No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes

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Abstract

I tested relationships between fish predator and prey densities or size across 66 lakes of the European temperate zone, covering mean depths between 1 and 22 m and a phytoplankton biomass range between 1 and 270 mg m^{-3} chlorophyll *a*. I hypothesized that in lakes of comparable phytoplankton biomass or depth, prey fish densities and size were lower at high predator densities or size than in systems with lower piscivory. Accordingly, I also expected a stronger trophic cascade from predatory fish to phytoplankton biomass in high-piscivory systems. None of the hypotheses were confirmed. Prey abundances and biomasses were consistently higher in high-piscivory than in low-piscivory lakes, if the effects of trophic state or lake depth on fish densities were accounted for. Chlorophyll *a* concentrations in lakes of similar depth did not differ between high and low piscivory, suggesting no difference in the strength of the trophic cascade. The overall size of prey was slightly higher in lakes with larger predators. The weak top-down influence of predatory fish on lower trophic levels may be attributable to the fact that the numerically dominant predator, perch, has to recruit through smaller ontogenetic stages, which dominate the prey community in most of the lakes. The availability of size refuges for prey and the overall omnivory of predators may contribute to the weak evidence for a trophic cascade.

Predator-controlled models of the structure of food webs predict reciprocal effects of predators on prey that alter the biomass of a trophic level across more than one link in the food chain, a community-wide interaction called trophic cascades (Shurin et al. 2002). In aquatic systems, there is much empirical evidence for community-wide cascades (Brett and Goldman 1997; Carpenter et al. 2001; Shurin et al. 2002). Strong tritrophic pelagic interactions between fish, zooplankton, and phytoplankton biomasses have been identified, with negative correlations observed between zooplanktivorous fish and zooplankton biomasses as well as between zooplankton and phytoplankton biomasses (Brett and Goldman 1997; Jeppesen et al. 2003). Furthermore, fish predation has been shown to shift the size structure of aquatic prey assemblages toward smaller average sizes (Brooks and Dodson 1965; Jeppesen et al. 2003).

In far fewer cases has the interaction between piscivorous fish predators and their fish prey been included in the exploration of trophic cascades in lakes. Single-system studies demonstrated that a change of fish predator populations may cause a reciprocal effect in the population density of their fish prey (Tonn et al. 1992; Carpenter et al. 2001; Potthoff et al. 2008). Furthermore, since piscivorous fish are gape limited and thus feed-size selective, strong predation may modify the average prey size (Hambright et al. 1991; Tonn et al. 1992; Nowlin et al. 2006). The existence of piscivore-induced trophic cascades was mainly suggested from the observation that the proportion of piscivores in the entire fish community was highest in lakes where large cladocerans were frequent and the phytoplankton biomass relatively low (Persson et al. 1992; Jeppesen et al. 2000). However, by comparing 17 piscivore manipula-

tions not confounded by other food web effects, trophic cascades from piscivores to phytoplankton biomass were observed in only seven studies (Drenner and Hambright 2002).

Piscivorous fish were suggested to be functionally important only in a limited set of lakes. Persson et al. (1992) showed that fish predators are frequent only at intermediate trophic state of lakes, whereas piscivore biomasses are low and functionally unimportant at low productivity due to nutrient limitation and at high productivity due to size-related competitive interactions between the dominant fish species. Accordingly, the proportion of predatory fish in the total fish community was shown to be highest at intermediate phytoplankton biomass (Persson et al. 1992; Jeppesen et al. 2000).

In a similar way, the intensity of trophic interactions was suggested to vary systematically with the physical dimension of the system. Higher interaction strengths were predicted in lakes with low volume-to-area ratios (Jeppesen et al. 1997; Benndorf et al. 2002) because productivity of lakes scales mainly to lake area, and thus the abundances and biomasses of individuals per volume are higher in shallow than in deep lakes. However, the majority of available across-system studies focused on tritrophic fish–zooplankton–phytoplankton cascades in lakes of varying depth (Jeppesen et al. 2003), with little empirical support that the link between fish predators and their fish prey responds similarly to a lake-depth gradient.

Here I present fish community data obtained by standardized gill-net sampling from 66 European lakes over large phytoplankton biomass and depth gradients. I calculated abundances, biomasses, and lengths of piscivorous fish and their fish prey for each of the lakes and split the data sets into groups of lakes with either high or low piscivory. I correlated prey abundance, biomass, and length to chlorophyll *a* (Chl *a*) and depth and compared the

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resulting regressions between the high- and low-piscivory lake sets. I hypothesized that across the lakes (1) abundance, biomass, and size of prey are lower in lakes with high piscivory than in lakes with low piscivory, if the confounding effects of trophic state and lake depth on fish densities are accounted for. I further hypothesized that the differences of prey biomasses and sizes between low- and high-piscivory lakes are (2) greater in lakes of low to intermediate Chl *a* concentrations than in lakes with higher phytoplankton biomass, and (3) greater in shallow than in deep lakes. Accordingly, I expected (4) stronger trophic cascades down to phytoplankton in high-piscivory than in low-piscivory lakes, reflected by a lower phytoplankton biomass at similar mean depths in the lakes with more predators.

Methods

Sampling—Sixty-seven natural lakes in the northeastern German lowlands were sampled once, the entire fish surveys encompassing the summers of 2001 through 2003. The area of the lakes ranged between 0.5 and 105 km², and their maximum depths varied between 2 and 69 m; thus the lake set encompassed 27 polymictic and 40 stratified lakes. All fish communities were near-natural and not influenced by heavy predator stocking or prey removal for biomanipulation purposes.

Two lake variables were included in the detailed analyses. Mean depths of lakes (Z_{mean}, range 1.0 to 22.5 m) were obtained from regional databases. Trophic state of lakes, as measured by Chl *a* concentrations (range 1.5 to 269.3 mg m^{-3}), was based on arithmetic means of at least three standardized samplings from epilimnetic layers during the summer months (April to October) and followed standard sample processing (DIN 1985) provided by state authorities (Ministry of the Environment, State of Mecklenburg–Vorpommern, Schwerin; Landesumweltamt, State of Brandenburg, Potsdam).

