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Contact CEH NORA team at  
[noraceh@ceh.ac.uk](mailto:noraceh@ceh.ac.uk)



31 **Abstract**

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

51

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

53

54 **Introduction**

55       Following two seminal papers on the effect of predation by planktivorous fish on zooplankton  
56 communities (Hrbacek et al. 1961; Brooks and Dodson 1965), pelagic food webs have long been  
57 considered classical examples for the structuring effects of predation in lakes. Numerous subsequent  
58 studies have shown that planktivorous fish predators can have profound effects on the densities,  
59 species composition and size structure of prey communities (e.g. Post and McQueen 1987; Carpenter  
60 et al. 2001; Brucet et al. 2010). Similar predation effects have also been found for benthivorous  
61 predatory fishes feeding upon macroinvertebrate prey (e.g. Brönmark et al. 1992; Diehl 1992;  
62 Blumenshine et al. 2000). In large-scale comparisons between lakes, negative correlations between  
63 predator and prey densities or size have supported the assumption that predation can explain a large  
64 part of between-lake variability in zooplankton densities or size (Jeppesen et al. 2003; Matveev  
65 2003).

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

79 publications have indicated that fish prey-size metrics may be sensitive to the strength of predation  
80 by piscivorous fish (Mehner 2010; Emmrich et al. 2011).

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

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

102 The aim of this study was to elucidate whether the strong predation effects on prey density and  
103 size demonstrated for planktivorous and benthivorous fish predators in aquatic food webs can

104 likewise be found for piscivorous fish predators in lakes. In contrast to earlier studies with a more  
105 regional focus (Bertolo et al. 2005; Mehner 2010; Friederichs et al. 2011), we included information  
106 on 356 lakes of the European continent, thus accounting for substantial variation of fish community  
107 composition in response to geographical location and environmental temperature (see Bruzet et al.  
108 2013). Individual fish were classified as piscivores, non-piscivores or piscivore prey, depending on  
109 species and size for facultative piscivores (Mittelbach and Persson 1998). We correlated piscivore  
110 with non-piscivore or piscivore prey densities, and expected to find a negative relationship across the  
111 lakes. Furthermore, we calculated linear abundance size spectra separately for piscivores non-  
112 piscivores and piscivore prey communities, thus explicitly searching for patterns in size structure in  
113 response to predation that go beyond the analysis of shifts in mean size (Mehner 2010; Bruzet et al.  
114 2013). Although changes of size spectra of prey communities in response to predation have been  
115 studied occasionally (Zimmer et al. 2001; Jonsson et al. 2005; Bruzet et al. 2010; Murry and Farrell  
116 2014), a simultaneous inspection and comparison of slopes of size spectra from both predator and  
117 prey communities across several lakes is not yet available. We expected to find steeper slopes of size  
118 spectra of non-piscivores and in particular of piscivore prey fish communities indicating a dominance  
119 of smaller fish in lakes where their piscivorous predators were large due to size-selective predation  
120 on larger prey (see Blumenshine et al. 2000; Blanchard et al. 2009). To account for confounding  
121 effects of lake productivity, morphometry and temperature on prey density and size, we included  
122 lake depth, lake area, total phosphorus concentration and maximum air temperature as covariates  
123 into our analyses. Finally, we tested for geographical effects by splitting the dataset into regional  
124 subsets from Northern and Central Europe.

125

## 126 **Methods**

### 127 *Sampling*

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

142 Fish in these lakes were caught by stratified multimesh gill-net sampling according to the EU  
143 standard for such sampling (CEN 2015). Each lake was divided into depth strata, and each stratum  
144 was randomly sampled by a pre-defined number of benthic gill-nets (type NORDEN: length 30 m;  
145 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,  
146 24, 29, 35, 43 and 55 mm), depending on lake area and maximum depth (Appelberg 2000; CEN 2015).  
147 Deep lakes (maximum depth >6 m) were additionally sampled with a row of pelagic nets [similar type  
148 as the benthic ones, but of 3 m height and 27.5 m length (5 mm mesh panel missing)] placed over the  
149 deepest location in each lake. The number of pelagic nets was defined by the maximum lake depth  
150 (i.e., number of nets = depth divided by the 3 m height of the pelagic nets) such that the pelagic net  
151 row fished the entire water column in deep lakes. All sampling was conducted during late summer to  
152 early autumn periods (CEN 2015). Catch was expressed as lake-specific number per unit effort (NPUE,  
153 fish net<sup>-1</sup> night<sup>-1</sup>), averaged from all nets set per lake (but pelagic nets of 3 m height counted as two

154 nets because the net area was about twice as large as the one of benthic nets), and hence this NPUE  
155 reflects primarily the catch in the benthic gill-nets (for an overview on numbers of nets set per lake,  
156 see Supplementary Material Table S1).

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

169

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

171 We visualized the frequency distributions of NPUEpiscivores, NPUEnon-piscivores and  
172 NPUEpiscivore-prey across the lakes by histograms, compared the NPUE between piscivores, non-  
173 piscivores and piscivore prey across all lakes by Wilcoxon rank sum tests, and calculated Spearman's  
174 rank correlation coefficient  $r_s$  between either  $\log_{10}$  NPUEpiscivores and  $\log_{10}$  NPUEnon-piscivores, or  
175 between  $\log_{10}$  NPUEpiscivores and  $\log_{10}$  NPUEpiscivore-prey to document the raw correspondence  
176 between predator and prey densities. Non-parametric tests were appropriate because of non-normal  
177 distribution and heteroscedasticity in the total, untransformed dataset.



