caution due to differences in the composition of the fish population and consequently in gill net catch efficiency among the regions. Moreover, differences in the composition of *Daphnia* species (for example, only a few large species are present in G and NZ lakes) and their pigmentation may have influenced their vulnerability to predation (Sægvog and others 1996); finally, temperature varied significantly among the regions. However, the relationship fits well with the pattern for N and DK lakes shown in Figure 1A, as well as the arguments for a high predation risk in oligotrophic lakes outlined above.

The significant difference in the median percent-

age of *Daphnia* between shallow and deep lakes at all TP levels (Figure 2 and Table 2) indicates that their predation risk is generally higher in shallow lakes than deep ones. According to Keller and Conlon (1994) and Jeppesen and others (1997), this higher risk can be attributed to an overall greater volumetric density of potentially planktivorous fish. In addition, it might reflect a proportionately higher production of benthic consumers relative to zooplankton than is found in deep lakes, either because of higher benthic primary production (clear shallow lakes) or because more of the phytoplankton production reaches the sediment surface (turbid shallow lakes) (Table 3). Thus, because fish are sustained to a larger extent by benthic invertebrates in shallow lakes, predation pressure on large-bodied zooplankton is consistently high. Moreover, there are fewer refuges for zooplankton in shallow lakes, with the exception of those (depending on the fish species present) with extensive growth of submerged macrophytes (Burks and others 2002).

It could be argued that relationships based on data from snapshot sampling events, as in the present study, are unreliable. However, we sampled all lakes in late summer, when fish predation is usually at the seasonal maximum avoiding the clearwater spring phase. Moreover, we found similar patterns and relationships between the percentage of *Daphnia*, TP, and CPUE when we compared the percentage of *Daphnia* ephippia to the total sum of *Daphnia* and *Bosmina* ephippia recorded in the uppermost 1 cm of the sediment with contemporary CPUE data from 135 DK, G, and NZ lakes (Jeppesen and others Forthcoming). The sediment record provides a time-integrated picture of the relationship, because the upper 1 cm represents the past 2–100 years, depending on the sedimentation rate. Thus, it provides data for many years in the oligotrophic lakes for which only one sample per lake was available. This sediment record, which might be considered more “robust”, fully supports our contemporary snapshot observations.

