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Effects of fish predation on density and size spectra of prey fish communities in lakes

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Abstract

Planktivorous and benthivorous fish have been documented to influence the density and size structure of their prey communities in lakes. We hypothesized that piscivorous fish modify their prey fish communities in the same way and sought to find evidence for such predation effects from a comparison across 356 lakes located in nine European ecoregions. We categorized individual fish as being either piscivore, non-piscivore or prey of piscivores, depending on species and individual size. We calculated piscivore, non-piscivore and piscivore prey densities, respectively, and fit linear abundance size spectra (SS) on lake-specific piscivore, non-piscivore and piscivore prey size distributions. Multiple linear regressions were calculated to quantify the effect of piscivore density and SS slopes on non-piscivore and piscivore prey densities and SS slopes, by accounting for potentially confounding factors arising from lake morphometry, productivity and local air temperature. Piscivore density correlated positively with piscivore prey density, but was uncorrelated to density of non-piscivores. Across a subset of 76 lakes for which SS slopes of piscivores were statistically significant, SS slopes of piscivores were uncorrelated with SS slopes of either non-piscivores or piscivore prey. However, densities of piscivores, non-piscivores or piscivore prey were a significant negative predictor of SS slopes of the respective groups. Our analyses suggest that direct predation effects by piscivorous fish on density and size structure of prey fish communities are weak in European lakes, likely caused by low predator-prey size ratios and the resulting size refuges for prey fish. In contrast, competition may substantially contribute to between-lake variability in fish density and size.

Key words: abundance size spectra, predator-prey interaction, across-lake comparison
Introduction

Following two seminal papers on the effect of predation by planktivorous fish on zooplankton communities (Hrbacek et al. 1961; Brooks and Dodson 1965), pelagic food webs have long been considered classical examples for the structuring effects of predation in lakes. Numerous subsequent studies have shown that planktivorous fish predators can have profound effects on the densities, species composition and size structure of prey communities (e.g. Post and McQueen 1987; Carpenter et al. 2001; Brucet et al. 2010). Similar predation effects have also been found for benthivorous predatory fishes feeding upon macroinvertebrate prey (e.g. Brönmark et al. 1992; Diehl 1992; Blumenshine et al. 2000). In large-scale comparisons between lakes, negative correlations between predator and prey densities or size have supported the assumption that predation can explain a large part of between-lake variability in zooplankton densities or size (Jeppesen et al. 2003; Matveev 2003).

There is a much smaller body of literature showing the same strong predation effects for piscivorous fish feeding upon fish prey. In some lakes, massive disturbances of predator communities after winter fish kills or by fish stocking or removal have induced correlated, often short-term, changes in prey communities (Benndorf et al. 1984; Mittelbach et al. 1995; Potthoff et al. 2008). In regional studies, the effect of predation by piscivores on prey fish densities has been compared across several lakes (Nowlin et al. 2006; Mehner 2010; Friederichs et al. 2011). In one of these analyses, predator and prey densities were positively correlated (Mehner 2010), whereas in others the expected negative correlations of prey density with predator density were found only for a limited number of small prey species (Nowlin et al. 2006; Friederichs et al. 2011). These studies also revealed that lake productivity and morphometry may confound the potential effects of predators on prey, and hence have to be taken into account when analysing correlations between abundances of predator and prey across lakes (Mehner 2010). Shifts in the size structure of prey fish communities in response to fish predation across lakes have not yet been explicitly demonstrated, although recent
publications have indicated that fish prey-size metrics may be sensitive to the strength of predation by piscivorous fish (Mehner 2010; Emmrich et al. 2011).

Body size is one of the most important traits of animals, being linked to physical activities, biological rates, the strength of ecological interactions and selective fisheries (Brown et al. 2004; Shin et al. 2005; Brose et al. 2006). Therefore, characterizing the size distributions of animal communities may capture much of the biologically meaningful variation in a relatively straightforward manner (Woodward et al. 2005). In aquatic systems, indeterminate growth of organisms dominates and ontogenetic changes in diet are common, hence the concept of species belonging to a single niche or trophic level is less plausible and the size-based view has been more widely appreciated than in terrestrial ecosystems (Trebiolco et al. 2013). Furthermore, the main determinant of the trophic position of an aquatic predator within a food web is often its size rather than its taxonomic identity (Woodward et al. 2005), and strong patterns in food web structure related to body size in aquatic systems become evident when analyzed using size-class subdivisions (Jennings et al. 2002).

Predators in aquatic environments face the problem that they generally have to swallow their prey as a single intact item because if they eat only pieces of it, they risk the loss of the rest of the prey item due to sinking or water flow (Brose et al. 2006). Accordingly, aquatic predator-prey interactions depend strongly on predator and prey sizes and the maximum prey size is determined by the predator gape size (Hambright 1994; Arim et al. 2010). Hence, comparative inspection of the distribution of abundance among body sizes in predator and prey communities may generate insight into the interaction strength between adjacent trophic levels (Emmerson and Raffaelli 2004; Brose et al. 2006; Trebilco et al. 2013). A suitable approach to compare size distributions is the linear size spectrum (Vidondo et al. 1997; Kerr and Dickie 2001), which captures the decline of number of organisms with increasing size without considering taxonomic differences.

The aim of this study was to elucidate whether the strong predation effects on prey density and size demonstrated for planktivorous and benthivorous fish predators in aquatic food webs can
likewise be found for piscivorous fish predators in lakes. In contrast to earlier studies with a more regional focus (Bertolo et al. 2005; Mehner 2010; Friederichs et al. 2011), we included information on 356 lakes of the European continent, thus accounting for substantial variation of fish community composition in response to geographical location and environmental temperature (see Brucet et al. 2013). Individual fish were classified as piscivores, non-piscivores or piscivore prey, depending on species and size for facultative piscivores (Mittelbach and Persson 1998). We correlated piscivore with non-piscivore or piscivore prey densities, and expected to find a negative relationship across the lakes. Furthermore, we calculated linear abundance size spectra separately for piscivores non-piscivores and piscivore prey communities, thus explicitly searching for patterns in size structure in response to predation that go beyond the analysis of shifts in mean size (Mehner 2010; Brucet et al. 2013). Although changes of size spectra of prey communities in response to predation have been studied occasionally (Zimmer et al. 2001; Jonsson et al. 2005; Brucet et al. 2010; Murry and Farrell 2014), a simultaneous inspection and comparison of slopes of size spectra from both predator and prey communities across several lakes is not yet available. We expected to find steeper slopes of size spectra of non-piscivores and in particular of piscivore prey fish communities indicating a dominance of smaller fish in lakes where their piscivorous predators were large due to size-selective predation on larger prey (see Blumenshine et al. 2000; Blanchard et al. 2009). To account for confounding effects of lake productivity, morphometry and temperature on prey density and size, we included lake depth, lake area, total phosphorus concentration and maximum air temperature as covariates into our analyses. Finally, we tested for geographical effects by splitting the dataset into regional subsets from Northern and Central Europe.