178 Non-piscivore fish were found in 332 lakes only. The remaining 24 lakes contained only  
179 piscivorous species. To evaluate the effects of piscivore density (NPUEpiscivores) on non-piscivore  
180 density (NPUEnon-piscivores) in these 332 lakes while accounting for the confounding effects of lake  
181 morphometry, productivity and temperature, we calculated linear models with  $\log_{10}$  NPUEnon-  
182 piscivores as the dependent variable and  $\log_{10}$  NPUEpiscivores,  $\log_{10}$  lake area,  $\log_{10}$  lake depth,  $\log_{10}$   
183 TP and maximum air temperature as independent variables. We did not consider interactions  
184 between the continuous predictor variables. We sought for the most parsimonious linear model by  
185 backwards elimination of the predictor with lowest significance from the initially full model, thus  
186 stepwisely declining the Akaike Information Criterion (AIC) of the models. Accordingly, the final  
187 model was the one with the lowest AIC (Faraway 2005). In addition, we compared the two models  
188 with lowest AIC by ANOVA to decide whether to retain the respective predictor. We checked residual  
189 plots of the final model for deviations from normality and homoskedasticity, and calculated variance  
190 inflation factors (VIF) to detect potential collinearity between predictor variables. To compare the  
191 relative strength of the significant predictors, we additionally calculated their standardized (beta)  
192 coefficients. In a similar way, we calculated linear models with  $\log_{10}$  NPUEpiscivore-prey (n=354  
193 lakes) as the dependent variable and  $\log_{10}$  NPUEpiscivores,  $\log_{10}$  lake area,  $\log_{10}$  lake depth,  $\log_{10}$  TP  
194 and maximum air temperature as independent variables.

195

#### 196 *Evaluating the effect of predator size on prey size*

197 To evaluate the effect of piscivore size structure on non-piscivore and piscivore-prey size  
198 structure, we accumulated information on the size of fish. All fish caught were individually measured  
199 (rounded to cm total length, TL) and directly weighed (g wet mass, wm) in most cases. For several  
200 lakes, wm was calculated from TL by regional species-specific regressions. The multimesh gill-nets  
201 used underestimate the proportion of fish smaller than 4-6 cm TL (Prchalova et al. 2009), and hence  
202 fish of 1 to 4 g wm (i.e., fish in first year of life) were under-represented in our catches. To avoid a

203 bias in estimating the fish size structures, we excluded all fish  $\leq 4$  g from subsequent calculations, and  
204 numbers of non-piscivores were accumulated into 13  $\log_2$  size classes (1<sup>st</sup> class:  $>2^2=4$  g to  $\leq 2^3=8$  g,  
205 2<sup>nd</sup> class:  $>2^3=8$  to  $\leq 2^4=16$  g, etc., 13<sup>th</sup> class:  $>2^{14}=16,384$  to  $\leq 2^{15}=32,768$  g). The size structure of  
206 piscivores encompassed only 10 size classes ( $>32$  to  $\leq 32,768$  g). The size structure of piscivore prey  
207 encompassed only four size classes ( $>8$  to  $\leq 128$  g, see above). For overall inspection purposes, we  
208 accumulated all piscivore, non-piscivore and piscivore prey fishes per size class across all 356 lakes  
209 into a cumulative size spectrum. Cumulative size spectra represent the average decline of fish  
210 numbers by size across all lakes, but weighted by the number of fish caught per lake. Accordingly,  
211 these plots are biased towards the size structure of those lakes which contributed most fish to the  
212 overall number. To check for regional differences in the cumulative size spectra, we split the total  
213 lake dataset into two geographical subsets (Northern Europe with  $n=193$  lakes from Norway and  
214 Sweden; Central Europe with  $n=163$  lakes primarily from Germany and France, accompanied by a few  
215 lakes from U.K., Ireland, Northern Italy, Estonia and Slovenia), and compared the slopes of the  
216 regional size spectra (see below) by ANCOVA.

217 Linear abundance size spectra (SS) as obtained by logarithmic binning (Kerr and Dickie 2001) were  
218 calculated as linear least-square regressions between  $\log_2$  numbers accumulated per size class and  
219  $\log_2$  midpoint of size classes (g). The slopes of SS indicate the rate of decrease in numbers with  
220 increasing body size, a parameter that may be sensitive to size-selective predation of piscivores. In  
221 some of the lakes, a few size classes did not contain fish, and these empty size classes were excluded  
222 from linear regressions (White et al. 2008). Furthermore, in some lakes, fish covered only one or two  
223 size classes, and hence SS could not be calculated. Ultimately, separate slopes for piscivores, non-  
224 piscivores and piscivore prey fish communities were calculated for 353, 317 and 317 lakes,  
225 respectively. We visualized the frequency distributions of piscivore, non-piscivore and piscivore-prey  
226 SS slopes by histograms, compared the SS slopes between piscivores and non-piscivores or between  
227 piscivores and piscivore prey across all lakes by Wilcoxon rank sum tests, and calculated the

228 Spearman's rank correlation coefficient  $r_s$  between piscivore SS slopes and non-piscivore or piscivore-  
229 prey SS slopes to document the raw correspondence between predator and prey size spectra.

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

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

248 With the subsets with significant and informative SS slopes, we conducted two additional  
249 analyses. First, we split the lakes into Northern or Central European origin (see above) and re-  
250 calculated the linear models with SS slope of non-piscivores or piscivore prey as the dependent  
251 variable separately for both geographical subsets. Second, we reversed the analyses and tested  
252 whether the SS slopes of non-piscivores or piscivore prey (independent variables) had an effect on SS

253 slopes of piscivores (dependent variable). We included  $\log_{10}$  NPUEpiscivores as predictor, and  $\log_{10}$   
254 lake area,  $\log_{10}$  lake depth,  $\log_{10}$  TP and maximum air temperature as covariates.

255

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

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

278 comparative way, and hence we are convinced that the general trends found by our analyses are  
279 robust and valid.

