Arranz, Ignasi; Mehner, Thomas; Benejam, Lluís; Argillier, Christine; Holmgren, Kerstin; Jeppesen, Erik; Lauridsen, Torben L.; Volta, Pietro; Winfield, Ian J.; Brucet, Sandra. 2016. **Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe** [in special issue: Size-based approaches in aquatic ecology and fisheries science: a symposium in honour of Rob Peters]. *Canadian Journal of Fisheries and Aquatic Sciences*, 73 (4). 519-534. 10.1139/cjfas-2014-0508

Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe

Ignasi Arranz, Thomas Mehner, Lluís Benejam, Christine Argillier, Kerstin Holmgren, Erik Jeppesen, Torben L. Lauridsen, Pietro Volta, Ian J. Winfield and Sandra Brucet

I. Arranz (ignasi.arranz@uvic.cat) and L. Benejam, Aquatic Ecology Group, BETA Technology Centre, University of Vic - Central University of Catalonia, Vic, Catalonia, Spain

T. Mehner, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, Berlin, Germany

C. Argillier, Irstea UR HYAX, Centre d'Aix-en-Provence, F-13182, France

K. Holmgren, Institute of Freshwater Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Stångholmsvägen 2, SE 178 93 Drottningholm, Sweden

E. Jeppesen and T. L. Lauridsen, Lake Ecology Section and Arctic Research Centre, Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark; Sino-Danish Center for Education and Research (SDC), Beijing, China,

P. Volta, CNR Institute of Ecosystem Study, L.go Tonolli 50, 28922 Verbania Pallanza, Italy

I. J. Winfield, Lake Ecosystems Group, Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, U.K.

S. Brucet, Lake Ecology Section, Department of Bioscience, Aarhus University, Vejløovej 25, 8600 Silkeborg, Denmark & Aquatic Ecology Group, BETA Technology Centre, University of Vic - Central University of Catalonia, Vic, Catalonia, Spain;

ABSTRACT

We studied fish size structure by using mean size, size diversity and the slope of linear size spectra of six common European fish species and compared whether these variables responded to the same large-scale continental gradients. We also included relative estimates of abundance (catch per unit effort, CPUE) as an indicator of density-dependent effects in order to assess whether they also modify the size structure of fish populations. We found differences in the strength of main predictors of size structure between the six species, but the direction of the response was relatively similar and consistent for most of the size metrics. Mean body size was negatively related to temperature, for perch, roach and ruffe. Lake productivity (expressed as total phosphorus concentration) and lake depth were also predictors of size structure for four out of six species. Moreover, we found a strong density dependence of size structure for all species, resulting in lower mean body size and size diversity and steeper size spectra slopes. This suggests that density dependence is a key driver of fish size structure.

Key words: environmental gradient, density-dependent effect, size structure, fish life history

Introduction

Size structure has traditionally been used for elucidating trophic interactions and patterns of energy transfer through trophic levels (Jennings et al. 2002; Woodward et al. 2005; Trebilco et al. 2013). Recent studies have revealed variation in the size structure of fish communities across continental gradients induced by climate-related variables as well as variations in taxonomic composition (Mims and Olden 2012; Emmrich et al. 2014).

Besides temperature, productivity of local systems also modifies fish community size structure (Jeppesen et al. 2000; Brucet et al. 2013). In Northern temperate regions, the shift in fish size structure along the productivity gradient is reflected in part by changes in species composition from nutrient-rich lakes being dominated by cyprinids to more nutrient-poor lakes dominated by percids or salmonids (Persson et al. 1988; Bergman 1991), but also by intra- and interspecific competition and perhaps reduced predation by piscivores (Persson et al., 1998; Jeppesen et al. 2000; Brucet et al. 2013). Lake morphometry (area and depth) also influences the shape of the size structure of fish communities (Holmgren and Appelberg 2000; Emmrich et al. 2014) due to its strong impact on structural complexity, niche availability and temperature. The ecosystem size rules predict that the shape of body size distributions will change because of the increase of number of trophic levels (Vander Zanden et al. 1999) and the higher abundance of predatory fish species (Allen et al. 2006). As such, high habitat diversity is more likely to exhibit a higher abundance of large fish and a wider range of size classes (Holmgren and Appelberg 2000; Emmrich et al. 2011).

