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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 Brucet 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; Brucet 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; Brucet 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; Bruce 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^{-3} , measured as the mean of a minimum of four samples taken in a single year), lake maximum
136 depth (m) and lake area (km^2). 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 $\text{fish net}^{-1} \text{night}^{-1}$), 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 ≤ 32 g and
167 all non-piscivores in the size range >8 g to ≤ 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 ≤ 4 g from subsequent calculations, and
204 numbers of non-piscivores were accumulated into 13 \log_2 size classes (1st class: $>2^2=4$ g to $\leq 2^3=8$ g,
205 2nd class: $>2^3=8$ to $\leq 2^4=16$ g, etc., 13th 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 ≤ 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⁻¹ 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 fish net^{-1}
309 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_{non-piscivores} 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_{piscivores} as significant predictor variables (AIC=-504.9). The next best model (AIC=-503.4)
320 excluded \log_{10} NPUE_{piscivores}, but this model was not significantly different from the model
321 including NPUE_{piscivores} (ANOVA, $P=0.49$), and hence we excluded NPUE_{piscivores} 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_{non-piscivores} were found for TP, temperature and lake area, whereas
324 NPUE_{non-piscivores} 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_{piscivore-prey} 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 adj.R²=0.16, F_{2,73}=7.89, P=0.0008, AIC=-127.9). The better model (AIC=-129.3) included also log₁₀ 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 adj.R²=0.38, F_{1,74}=47.3, P<0.0001, log₁₀
418 NPUEpiscivores t=-6.88, P<0.0001; for piscivore SS slopes including piscivore prey as predictor: final
419 model adj.R²=0.33, F_{1,74}=37.9, P<0.0001, log₁₀ 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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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⁻¹ night⁻¹, upper part) or \log_{10} NPUEpiscivore-prey fish (in fish net⁻¹ night⁻¹, 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⁻¹ night⁻¹), lake area (in ha), lake maximum depth
 767 (max_depth, in m), total phosphorus concentration (TotalP, in mg m⁻³) 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
$\log_{10}(\text{lake_area})$	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
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
$\log_{10}(\text{NPUE_Pisc})$	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
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⁻¹ night⁻¹), SS slope of piscivores (SlopeSS_Pisc), lake area (in km²),
 778 total phosphorus concentration (TotalP, in mg m⁻³) 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

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⁻¹ night⁻¹) 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 log₁₀ NPUEpiscivores versus log₁₀ NPUEnon-piscivores (d)
 789 and log₁₀ NPUEpiscivores versus log₁₀ 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 log₂ size classes of fish (g
 793 wm) is plotted against log₂ 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 ($P<0.05$).