280

### 281 *Testing for potential bias in the dataset caused by fisheries*

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

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

299

## 300 **Results**

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

317 The best linear model for the 332 lakes with  $\log_{10}$  NPUE<sub>non-piscivores</sub> as the dependent variable  
318 contained  $\log_{10}$  TP,  $\log_{10}$  maximum lake depth,  $\log_{10}$  lake area, maximum air temperature and  $\log_{10}$   
319 NPUE<sub>piscivores</sub> as significant predictor variables (AIC=-504.9). The next best model (AIC=-503.4)  
320 excluded  $\log_{10}$  NPUE<sub>piscivores</sub>, but this model was not significantly different from the model  
321 including NPUE<sub>piscivores</sub> (ANOVA,  $P=0.49$ ), and hence we excluded NPUE<sub>piscivores</sub> as predictor  
322 (Table 1,  $\text{adj.}R^2=0.47$ ,  $F_{4,327}=73.7$ ,  $P<0.0001$ ). All variance inflation factors were  $<1.5$  (Table 1). Positive  
323 relationships to NPUE<sub>non-piscivores</sub> were found for TP, temperature and lake area, whereas  
324 NPUE<sub>non-piscivores</sub> declined with lake depth (Table 1). According to beta coefficients, air  
325 temperature was the strongest predictor, whereas the effect of lake area was the weakest (Table 1).  
326 The most parsimonious linear model for the 354 lakes with  $\log_{10}$  NPUE<sub>piscivore-prey</sub> as the

327 dependent variable variable contained  $\log_{10}$  TP,  $\log_{10}$  maximum lake depth,  $\log_{10}$  lake area, maximum  
 328 air temperature and  $\log_{10}$  NPUepiscivores as significant predictor variables (Table 1,  $\text{adj.}R^2=0.48$ ,  
 329  $F_{5,348}=65.1$ ,  $P<0.0001$ ,  $\text{AIC}=-723.4$ ). The next best model ( $\text{AIC}=-720.4$ ) excluded  $\log_{10}$  TP, but was  
 330 significantly different from the model including TP (ANOVA,  $P=0.026$ ), and hence we kept TP as  
 331 predictor variable. All variance inflation factors were  $<1.65$  (Table 1). In contrast to our expectations,  
 332 the NPUepiscivores was positively related to NPUepiscivore-prey. Positive relationships to  
 333 NPUepiscivore-prey were likewise found for TP, temperature and lake area, whereas NPUepiscivore-  
 334 prey declined with lake depth (Table 1). According to beta coefficients, air temperature was the  
 335 strongest predictor, whereas the effects of TP and NPUepiscivores were the weakest (Table 1).

336 The piscivore sizes ranged between the lower threshold size of 32 g (several species) and the  
 337 maximum of 11,124 g (a pike). The size of non-piscivores ranged between 1 g (several species) and  
 338 20,000 g (a bighead carp, *Hypophthalmichthys nobilis*). The size of piscivore prey was defined  
 339 according to our thresholds between 9 g and 128 g. The cumulative size spectrum across all 356 lakes  
 340 had a slope of -1.68 for piscivores, -1.35 for non-piscivores, and -0.86 for piscivore prey  
 341 (Supplementary Material, Fig. S1a). The total size range of piscivores and non-piscivores was very  
 342 similar, except the missing smallest size classes of predators ( $<32$  g) which were classified as piscivore  
 343 prey. If the lake dataset was split into subsets from two geographical regions, the resulting slopes of  
 344 cumulative size distributions of piscivores, non-piscivores and piscivore prey for the Northern and  
 345 Central European regions were similar (Supplementary Material Fig. S1b,c) and did not differ  
 346 between the geographical subsets (ANCOVA, piscivores:  $F_{2,20}=0.47$ ,  $P=0.63$ ; non-piscivores:  $F_{2,30}=2.1$ ,  
 347  $P=0.13$ ; piscivore prey:  $F_{2,6}=0.65$ ,  $P=0.55$ ).

348 Among the 356 lakes, there were combinations of shallow piscivore but steep non-piscivore and  
 349 piscivore-prey SS slopes (Mirower See, Fig. 3a), intermediate SS slopes for piscivores, non-piscivores  
 350 and piscivore prey (Wummsee, Fig. 3b), or steep piscivore but shallow non-piscivore and piscivore-  
 351 prey SS slopes (Fleesensee, Fig. 3c). Overall, the slopes of the SS of piscivores in the 353 lakes for  
 352 which SS could be calculated ranged between -2.93 and 0.50 (median= -0.828, Supplementary

353 Material Table S1), but the slopes were between -0.50 and -1.00 in about half of the lakes (Fig. 4a).  
354 The slopes of the SS of non-piscivores in the 317 lakes for which SS could be calculated ranged  
355 between -2.64 and 1.04 (median=-0.614, Fig. 4b; Supplementary Material Table S1), and non-  
356 piscivore SS slopes were shallower than piscivore SS slopes (Wilcoxon rank sum test,  $W=65,055$ ,  
357  $P<0.0001$ ). There was a slightly negative correlation between piscivore and non-piscivore SS slopes  
358 across the 315 lakes for which SS could be calculated for both fish groups (Fig. 4c; Spearman's  
359  $r_s=-0.118$ ,  $P=0.036$ ). The slopes of the SS of piscivore prey in the 317 lakes for which SS could be  
360 calculated ranged between -3.33 and 1.36 (median=-0.883, Fig. 4e; Supplementary Material Table  
361 S1), and piscivore-prey SS slopes did not differ from piscivore SS slopes (Wilcoxon rank sum test,  
362  $W=46,694$ ,  $P=0.23$ ). There was no correlation between piscivore SS slopes and piscivore-prey SS  
363 slopes across the 314 lakes for which size spectra could be calculated for both fish groups (Fig. 4f;  
364 Spearman's  $r_s=-0.016$ ,  $P=0.77$ ).