Methods

Sampling
Lake fish communities were sampled in about 1800 European lakes between 1990 and 2010, and data have been accumulated into a database within the EU-project WISER (see for details Argillier et al. 2013; Brucet et al. 2013). Complete information on fish size, lake productivity and lake morphometry were available only for a subset of these 1800 lakes. We focused on those 356 lakes located in nine European ecoregions (Illies 1978) which are dominated by percid (perch *Perca fluviatilis* and/or pikeperch *Sander lucioperca*) or salmonid predators (mainly brown trout, *Salmo trutta*) (Fig. 1). For these lakes, we acquired information on lake total phosphorus concentration (TP, mg m\(^{-3}\), measured as the mean of a minimum of four samples taken in a single year), lake maximum depth (m) and lake area (km\(^2\)). Maximum air temperature at the geographic location of the lake was calculated from the climate CRU model (New et al. 2002) and was used as an approximation to maximum lake temperature. Earlier calculations have shown that size structure of fish communities is more sensitive to maximum than to average local temperatures (Emmrich et al. 2014). An overview about mean values and value ranges for all variables within the 356 lakes is given in the Supplementary Material (Table S1).

Fish in these lakes were caught by stratified multimesh gill-net sampling according to the EU standard for such sampling (CEN 2015). Each lake was divided into depth strata, and each stratum was randomly sampled by a pre-defined number of benthic gill-nets (type NORDEN: length 30 m; height 1.5 m; 12 panels of 2.5 m each with mesh sizes (knot to knot) of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm), depending on lake area and maximum depth (Appelberg 2000; CEN 2015). Deep lakes (maximum depth >6 m) were additionally sampled with a row of pelagic nets [similar type as the benthic ones, but of 3 m height and 27.5 m length (5 mm mesh panel missing)] placed over the deepest location in each lake. The number of pelagic nets was defined by the maximum lake depth (i.e., number of nets = depth divided by the 3 m height of the pelagic nets) such that the pelagic net row fished the entire water column in deep lakes. All sampling was conducted during late summer to early autumn periods (CEN 2015). Catch was expressed as lake-specific number per unit effort (NPUE, fish net\(^{-1}\) night\(^{-1}\), averaged from all nets set per lake (but pelagic nets of 3 m height counted as two
nets because the net area was about twice as large as the one of benthic nets), and hence this NPUE reflects primarily the catch in the benthic gill-nets (for an overview on numbers of nets set per lake, see Supplementary Material Table S1).

In predator fish, ontogenetic diet shifts are common and piscivory is the dominant feeding strategy only beyond a certain fish size. Therefore, all individuals $>2^{5}=32$ g (roughly equivalent to 15 cm total length) of pike *Esox lucius*, pikeperch, catfish *Silurus glanis*, asp *Aspius aspius*, burbot *Lota lota*, perch, brown trout, rainbow trout *Oncorhynchus mykiss*, Arctic charr *Salvelinus alpinus*, lake trout *Salvelinus namaycush* and largemouth bass *Micropterus salmoides* were classified as piscivores. All other 45 species were classified as non-piscivores, and were considered potential prey of the piscivores. However, to account for the potentially underestimated proportion of small-sized fish in gill-net catches and to prevent the inclusion of all non-piscivores that were definitely too large to be fed upon by piscivores, we defined the narrow-sized group of piscivore prey (i.e., suitably sized prey for the piscivores) which included the sum of all young piscivores in the size range $>8$ g to $\leq 32$ g and all non-piscivores in the size range $>8$ g to $\leq 128$ g. This group hence reflects all fish in the size range between 8 g and 128 g except piscivores $>32$ g.

**Evaluating the effect of piscivore density on non-piscivore and piscivore prey densities**

We visualized the frequency distributions of NPUEpiscivores, NPUEnon-piscivores and NPUEpiscivore-prey across the lakes by histograms, compared the NPUE between piscivores, non-piscivores and piscivore prey across all lakes by Wilcoxon rank sum tests, and calculated Spearman’s rank correlation coefficient $r_S$ between either $\log_{10}$ NPUEpiscivores and $\log_{10}$ NPUEnon-piscivores, or between $\log_{10}$ NPUEpiscivores and $\log_{10}$ NPUEpiscivore-prey to document the raw correspondence between predator and prey densities. Non-parametric tests were appropriate because of non-normal distribution and heteroscedasticity in the total, untransformed dataset.
Non-piscivore fish were found in 332 lakes only. The remaining 24 lakes contained only piscivorous species. To evaluate the effects of piscivore density (NPUEpisivores) on non-piscivore density (NPUEnon-piscivores) in these 332 lakes while accounting for the confounding effects of lake morphometry, productivity and temperature, we calculated linear models with log_{10} NPUEnon-piscivores as the dependent variable and log_{10} NPUEpisivores, log_{10} lake area, log_{10} lake depth, log_{10} TP and maximum air temperature as independent variables. We did not consider interactions between the continuous predictor variables. We sought for the most parsimonious linear model by backwards elimination of the predictor with lowest significance from the initially full model, thus stepwisely declining the Akaike Information Criterion (AIC) of the models. Accordingly, the final model was the one with the lowest AIC (Faraway 2005). In addition, we compared the two models with lowest AIC by ANOVA to decide whether to retain the respective predictor. We checked residual plots of the final model for deviations from normality and homoskedasticity, and calculated variance inflation factors (VIF) to detect potential collinearity between predictor variables. To compare the relative strength of the significant predictors, we additionally calculated their standardized (beta) coefficients. In a similar way, we calculated linear models with log_{10} NPUEpisivore-prey (n=354 lakes) as the dependent variable and log_{10} NPUEpisivores, log_{10} lake area, log_{10} lake depth, log_{10} TP and maximum air temperature as independent variables.