Fishes were obtained from the benthic and pelagic habitats by stratified random sampling with benthic Norden multimesh gill nets, following the European standard for gill-net surveys (CEN 2005). All gill nets were set before dusk and lifted after dawn to assure fishing of the likely maximum activity periods for all fish species. Benthic gill nets (length 30 m, height 1.5 m; 12 mesh size panels each being 2.5 m long with 5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43, and 55 mm) were randomly distributed over the whole lake area and systematically placed in all depth layers, the number of nets (range 16 to 101 per lake) increasing in a standardized way with lake area and maximum depth (Appelberg 2000). These nets proved to be reliable gear to sample lake fish communities (Kurkilahti and Rask 1996). Pelagic Norden multimesh gill nets (length 30 m, height 3 m; 12 mesh sizes from 5 to 55 mm as given above) were set stepwise from the surface to the bottom over the deepest point of all those lakes with a maximum depth of 6 m and more (58 of the total of 67 lakes, the number of nets per lake ranging between 1 and 23). For more details of the sampling and the lakes included, *see* Mehner et al. (2005).

In one lake (Schwielochsee), several hundred under-yearling zander (*Zander lucioperca* (L.)) were caught by one benthic net. Multivariate Bray–Curtis distances indicated that this lake was therefore an extreme outlier in the total set of the 67 lakes (>7 standard deviations distant from the grand mean distance). Accordingly, this lake was excluded from subsequent analyses.

Calculations and statistics—For all fish, species, number, total length (TL, nearest cm), and wet weight (ww, ±1 g) were determined. Relative abundance (number of fish per unit effort, NPUE) and relative biomass (weight per unit effort, WPUE) of species-specific gill-net catches were calculated based on the number of standard nets (1.5 m high, 30 m long) set per lake (ind. or g ww net^{-1}). To obtain lakewide abundances or biomasses, average unit catches from benthic and pelagic habitats were calculated. Since the net area of pelagic nets was exactly twice the area of benthic nets, the catch per pelagic net was assumed to be obtained from two standard nets. This procedure was similar to the approach applied recently to explore fish assemblage types in lakes of the European ''Central Plains'' ecoregion (Mehner et al. 2007). My preliminary tests suggested that direction and strength of correlations between abundances of single species were qualitatively similar, whether based on benthic or pelagic catches in all lakes, similar to other studies (Lauridsen et al. 2008). Therefore, the combination of catches from both habitats seems to be appropriate to analyze the overall predation strength of piscivorous fish on prey fish.

Among the total of 34 fish species and one cyprinid hybrid caught in the lakes (Mehner et al. 2005), the following five species were considered as obligatory piscivores: Pike (*Esox lucius* L., *n* = 64 lakes), zander (*n* = 35 lakes), burbot (*Lota lota* L., *n* = 25 lakes), asp (*Aspius aspius* (L.), *n* = 4 lakes), and European catfish (*Silurus glanis* L., *n* = 5 lakes). Perch (*Perca fluviatilis* L.) display a switch from zooplankton and zoobenthos as a main food source (juvenile perch) to fish (adult perch) during ontogeny (Persson 1986). Therefore, perch were divided into nonpiscivorous (TL < 15 cm, *n* = 66 lakes) and piscivorous (TL ≥ 15 cm, *n* = 66 lakes) individuals (Persson et al. 1992). The other 28 species were treated as nonpiscivores and considered as potential prey of the fish predators.

Relative abundances (NPUE) and biomasses (WPUE) were summed for either piscivorous or nonpiscivorous fish. The average size per group of piscivores or nonpiscivores was calculated as arithmetic mean TL of all piscivores or nonpiscivores caught per lake. All fish variables as well as mean depth (Z_{mean}) and Chl *a* concentration from the 66 lakes were $\log_{10}$ transformed to approximate to normal distributions and stabilize homogeneity of variances. Subsequent Kolmogorov–Smirnov exact tests, scatterplots of residuals, and Durbin–Watson tests indicated normal distributions, homoscedasticity, and no autocorrelation of residuals for all variables ($p > 0.05$).

Consistent predator : prey ratios were calculated by dividing the sum of abundance or biomass or the average size of piscivores (subsequently referred to as predators) by

the identical variable obtained from nonpiscivores (subsequently referred to as prey). The resulting ratios are not identical to the proportion of predators in the entire community (i.e., predator biomass/(prey biomass + predator biomass)) as used, for example, by Jeppesen et al. (2000) but can easily be converted into abundance and biomass proportions (no conversion possible for the length ratio). I directly tested for significant linear or unimodal relationships between the predator : prey abundance, biomass, and length ratios and $\log_{10}$ Chl a and Z_{mean} of all 66 lakes. These tests allow for a comparison with earlier studies in which the relationships between proportion of predators and lake productivity or depth have been discussed (Persson et al. 1992; Jeppesen et al. 1997; Jeppesen et al. 2000).

To evaluate the top-down influence of predators on prey over gradients of lake trophic state and depth, I followed the conceptual approach suggested for comparing the effect of zooplankton grazers on algal biomass between odd- and even-link lakes (Mazumder 1994). I first split the 66 lakes into two groups with either high or low piscivory. To account for the confounding effects of lake trophic state and depth on predator densities, the split was based on linear regressions between predator abundance or biomass, and Chl a or Z_{mean} of the lakes (*see* Results). Lakes with predator densities above the regression line were considered high-piscivory lakes, whereas lakes with predator densities below the regression line were grouped into the low-piscivory lakes. Because predator length was independent of Chl a or Z_{mean} (*see* Results), splitting the lake set into high- and low-piscivory lakes according to predator length was performed at the median length of predators in the 66 lakes. Subsequently, I calculated linear regressions between $\log_{10}$ prey abundance, biomass, or size and $\log_{10}$ Chl a or Z_{mean} separately for the groups of high-piscivory and low-piscivory lakes. I expected that prey abundance, biomass, and size increase with Chl a in both high-piscivory and low-piscivory lakes but with a steeper slope in high-piscivory lakes, which reflects the stronger top-down control a low to intermediate Chl a. Similarly, I expected prey abundance, biomass, and size to decline with mean lake depth at both low and high piscivory, but with a shallower slope in high-piscivory lakes, reflecting stronger top-down control in the shallower lakes. To test for these expected differences between high- and low-piscivory lakes, slopes and intercepts of linear regressions were compared by analysis of covariance (ANCOVA). For consistency, I tested unimodal (quadratic) regressions between prey and Chl a or Z_{mean} in addition. These quadratic regressions were considered significant when *t*-tests revealed significance of both the linear and the quadratic terms. This was the case only for the prey abundance–Chl a relationship in high-piscivory lakes (*see* Results).

To evaluate whether the community-wide relationships mask negative correlations between predators and single prey fish species, I calculated Spearman's rank correlation coefficients (R_s) between the abundance sum of all predators and the abundance of all those single prey species that occurred in at least a quarter (17 out of 66) of all lakes. This set included small perch ($n = 65$ lakes), roach

(*Rutilus rutilus* (L.), $n = 66$), bream (*Abramis brama* (L.), $n = 66$), silver bream (*Blicca bjoerkna* (L.), $n = 57$), tench (*Tinca tinca* (L.), $n = 41$), ruffe (*Gymnocephalus cernuus* (L.), $n = 66$), bleak (*Alburnus alburnus* (L.), $n = 55$), spined loach (*Cobitis taenia* L., $n = 25$), gudgeon (*Gobio gobio* (L.), $n = 17$), and vendace (*Coregonus albula* (L.), $n = 31$).