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

375 We excluded two lakes with outlier SS slopes of piscivores or piscivore prey (Fig. 4f) to reduce  
376 heteroskedasticity. The best linear model for the remaining 312 lakes with SS slopes of piscivore prey  
377 as the dependent variable contained  $\log_{10}$  maximum depth,  $\log_{10}$  TP and  $\log_{10}$  NPUEpiscivore-prey as  
378 significant predictor variables (AIC=-284.0). However, the next best model (AIC=-283.5) excluded



379 maximum depth, and this model was not significantly different to the one including depth (ANOVA,  
380  $P=0.15$ ). Therefore, we excluded maximum depth from the final model (Table 2,  $\text{adj.}R^2=0.10$ ,  
381  $F_{2,309}=19.0$ ,  $P<0.0001$ ). According to beta coefficients, NPUepiscivore-prey was the strongest  
382 predictor of SS slopes of piscivore prey (Table 2).

383 By considering only significant ( $P<0.05$ ) and informative ( $R^2>0.5$ ) SS slopes, the range of SS slopes  
384 for piscivores in the remaining 185 lakes became narrower than that calculated from all lakes  
385 (median  $=-1.01$ ), but the majority of slopes was still found between  $-0.50$  and  $-1.0$  (Fig. 4g). The range  
386 of significant and informative non-piscivore SS slopes in 137 lakes became likewise narrower (median  
387  $=-0.843$ , Fig. 4h), but non-piscivore SS slopes still were significantly shallower than piscivore SS slopes  
388 (Wilcoxon rank sum test,  $W=16,457$ ,  $P<0.0001$ ). There was no significant correlation between  
389 piscivore and non-piscivore SS slopes in the 76 lakes for which significant and informative SS could be  
390 calculated (Fig. 4i; Spearman's  $r_s=-0.102$ ,  $P=0.39$ ). The median of significant ( $P<0.1$ ) and informative  
391 ( $R^2>0.5$ ) SS slopes of piscivore prey in 123 lakes was steeper than the one in all lakes (median  
392  $=-1.184$ , Fig. 4k), and SS slopes of piscivore prey were significantly steeper than piscivore SS slopes  
393 (Wilcoxon rank sum test,  $W=9,072$ ,  $P=0.003$ ). There was no significant correlation between SS slopes  
394 of piscivores and SS slopes of piscivore prey in the 76 lakes for which significant and informative SS  
395 could be calculated (Fig. 4l; Spearman's  $r_s=0.063$ ,  $P=0.56$ ).

396 The best linear model for the 76 lakes with significant SS slopes of non-piscivores as the  
397 dependent variable contained SS slopes of piscivores, maximum temperature and  $\log_{10}$  NPUEnon-  
398 piscivores as significant predictor variables (AIC=-247.5). However, the next best model (AIC=-247.0)  
399 excluded SS slopes of piscivores, and this model was not significantly different to the one including  
400 piscivore slopes (ANOVA,  $P=0.23$ ). Therefore, we excluded SS slopes of piscivores from the final  
401 model (Table 2,  $\text{adj.}R^2=0.36$ ,  $F_{2,73}=21.9$ ,  $P<0.0001$ ). The negative effect of NPUEnon-piscivores on SS  
402 slopes of non-piscivores was stronger than the positive effect of temperature on SS slopes (Table 2).  
403 Similarly, the most parsimonious model for significant SS slopes of piscivore prey in 76 lakes  
404 contained only maximum temperature and NPUepiscivore-prey as significant predictors (Table 2,

405  $\text{adj.}R^2=0.16$ ,  $F_{2,73}=7.89$ ,  $P=0.0008$ ,  $\text{AIC}=-127.9$ ). The better model ( $\text{AIC}=-129.3$ ) included also  $\log_{10}$  TP,  
406 but this model was not significantly better than the one without TP (ANOVA,  $P=0.53$ ).

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

412 In the reversed analyses, we calculated the most parsimonious linear model with SS slopes of  
413 piscivores as the dependent variable, and TP, lake area, lake depth, maximum temperature, SS slope  
414 of non-piscivores or piscivore prey, and NPUEpiscivores as predictors. In both linear models, all lake  
415 descriptors and SS slopes of non-piscivores or piscivore prey were excluded, and NPUEpiscivores was  
416 the single significant independent variable for SS slopes of piscivores (for piscivore SS slopes  
417 including non-piscivores as predictor: final model  $\text{adj.}R^2=0.38$ ,  $F_{1,74}=47.3$ ,  $P<0.0001$ ,  $\log_{10}$   
418 NPUEpiscivores  $t=-6.88$ ,  $P<0.0001$ ; for piscivore SS slopes including piscivore prey as predictor: final  
419 model  $\text{adj.}R^2=0.33$ ,  $F_{1,74}=37.9$ ,  $P<0.0001$ ,  $\log_{10}$  NPUEpiscivores  $t=-6.19$ ,  $P<0.0001$ ).

420

## 421 Discussion

422 The correspondence between the density and size of piscivorous fish and the density and size of  
423 non-piscivores or piscivore prey fish produced by our calculations was in part unexpected. Piscivore  
424 density correlated positively with piscivore prey density. Piscivore SS slopes did not predict the non-  
425 piscivore and piscivore-prey SS slopes in the linear models in any of the subsets including only  
426 significant slopes. In contrast, the SS slopes of piscivores, non-piscivores and piscivore prey were  
427 strongly negatively correlated with NPUE of the respective groups in all datasets, suggesting that the  
428 size structure of fish in lakes is primarily density-dependent. A substantial decline of prey fish  
429 densities or a consistent removal of maximum-sized piscivore prey fish from predation by piscivorous

430 fish, similar to the patterns found for example for the interactions between planktivorous fish and  
431 zooplankton prey in the pelagic area of lakes (Brooks and Dodson 1965; Jeppesen et al. 2003), could  
432 not be detected by the ataxonomic approach as used here.