Evaluating the effect of predator size on prey size

To evaluate the effect of piscivore size structure on non-piscivore and piscivore-prey size structure, we accumulated information on the size of fish. All fish caught were individually measured (rounded to cm total length, TL) and directly weighed (g wet mass, wm) in most cases. For several lakes, wm was calculated from TL by regional species-specific regressions. The multimesh gill-nets used underestimate the proportion of fish smaller than 4-6 cm TL (Prchalova et al. 2009), and hence fish of 1 to 4 g wm (i.e., fish in first year of life) were under-represented in our catches. To avoid a
bias in estimating the fish size structures, we excluded all fish ≤4 g from subsequent calculations, and
digits of non-piscivores were accumulated into 13 log₂ size classes (1st class: >2²=4 g to ≤2³=8 g,
2nd class: >2³=8 to ≤2⁴=16 g, etc., 13th class: >2¹⁵=16,384 to ≤2¹⁶=32,768 g). The size structure of
piscivores encompassed only 10 size classes (>32 to ≤32,768 g). The size structure of piscivore prey
encompassed only four size classes (>8 to ≤128 g, see above). For overall inspection purposes, we
accumulated all piscivore, non-piscivore and piscivore prey fishes per size class across all 356 lakes
into a cumulative size spectrum. Cumulative size spectra represent the average decline of fish
numbers by size across all lakes, but weighted by the number of fish caught per lake. Accordingly,
these plots are biased towards the size structure of those lakes which contributed most fish to the
overall number. To check for regional differences in the cumulative size spectra, we split the total
lake dataset into two geographical subsets (Northern Europe with n=193 lakes from Norway and
Sweden; Central Europe with n=163 lakes primarily from Germany and France, accompanied by a few
lakes from U.K., Ireland, Northern Italy, Estonia and Slovenia), and compared the slopes of the
regional size spectra (see below) by ANCOVA.

Linear abundance size spectra (SS) as obtained by logarithmic binning (Kerr and Dickie 2001) were
calculated as linear least-square regressions between log₂ numbers accumulated per size class and
log₂ midpoint of size classes (g). The slopes of SS indicate the rate of decrease in numbers with
increasing body size, a parameter that may be sensitive to size-selective predation of piscivores. In
some of the lakes, a few size classes did not contain fish, and these empty size classes were excluded
from linear regressions (White et al. 2008). Furthermore, in some lakes, fish covered only one or two
size classes, and hence SS could not be calculated. Ultimately, separate slopes for piscivores, non-
piscivores and piscivore prey fish communities were calculated for 353, 317 and 317 lakes,
respectively. We visualized the frequency distributions of piscivore, non-piscivore and piscivore-prey
SS slopes by histograms, compared the SS slopes between piscivores and non-piscivores or between
piscivores and piscivore prey across all lakes by Wilcoxon rank sum tests, and calculated the
Spearman’s rank correlation coefficient $r_s$ between piscivore SS slopes and non-piscivore or piscivore-prey SS slopes to document the raw correspondence between predator and prey size spectra.

To evaluate more precisely the effect of predator size distributions on prey size distributions, we calculated linear models with non-piscivore SS slopes as the dependent variable, and piscivore SS slopes as the independent variable. To consider potential density effects on non-piscivore slopes, $\log_{10} NPUE_{\text{non-piscivores}}$ was added to the set of predictor variables. We further added $\log_{10}$ lake area, $\log_{10}$ lake depth, $\log_{10}$ TP and maximum air temperature as potentially confounding variables. The most parsimonious model was found according to minimized AIC and ANOVA as described above. Similarly, we calculated linear models with piscivore-prey SS slopes as the dependent variable, and piscivore SS slopes as the independent variable, and added $\log_{10} NPUE_{\text{piscivore-prey}}$, $\log_{10}$ lake area, $\log_{10}$ lake depth, $\log_{10}$ TP and maximum air temperature as predictors.

The SS of fish communities were non-linear in some lakes (Emmrich et al. 2014). Therefore, we created a lake subset by including only significant ($P<0.05$) and informative ($R^2>0.5$) SS slopes for piscivores (185 lakes) and non-piscivores (137 lakes). For piscivore prey (123 lakes), we applied a less strict significance threshold ($P<0.10$) because these SS regressions were based on four value pairs only. Significant and informative SS for both piscivores and non-piscivores in the same lake were found in 76 lakes. Similarly, significant and informative SS for both piscivores and piscivore prey in the same lake were found in 76 lakes. For these subsets, we repeated the visualization and all calculations as described above, to evaluate whether the size structure of piscivores had a correlative effect on the size structure of non-piscivores of piscivore-prey fish.

With the subsets with significant and informative SS slopes, we conducted two additional analyses. First, we split the lakes into Northern or Central European origin (see above) and re-calculated the linear models with SS slope of non-piscivores or piscivore prey as the dependent variable separately for both geographical subsets. Second, we reversed the analyses and tested whether the SS slopes of non-piscivores or piscivore prey (independent variables) had an effect on SS
slopes of piscivores (dependent variable). We included log$_{10}$ NPUEpiscivores as predictor, and log$_{10}$ lake area, log$_{10}$ lake depth, log$_{10}$ TP and maximum air temperature as covariates.

Potential bias of gill-net catches for fish density and size estimates

All analyses were based on standardized catches by multi-mesh gill nets, and gill-net catches can be biased with respect to abundance estimates and size distributions (Prchalova et al. 2009; Prchalova et al. 2011; Clement et al. 2014). Saturation effects may lead to underestimation of fish abundances if soaking time of gill-nets is long, and correction has been recommended for catches >3 kg per standard multi-mesh gill-net per night (Prchalova et al. 2011). However, the average biomass per net exceeded 3 kg in only 41 out of the 356 lakes, and was higher than 6 kg net$^{-1}$ in only four lakes. Therefore, saturation may have only marginally biased our results. It has been shown that gill-nets consistently underestimate the relative proportions of fish smaller than about 6 cm (Prchalova et al. 2009). However, there is a strong correspondence between catches by multi-mesh gill-nets and fish densities calculated from hydroacoustic records (Emmrich et al. 2012), suggesting that the fish-catch index (NPUE) obtained from gill-nets is a relatively unbiased approximation to lake-specific fish densities. Therefore, we assumed that the consistent underestimation of the smallest size classes of fish by gill-net catches has no systematic effect on comparison of fish NPUE between the lakes. In addition to the underestimation of small fish <4 g, the abundance of very large fish may also be underestimated (Psuty and Borowski 1997; Prchalova et al. 2009; Smejkal et al. 2015). The cumulative size spectra (Supplementary Material Fig. S1) suggest an underestimation of fish >4096 g. However, this uncertainty for fish >4 kg may have had no substantial effect on the estimates of total piscivore abundances or piscivore SS slopes. Overall, the SS slopes of piscivores and non-piscivores were determined by the numbers of fish in up to 11 (usually 5-7) size classes in our dataset (compare Fig. 3), and hence uncertainties for abundances in single size classes have not too strong effects on the slope estimates. Furthermore, the biases introduced by gill-nets apply to all lakes in a
comparative way, and hence we are convinced that the general trends found by our analyses are robust and valid.