Finally, I analyzed whether the strength of the trophic cascade differed between lakes at high or low piscivory. I used the same split of lakes into high- or low-piscivory systems according to the regressions between predator densities and Chl a or Z_{mean} as described above. For consistency, I considered only those lakes that were grouped into the same high-piscivory or low-piscivory sets by regressions from both Chl a and Z_{mean} (three lakes omitted according to contrasting grouping from predator abundance, six omitted according to different grouping from predator biomass). I then calculated linear relationships between $\log_{10} Z_{mean}$ and $\log_{10}$ Chl a separately for the two lake groups. I expected a functionally similar regression for both lake data sets (identical slopes), but I predicted a lower phytoplankton biomass (Chl a) at similar lake depth in lakes with high piscivory (smaller intercept) due to the cascading effect of high piscivory on fish prey, zooplankton, and phytoplankton. Slopes and intercepts of the regressions were compared by ANCOVA. All statistical calculations were performed by SPSS 14.0 (SPSS 2005).

Results

In total, 166,221 fish from 34 species and one hybrid were caught (Fig. 1). The entire and detailed list of species is available elsewhere (Mehner et al. 2005). Size of fish ranged between 2 and 110 cm TL, with numerical peaks at 7 to 10 cm for predators and prey (Fig. 1). Perch was the dominant species (45.2% of total fish numbers, Fig. 1B). If perch were split between prey and predators at 15 cm TL, the resulting 9448 predators (large perch, pike, zander, wels, burbot, asp) constituted 5.7% of the total catch.

Predator : prey ratios were variable between the 66 lakes. The median of the abundance ratio was 0.0496 (range 0.014 to 0.445), reflecting that at least some predators were present in all lakes. The median of the predator : prey biomass ratio was 0.321 (range 0.061 to 1.384) (Fig. 2), suggesting that the biomass of prey was on average three times larger than that of predators. Overall, mean predator lengths were about twice the mean length of prey fish in the 66 lakes but with substantial between-lake variability (range 1.27 to 3.50) (Fig. 2). These predator : prey abundance, biomass, and length ratios were in no case significantly linearly or unimodally related to $\log_{10}$ Chl a or $\log_{10} Z_{mean}$ of the 66 lakes ($F_{1,64} < 1.84$, $p > 0.17$).

Predator abundance increased weakly significantly ($p = 0.096$) with Chl a (Fig. 3A; Table 1) and decreased with Z_{mean} of lakes (Fig. 3D; Table 1). Stronger relationships with similar directions were found between predator biomass and Chl a and Z_{mean} (Fig. 3B,E; Table 1). Accordingly, the 66 lakes were split into high- and low-piscivory systems according to the linear regressions of predator abundance or biomass to Chl a and Z_{mean}. In the high-piscivory systems, predators had 3.3 times more
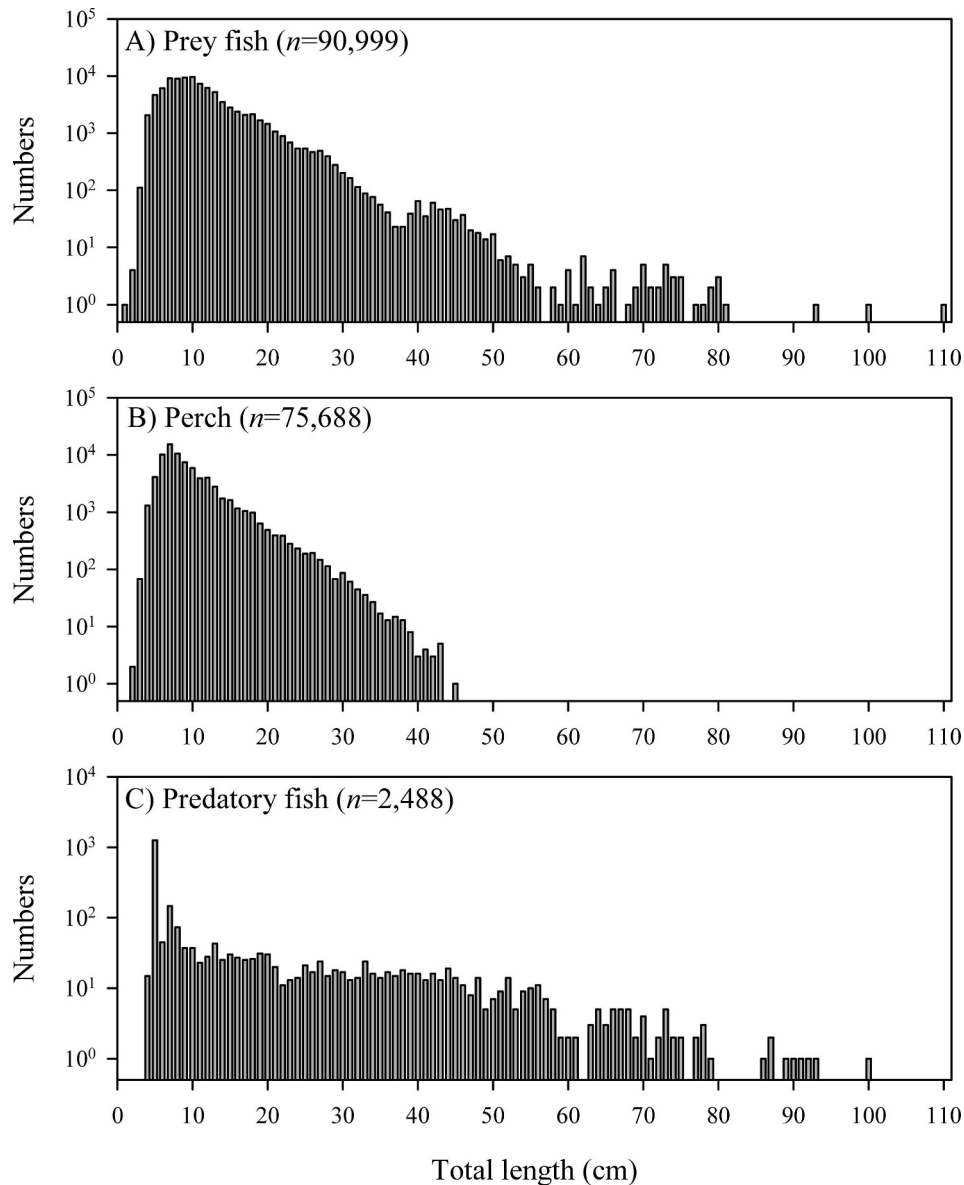
Fig. 1.   Total numbers per 1-cm length class of (A) prey fish, (B) perch, and (C) predatory
fish caught by multimesh gill nets in 66 German lakes. Note the logarithmic *y*-axes.