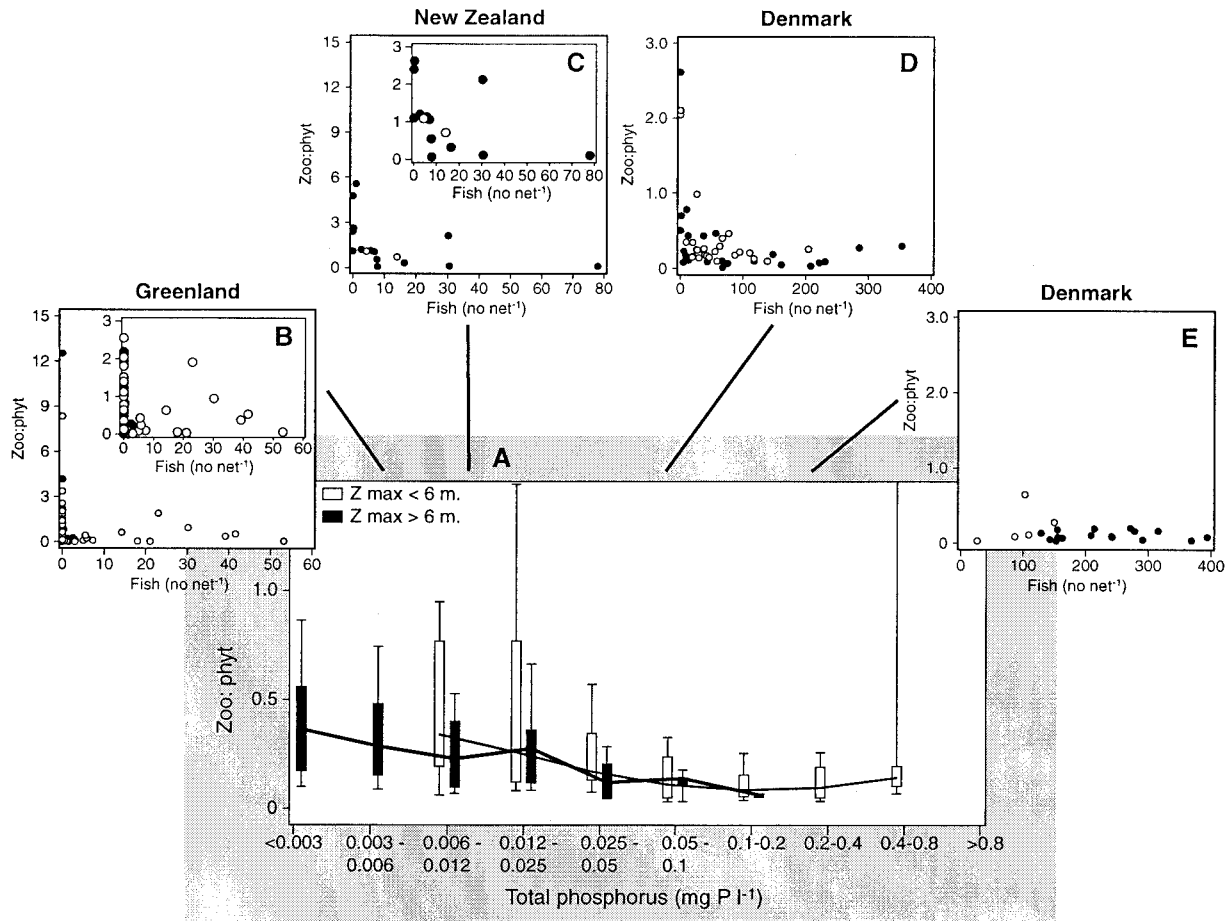


Figure 3. (A) Boxplots showing the biomass ratio of zooplankton to phytoplankton (averages for July–August) in deep (more than 6 m) and shallow (less than 6 m) Danish and Norwegian lakes. (B) (C) (D) (E) The same ratio versus the total catch of planktivorous fish. The insets in B and D represent lakes with the same range of zooplankton–phytoplankton ratios as in D and E. See also Figure 1.

We used the zooplankton–phytoplankton (zoo:phyt) biomass ratio as an indicator of the cascading effects on phytoplankton. This ratio decreased with increasing TP in both shallow and deep lakes (Figure 3 and Table 2) from a mean value of 0.35 in the most oligotrophic lakes to less than 0.1–0.2 in the most eutrophic lakes. Thus, the suggested high predation pressure on large-bodied zooplankton in oligotrophic and eutrophic lakes seems to have the strongest cascading effect on the zoo:phyt ratio (and most likely also on the zooplankton grazing capacity) in the eutrophic lakes. Yet we found that fish have a clear effect at all TP levels, since the zoo:phyt ratio was significantly negatively related to CPUE (both log-transformed) in G ($P < 0.0001$, $r^2 = 0.65$) (Figure 3B), NZ ($P < 0.001$, $r^2 = 0.80$) (Figure 3C), and DK lakes ($P < 0.004$, $r^2 = 0.12$) (Figure 3D and E). In a multiple regression of the pooled data set, CPUE but not TP contributed significantly and neg-

atively to the variation in the zoo:phyt ratio (Table 4), suggesting that the higher predation risk for large-bodied zooplankton per unit of CPUE at low TP is not transferred to the zoo:phyt ratio.