Testing for potential bias in the dataset caused by fisheries

Exploitation of fish communities by commercial or recreational fisheries may modify fish abundance and size spectra (Jennings and Blanchard 2004). We tested for a potential bias of our analyses induced by fisheries intensity within the total dataset of 356 lakes by comparing NPUE and SS slopes of piscivores, non-piscivores and piscivore prey between 47 lakes with reported high fisheries intensity (categorized according to local expert opinion), and 112 lakes with no or very low fisheries intensity. For the remaining lakes, no information was available, or fisheries intensity was considered intermediate. We ran linear models with fisheries (low or high) as the main categorical factor, and lake area, lake depth, TP concentration and maximum air temperature as covariates. We further included all two-way interactions between fisheries intensity and the four covariates. Fisheries intensity had no effect on NPUEpiscivores (P=0.20). However, NPUEnon-piscivores (P=0.042) and NPUEpiscivore-prey (P=0.012) were slightly higher in lakes with high fisheries intensity indicating that more non-piscivore and prey fish are found in lakes with stronger fisheries. However, the SS slopes of piscivores (P=0.89), non-piscivores (P=0.21) and piscivore prey (P=0.22) did not differ between the low and high fisheries lakes. We conclude that fisheries intensity is likely to have had only marginal effects on the validity of our analyses which focused on the effects of predator on prey fish.

All statistical calculations were performed in R 3.1.2 (R Development Core Team 2014).

Results
In total, n=39,066 piscivore predators were caught in the 356 lakes, and the median standardized NPUE of piscivores was 3.5 fish net\(^{-1}\) night\(^{-1}\) (Supplementary Material Table S1). In the majority of lakes, NPUE of piscivores ranged between 1 and 10 fish net\(^{-1}\) night\(^{-1}\) (Fig. 2a), but the maximum piscivore NPUE was 26 fish net\(^{-1}\) night\(^{-1}\). A total of n=163,562 non-piscivore fish was caught in 332 lakes (the remaining lakes had fish communities exclusively composed of juvenile and adult piscivores). The median NPUE of non-piscivores was 11.4 fish net\(^{-1}\) night\(^{-1}\), and non-piscivore NPUE was significantly higher than piscivore NPUE in these lakes (Wilcoxon rank sum test, W=94,828, P<0.0001). In the majority of the lakes, NPUE of non-piscivores ranged between 1 and 50 fish net\(^{-1}\) night\(^{-1}\), but higher NPUE up to the maximum of 244 fish net\(^{-1}\) night\(^{-1}\) were found in some of the remaining lakes (Fig. 2b, Supplementary Material Table S1). There was a weak negative correlation between the log\(_{10}\)-transformed piscivore and non-piscivore NPUEs across the 332 lakes (Fig. 2d; Spearman’s \(r_s\)=−0.113, \(P=0.039\)). A total of n=188,868 piscivore prey fish was caught in 354 lakes, with a median NPUE of piscivore prey of 15.5 fish net\(^{-1}\) night\(^{-1}\) (Fig. 2c) which was higher than the median piscivore NPUE in all lakes (Wilcoxon rank sum test, W=108,705, \(P<0.0001\)). There was no correlation between the log\(_{10}\)-transformed NPUE of piscivore and NPUE of piscivore prey across the 354 lakes (Fig. 2e; Spearman’s \(r_s\)=0.023, \(P=0.67\)).

The best linear model for the 332 lakes with log\(_{10}\) NPUEnon-piscivores as the dependent variable contained log\(_{10}\) TP, log\(_{10}\) maximum lake depth, log\(_{10}\) lake area, maximum air temperature and log\(_{10}\) NPUEpiscivores as significant predictor variables (AIC=-504.9). The next best model (AIC=-503.4) excluded log\(_{10}\) NPUEpiscivores, but this model was not significantly different from the model including NPUEpiscivores (ANOVA, \(P=0.49\)), and hence we excluded NPUEpiscivores as predictor (Table 1, adj.\(R^2\)=0.47, \(F_{4,327}=73.7\), \(P<0.0001\)). All variance inflation factors were <1.5 (Table 1). Positive relationships to NPUEnon-piscivores were found for TP, temperature and lake area, whereas NPUEnon-piscivores declined with lake depth (Table 1). According to beta coefficients, air temperature was the strongest predictor, whereas the effect of lake area was the weakest (Table 1). The most parsimonious linear model for the 354 lakes with log\(_{10}\) NPUEpiscivore-prey as the
dependent variable contained $\log_{10}$ TP, $\log_{10}$ maximum lake depth, $\log_{10}$ lake area, maximum
air temperature and $\log_{10}$ NPUEpiscivores as significant predictor variables (Table 1, adj.$R^2=0.48$, $F_{5,348}=65.1$, $P<0.0001$, AIC=-723.4). The next best model (AIC=-720.4) excluded $\log_{10}$ TP, but was
significantly different from the model including TP (ANOVA, $P=0.026$), and hence we kept TP as
predictor variable. All variance inflation factors were <1.65 (Table 1). In contrast to our expectations,
the NPUEpiscivores was positively related to NPUEpiscivore-prey. Positive relationships to
NPUEpiscivore-prey were likewise found for TP, temperature and lake area, whereas NPUEpiscivore-
prey declined with lake depth (Table 1). According to beta coefficients, air temperature was the
strongest predictor, whereas the effects of TP and NPUEpiscivores were the weakest (Table 1).

The piscivore sizes ranged between the lower threshold size of 32 g (several species) and the
maximum of 11,124 g (a pike). The size of non-piscivores ranged between 1 g (several species) and
20,000 g (a bighead carp, Hypophthalmichthys nobilis). The size of piscivore prey was defined
according to our thresholds between 9 g and 128 g. The cumulative size spectrum across all 356 lakes
had a slope of -1.68 for piscivores, -1.35 for non-piscivores, and -0.86 for piscivore prey
(Supplementary Material, Fig. S1a). The total size range of piscivores and non-piscivores was very
similar, except the missing smallest size classes of predators (<32 g) which were classified as piscivore
prey. If the lake dataset was split into subsets from two geographical regions, the resulting slopes of
cumulative size distributions of piscivores, non-piscivores and piscivore prey for the Northern and
Central European regions were similar (Supplementary Material Fig. S1b,c) and did not differ
between the geographical subsets (ANCOVA, piscivores: $F_{2,20}=0.47$, $P=0.63$; non-piscivores: $F_{2,30}=2.1$, $P=0.13$; piscivore prey: $F_{2,6}=0.65$, $P=0.55$).