abundance or 3.1 times more biomass than in the low-piscivory systems. Predator length was not at all related to Chl *a* or Z_{mean} (Fig. 3C,F; Table 1), and accordingly the lakes were split into high- and low-piscivory systems at the median predator length (20.8 cm, predators 1.26 times larger in high-piscivory than in low-piscivory systems). The resulting lake groups of high or low piscivory did not differ in arithmetic means of $\log_{10}$ Chl *a* or Z_{mean} (*t*-tests, df = 64, $p > 0.06$), thus suggesting that any differences in prey densities or size between high- and low-piscivory systems cannot exclusively be explained by the confounding effects of Chl *a* or mean depth.

Prey abundance increased with increasing Chl *a* in both low- and high-piscivory lakes with no difference in slopes (Fig. 4A; Table 1; ANCOVA, $F_{1,62} = 0.01$, $p = 0.92$). In the high-piscivory system, a quadratic regression provided

a comparable fit to the data ($F_{2,27} = 5.7$, $p = 0.009$) as found for the linear regression ($F_{1,28} = 6.1$, $p = 0.02$). Prey was more abundant in the high- than in the low-piscivory lakes over the entire Chl *a* range (ANCOVA on linear regressions, intercepts, $F_{1,63} = 26.2$, $p < 0.0001$). The overall patterns found for prey abundance were corroborated from the regressions on prey biomass (Fig. 4B; Table 1). Prey biomasses were consistently higher in lakes with high predator biomasses than in lakes with low predator biomasses (ANCOVA, slopes, $F_{1,62} = 0.01$, $p = 0.91$; intercepts, $F_{1,63} = 18.6$, $p < 0.0001$).

Prey abundance and biomass were negatively linearly related to mean depth in both high- and low-piscivory systems (Fig. 4D,E; Table 1). Whereas the slopes of the high-piscivory vs. low-piscivory groups of lakes did not differ (ANCOVA, abundance, $F_{1,62} = 0.56$, $p = 0.46$;
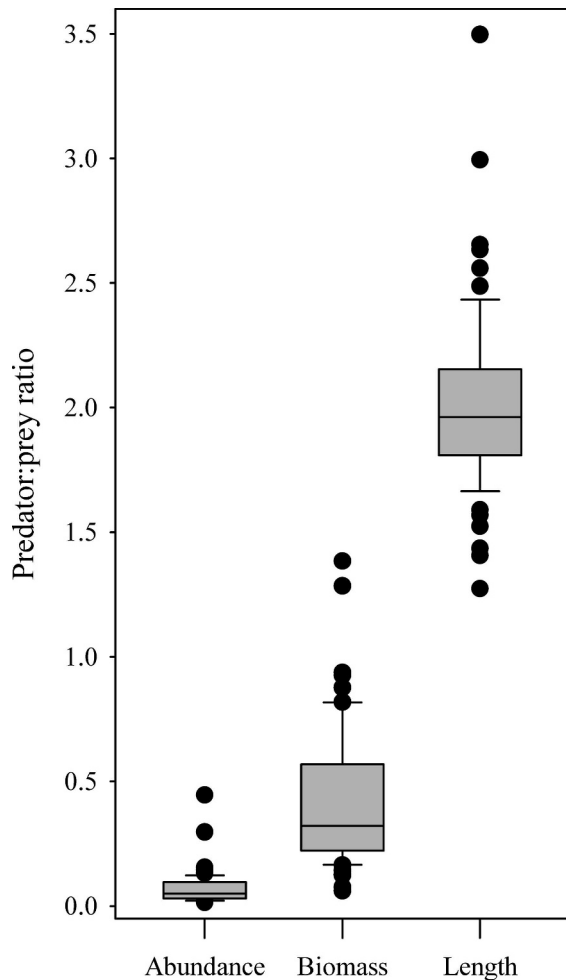
Fig. 2. Box plots of predator : prey ratios of abundances, biomasses, and lengths in 66 German lakes. Plots show medians, 25th and 75th percentiles (boxes), 10th and 90th percentiles (whiskers), and all outliers (dots).

biomass, $F_{1,62} = 0.15$, $p = 0.70$), the intercept of the linear regression was larger in the high-piscivory lakes (ANCOVA, abundance, $F_{1,63} = 14.1$, $p < 0.0001$; biomass, $F_{1,63} = 15.9$, $p < 0.0001$), suggesting that prey abundances and biomasses were consistently higher in the high-piscivory than in the low-piscivory lakes, independent of mean depth of lakes.

The mean prey length was not at all correlated to Chl a or Z_{mean} (Fig. 4C,F; Table 1), but prey was on average 1.12 times larger in lakes with large (high piscivory) predators than in lakes with smaller (low piscivory) predators (t-test on $\log_{10}$ prey lengths, df $= 64$, $t = 3.92$, $p = 0.0002$).

The total predator abundance was significantly correlated to abundances of five out of those ten single prey species that occurred in at least 17 of the 66 lakes. However, the significant correlations were in all cases positive, reflecting that in particular the abundances of small perch, but also the abundances of ruffe, bream, roach, and bleak, increased with increasing predator abundances (Fig. 5). A weakly significant negative rank correlation ($R_s = -0.32$, df $= 31$, $p = 0.074$) was found only between predator and vendace abundances (Fig. 5).

The level of piscivory had no influence on the relationships between Z_{mean} and Chl a of the lakes (Fig. 6; Table 1). Slopes and intercepts of the high-piscivory vs. low-piscivory groups of lakes did not differ, whether level of piscivory was estimated by predator abundance (Fig. 6A; ANCOVA, slope, $F_{1,59} = 1.07$, $p = 0.30$; intercept, $F_{1,60} = 1.46$, $p = 0.23$), predator biomass (Fig. 6B; ANCOVA, slope, $F_{1,56} = 0.01$, $p = 0.92$; intercept, $F_{1,57} = 0.08$, $p = 0.78$), or predator length (Fig. 6C; ANCOVA, slope, $F_{1,62} = 0.65$, $p = 0.42$; intercept, $F_{1,63} = 0.20$, $p = 0.66$). Accordingly, in opposition to my expectation, the trophic cascade down to phytoplankton was not stronger in lakes with high piscivory than in lakes with low piscivory.