The chlorophyll *a*–TP (Chla:TP) ratio provides further evidence that fish have stronger cascading effects on phytoplankton at high TP (Figure 1B–E). Although this ratio was not related to CPUE in the nutrient-poor G lakes ($P > 0.7$) (Figure 1B), it increased significantly in the slightly more nutrient-rich NZ lakes ($P < 0.04$, $r^2 = 0.29$) (Figure 1C) and in the eutrophic DK lakes ($P < 0.0001$, $r^2 = 0.29$) (Figure 1D and E), most likely reflecting a reduction in the impact exerted by zooplankton grazing on phytoplankton at increasing TP. Moreover, a recent study of 130 oligotrophic lakes in Greenland, 60% without fish, found no difference in the chlorophyll *a* or the Chla:TP ratio between lakes with and without fish (E. Jeppesen and others unpublished).

The zoo:phyt ratio did not differ markedly among deep and shallow lakes. This may, however, be a result of our sampling strategy. Although zooplankton were sampled in the entire water column in DK lakes and at a depth of at least 20 m in N lakes, the phytoplankton sampling covered only the photic zone in both countries. If phytoplankton had been sampled in the same layer as zooplankton, the zoo:phyt ratio per square meter would have been higher in deeper lakes, as would be expected given the lower predation pressure in such lakes (Table 3).

In accordance with the results of several other studies (see review by Pace and others 1999), our results indicate that the trophic cascade is highest in nutrient-rich lakes (Table 3). Numerous biomanipulation experiments also support our results. For example, the mass removal of cyprinids in eutrophic lakes often resulted in low chlorophyll *a* and high zoo:phyt ratios that exceeded 0.6–1 throughout the summer, as compared with a ratio of less than 0.2 in July–August before a biomanipulation scheme was implemented to control fish predation (Jeppesen and others 2002b). By contrast, but also in accordance with our data, several fish manipulation experiments conducted at low TP had only minimal cascading effects on phytoplankton biomass (Ramcharan and others 1995; Bizina 2000). Therefore, our results do not support the assertion that the cascading effect of fish on phytoplankton is higher in oligotrophic than in eutrophic lakes, as suggested by McQueen and others (1986, 1989) and Brett and Goldman (1997).

Our results, which showed that large-bodied *Daphnia* exert the greatest influence at intermediate TP concentrations confirm in part the intermediate-state hypothesis of Carney and Elser (1990). However, the potential zooplankton grazing pressure is apparently not low in oligotrophic lakes, as suggested by the hypothesis. The zoo:phyt ratio for these types of lakes was high in our study, possibly because the zooplankton were subsidized by organic matter from a terrestrial input or from the sediment, not least in systems where the contribution of phytoplankton to the total particulate organic input (whether externally derived or produced in the lake) is low (Del Giorgio and Peters 1993; Jeppesen and others 1997; Hessen and others forthcoming).

Although our data are generally in accordance with the food web theory (even–odd links) (Persson and others 1988) for mesotrophic and eutrophic lakes, they deviate for oligotrophic lakes. We found a high risk of loss of *Daphnia* and a relatively low cascading effect of fish on phytoplankton bio-

mass in lakes both with and without piscivores (four and three links, respectively) (E. Jeppesen and others unpublished) (Figures 1 and 3). Recently, Carpenter and others (2001) observed that a clearwater state mediated by the addition of piscivorous fish could be maintained for a minimum of 7 years irrespective of the loading, resulting in high grazing effects on phytoplankton at all TP loads. Based on these results, the authors concluded that the piscivorous state can be maintained at a broad range of nutrient loads. Our data support the idea that large-bodied grazers, and consequently the grazing pressure on phytoplankton, may be high at all TP levels (Figure 2). Yet they also strongly suggest that the most likely state in eutrophic lakes is one where small-bodied cladocerans are dominant and the grazing pressure on phytoplankton, as low, suggested by Persson and others (1988) and Jeppesen and others (1997, 2000a).

Our findings have implications for the use of biomanipulation as a restoration tool (Table 3). Although predation release seems to affect the abundance of large-bodied zooplankton at all nutrient levels, at high TP the most likely state is the turbid one, with low grazing of zooplankton phytoplankton. It is therefore likely that high-TP lakes will be resilient to fish manipulation—that is, the lake will return to the turbid state after a temporary clearwater state, as has been observed in several biomanipulation studies (Meijer and others 1999; Van De Bund and Van Donk 2002). At moderate eutrophication, the cascading effect may be long-lasting, whereas in oligotrophic lakes fish manipulation may have a strong impact on large-bodied zooplankton but low cascading effects on phytoplankton biomass.