Among the 356 lakes, there were combinations of shallow piscivore but steep non-piscivore and
piscivore-prey SS slopes (Mirower See, Fig. 3a), intermediate SS slopes for piscivores, non-piscivores
and piscivore prey (Wummsee, Fig. 3b), or steep piscivore but shallow non-piscivore and piscivore-
prey SS slopes (Fleesensee, Fig. 3c). Overall, the slopes of the SS of piscivores in the 353 lakes for
which SS could be calculated ranged between -2.93 and 0.50 (median= -0.828, Supplementary
The slopes of the SS of non-piscivores in the 317 lakes for which SS could be calculated ranged between -2.64 and 1.04 (median=-0.614, Fig. 4b; Supplementary Material Table S1), and non-piscivore SS slopes were shallower than piscivore SS slopes (Wilcoxon rank sum test, W=65,055, P<0.0001). There was a slightly negative correlation between piscivore and non-piscivore SS slopes across the 315 lakes for which SS could be calculated for both fish groups (Fig. 4c; Spearman’s r_s=-0.118, P=0.036). The slopes of the SS of piscivore prey in the 317 lakes for which SS could be calculated ranged between -3.33 and 1.36 (median=-0.883, Fig. 4e; Supplementary Material Table S1), and piscivore-prey SS slopes did not differ from piscivore SS slopes (Wilcoxon rank sum test, W=46,694, P=0.23). There was no correlation between piscivore SS slopes and piscivore-prey SS slopes across the 314 lakes for which size spectra could be calculated for both fish groups (Fig. 4f; Spearman’s r_s=-0.016, P=0.77).

We excluded two lakes with outlier SS slopes of piscivores or non-piscivores (Fig. 4c) to reduce heteroskedasticity and one lake for which no information on maximum depth was available. The best linear model for the remaining 312 lakes with non-piscivore SS slope as the dependent variable contained piscivore SS slopes, maximum temperature, log_{10} TP, log_{10} lake area and log_{10} NPUEnon-piscivores as significant predictor variables (AIC=-615.7). However, the next best model (AIC=-613.8) excluded maximum temperature, and this model was not significantly different to the one including temperature (ANOVA, P=0.076). Therefore, we excluded maximum temperature from the final model (Table 2, adj.R^2=0.35, F_{4,307}=41.4, P<0.0001). According to beta coefficients, the negative effect of the piscivore SS slopes on non-piscivore SS slopes was the weakest among the significant predictors, whereas NPUEnon-piscivores was the strongest predictor (Table 2).

We excluded two lakes with outlier SS slopes of piscivores or piscivore prey (Fig. 4f) to reduce heteroskedasticity. The best linear model for the remaining 312 lakes with SS slopes of piscivore prey as the dependent variable contained log_{10} maximum depth, log_{10} TP and log_{10} NPUEpiscivore-prey as significant predictor variables (AIC=-284.0). However, the next best model (AIC=-283.5) excluded
maximum depth, and this model was not significantly different to the one including depth (ANOVA, $P=0.15$). Therefore, we excluded maximum depth from the final model (Table 2, adj.$R^2=0.10$, $F_{2,309}=19.0$, $P<0.0001$). According to beta coefficients, NPUEpiscivore-prey was the strongest predictor of SS slopes of piscivore prey (Table 2).

By considering only significant ($P<0.05$) and informative ($R^2>0.5$) SS slopes, the range of SS slopes for piscivores in the remaining 185 lakes became narrower than that calculated from all lakes (median $=-1.01$), but the majority of slopes was still found between -0.50 and -1.0 (Fig. 4g). The range of significant and informative non-piscivore SS slopes in 137 lakes became likewise narrower (median $=-0.843$, Fig. 4h), but non-piscivore SS slopes still were significantly shallower than piscivore SS slopes (Wilcoxon rank sum test, $W=16,457$, $P<0.0001$). There was no significant correlation between piscivore and non-piscivore SS slopes in the 76 lakes for which significant and informative SS could be calculated (Fig. 4i; Spearman’s $r_s=-0.102$, $P=0.39$). The median of significant ($P<0.1$) and informative ($R^2>0.5$) SS slopes of piscivore prey in 123 lakes was steeper than the one in all lakes (median $=-1.184$, Fig. 4k), and SS slopes of piscivore prey were significantly steeper than piscivore SS slopes (Wilcoxon rank sum test, $W=9,072$, $P=0.003$). There was no significant correlation between SS slopes of piscivores and SS slopes of piscivore prey in the 76 lakes for which significant and informative SS could be calculated (Fig. 4i; Spearman’s $r_s=0.063$, $P=0.56$).

The best linear model for the 76 lakes with significant SS slopes of non-piscivores as the dependent variable contained SS slopes of piscivores, maximum temperature and $\log_{10}$ NPUEnon-piscivores as significant predictor variables (AIC=-247.5). However, the next best model (AIC=-247.0) excluded SS slopes of piscivores, and this model was not significantly different to the one including piscivore slopes (ANOVA, $P=0.23$). Therefore, we excluded SS slopes of piscivores from the final model (Table 2, adj.$R^2=0.36$, $F_{2,73}=21.9$, $P<0.0001$). The negative effect of NPUEnon-piscivores on SS slopes of non-piscivores was stronger than the positive effect of temperature on SS slopes (Table 2). Similarly, the most parsimonious model for significant SS slopes of piscivore prey in 76 lakes contained only maximum temperature and NPUEpiscivore-prey as significant predictors (Table 2,
adj. R²=0.16, F_{2,73}=7.89, P=0.0008, AIC=-127.9). The better model (AIC=-129.3) included also \log_{10} TP, but this model was not significantly better than the one without TP (ANOVA, P=0.53).

When the lake dataset with significant and informative SS slopes was split into regional subsets, the linear models revealed that the NPUE of non-piscivores or piscivore prey were the strongest predictors for SS slopes on non-piscivores or piscivore prey, respectively, in particular for the region Central Europe (Table S2, Supplementary Material). A negative effect of piscivore SS slopes on non-piscivore or piscivore-prey SS slopes could not be found in these geographical subsets.

In the reversed analyses, we calculated the most parsimonious linear model with SS slopes of piscivores as the dependent variable, and TP, lake area, lake depth, maximum temperature, SS slope of non-piscivores or piscivore prey, and NPUEpiscivores as predictors. In both linear models, all lake descriptors and SS slopes of non-piscivores or piscivore prey were excluded, and NPUEpiscivores was the single significant independent variable for SS slopes of piscivores (for piscivore SS slopes including non-piscivores as predictor: final model adj. R²=0.38, F_{1,74}=47.3, P<0.0001, \log_{10} NPUEpiscivores t=-6.88, P<0.0001; for piscivore SS slopes including piscivore prey as predictor: final model adj. R²=0.33, F_{1,74}=37.9, P<0.0001, \log_{10} NPUEpiscivores t=-6.19, P<0.0001).