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

449 The overall positive correlation between piscivore density and piscivore-prey density contrasts  
450 with the findings of lake-specific studies in which massive interventions for piscivorous fish  
451 communities changed the equilibrium between predator and prey. For example, experimental  
452 stocking or removal of piscivores conducted in small lakes induced correlated short-term changes in  
453 prey fish communities (Benndorf et al. 1984; Mittelbach et al. 1995; Potthoff et al. 2008). However,  
454 in most of these cases, after a few years the predator-to-prey density or species ratios returned to  
455 the original values observed before disturbance, hence suggesting that strong negative density

456 effects of piscivores on prey communities may reflect transient states which cannot be upheld  
457 without permanent disturbance (Mittelbach et al. 1995; Donald and Anderson 2003). In studies  
458 comparing fish communities across several lakes, densities and size of single, usually small, prey fish  
459 species have been found to correlate negatively to predator fish densities (Nowlin et al. 2006;  
460 Friederichs et al. 2011). One may argue that our sampling approach was not suitable to find a  
461 negative effect of predation on densities of small-sized fish because piscivore prey individuals smaller  
462 than 2 g (about 6 cm length) representing the newly hatched cohorts in the year of catch were  
463 underrepresented in the gill-nets (Prchalova et al. 2009). Hence, we cannot totally exclude the  
464 possibility that fish predation reduces in particular the densities of newly hatched fish. However, this  
465 effect obviously does not translate into lower recruitment and likewise lower densities of fish at  
466 higher age because our analyses demonstrate that the total densities of piscivores and piscivore prey  
467 in lakes tend to be positively correlated. This positive correlation suggests that productivity and  
468 competition strength keep predator and prey densities in equilibrium and override potential local  
469 predation effects. It has to be noted that there was no positive correlation between densities of  
470 piscivores and non-piscivores, but only between piscivores and piscivore prey. The group of piscivore  
471 prey also included the smallest size groups (<32 g or about <15 cm) of predators (primarily perch and  
472 zander in European lakes) which can form a substantial proportion of total fish abundance in the 8 g  
473 to 32 g size classes. Therefore, piscivores are more abundant in lakes where young piscivores are  
474 likewise more abundant, and hence intra-guild predation and cannibalism within and among  
475 piscivorous fish populations (e.g., Schulze et al. 2006) contribute to the energy transfer from primary  
476 production to production of piscivores.

477       Increasing fish density might be compensated for by reduced average individual growth  
478 (Holmgren and Appelberg 2001; Rose et al. 2001). Therefore, fish achieve a relatively smaller size at  
479 higher densities, as indicated by the dominant negative correlation between SS slopes of piscivores,  
480 non-piscivores or piscivore prey, and the NPUE of the respective groups. This strong negative density  
481 dependence has been found by several previous analyses on the fish communities of European lakes

482 (Emmrich et al. 2011; Arranz et al. 2015). Lowered growth rates leading to 'stunted' fish populations  
483 are well described in response to strong competition for resources at high fish densities (Ylikarjula et  
484 al. 1999; Amundsen et al. 2007). Stunting can be seen as an adaptive response of life history by  
485 which age and size at maturity and investment into reproduction are adjusted to the local conditions.  
486 It can be expected for fish that live in environments characterized by steep size spectra (i.e., low  
487 average size of food resources) and low overall resource abundance such that growth is limited by  
488 high foraging activity (Giacomini et al. 2013).

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

506 Based on this low PPMR, the range of piscivore-prey sizes still available to the piscivorous  
507 predators is surprisingly small. An upper threshold for vulnerable size classes of prey fish can be

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

530 The lack of significant slopes in many lakes indicates that linear SS may not be an ideal approach  
531 for characterizing the size structure of fish communities. Only in about half of all lakes we obtained  
532 significant and informative SS slopes by logarithmic binning and least-square estimation. Continuous  
533 approaches such as the fit by maximum likelihood of a Pareto I cumulative distribution function are

534 recommended (White et al. 2008), but are likewise inappropriate if the log-log relationship between  
535 numbers and size is not linear (Emmrich et al. 2011; Emmrich et al. 2014). The cumulative size  
536 spectra shown here likewise indicated a tendency towards a non-linear log-log size-density  
537 relationship. Our own tests showed that Bayesian minimum mean square error estimations of Pareto  
538 II functions result in somehow improved fits of the size distributions, probably because Pareto II  
539 models approximate to non-linear log-log relationships between numbers and size (results not  
540 shown). However, the resulting Pareto II function has two or even three parameters which are  
541 strongly correlated to each other. Accordingly, the ecological interpretation of the form of Pareto II  
542 curves is not straightforward (Vidondo et al. 1997), and a meaningful conclusion with respect to the  
543 effect of predator size on prey size could not be drawn. Accordingly, we had to base our conclusions  
544 primarily on the relationship between SS of piscivores and non-piscivores or piscivore prey for the  
545 subsets of lakes with significant SS slopes.

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

556

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574

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762 **Table 1:** Coefficients (estimates  $\pm$  standard error, S.E.), beta (standardized) coefficients and variance  
 763 inflation factors (VIF) of the most parsimonious linear model of  $\log_{10}$  NPUEnon-piscivore fish (in fish  
 764 net<sup>-1</sup> night<sup>-1</sup>, upper part) or  $\log_{10}$  NPUEpiscivore-prey fish (in fish net<sup>-1</sup> night<sup>-1</sup>, lower part) as the  
 765 dependent variable in 332 and 354 European lakes, respectively. Significant predictors were  $\log_{10}$   
 766 piscivore fish density (NPUE\_Pisc, in fish net<sup>-1</sup> night<sup>-1</sup>), lake area (in ha), lake maximum depth  
 767 (max\_depth, in m), total phosphorus concentration (TotalP, in mg m<sup>-3</sup>) and maximum air  
 768 temperature (max\_temperature, in °C).