Discussion

I found little evidence that predatory fish in lakes exert strong community-wide top-down control on their prey fishes in lakes. Furthermore, I found no evidence that the trophic cascade from piscivores down to phytoplankton was stronger in lakes with high piscivory than in lakes with functionally less important piscivory. Since these patterns were corroborated also by positive correlations between predator abundance and abundance of single dominant species, my results contrast earlier studies, which have suggested that strong trophic cascades from predatory fish down to phytoplankton may occur in lakes (Persson et al. 1992; Carpenter et al. 2001; Potthoff et al. 2008).

Since my comparative approach is based on fish catches by gill nets, I discuss methodological uncertainties that may have contributed to the differences to previous studies. First, the size-selective catch by gill nets may bias size distribution and proportion of certain fish species (Hamley 1975). The multimesh gill-net type as applied in my study has been specifically designed to reduce size selectivity (Kurkilahti and Rask 1996), and comparative tests indicated high reliability of catches for fish >6 cm (Prchalova et al. 2009). Unbiased catches for fish >6 cm were also suggested by the continuous slope of the logarithmic length distributions shown here. A recent study found similar catches of large fish in gill nets and beach seines with no evidence for underestimation of large predators in gill nets (Prchalova et al. 2009). Therefore, a systematic bias of the predator : prey biomass or length ratios from catches by multimesh gill nets is unlikely.

A second issue of concern is the pooling of catches from benthic and pelagic habitats. Because substantially less pelagic than benthic nets have been used in all lakes, this procedure may underestimate the true densities of exclusively pelagic species in very deep lakes relative to those predominantly occupying benthic habitats. To overcome this bias, weighing the gill-net catch per depth with the water volume of the respective depth stratum is recommended (Lauridsen et al. 2008), but lack of respective data prevented the application in my study. Earlier comparisons indicated that all fish species occurring in pelagic nets are also caught by benthic nets (Diekmann et al. 2005). Furthermore, the observed succession of fish community composition along productivity gradients in lakes was
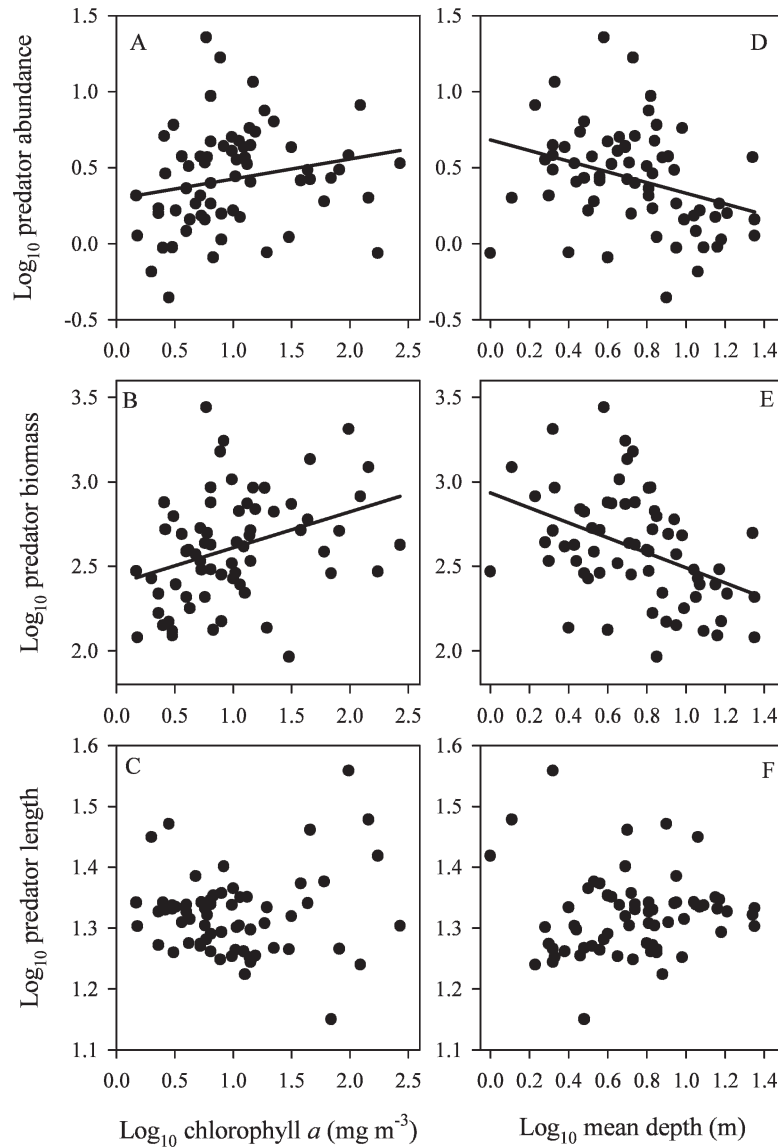
Fig. 3. Scatter plots between (A, B, C) lake productivity ($\log_{10}$ Chl a, mg m^{-3}) or (D, E, F) lake mean depth ($\log_{10}$ Z_{mean}, m) and (A, D) $\log_{10}$ abundances (ind. standard gill net^{-1}), (B, E) $\log_{10}$ biomasses (g wet weight standard gill net^{-1}), or (C, F) $\log_{10}$ lengths (cm) of predatory fish in 66 German lakes (*see* Table 1 for regression details).

predominantly based on catches from benthic nets (Persson et al. 1992; Jeppesen et al. 2000) suggesting that the lower representation of pelagic catches may have had little consequences for the overall interpretation.

A third potential concern refers to the question of whether the chosen lakes were typical for the geographical area or substantially deviated from the expected predator:prey ratios. The fish communities studied here contributed to developing a fish-based typology for the entire European ecoregion "Central Plains," encompassing lakes in Denmark, southern Sweden, and northern Germany (Mehner et al. 2007). Therefore, the north German lakes are a representative selection with respect to fish species composition, lake productivity, and morphometry. The predator proportions in these lakes were also within the expected range. Based on bioenergetics

balances, we have estimated that about 25% predator biomass would be sufficient to control the average annual production of prey fishes in lakes (Wysujack and Mehner 2002). The median biomass proportion of predators in the 66 lakes, as estimated from the predator:prey ratio, was 24% (0.321/(0.321 + 1)). Because the theoretical estimate corresponds to the average predator proportion found empirically, it is suggested that the lake fish communities studied here do have functionally significant predator levels. Therefore, I assume that the extensive sampling protocol as applied in my study was appropriate and none of my conclusions are seriously violated by methodological shortcomings.