Discussion

The correspondence between the density and size of piscivorous fish and the density and size of non-piscivores or piscivore prey fish produced by our calculations was in part unexpected. Piscivore density correlated positively with piscivore prey density. Piscivore SS slopes did not predict the non-piscivore and piscivore-prey SS slopes in the linear models in any of the subsets including only significant slopes. In contrast, the SS slopes of piscivores, non-piscivores and piscivore prey were strongly negatively correlated with NPUE of the respective groups in all datasets, suggesting that the size structure of fish in lakes is primarily density-dependent. A substantial decline of prey fish densities or a consistent removal of maximum-sized piscivore prey fish from predation by piscivorous
fish, similar to the patterns found for example for the interactions between planktivorous fish and zooplankton prey in the pelagic area of lakes (Brooks and Dodson 1965; Jeppesen et al. 2003), could not be detected by the ataxonomic approach as used here.

The strong positive correlations between non-piscicivore or piscivore-prey densities and temperature, lake productivity or morphometry confirm earlier studies which have used various subsets of European lakes (Jeppesen et al. 2000; Mehner et al. 2005; Brucet et al. 2013). Usually, higher TP concentrations directly boost the biomass of primary producers and indirectly increase the biomass of primary consumers (zooplankton and macroinvertebrates), and hence the resource availability becomes similarly higher for fish as secondary consumers. The positive correlation between piscivore densities and piscivore prey densities found in our data suggests that the enhanced resource availability translates even into tertiary consumers. A similar positive correlation between predator and prey fish densities has already been found in a subset of about 60 German lakes (Mehner 2010). The correspondence between resource availability and fish density is further modified by lake morphometry. Polymictic shallow, large and warm lakes facilitate a stronger response of fish density to productivity than observed in stratified lakes with a cool hypolimnetic area (Brucet et al. 2013). In polymictic lakes, TP concentrations are translated into higher primary productivity than in stratified lakes at comparable TP concentrations, attributable to the interaction between frequent mixing and hence continuous nutrient availability for phytoplankton, and the higher average temperatures (Jeppesen et al. 1997).

The overall positive correlation between piscivore density and piscivore-prey density contrasts with the findings of lake-specific studies in which massive interventions for piscivorous fish communities changed the equilibrium between predator and prey. For example, experimental stocking or removal of piscivores conducted in small lakes induced correlated short-term changes in prey fish communities (Benndorf et al. 1984; Mittelbach et al. 1995; Potthoff et al. 2008). However, in most of these cases, after a few years the predator-to-prey density or species ratios returned to the original values observed before disturbance, hence suggesting that strong negative density
effects of piscivores on prey communities may reflect transient states which cannot be upheld without permanent disturbance (Mittelbach et al. 1995; Donald and Anderson 2003). In studies comparing fish communities across several lakes, densities and size of single, usually small, prey fish species have been found to correlate negatively to predator fish densities (Nowlin et al. 2006; Friederichs et al. 2011). One may argue that our sampling approach was not suitable to find a negative effect of predation on densities of small-sized fish because piscivore prey individuals smaller than 2 g (about 6 cm length) representing the newly hatched cohorts in the year of catch were underrepresented in the gill-nets (Prchalova et al. 2009). Hence, we cannot totally exclude the possibility that fish predation reduces in particular the densities of newly hatched fish. However, this effect obviously does not translate into lower recruitment and likewise lower densities of fish at higher age because our analyses demonstrate that the total densities of piscivores and piscivore prey in lakes tend to be positively correlated. This positive correlation suggests that productivity and competition strength keep predator and prey densities in equilibrium and override potential local predation effects. It has to be noted that there was no positive correlation between densities of piscivores and non-piscivores, but only between piscivores and piscivore prey. The group of piscivore prey also included the smallest size groups (<32 g or about <15 cm) of predators (primarily perch and zander in European lakes) which can form a substantial proportion of total fish abundance in the 8 g to 32 g size classes. Therefore, piscivores are more abundant in lakes where young piscivores are likewise more abundant, and hence intra-guild predation and cannibalism within and among piscivorous fish populations (e.g., Schulze et al. 2006) contribute to the energy transfer from primary production to production of piscivores.

Increasing fish density might be compensated for by reduced average individual growth (Holmgren and Appelberg 2001; Rose et al. 2001). Therefore, fish achieve a relatively smaller size at higher densities, as indicated by the dominant negative correlation between SS slopes of piscivores, non-piscivores or piscivore prey, and the NPUE of the respective groups. This strong negative density dependence has been found by several previous analyses on the fish communities of European lakes.
(Emmrich et al. 2011; Arranz et al. 2015). Lowered growth rates leading to ‘stunted’ fish populations are well described in response to strong competition for resources at high fish densities (Ylikarjula et al. 1999; Amundsen et al. 2007). Stunting can be seen as an adaptive response of life history by which age and size at maturity and investment into reproduction are adjusted to the local conditions. It can be expected for fish that live in environments characterized by steep size spectra (i.e., low average size of food resources) and low overall resource abundance such that growth is limited by high foraging activity (Giacomini et al. 2013).

The median SS slopes of piscivores, non-piscivores and piscivore prey were relatively similar, and the majority of the slopes ranged between -0.5 and -1.0, in particular in the subsets with significant SS slopes. However, SS slopes of piscivores were unrelated to SS slopes of non-piscivores or piscivore prey. Obviously, the correspondence between size distributions of piscivores and piscivore prey is much weaker than the strong negative effect of planktivorous fish predators on zooplankton size (Brooks and Dodson 1965). The decisive difference to the fish-zooplankton interaction is the very similar and largely overlapping size range of piscivores and non-piscivores. We found both piscivores and non-piscivores between 1 g and >10 kg in the catches. This feature characterizes size-structured populations in which adult fish have to recruit through much smaller juvenile stages during which juvenile piscivores can be competitors of piscivore prey fish (Werner and Gilliam 1984). In contrast, there is almost no size overlap between the largest zooplankton (about 5 mm) and the smallest zooplanktivorous fish (fish larvae of about 5-6 mm) and predator-to-prey length ratio (PPLR) in interactions between adult fish and zooplankton is in most cases >100 which translates into a predator-to-prey mass ratio (PPMR) of at least $100^3=1,000,000$. In contrast, the PPLR of piscivore fish in temperate European lakes is only around 4 to 5 (Mittelbach and Persson 1998; Wysujack and Mehner 2005; Dörner et al. 2007), and hence their average PPMR is about $4^3=64$ to $5^3=125$ (Brose et al. 2006).