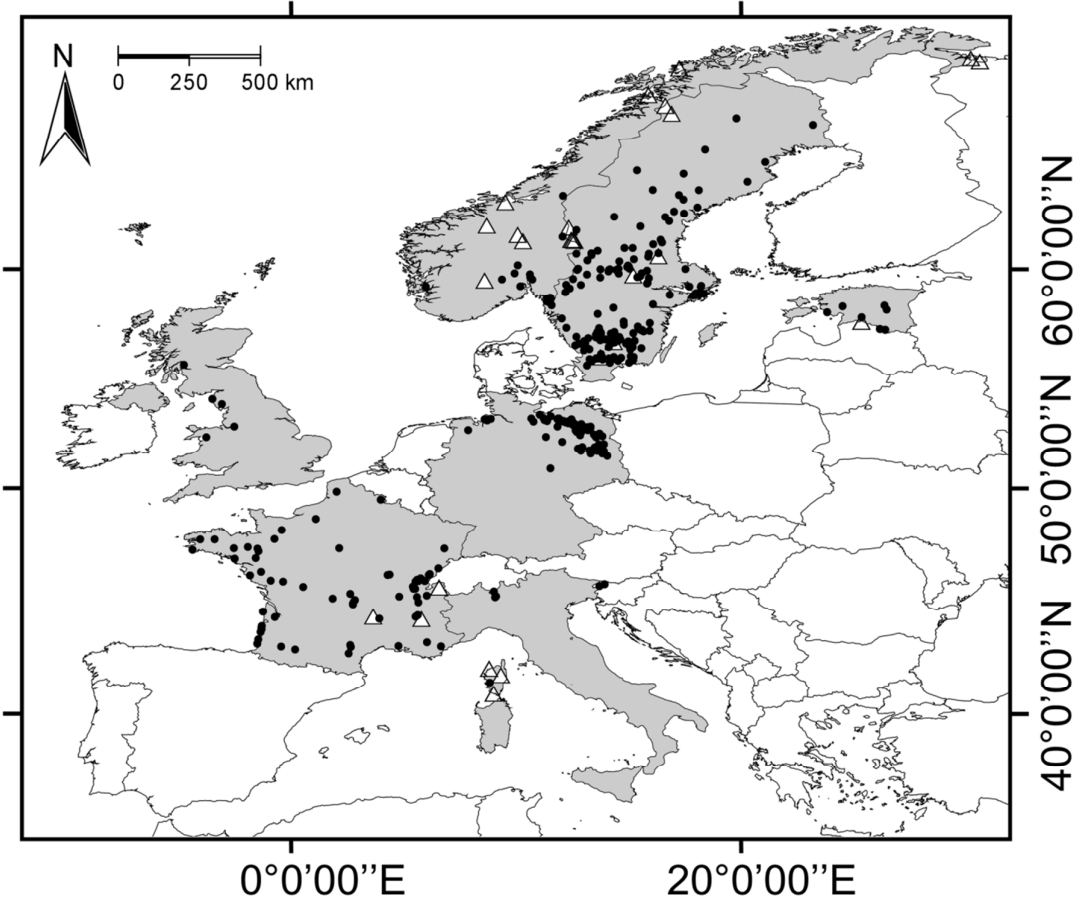
800 Fig. 4: Frequency distribution of the slopes of abundance size spectra (SS) of fish caught by multi-
 801 mesh gill nets in European lakes, split into predators (a,d, g, j), non-piscivores (b,h) and piscivore prey
 802 fish (e, k). Note that plots (a) and (d), and (g) and (j), show the same dataset. 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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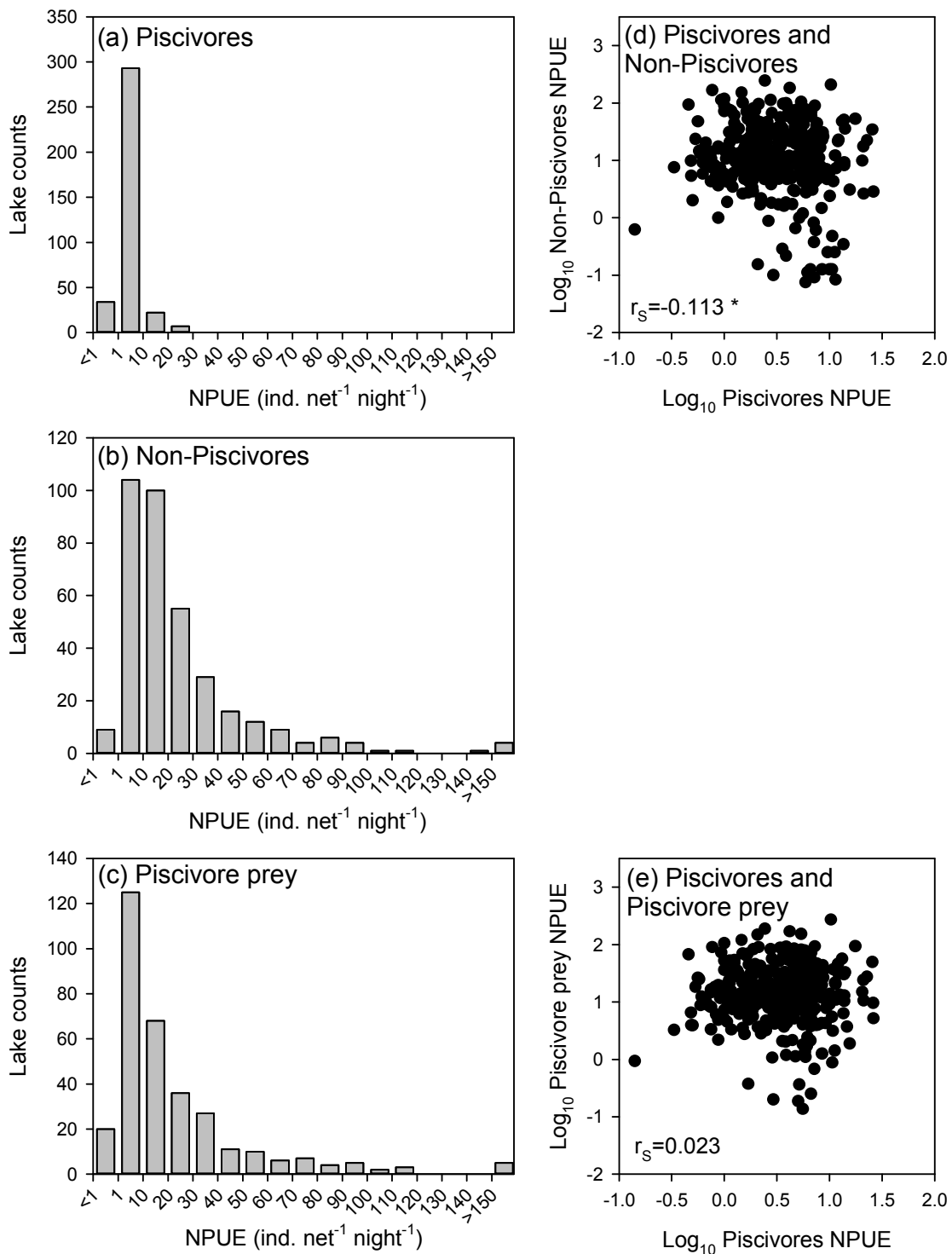