Methodological details may have contributed to the differences between my study and earlier studies with respect to the proportion of predators over the productivity

Table 1. Results of linear regressions between $\log_{10}$ predator or prey fish abundance (ind. standard net^{-1}), biomass (g wet weight standard net^{-1}), or mean length (cm) and lake productivity ($\log_{10}$ Chl *a* concentration, mg m^{-3}) or $\log_{10}$ mean depth (Z_{mean}, m) in 66 German lakes. Prey variables were split into lake groups with either high or low piscivory according to the regressions between predator variables and lake productivity or depth. Regression coefficients a (intercept) and b (slope) are indicated with their 95% confidence intervals (CI, in parentheses). *See* Figs. 3, 4, and 6 for the bivariate plots.

Piscivory	No. of lakes	R^2	p	a (95% CI)	b (95% CI)
Predator abundance vs. lake productivity					
	66	0.043	0.096	0.29(0.09)	0.13(0.08)
Predator abundance vs. lake depth					
	66	0.105	0.008	0.68(0.10)	−0.35(0.13)
Predator biomass vs. lake productivity					
	66	0.120	0.004	2.40(0.08)	0.21(0.07)
Predator biomass vs. lake depth					
	66	0.181	<0.0001	2.93(0.09)	−0.44(0.12)
Predator length vs. lake productivity					
	66	—	0.543	—	—
Predator length vs. lake depth					
	66	—	0.798	—	—
Prey abundance vs. lake productivity					
Low	36	0.232	0.003	1.30(0.09)	0.26(0.08)
High	30	0.179	0.020	1.64(0.10)	0.24(0.10)
Prey biomass vs. lake productivity					
Low	33	0.255	0.003	2.67(0.09)	0.28(0.08)
High	33	0.291	0.001	2.94(0.08)	0.26(0.07)
Prey length vs. lake productivity					
Low	33	—	0.837	—	—
High	33	—	0.584	—	—
Prey abundance vs. lake depth					
Low	37	0.387	<0.0001	2.05(0.11)	−0.61(0.13)
High	29	0.248	0.006	2.16(0.11)	−0.45(0.15)
Prey biomass vs. lake depth					
Low	33	0.531	<0.0001	3.43(0.09)	−0.63(0.11)
High	33	0.323	0.001	3.59(0.10)	−0.56(0.16)
Prey length vs. lake depth					
Low	33	—	0.079	—	—
High	33	—	0.084	—	—
Lake productivity vs. lake depth at differing predator abundances					
Low	35	0.542	<0.0001	2.02(0.18)	−1.31(0.21)
High	28	0.310	0.002	1.63(0.19)	−0.93(0.27)
Lake productivity vs. lake depth at differing predator biomasses					
Low	30	0.510	<0.0001	1.90(0.19)	−1.18(0.22)
High	30	0.346	0.001	1.84(0.22)	−1.14(0.30)
Lake productivity vs. lake depth at differing predator lengths					
Low	33	0.287	0.001	1.69(0.19)	−0.95(0.27)
High	33	0.515	<0.0001	1.93(0.19)	−1.23(0.21)

gradient in lakes. Persson et al. (1992) compared 11 stratified lakes with and without predators in Sweden. They demonstrated that the highest proportion of predators occurred at intermediate phytoplankton biomasses. However, the switch from systems without predators to systems with abundant predators was observed over a narrow range of 1.6 to 4.5 mg m^{-3} Chl *a*, far below the productivity measured in the majority of the lakes of my study (range 1.5 to 269 mg m^{-3}). Furthermore, in contrast to the multimesh gill nets with 5.0-mm minimum mesh size as I have applied, the survey nets applied in Sweden had 8-mm (pelagic nets) or even 9.5-mm (benthic nets) minimum mesh sizes (Persson et al. 1992). Accordingly, all fishes with length smaller than about 9 cm (M. Prchalova, Institute of Hydrobiology, Ceske Budejovice pers. comm.) were certainly not quantitatively included in the calculation of predator proportions in the Swedish lakes. In my surveys, fish between 2 and 9 cm constituted 56% of all prey fish sizes but only 3% of all predator fish sizes due to the dominance of perch among the piscivores. Therefore, it is
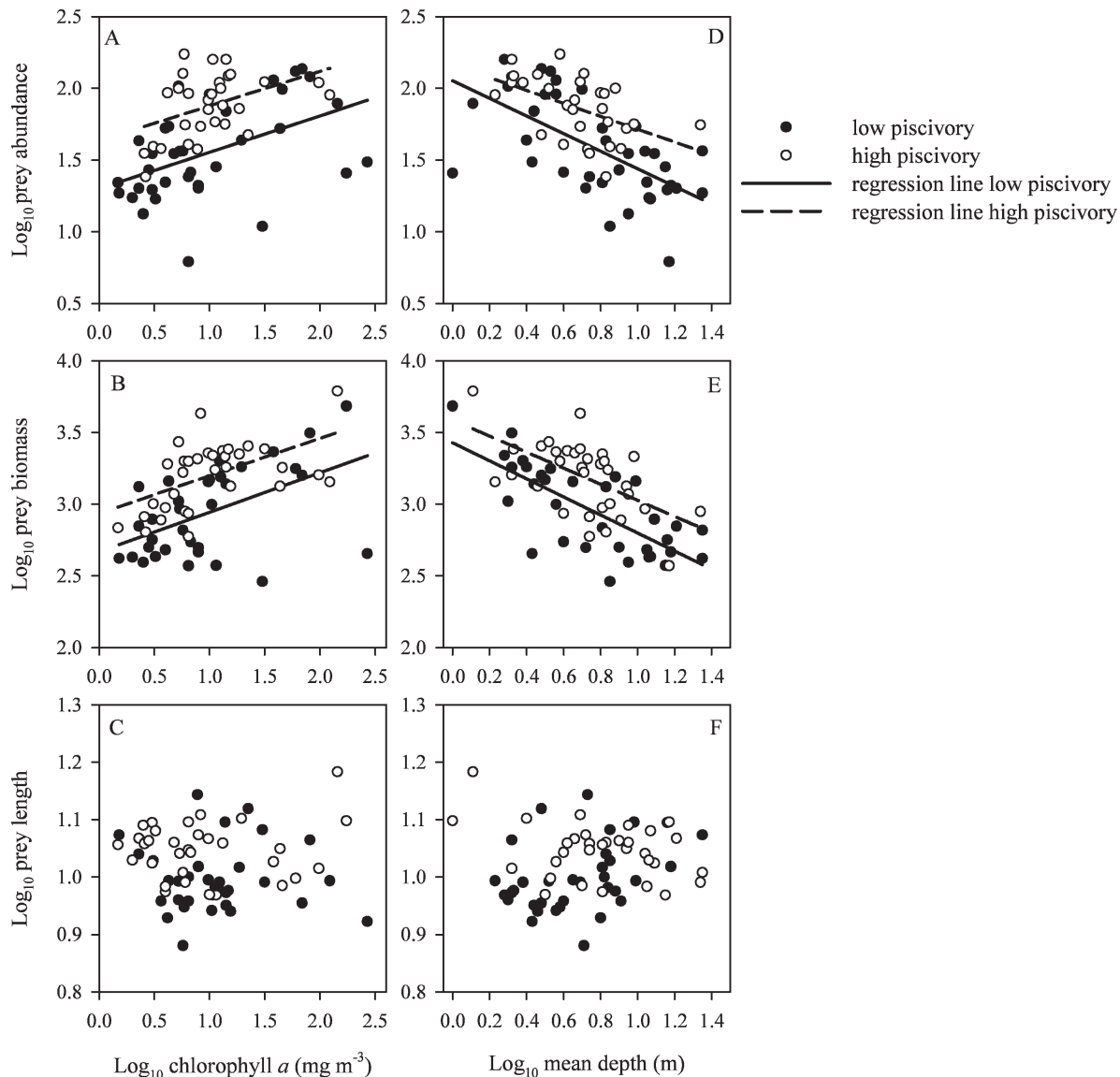
Fig. 4.   Scatter plots between (A, B, C) lake productivity (log$_{10}$ Chl a, mg m^{-3}) or (D, E, F) lake mean depth (log$_{10}$ Z_{mean}, m) and (A, D) log$_{10}$ abundances (ind. standard gill net^{-1}), (B, E) log$_{10}$ biomasses (g wet weight standard gill net^{-1}), or (C, F) log$_{10}$ lengths (cm) of prey fish in 66 German lakes. The data set was split into lake groups with either low or high piscivory according to (A, D) predator abundance, (B, E) predator biomass, or (C, F) predator length, and regressions were separately calculated for these lake sets (*see* Table 1 for regression details).