In conclusion, we have provided evidence that (a) fish predation pressure on large-bodied cladocerans is overall unimodally related to TP in both shallow and deep lakes; (b) the effect generally cascades to the phytoplankton biomass level in eutrophic lakes, but less significantly so in oligotrophic lakes; and (c) predator control of large-bodied zooplankton tends to be higher in shallow lakes than in deep lakes. However, our results also demonstrate that these general patterns occur over a broad spectrum of possible alternatives. At both low and high TP, predator and grazer control ranged from high to low in the lakes included in the analysis. We conclude that in the short-term the probability that biomanipulation will prove successful in reducing phytoplankton biomass increases with TP, but the likelihood of achieving a long-term effect is highest at intermediate TP levels.

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REFERENCES

- Anderson RS. 1982. Zooplankton composition and change in an alpine lake. *Ver Int Verein Limnol* 18:264–8.
- Bizina EV. 2000. Interplay of “top-down” and “bottom-up” factors in the regulation of plankton communities in freshwater oligotrophic ecosystems. *Ver Int Verein Limnol* 27:1752–6.
- Bottrell HH, Duncan A, Gliwicz ZM, Grygierek E, Herzig A, Illbrich-Ilkowska A, Kurasawa H, Larsson P, Weglenska T. 1976. A review of some problems in zooplankton production studies. *Norw J Zool* 24:419–56.
- Brett MT, Goldman CR. 1996. Consumer versus resource control in freshwater pelagic food webs. *Science* 275:384–6.
- Brooks JL. 1969. Eutrophication and changes in the composition of zooplankton. In: *Eutrophication: causes, consequences, correctives* (Ed. Anon). National Academy of Sciences, Washington D.C. p 236–55.
- Brooks JL, Dodson SI. 1965. Predation, body size and composition of plankton. *Science* 150:28–35.
- Burks R, Lodge DM, Jeppesen E, Lauridsen TL. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting littoral zones. *Freshwat Biol* 47:343–65.
- Cade BS, Terrell JW, Schroeder RL. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–23.
- Carney JJ, Elser JJ. 1990. The strength of zooplankton–phytoplankton coupling in relation to trophic state. In: Tilzer MM, editor. *Ecology of large lakes*. New York: Springer-Verlag. p 616–31.
- Carpenter SR, Cole JJ, Hodgson JR, Kitchell JF, Pace ML, Bade D, Cottingham DL, Essington TE, Houser JN, Schindler DE. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecol Monogr* 71:163–86.
- Carpenter SR, Kitchell JF. 1993. *The trophic cascade in lakes*. Cambridge (UK): Cambridge University Press. 385 p.
- Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–9.
- Carpenter SR, van Donk E, Wetzel RG. 1997. Nutrient loading gradient in shallow lakes: report of the group discussion. In: Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K, editors. *The structuring role of submerged macrophytes in lakes*. New York: Springer Verlag. p 393–6.