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813 Fig. 1

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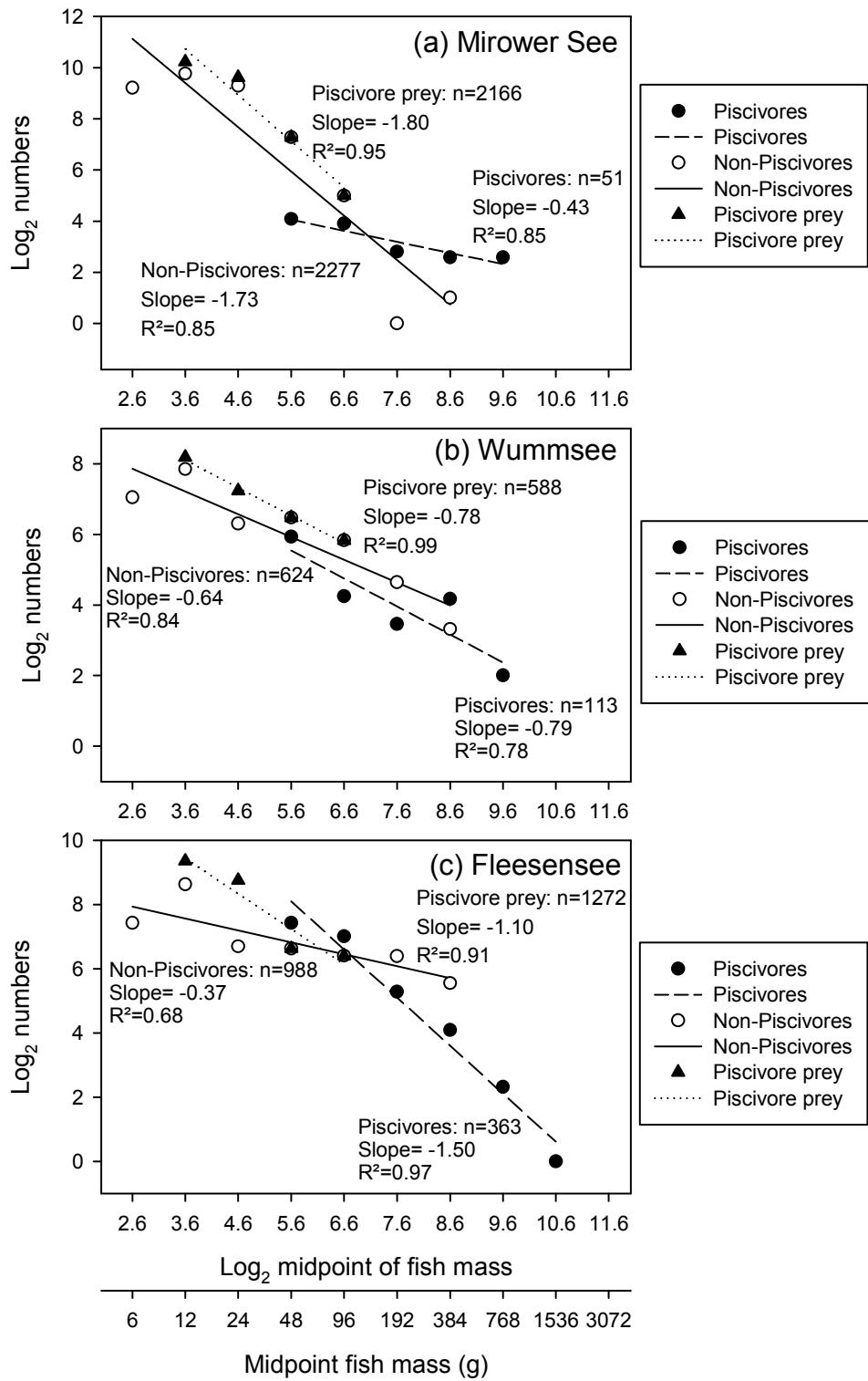