not surprising that my results do not correspond to the high proportions and the unimodal relationship between fish predators and lake productivity suggested by Persson et al. (1992).

Similarly, a peak with 45% to 65% piscivores was found at low to intermediate phytoplankton biomass (<30 mg Chl a m^{-3}) in shallow Danish lakes (Jeppesen et al. 2000), substantially exceeding the majority of predator : prey ratios that I have found in my study. However, Jeppesen et al. (2000) assigned all perch independent of lengths into the predatory fish group, in contrast to splitting perch into predators and prey at 15 cm length as I have done. Therefore, my results and the study by Jeppesen et al. (2000) are in fact congruent in finding high perch biomasses in lakes at intermediate phytoplankton biomass and of

intermediate depths. However, only a minority of these perch are large predators, and therefore I could not confirm a unimodal relationship between the predator : prey ratio and Chl a.

My results contradict the trophic cascade hypothesis (Carpenter et al. 1985) and a number of studies in which strong negative interactions in the food chain from piscivores to phytoplankton have been demonstrated, mainly in small, species-poor lakes (Benndorf et al. 1984; Carpenter et al. 2001; Potthoff et al. 2008). In contrast, weak community-wide relationships between predatory fish and their prey and low evidence for piscivore-induced trophic cascades have been demonstrated in other experiments (Nowlin et al. 2006) and by comparative analyses (Drenner and Hambright 2002; Bertolo et al. 2005). I
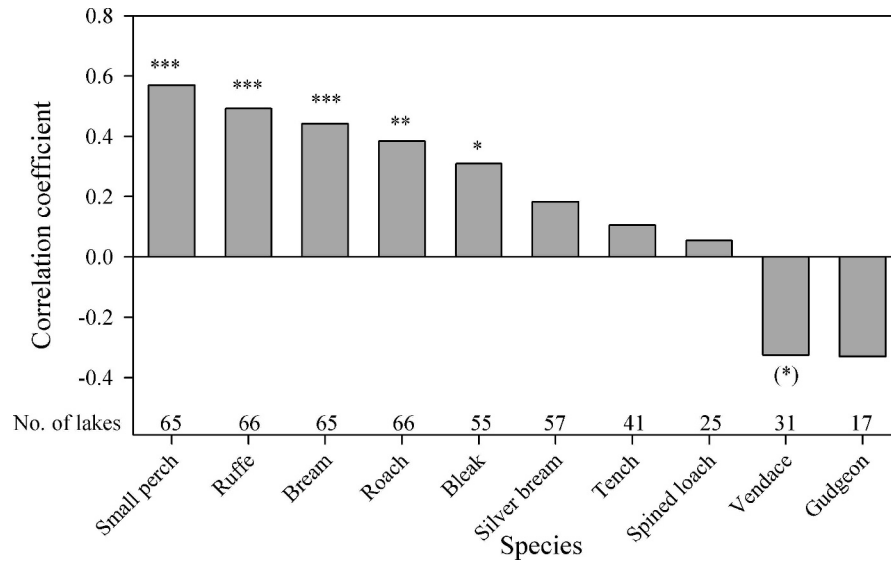
Fig. 5. Bivariate Spearman rank correlation coefficients between total abundance of all predators (ind. standard net^{-1}) and abundances of those 10 prey fish species (ind. standard net^{-1}) that occurred in at least 17 of the 66 lakes. Significance of correlations is indicated by asterisks (*** <0.001, ** <0.01, * <0.05, (*) <0.10).

discuss subsequently why an increase in predator densities does not necessarily cause reduced community-wide prey densities or sizes and a stronger trophic cascade.

First, the positive correlation between predator and prey densities was mainly attributable to perch, whose individuals were split between predators and prey at a certain length threshold, as also suggested in earlier comparative studies (Persson et al. 1992). Since predatory perch have to recruit through the smaller ontogenetic stages grouped into the prey category, densities of both small and large perch may be strongly positively correlated. Furthermore, perch was the numerically dominant fish species in the entire data set, and occurred in 65 of the 66 lakes. These details explain why perch is the most important species for the overall evaluation of predator–prey relationships in European lakes (Persson et al. 1992; Jeppesen et al. 2000). However, cannibalism may be strong in perch (Persson et al. 2000), and therefore negative density correlations between cannibalistic predators and smaller perch prey can be expected, which may induce lakewide trophic cascades down to zooplankton and phytoplankton (Persson et al. 2003). In contrast, my data suggest low levels of cannibalism, since the abundance of all predators (which was dominated by piscivorous perch) and the abundance of small perch were strongly positively correlated. Therefore, an efficient control of the dominant prey (small perch) by the dominant predator (large perch) is unlikely in the majority of larger European lakes as studied here. A similar compensation of the trophic cascade by strong recruitment of the dominant piscivore largemouth bass (*Micropterus salmoides* (Lacepede)) through younger planktivorous stages has been documented for a lake in North America (Post et al. 1997).