- Dahl-Hansen GAP. 1995. Long-term changes in crustacean zooplankton—the effects of a mass removal of arctic charr, *Salvelinus alpinus* (L.), from an oligotrophic lake. *J Plankton Res* 17:1819–33.
- Del Giorgio PA, Peters RH. 1993. Balance between phytoplankton production and plankton respiration in lakes. *Can J Fish Aquat Sci* 50:282–9.
- Dumont HJ, Van de Velde I, Dumont S. 1975. The dry weight estimate on a selection of cladocera, copepoda and rotifers from the plankton, periphyton and benthos of continental waters. *Oecologia* 19:75–97.
- Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Schulz KL, and others. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408:578–80.
- Elser JJ, Goldman CR. 1990. Zooplankton effects on phytoplankton in lakes of contrasting trophic status. *Limnol Oceanogr* 36:64–90.
- Faafeng B, Brettum P, Hessen DO. 1995. Landsomfattende undersøkelse av trofistanden i 355 innsjøer i Norge [in Norwegian]. Report nr 2355. Oslo: NIVA. 575 p.
- Gliwicz ZM, Slusarczyk A, Slusarczyk M. 2001. Life-history synchronization in a long-lifespan single-cohort *Daphnia* population of an alpine lake free of fish. *Oecologia* 128:368–78.
- Gulati RD, Lammens EHRR, Meijer M-L, Van Donk E, editors. 1990. *Bio-manipulation—tools for water management*. Hydrobiologia 200/201. 628 p.
- Hansson L-A, Annadotter H, Bergman E, Hamrin SF, Jeppesen E, Kairesalo T, Luokkanen E, Nilsson P-Å, Søndergaard M, Strand J. 1998. Bio-manipulation as an application of food chain theory: constraints, synthesis and recommendations for temperate lakes. *Ecosystems* 1:558–74.
- Hessen DO. 1992. Nutrient element limitation of zooplankton production. *Am Nat* 140:799–814.
- Hessen DO, Alstad NEW, Skardal L. 2000. Calcium limitation in *Daphnia magna*. *J Plankton Res* 22:553–68.
- Hessen DO, Faafeng B, Andersen T. 1995a. Competition or niche segregation between *Holopedium* and *Daphnia*; empirical light on abiotic key parameters. *Hydrobiologia* 307:253–261.
- Hessen DO, Faafeng B, Anderson T. 1995b. Replacement of herbivore zooplankton species along gradients of ecosystem productivity and fish predation pressure. *Can J Fish Aquat Sci* 52:733–42.
- Hessen DO, Faafeng B, Brettum P. Autotroph: herbivore biomass ratios: carbon deficits judged from planktonic data. *Hydrobiologia*. Forthcoming.
- Hrbacek J, Dvorakova V, Korinek V, Prochazkova L. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. *Verh Int Verein Limnol* 14:192–5.
- Jeppesen E, Christoffersen K, Landkildehus F, Lauridsen TL, Amsinck SL, Ríget F, Søndergaard M. 2001. Fish and crustaceans in northeast Greenland lakes with special emphasis on interactions between arctic charr (*Salvelinus alpinus*), *Lepidurus arcticus* and benthic chydorids. *Hydrobiologia* 442:329–37.
- Jeppesen E, Jensen JP, Lauridsen TL, Amsinck SL, Christoffersen K, Mitchell SF. Sub-fossils of cladocerans in the surface sediment of 135 lakes as proxies for community structure of