Variation in the size structure of selected species over large geographical gradients has occasionally been demonstrated (e.g. in Europe, Heibo et al. 2005; Blanck and Lamouroux 2007; or in North America, Knouft 2004). For example, at a continental scale, Eurasian perch (*Perca fluviatilis*) populations follow the temperature-size rule (Bergmann 1847) with fish body size being smaller in the warmer lakes (Heibo et al. 2005; Jeppesen et al. 2012). This pattern has repeatedly been found for the size structure of entire fish communities (Edeline et al. 2013; Brucet et al. 2013; Emmrich et al. 2014), but it is not universal at the species level (Belk and Houston 2002).

Variations in fish density typically induce substantial changes in the growth rates of individuals, triggered by food resource or habitat availability (Byström and García-Berthou 1999). Dietary shifts are furthermore expected to result from strong size-dependent intraspecific interactions (Persson 1987) and may lead to stunted populations (Ylikarjula et al. 2000). However, most previous work on size structure at the species level has been based on a few lakes or dynamical models, while potential density-dependent effects on the size structure of fish species over large-scale gradients have not yet been evaluated.

We analysed the size structure of six common freshwater fish species by measuring mean size, size diversity and the slope of linear size spectra in several hundred European lakes. Our objective was to assess which environmental variables influenced the variation in size structure of the selected fish species at continental scale. We hypothesised that the changes in size structure for all species in response to local temperature, productivity and lake morphometry would be consistent with those found for the community-wide variation in fish size structure (Emmrich et al. 2014). Since fish density modifies the availability of food resources, which affects fish growth rates, we hypothesised that density-dependent effects would also contribute to shifts in species-specific size structures by decreasing mean body size, size diversity and size spectra slopes when density increases. We therefore included relative estimates of abundance (catch per unit effort, CPUE) as an approximation of density dependence to explore potential modifications in size structure, and hence life history, caused by fish density in the lakes.

Material and methods

Dataset

We used the dataset from the EU project WISER (Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery) created during a European intercalibration process with 1632 lakes, considering exclusively, though, the lakes based on the same systematic approach with complete fish assemblage and limnological information (Brucet et al. 2013). Individual body-size information was only available on a subset of 356 lakes (317 natural lakes and 39 reservoirs) covering nine European ecoregions (Illies 1978) and eight countries along a latitudinal gradient between 41.96 and 69.69ºN and a longitudinal gradient between 10.17 and 31.30°E (Fig. 1).

In cases of multiple sampling years (mainly Swedish lakes), we always selected the data from the most recent sampling campaign. In addition, we obtained corresponding information on 19 reservoirs from the Ebro River basin in Spain, which were sampled following the same standardised procedure (CEN 2005) (reports from *Confederación Hidrográfica del Ebro*, CHE 2008-2012); the data were, therefore, comparable with the European lakes included in the WISER project. In summary, our dataset encompassed a total of 375 European lakes and reservoirs from nine countries and ten ecoregions along a latitudinal gradient between 40.81 and 69.69ºN (Fig. 1).

Sampling

All fish were caught in accordance with the European standard (CEN 2005) during late summer and early autumn by using benthic multi-mesh gillnets (type NORDEN: length 30 m; height 1.5 m; 12 panels of 2.5 m each with mesh sizes between 5.0 and 55 mm knot to knot in a geometric series). These different mesh sizes allow catching of a wide range of fish sizes and can be used to estimate the size structure of fish populations in a cost-effective way (Appelberg et al. 1995; CEN 2005). The number of nets to be used is determined by lake morphology (area and depth) and these nets were set randomly in all depth strata of the lakes. All nets were left for approximately 12 hours overnight due to the fact that gillnet catch is highly dependent on fish activity (Prchalová et al. 2009). To ensure comparable individual body size measurements and fish densities, the total fishing effort per lake (number of nets) was standardised by lake area and maximum depth according to CEN 14757 (2005). Fish catches were expressed as lake-specific catch per unit effort (CPUE) and were standardised by calculating the average number of fish caught per net and night in each lake. We used four lakes sampled for more than 20 years to estimate the inter-annual variability (and hence uncertainty) of CPUE values (unpublished data). CPUE of the three species found in these lakes, perch, roach (*Rutilus rutilus*), and ruffe (*Gymnocephalus cernuus*), showed relatively low variability (CPUE averages ±SD 19.71±14.48, 8.34±3.07 and 0.73±0.32, in the lake with highest variability for perch, roach and ruffe, respectively). The exception was perch population in the lake with at the highest latitude for which one-year-old individuals dominated the catches in 1997. Perch populations in lakes far north at the latitudinal edges of their distribution areas are the most outstanding exceptions from low between-year variation (Holmgren 2013). Fish species were identified, counted and individually measured to determine total length (TL, nearest cm) and fresh body mass (FM, nearest g). For all Swedish lakes, FM was estimated by length-mass relationships from lakes in other countries at the same latitudinal range. For German lakes, the sampling protocol was divided into two different periods: autumn (late August to early October) and the subsequent spring (Mehner et al. 2005). The catches from both periods were summed up. For more details see Brucet et al. (2013).