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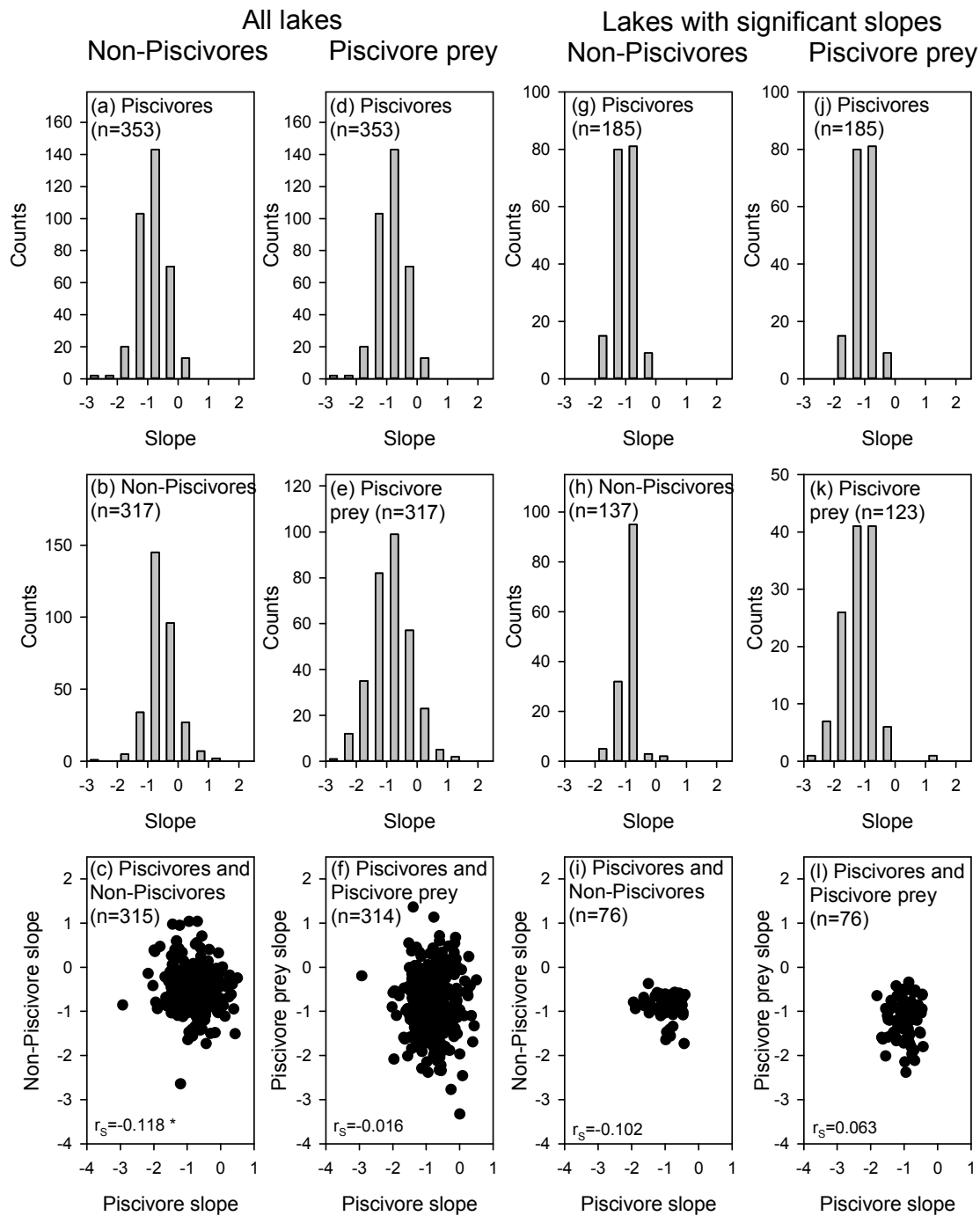
817 Fig. 2

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820 Fig. 3



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823 Fig. 4