- zooplankton, fish abundance and lake temperature. *Hydrobiologia*. Forthcoming.
- Jeppesen E, Jensen JP, Søndergaard M. 2002. Response of phytoplankton, zooplankton and fish to re-oligotrophication: an 91-year study of 23 Danish lakes. *Aquat Ecosys Health Manage* 5:31–43.
- Jeppesen E, Jensen JP, Søndergaard M, Lauridsen TL, Landkildehus F. 2000a. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwat Biol* 45:201–13.
- Jeppesen E, Jensen JP, Søndergaard M, Lauridsen TL, Pedersen LJ, Jensen L. 1997. Top-down control in freshwater lakes: the role of nutrients, submerged macrophytes and water depth. *Hydrobiologia* 342/345:151–64.
- Jeppesen E, Lauridsen TL, Mitchell SF, Christoffersen K, Burns CW. 2000b. Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *J Plankton Res* 22:951–68.
- Keller W, Conlon M. 1994. Crustacean zooplankton communities and lake morphometry in Precambrian shield lakes. *Can J Fish Aquat Sci* 51:2424–34.
- Koenker R, d'Orey V. 1987. Computing regression quantiles. *Appl Stat* 36:245–54.
- Koenker R, d'Orey V. 1994. A remark on Algorithm AS220: computing dual regression quantiles and regression rank scores. *Appl Stat* 43:410–4.
- Koroleff F. 1970. Determination of total phosphorus in natural waters by means of persulphate oxidation. An Interlab. report nr 3. Cons. Int. pour l'Exploration de la Mer.
- Lauridsen TL, Jeppesen E, Landkildehus F, Søndergaard M. 2001. Horizontal distribution of cladocerans in arctic Greenland lakes. *Hydrobiologia* 442:107–16.
- Leibold MA. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am Nat* 134:922–49.
- McQueen DJ, Johannes MRS, Post JR, Steward TJ, Lean DRS. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecol Monogr* 59:289–310.
- McQueen DJ, Post JR, Mills EL. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can J Fish Aquat Sci* 43:1571–81.
- Meijer M-L, de Boois I, Scheffer M, Portielje R, Hospe H. 1999. Biomanipulation in the Netherlands: an evaluation of 18 case studies in shallow lakes. *Hydrobiologia* 408/409:13–30.
- Mortensen E, Jensen HJ, Müller JP, Timmermann M. 1990. Fiskeundersøgelser i søer: Øvervågningsprogram. Undersøgelsesprogram, fiskeredskaber og metoder [in Danish]: Teknisk anvisning nr 3. Silkeborg (Denmark): Danmarks Miljøundersøgelser. 60 p.
- Murphy J, Riley JR. 1972. A modified single solution method for the determination of phosphate in natural waters. *Analyt Chim Acta* 27:21–6.
- Pace M, Cole JJ, Carpenter SR, Kitchell JF. 1999. Trophic cascades revealed in diverse ecosystems. *Trends Ecol Evol* 14: 483–8.
- Paul AJ, Leavitt PR, Schindler DW, Hardie AK. 1995. Direct and indirect effects of predation by a calanoid copepod (subgenus: *Hesperodiptomus*) and of nutrients in a fishless alpine lake. *Can J Fish Aquat Sci* 52:2628–38.
- Perrow MR, Meijer M-L, Dawidowicz P, Coops H. 1997. Biomanipulation in shallow lakes: state of the art. *Hydrobiologia* 342/343:355–65.
- Persson L, Anderson G, Hamrin SF, Johanson L. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In: Carpenter SR, editor. *Complex interactions in lake communities*. New York: Springer-Verlag. p 45–65.
- Persson L, Diehl S, Johansson L, Andersson G, Hamrin SF. 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *Am Nat* 140:59–84.
- Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J. 2000. When is a trophic cascade a trophic cascade? *Trends Ecol Evol* 15:473–5.
- Ramcharan CW, McQueen DJ, Demers E, Popiel SA, Rocchi AM, Yan ND, Wong AH, Hughes KD. 1995. A comparative approach to determining the role of fish predation in structuring limnetic ecosystems. *Arch Hydrobiol* 133:389–416.
- Sægrov H, Hobæk A, Låbe-Lund HH. 1996. Vulnerability of melanistic *Daphnia* to brown trout predation. *J Plankton Res* 18:2113–8.
- Sarnelle O. 1992. Nutrient enrichment and grazer effects of phytoplankton in lakes. *Ecology* 73:551–60.
- Sterner RW, Hessen DO. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu Rev Ecol Syst* 25:1–29.
- Vadeboncoeur Y, Steinman AD. 2002. Periphyton function in lake ecosystems. *Sci World* 2:1449–68.
- Vadeboncoeur Y, Vander Zanden MJ, Lodge D. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. *BioScience* 52:44–54.
- Van De Bund WJ, Van Donk E. Short-term and long-term effects of zooplanktivorous fish removal in a shallow lake: a synthesis of 15 years of data from Lake Zwemlust. *Freshwat Biol*. Forthcoming.
- Vander Zanden MJ, Vadeboncoeur Y. 2002. Fish as integrators of benthic and pelagic food webs in lakes. *Ecology* 83:2152–2161.