Fish species selected

Species selection was hierarchically guided by the following requirements: (1) the species had to be present in a representative number of lakes (minimum 20 lakes, Table 1); (2) their presence should encompass a sufficiently widespread area (minimum five ecoregions, Table 1). Accordingly, six species were chosen (Table 1): the percids perch, ruffe and zander (*Sander lucioperca*), and the cyprinids roach, common bream (*Abramis brama*) and white bream (*Blicca bjoerkna*). Perch and zander are typically piscivorous fish, and both undergo size-related ontogenetic niche shifts. Ruffe, common bream and white bream feed on cladocerans, copepods and benthic macroinvertebrates such as midge larvae (Chironomidae) or mussels (Nagelkerke and Sibbing 1996; Volta et al. 2013). Roach is a typical omnivorous feeder with a diet mainly based on zooplankton, plant material and detritus (Bergman and Greenberg 1994; García-Berthou 1999). Despite their presence in many lakes, we did not consider typical pelagic species such as bleak (*Alburnus alburnus*) and vendace (*Coregonus albula*) because these are not quantitatively well represented in benthic gillnet catches (Emmrich et al. 2012). To ensure a reliable representation of each selected species, we included only lakes with at least 25 measured individuals, which corresponds to an approximate 30% error of size diversity estimation.

Size metrics corresponding to size structure

Three size metrics were calculated from the measurements of individual fish body size for each population: geometric mean body size, the slope of linear size spectrum (both based on fish mass), and size diversity (based on fish length). We combined metrics for fish mass and length to ensure that the response of fish size structure along gradients is adequately captured.

Mean body size expressed as geometric mean mass is a general descriptor for assessing interspecific gradients in the size structure of fish communities (Emmrich et al. 2011, 2014). Size diversity was calculated following a nonparametric methodology of Quintana et al. (2008), which is an analogue of the Shannon diversity index but adapted for continuous variables (herein fish total length). For size diversity, we used fish total lengths because our earlier work showed a significant response of length diversity to environmental gradients (Emmrich et al. 2011). The index was computed using individual size measurements (Brucet et al. 2006; Quintana et al. 2008) for each lake following an integral formula:

$$\mu_2(\mathrm{x}) = -\int_0^\infty \rho_x(x) log_2 p_x(x) dx \tag{1}$$

Where $\boldsymbol{\mu_2}$ is the Shannon size diversity index and $\boldsymbol{\rho_x}$ is the probability density function (pdf; function that describes the relative likelihood for a random variable to take on a given value) that an organism belongs to a certain size class. The most appropriate approach to calculate the pdf is by using a non-parametric Kernel estimation (Quintana et al. 2008). A kernel estimation is essentially a pdf, usually symmetric, whose dispersion is controlled by a bandwidth parameter. The estimator is a sum of kernel functions centered at the samples points, which can be applicable for most size distributions. Before computing size diversity, the data is double standardised to 1) make the size data adimensional and 2) make size data comparable with other studies whose samples are measured with different units, such as length, weight or volume, without altering the results (Quintana et al. 2008). Size diversity integrates the range of the size classes and the evenness, that is, the equitability of frequency across the size range; in the same way as the Shannon diversity integrates the species composition and species relative abundances. The single-value index condenses many different aspects of other size metrics into a single comparable value (Brucet et al. 2006, 2010; Emmrich et al. 2011). Furthermore, size diversity is easy to interpret since the concept of diversity has been well established. Low size diversity values imply high accumulation of abundance within a specific size range, whereas high values mean similar proportions of the different sizes along the size distribution. Negative values of size diversity may be found since the method uses a continuous pdf for the probability estimation, and probability densities above one may occur (Quintana et al. 2008).