	Estimate	S.E.	Beta coeff.	VIF	t-value	Pr(> t )
<u>Non-Piscivores (n=332 lakes)</u>						
(Intercept)	-0.892	0.219			-4.067	<0.0001
log10(lake_area)	0.155	0.049	0.14	1.20	3.171	0.0017
log10(max_depth)	-0.495	0.073	-0.31	1.30	-6.806	<0.0001
log10(TotalP)	0.258	0.064	0.20	1.47	4.018	<0.0001
max_temperature	0.135	0.014	0.45	1.36	9.600	<0.0001
<u>Piscivore prey (n=354 lakes)</u>						
(Intercept)	-0.246	0.171			-1.432	0.1531
log10(NPUE_Pisc)	0.189	0.053	0.14	1.11	3.546	0.0004
log10(lake_area)	0.142	0.037	0.17	1.23	3.867	0.0001
log10(max_depth)	-0.460	0.056	-0.37	1.34	-8.217	<0.0001
log10(TotalP)	0.109	0.049	0.11	1.61	2.225	0.0267
max_temperature	0.107	0.010	0.49	1.45	10.535	<0.0001

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771 **Table 2:** Coefficients (estimates  $\pm$  standard error, S.E.), beta (standardized) coefficients and variance  
 772 inflation factors (VIF) of the most parsimonious linear models of the slope of abundance size spectra  
 773 (SS) of non-piscivore or piscivore prey fish communities as the dependent variables. Linear models  
 774 were calculated for the entire dataset (all lakes with SS slopes) and for subsets with significant  
 775 ( $P < 0.05$  for non-piscivores,  $P < 0.10$  for piscivore prey) and informative ( $R^2 > 0.5$ ) SS slopes only.  
 776 Significant predictors were density of non-piscivores or piscivore prey (NPUE\_Non-Pisc;  
 777 NPUE\_PiscPrey; both in fish net<sup>-1</sup> night<sup>-1</sup>), SS slope of piscivores (SlopeSS\_Pisc), lake area (in km<sup>2</sup>),  
 778 total phosphorus concentration (TotalP, in mg m<sup>-3</sup>) and maximum air temperature  
 779 (max\_temperature, in °C).  
 780

	Estimate	S.E.	Beta coeff.	VIF	t-value	Pr(> t )
<u>Non-Piscivores</u>						
<u>All lakes (n=312)</u>						
(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	<0.0001
<u>Lakes with significant slopes only (n=76)</u>						
(Intercept)	-1.204	0.221			-5.441	<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	<0.0001
<u>Piscivore prey</u>						
<u>All lakes (n=314)</u>						
(Intercept)	-0.558	0.122			-4.557	<0.0001

log10(TotalP)	0.291	0.080	0.21	1.16	3.628	0.0003
log10(NPUE_PiscPrey)	-0.537	0.090	-0.34	1.16	-5.967	<0.0001
<u>Lakes with significant slopes only (n=76)</u>						
(Intercept)	-1.754	0.484			-3.625	0.0005
max_temperature	0.076	0.032	0.28	1.24	2.392	0.0194
log10(NPUE_PiscPrey)	-0.518	0.133	-0.46	1.24	-3.902	0.0002

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781

782 **Captions for figures**

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

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

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

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

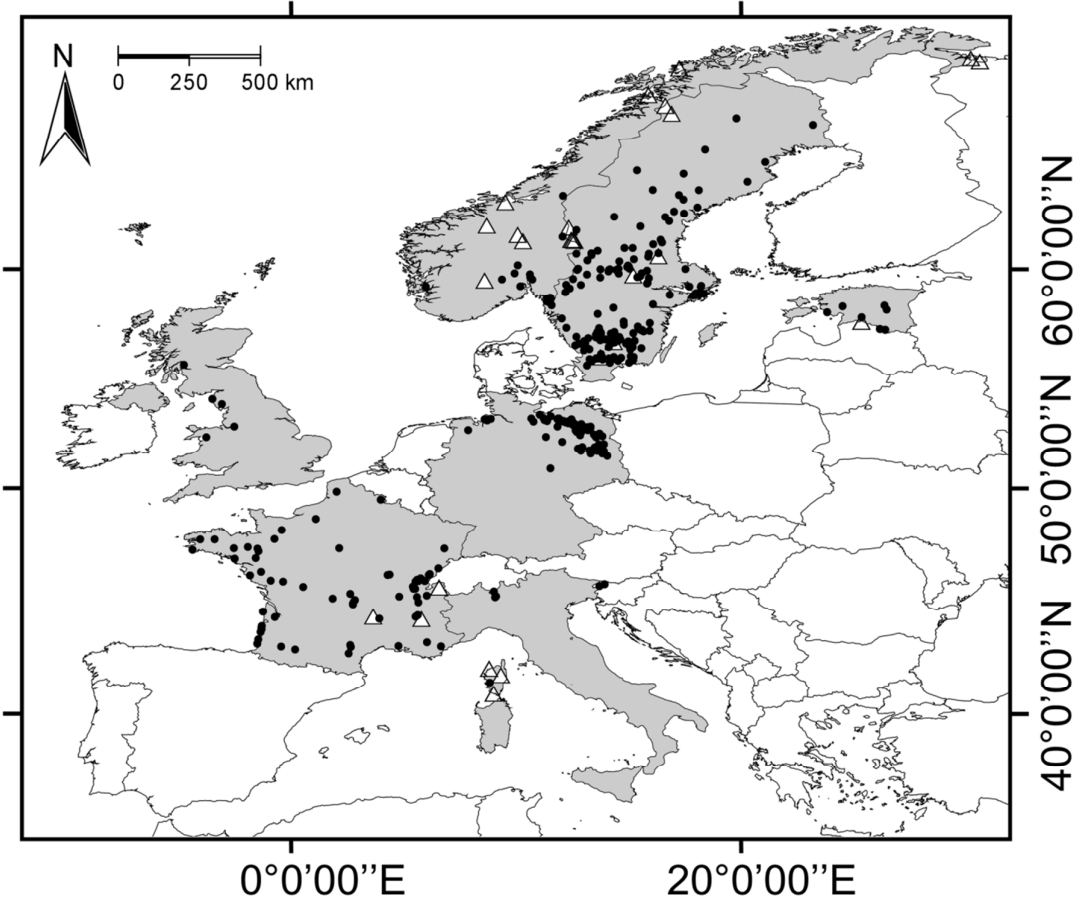


806 In the right part (g-l), only lakes are included for which SS slopes were significant ( $P < 0.05$  for  
807 piscivores and non-piscivores,  $P < 0.10$  for piscivore prey) and informative ( $R^2 \geq 0.5$ ).