Second, the intensity of predator–prey interactions and the resulting trophic cascade may be modified by the size relationships of the involved species. Empirical research has demonstrated that interaction strength increases with larger size ratios between predator and prey (Emmerson and Raffaelli 2004). In my study, the lengths of fish predators were about twice the lengths of their prey, and thus much smaller than the average found for predator–prey length relationships in freshwater systems (log$_{10}$ mass ratio of 4.15, equivalent to a length ratio of about 24) (Brose et al. 2006). The dominant predators in the lakes studied here, pike, zander, and perch, are able to ingest prey that is at maximum about one-third of their own length due to gape limitations (Mittelbach and Persson 1998). Therefore, an efficient control of the larger prey is prevented by a size refuge (Hambright et al. 1991), and negative correlations had to be expected mainly between predator abundance and abundance of small, juvenile fishes. However, because the overall catch was dominated by fish smaller than 15 cm length (90% of all prey individuals), the lack of negative correlations in the entire data set suggests that there was also no top-down control of smaller fish. The average size of prey was significantly larger in high-piscivory lakes (larger predators) than in low-piscivory lakes, suggesting that predator and prey sizes are positively coupled. However, the overall effect size of larger predators on prey size (1.12) was small only. To understand mechanistically the potentially subtle response of prey to predator lengths, more detailed analyses of size spectra within the fish communities may be required (Jennings et al. 2001).

Finally, omnivory, i.e., feeding from several trophic levels, is common in freshwater fishes. Recent studies using stable isotopes have suggested that many piscivores frequently feed upon invertebrate prey items originating from benthic lake habitats (Vander Zanden and Vadeboncoeur 2002). Accordingly, a part of the required energy is diverted away from the predatory fish–prey fish link, thus lowering the predicted top-down control by the predators. If littoral and pelagic food webs are largely uncoupled, as found, for example, in oligotrophic Canadian lakes,
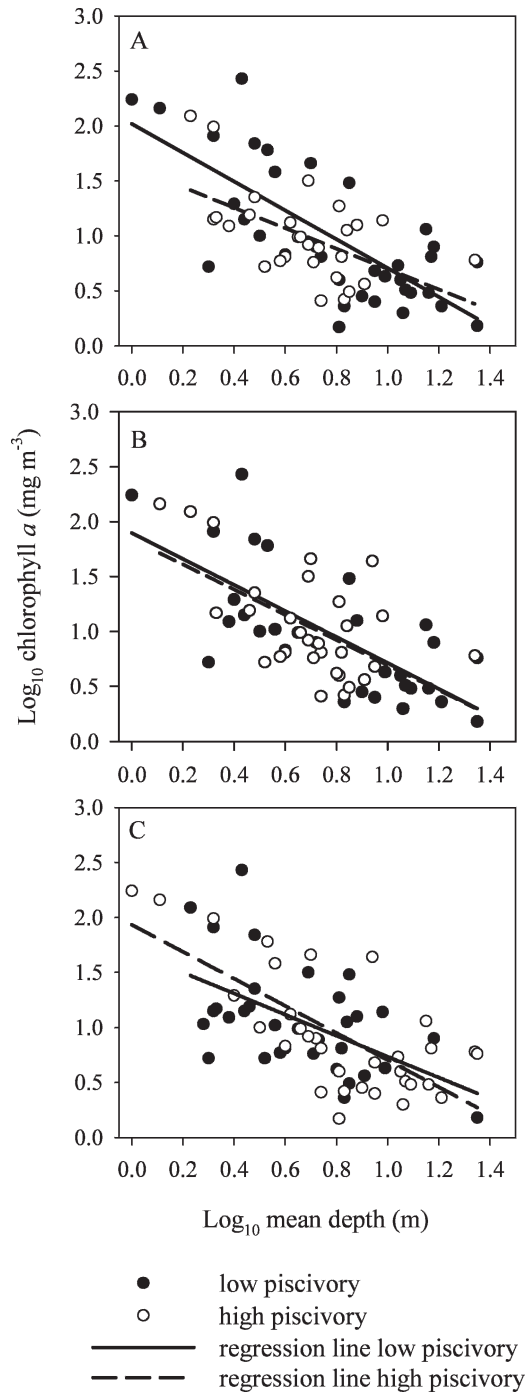
Fig. 6. Scatter plots between lake productivity (log$_{10}$ Chl a, mg m^{-3}) and lake mean depth (log$_{10}$ Z_{mean}, m) of 66 German lakes. The data set was split into lake groups with either low or high piscivory according to (A) predator abundance, (B) predator biomass, or (C) predator length, and regressions were separately calculated for these lake sets (*see* Table 1 for regression details).

predation by piscivores may have little effect on phytoplankton biomass (Bertolo et al. 2005).

Detailed analyses of predator manipulations in lakes revealed that size or biomass of single prey species responded negatively to enhanced predation, whereas community-wide effects of piscivore feeding were rare

(Hambright et al. 1991; Tonn et al. 1992; Nowlin et al. 2006). Therefore, I have also checked for effects of high piscivory on single prey species in my data set. I found mainly positive correlations between piscivores and prey fish abundances except for the weakly significant negative relationship between vendace and predators. In a comparative study in Canadian lakes that differed in the presence and biomasses of several piscivorous fish species, Bertolo et al. (2005) likewise found positive correlations between predator biomass and the biomasses of the dominant prey species. Only a group of small-sized planktivores constituting in sum less than 5% of total fish biomass responded negatively to piscivore predation. Therefore, I cannot exclude that predation has modified the biomass or presence–absence structure of those small fish that occurred in less than a quarter of the 66 lakes included in my study. However, owing to their rarity and the very low proportion of overall fish biomass, they do not contribute decisively to the strength of a trophic cascade.

In summary, community-wide effects of predatory fish on prey fish abundance or biomass and a trophic cascade induced by fish predators were not found. Furthermore, the predator : prey ratios were not at all related to phytoplankton biomass or mean depth of lakes. These results do not question that community-wide trophic cascades do exist in lakes, but the strongest evidence comes from cascades induced by planktivorous and benthivorous fishes (Jeppesen et al. 2003). In contrast, evidence for strong top-down interactions between piscivores and their prey fish is rather weak (Drenner and Hambright 2002; Nowlin et al. 2006). It needs to be studied which specific features of predator and prey fish prevent the predation effect from being comparatively strong as observed between fish and zooplankton or zooplankton and phytoplankton.

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