The linear size spectrum was calculated as the regression between $\log_2$ midpoint of size classes (axis x) and $\log_2$ total numbers per size class (axis y). The slope of the linear size spectrum is usually described by a decreasing linear function in fish numbers as midpoint size class increases. Steeper slopes from the linear size spectrum reflect high proportions of small fish, whereas flatter (less negative) slopes indicate a high proportion of large fish (Emmrich et al. 2011). The number of size classes varied between the species (Table 1) but always followed a $\log_2$ scale (1st class: 2^2=4 g to 2^3=8 g, 2nd class: 2^3=8 to 2^4=16 g, etc.). Multimesh gillnets have been shown to describe well the size structure of populations of perch and roach despite underestimation of the proportion of fish smaller than 6-8 cm TL (Prchalova et al. 2009). Hence, 1 to 4 g fish (i.e. fish in the first year of life) were underrepresented in our catches. These small fish easily detect the wall of netting of the smallest mesh size and thus avoid it (Prchalová et al. 2009). Also, they tend to swim more slowly than larger fish and the probability of catching them is proportional to body length (Rudstam et al. 1984). Accordingly, the few small fishes (<4 g) caught were grouped in the first size class (2^2=4 g). Intermediate empty size classes were filled with zeroes. Although there is some debate about the most appropriate way to deal with intermediate empty size classes (Loder et al. 1997; Gómez-Canchong et al. 2013), we considered our approach appropriate for comparison of large-scale patterns in the slope of the linear size spectrum. Furthermore, the frequency of zero infilling for each of the species was less than 5% (less than 20% of the lakes had at least one intermediate empty bin for each species), with the exception of zander for which 17.7% of intermediate classes were filled by zeros (74% of the lakes had at least one intermediate empty size bin). Zander had more empty bins because more size classes were covered (size range of 11 classes, Table 1) than e.g. in ruffe (size range of 5 classes, Table 1).

Predictors of size structure

From a large set of predictors characterising lake geographical position, morphometry and productivity, we retained six variables but excluded others that were most strongly correlated with the retained predictors (Spearman's rank correlation r_s>0.6 or r_s<-0.6) (Emmrich et al. 2011).

We used four environmental and morphometric predictors (Table A1): (1) total phosphorus concentration (hereafter TP, $mg.m^{-3}$) as a surrogate of lake productivity, (2) maximum depth (m) and (3) lake area (ha). We excluded geographical position and instead used direct local climate data expressed as (4) maximum monthly mean air temperature (ºC), which was calculated using the climate CRU (Climatic Research Unit) model proposed by New et al. (2002). This specific model can obtain a spatial resolution of 10′ latitude/longitude and takes into account elevational differences between stations (New et al. 2002). Previous studies have successfully used air temperature instead of indirect temperature approximations based on geographical locations (Argillier et al. 2013; Brucet et al. 2013; Emmrich et al. 2014).

Furthermore, two biotic predictors were included. We used the CPUEs as indicators of fish density to infer their effects on size structure and assumed that high densities are approximations for low individual resource availability and strong competition. However, because resource similarity is usually stronger between individuals of the same species than between species, we split CPUE as a surrogate of density dependence into (5) the intraspecific density-dependent effect (CPUE of the focal species, hereafter, CPUEintra) and (6) the interspecific density-dependent effect (sum of CPUE of the other five potentially competing species, hereafter CPUEinter). The sum of the six species in each lake was 82.2 ± 29.9% (SD) of total CPUE, and hence intra- and interspecific CPUE covered the large majority of total fish available and the potential competition effects. No species in our list are strict feeding specialists and most of them undergo ontogenetic niche/diet shifts (see Persson and Hansson 1999 for perch, common bream and roach). Accordingly, all species were considered to compete for the same food resources, at least during some part of their life. Finally, we did not consider predation effects on size structure because earlier work in a subset of lakes has indicated an only limited effect of fish predation on fish prey density and average size (Mehner 2010).

Statistical analyses

Some fish populations were characterised by unimodal (hump-shaped) or multimodal size distributions (two or more distinct peaks) and hence deviated from linear size spectra. We only included linear slopes for which their significance was $p<0.10$. The two other size metrics (mean size and size diversity) were calculated for all lakes. We graphically represented the cumulative frequency distribution of sizes for the six species by using the total numbers per size class across all lakes (see Fig. A1).