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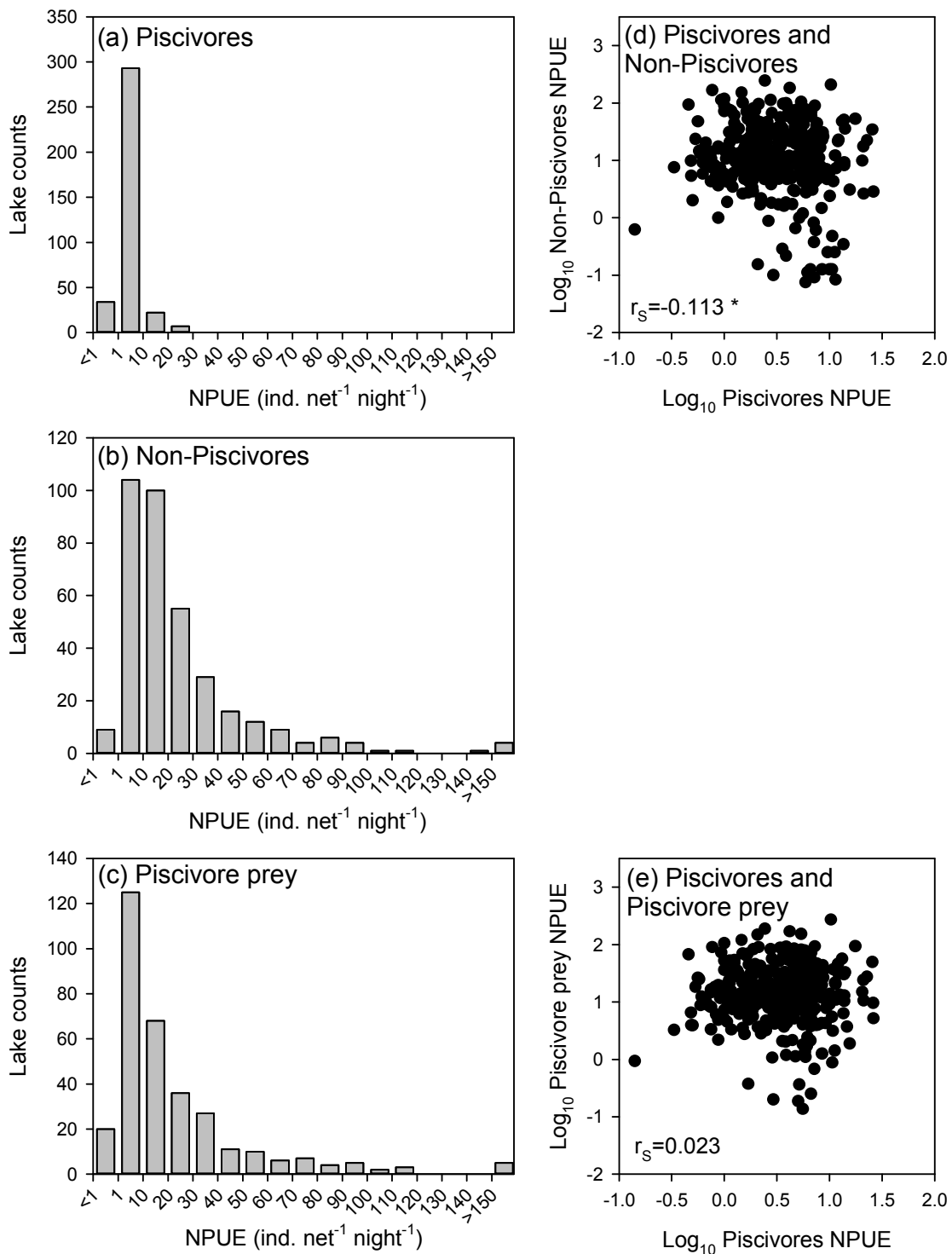