Based on this low PPMR, the range of piscivore-prey sizes still available to the piscivorous predators is surprisingly small. An upper threshold for vulnerable size classes of prey fish can be
estimated at about 100 g because piscivores capable of feeding on 100 g prey have to be 64 to 125 times heavier, i.e. their mass would exceed 6400 g. Piscivores of this size are rare in the lake fish communities analysed here (only 14 of the 39,066 piscivores were in the size classes >4096 g). In turn, prey fish bigger than about 100 g may reach a size refuge (Hambright 1994; Wysujack and Mehner 2005). According to the cumulative data from all 356 lakes in our dataset, size classes >128 g represent about 4.9% of all non-piscivore individuals, a proportion big enough to facilitate continued reproduction (Meijer et al. 1994). In addition, the largest female fish also have the highest absolute fecundity. Therefore, the size refuge may explain why there was no negative effect of piscivore densities on non-piscivore densities. However, we have also tested for a stronger negative effect of predation on structure of the most vulnerable prey sizes by limiting the size range of piscivore prey to between 8 and 128 g. This narrow size range of prey prevented inclusion of potentially underestimated small sizes and also prevented the inclusion of all non-piscivores that were definitely too large to be fed upon by piscivores. Accordingly, a negative correlation between SS slopes of piscivores and these four size classes of piscivore prey would have been expected if gape-size limitation is the single explanation for low predation effects on the size structure of the prey fish community. However, even by having these few prey size classes included, there was no response of piscivore-prey size structure to the piscivore size structure. These results suggest that the SS slopes of non-piscivore fish communities are relatively stable and independent of predation, and may reflect an emergent characteristics of the ecosystem (Sprules 2008; Yurista et al. 2014). This is confirmed by the fact that we found systematically steeper slopes at the higher fish densities which occur in more productive lakes, suggesting that there is a correspondence between fish density, ecosystem productivity and fish size structure.

The lack of significant slopes in many lakes indicates that linear SS may not be an ideal approach for characterizing the size structure of fish communities. Only in about half of all lakes we obtained significant and informative SS slopes by logarithmic binning and least-square estimation. Continuous approaches such as the fit by maximum likelihood of a Pareto I cumulative distribution function are
recommended (White et al. 2008), but are likewise inappropriate if the log-log relationship between numbers and size is not linear (Emmrich et al. 2011; Emmrich et al. 2014). The cumulative size spectra shown here likewise indicated a tendency towards a non-linear log-log size-density relationship. Our own tests showed that Bayesian minimum mean square error estimations of Pareto II functions result in somehow improved fits of the size distributions, probably because Pareto II models approximate to non-linear log-log relationships between numbers and size (results not shown). However, the resulting Pareto II function has two or even three parameters which are strongly correlated to each other. Accordingly, the ecological interpretation of the form of Pareto II curves is not straightforward (Vidondo et al. 1997), and a meaningful conclusion with respect to the effect of predator size on prey size could not be drawn. Accordingly, we had to base our conclusions primarily on the relationship between SS of piscivores and non-piscivores or piscivore prey for the subsets of lakes with significant SS slopes.

In summary, our analyses did not find evidence for predation effects of piscivorous fish on prey fish communities in European lakes which mimic the strong effects of planktivorous and benthivorous fish predators on size and density of their invertebrate prey groups. Size ranges were remarkably similar between piscivores and non-piscivore fish across all lakes included in the analyses, and hence there was no negative effect of piscivore density or size on non-piscivore or piscivore prey numbers and size structure. As a consequence of this lack of density control by predation, the density and size structure of non-piscivore fish communities were substantially predicted by variables related directly to temperature, resource availability and the correlated system size (see Chase 2003), indicating that the intensity of intra- and interspecific competition strongly modifies composition and size variability of fish communities in lakes.

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References


Table 1: Coefficients (estimates ± standard error, S.E.), beta (standardized) coefficients and variance inflation factors (VIF) of the most parsimonious linear model of \( \log_{10} \) \( NPUE \) non-piscivore fish (in fish \( \text{net}^{-1} \text{night}^{-1} \), upper part) or \( \log_{10} \) \( NPUE \) piscivore-prey fish (in fish \( \text{net}^{-1} \text{night}^{-1} \), lower part) as the dependent variable in 332 and 354 European lakes, respectively. Significant predictors were \( \log_{10} \) piscivore fish density (\( NPUE_{\text{Pisc}} \), in fish \( \text{net}^{-1} \text{night}^{-1} \)), lake area (in ha), lake maximum depth (\( \text{max} \_\text{depth}, \text{in m} \)), total phosphorus concentration (\( \text{TotalP}, \text{in mg m}^{-3} \)) and maximum air temperature (\( \text{max} \_\text{temperature}, \text{in °C} \)).

|                       | Estimate | S.E.  | Beta coeff. | VIF | t-value | Pr(>|t|) |
|-----------------------|----------|-------|-------------|-----|---------|----------|
| **Non-Piscivores (n=332 lakes)** |          |       |             |     |         |          |
| (Intercept)           | -0.892   | 0.219 | -4.067      | <0.0001 |         |          |
| \( \log_{10}(\text{lake area}) \) | 0.155    | 0.049 | 0.14        | 1.20 | 3.171   | 0.0017   |
| \( \log_{10}(\text{max_depth}) \) | -0.495   | 0.073 | -0.31       | 1.30 | -6.806  | <0.0001  |
| \( \log_{10}(\text{TotalP}) \) | 0.258    | 0.064 | 0.20        | 1.47 | 4.018   | <0.0001  |
| \( \text{max_temperature} \) | 0.135    | 0.014 | 0.45        | 1.36 | 9.600   | <0.0001  |
| **Piscivore prey (n=354 lakes)** |          |       |             |     |         |          |
| (Intercept)           | -0.246   | 0.171 | -1.432      | 0.1531 |         |          |
| \( \log_{10}(\text{NPUE}_{\text{Pisc}}) \) | 0.189    | 0.053 | 0.14        | 1.11 | 3.546   | 0.0004   |
| \( \log_{10}(\text{lake area}) \) | 0.142    | 0.037 | 0.17        | 1.23 | 3.867   | 0.0001   |
| \( \log_{10}(\text{max_depth}) \) | -0.460   | 0.056 | -0.37       | 1.34 | -8.217  | <0.0001  |
| \( \log_{10}(\text{TotalP}) \) | 0.109    | 0.049 | 0.11        | 1.61 | 2.225   | 0.0267   |
| \( \text{max_temperature} \) | 0.107    | 0.010 | 0.49        | 1.45 | 10.535  | <0.0001  |
Table 2: Coefficients (estimates ± standard error, S.E.), beta (standardized) coefficients and variance inflation factors (VIF) of the most parsimonious linear models of the slope of abundance size spectra (SS) of non-piscivore or piscivore prey fish communities as the dependent variables. Linear models were calculated for the entire dataset (all lakes with SS slopes) and for subsets with significant (P<0.05 for non-piscivores, P<0.10 for piscivore prey) and informative (R²>0.5) SS slopes only.