General linear models (GLM) were used to identify which predictors were significantly related to the size metrics of the six species. The six predictor variables mentioned above were $\log_{10}$ transformed to meet assumption of normality. Shapiro-Wilk tests and quartile-quartile plots indicated that the transformed variables closely followed normal distributions. We also included the interaction between density-dependent effects and productivity and lake depth (i.e. CPUEintra*TP, CPUEintra*Depth, CPUEinter*TP and CPUEinter*Depth) because the latter two variables may influence the density-dependent effects on fish size (i.e. in deeper lakes the effect of CPUEintra on fish size may be less intense than in shallow lakes because coexistence of all size classes is facilitated by the large pelagic volume). The response variables were mean body size, size diversity and the slope of linear size spectra. The level of significance for GLM was established at 95% (0.05). Using GLM, we searched for the most parsimonious model by an automatic stepwise backward selection of one predictor variable at a time, following the lowest Akaike's information criterion (AIC) (Akaike 1974). The most parsimonious model was the combination of variables having the strongest impact on outcomes. To account for moderate robustness of the stepwise selection of variables, we further applied ANOVA to compare the most parsimonious final model (i.e. the one with lowest AIC) with the next best model that included one more predictor. We used standardised regression beta coefficients and the percentage of variance explained to compare the relative strength of each significant predictor for each of the size metrics (Table 2). Multicollinearity can inflate the variance amongst the selected predictors in the model. To identify which predictor was highly correlated with the remaining ones, we examined the variance inflation factor (VIF) values. They were <2 in all analyses, indicating a low degree of multicollinearity (Belsley, Kuh & Welsch 1980). We also included a measure of model fitting to explain the deviance in percentage (Table 2). Residual partial plots for each significant variable were then drawn to show the relationship between the predictor and the response variables. All statistical analyses were conducted using package "MASS" (version 7.3; Venables and Ripley 2002), "car" (version 2.0; Fox and Weisberg 2011), "QuantPsy" (version 1.5; Fletcher 2012) and "BiodiversityR" (version 2.4-4; Kindt and Coe 2005) from the software R (version 3.0.2; R Development Core Team 2008).

Results

General patterns of occurrence and size structure

The temperature range at which fish were found was relatively similar for all species across the European lakes, the widest being recorded for roach and the narrowest for common bream (Table A1). The depth of the lakes in which the species were present was also similar, but the TP and lake area ranges differed among species (Table A1).

Zander had the highest number of size classes, from the smallest (1st class, 4-8 g) to the largest size class (11th class, 4096-8192 g), whereas ruffe sizes covered only five classes (maximum 5th class, 64-128 g). The proportion of lakes in which fish populations exhibited linear size spectra was relatively high for perch (62.9%), ruffe (46.9%) and white bream (41.7%). In contrast, non-linear (p>0.10) size distributions dominated in common bream, zander and roach populations (non-significant slopes in 76%, 75% and 68% of the lakes, respectively).

Size structure predicted by environmental variables

Mean body size of perch, roach and ruffe significantly decreased with increasing maximum temperatures (Table 2, Fig. A2). The slope of linear size spectra for zander was also negatively related to temperature, indicating a relative increase of small sizes in warmer lakes (e.g. Lake Figari from France 23.1 ºC; Table 2, Fig. A3). In contrast, the size diversity of white bream and roach showed a positive relationship with temperature, suggesting that a wider range of size classes occurred at warmer temperatures (Table 2, Fig. A4).

Lake productivity (TP) affected size metrics for five out of the six species (Table 2, Appendices 3, 4 and 5). The mean size of ruffe, white bream and common bream, as well as the slope of the linear spectra of ruffe and white bream, increased in highly productive lakes (e.g. Lake Audomarois from France 561 $\mu g\ L^{-1}$), whereas the mean size of perch decreased with productivity. The size diversity of perch and roach was negatively related to TP, indicating a narrower size range in highly productive lakes.

Size metrics were also influenced by lake depth and lake area. Size diversity increased with lake depth for three species, and the slope of the linear spectra increased with depth for zander, indicating a flatter size spectrum in deeper lakes (Table 2, Fig. A3). The slope of the linear spectra for perch became significantly steeper with increasing lake area (Table 2, Fig. A3). There were some relationships with lake area, with smaller sizes being observed for ruffe and perch and larger sizes for white bream in larger lakes (Table 2, Appendices 3, 4 and 5).