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813 Fig. 1

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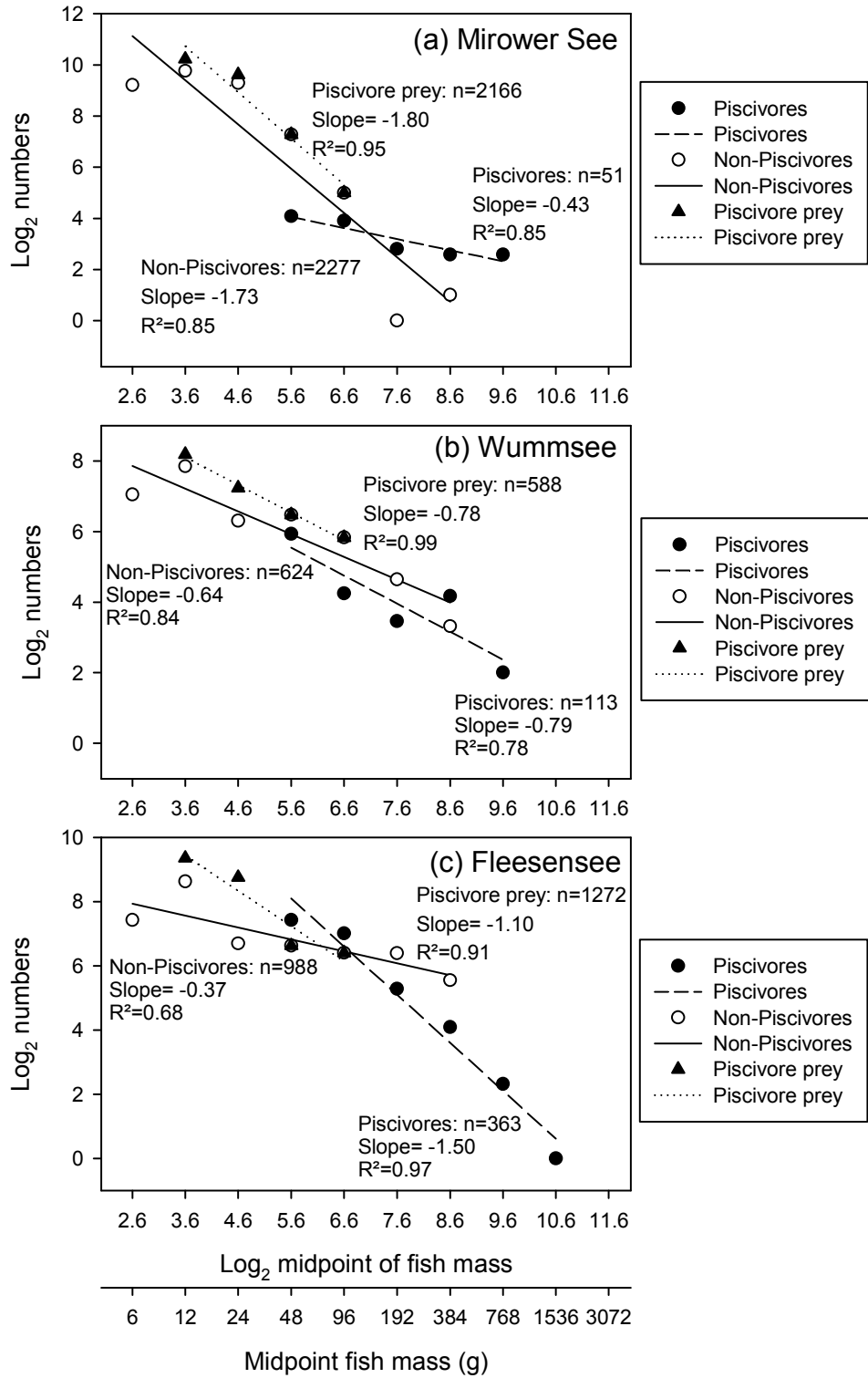


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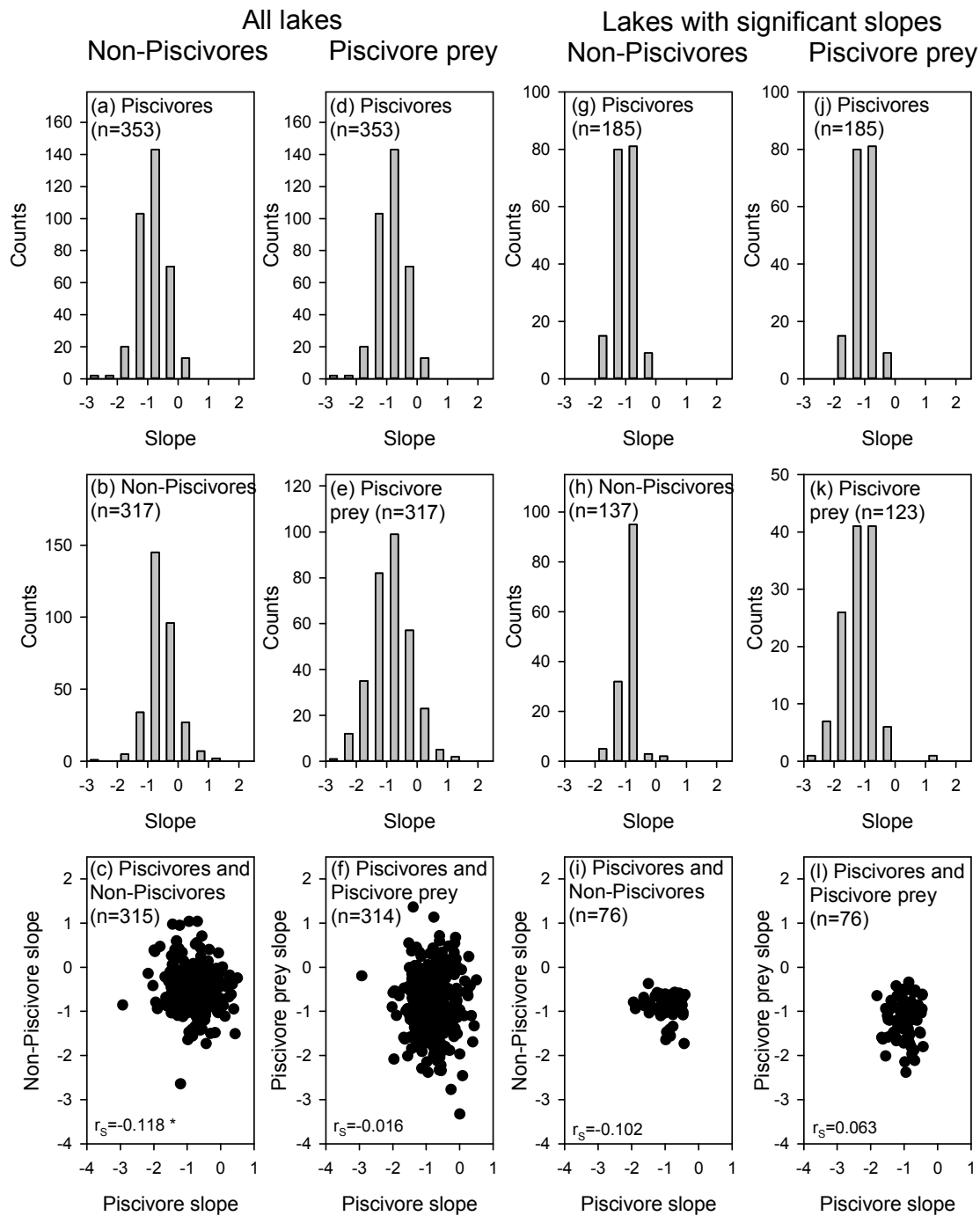
817 Fig. 2

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820 Fig. 3



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823 Fig. 4