Significant predictors were density of non-piscivores or piscivore prey (NPUE_Non-Pisc; NPUE_PiscPrey; both in fish net⁻¹ night⁻¹), SS slope of piscivores (SlopeSS_Pisc), lake area (in km²), total phosphorus concentration (TotalP, in mg m⁻³) and maximum air temperature (max_temperature, in °C).

<p>|                      | Estimate | S.E. | Beta coeff. | VIF | t-value | Pr(&gt;|t|) |
|----------------------|----------|------|-------------|-----|---------|---------|
| <strong>Non-Piscivores</strong>   |          |      |             |     |         |         |
| All lakes (n=312)    |          |      |             |     |         |         |
| (Intercept)          | -0.198   | 0.083| -2.392      |     | 0.0174  |         |
| log10(lake_area)     | -0.116   | 0.038| -0.15       | 1.05| -3.075  | 0.0023  |
| log10(TotalP)        | 0.117    | 0.051| 0.12        | 1.39| 2.267   | 0.0241  |
| SlopeSS_Pisc         | -0.119   | 0.048| -0.12       | 1.15| -2.485  | 0.0135  |
| log10(NPUE_Non-Pisc) | -0.510   | 0.046| -0.58       | 1.34| -10.993 | &lt;0.0001 |
| <strong>Lakes with significant slopes only (n=76)</strong> |          |      |             |     |         |         |
| (Intercept)          | -1.204   | 0.221| -5.441      |     | &lt;0.0001 |         |
| max_temperature      | 0.052    | 0.015| 0.38        | 1.30| 3.569   | 0.0006  |
| log10(NPUE_Non-Pisc) | -0.422   | 0.064| -0.70       | 1.30| -6.606  | &lt;0.0001 |
| <strong>Piscivore prey</strong>   |          |      |             |     |         |         |
| All lakes (n=314)    |          |      |             |     |         |         |
| (Intercept)          | -0.558   | 0.122| -4.557      |     | &lt;0.0001 |         |</p>
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**Lakes with significant slopes only (n=76)**

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Captions for figures

Fig. 1: Geographical map of Europe, indicating location of the 329 lakes dominated by percid predators (dots) and 27 lakes dominated by salmonid predators or without predators at all (triangles).

Fig. 2: Frequency distribution of the fish abundance index (NPUE, number net$^{-1}$ night$^{-1}$) of fish caught by multi-mesh gill nets in 356 European lakes, split into NPUE of piscivores (a), non-piscivores (b) and piscivore prey fish (c), and scatter plot of log$_{10}$ NPUEpiscivores versus log$_{10}$ NPUEnon-piscivores (d) and log$_{10}$ NPUEpiscivores versus log$_{10}$ NPUEpiscivore-prey (e) in all lakes. The Spearman rank correlation coefficients $r_s$ are indicated in addition (d,e; *=P<0.05).

Fig. 3: Examples of linear abundance size spectra (SS) with opposing slopes of piscivores and non-piscivores or piscivore prey fishes in three German lakes. The midpoint of log$_2$ size classes of fish (g wm) is plotted against log$_2$ numbers of fish in this size class, and the slope of the regression is determined by least-squares estimation. Examples show Lake Mirower See with shallow piscivore slope and steep non-piscivore and piscivore-prey slopes (a), Lake Wummsee with intermediate piscivore, non-piscivore and piscivore-prey slopes (b), and Lake Fleesensee with steep piscivore slope and shallow non-piscivore and piscivore-prey slopes (c). Number of fish included (n), SS slopes and variance predicted by linear regression ($R^2$) are shown for each plot. All SS slopes are significant (P<0.05).

Fig. 4: Frequency distribution of the slopes of abundance size spectra (SS) of fish caught by multi-mesh gill nets in European lakes, split into predators (a,d, g, j), non-piscivores (b,h) and piscivore prey fish (e, k). Note that plots (a) and (d), and (g) and (j), show the same dataset. Scatter plots show SS slopes of piscivores versus SS slopes of non-piscivores (c, f) or vs. piscivore prey (i, l). The Spearman rank correlation coefficient $r_s$ is indicated in addition (c, f i, l; *=P<0.05). In the left part (a-f), we included all lakes for which SS slopes could be calculated (number of lakes indicated in graph titles).
In the right part (g-I), only lakes are included for which SS slopes were significant (P<0.05 for piscivores and non-piscivores, P<0.10 for piscivore prey) and informative (R²≥0.5).
Fig. 2

(a) Piscivores

(b) Non-Piscivores

(c) Piscivore prey

(d) Piscivores and Non-Piscivores

(e) Piscivores and Piscivore prey

Log_{10} Piscivores NPUE

Log_{10} Piscivore prey NPUE

r_s = -0.113 *

r_s = 0.023
Fig. 3

(a) Mirower See

(b) Wummsee

(c) Fleesensee

Log$_2$ numbers

Log$_2$ midpoints of fish mass

Midpoint fish mass (g)

Non-Piscivores: n=2277
Slope= -1.73
R$^2=0.85$

Non-Piscivores: n=624
Slope= -0.64
R$^2=0.84$

Non-Piscivores: n=988
Slope= -0.37
R$^2=0.68$

Piscivores: n=363
Slope= -1.50
R$^2=0.97$

Piscivores: n=588
Slope= -0.79
R$^2=0.78$

Piscivores: n=1272
Slope= -1.10
R$^2=0.91$

Piscivores: n=2166
Slope= -1.80
R$^2=0.95$

Piscivores: n=51
Slope= -0.43
R$^2=0.85$

Piscivores: n=363
Slope= -1.50
R$^2=0.97$

Piscivores: n=1272
Slope= -1.10
R$^2=0.91$
Fig. 4

(a) Piscivores (n=353)

(b) Non-Piscivores (n=317)

(c) Piscivores and Non-Piscivores (n=315)

(d) Piscivores (n=353)

(e) Piscivore prey (n=317)

(f) Piscivores and Piscivore prey (n=314)

(g) Piscivores (n=185)

(h) Non-Piscivores (n=137)

(i) Piscivores and Non-Piscivores (n=76)

(j) Piscivores (n=185)

(k) Piscivore prey (n=123)

(l) Piscivores and Piscivore prey (n=76)

Lakes with significant slopes

Non-Piscivores  Piscivore prey

$r_{S} = -0.118 \ast$

$r_{S} = -0.016$

$r_{S} = 0.102$

$r_{S} = 0.063$