Size structure predicted by density-dependent effects

There was a strong density-dependent effect on the variation in size structure for all species (Table 2, Fig. 2 and Appendices 3 and 5). Particularly, lower mean size and steeper slopes (i.e. greater relative abundance of small-sized individuals) occurred at higher CPUEintra for five and four, respectively, out of the six species (Table 2). Additionally, a negative response of size diversity to CPUEintra was found for three species (Appendices 3 and 5). In contrast, there was a weaker and less consistent effect for

CPUEinter (mean beta coefficients for CPUEintra and CPUEinter: 0.53 and 0.31, respectively). The mean body size of perch and ruffe and the slope of the linear spectra of ruffe and zander responded negatively to CPUEinter (Table 2, Appendices 3 and 4). In contrast, CPUEinter positively affected roach size diversity and the slope of linear size spectra, suggesting a wider size range and flatter slopes at higher abundance of the other five coexisting fish species (Table 2, Fig. A4). Finally, interactions terms were not significant (p>0.05) except the interactions CPUEintra*TP and CPUEintra*Depth for the size diversity of perch (p≤0.001 and p≤0.01, respectively).

Discussion

Our results showed some difference in main predictors and response strength (Table 2) to continental environmental gradients between the six common fish species in European lakes, but the direction of the response was relatively similar and consistent for most of the size metrics. For example, temperature variations across Europe induced the same response for five of the six species, with fish size declining at higher temperatures. Furthermore, productivity and lake depth were predictors of size structure, whereas lake area had little effect on the size metrics. Overall, however, the potential intraspecific density-dependent effect was the strongest and most consistent predictor of the variation in the size structure of fish populations (Table 2).

Temperature affected the size metrics for perch, roach, ruffe, white bream and zander. These results are in accordance with the Bergmann (1847) and Atkinson (1994) rules explaining that ectothermic animals developing at higher temperature are relatively smaller as adults. However, temperature showed a weaker effect as a predictor of population size structure compared with the effect that it had on the size structure of the whole fish assemblage (Emmrich et al. 2014). Probably, the temperature effect is masked by the strong density-dependent effect which has not been considered in the community-wide analyses. Thus, our results suggest that, at least at species level, it is important to take into account density-dependent effects when studying the influence of temperature on fish size structure. Mean size of roach decreased at higher temperatures, but size diversity increased (Appendices 3 and 5). Studies in Swedish lakes have shown that roach populations may attain > 20 cm and > 100 g already in their 4th growth season in southern Sweden, whereas they often need at least twice as long to reach such size further north (Jeppesen et al. 2010; Holmgren 2013). Likewise, in France, in warmer lakes and reservoirs, high proportions of large roach often occur in the catches. These large roach have reached an anti-predation window and are no longer available for most of the carnivorous species such as pike (*Esox lucius*), pikeperch or perch (Wysujack and Mehner 2002; Schlumberger and Elie 2008).

Lake productivity (TP) mainly affected the size structure of perch, roach and ruffe and the congeneric species, i.e. common bream and white bream. At the community level, Jeppesen et al. (2000) and Brucet et al. (2013) have found a decrease in the mean body size of fish in lakes with increasing TP. Our results at species level partially contrast these findings since the mean body size of perch decreased, whereas the mean body size of white and common bream and ruffe, and the proportion of large individuals of ruffe and white bream, increased in highly productive lakes. The differing species responses may be due to their different feeding strategies. Perch is a visual hunter depending on good light conditions, and hence perch feeding rates may decrease at higher productivity and algal turbidity. In contrast, the other species are successful predators in turbid waters (Bergman 1991; Lammens et al. 1992). Studies on both bream species (Olin et al. 2002) and on ruffe (Persson et al. 1991) showed that these species dominated the catches at enhanced TP concentrations. There was a negative response of the size diversity of perch and roach to lake productivity as shown by low size diversity in the highly productive Lake Bordeaux (561 µg TP L^{-1}) and Lake Schwielochsee (260 µg TP L^{-1}). Roach can be both a prey and a competitor for perch (Persson 1988). Thus, the decrease in mean body size of perch with increasing productivity can be related to competition between small juvenile perch and roach, reducing both juvenile and adult growth and thereby the number of size classes of both species.

Lake morphometry (area and depth) affected the size structure of almost all species, but the strength of the response was relatively weak for all size metrics. Our results demonstrated that lake depth is a better predictor than lake area of the variation in size structure. Size diversity showed a consistent response to lake depth and area, and populations with large fish were found in deeper and larger lakes. However, the morphometric variables seem to be poor predictors of the shifts in slopes of linear size spectra. A (positive) correlation between lake depth and slope of the linear size spectra was found only for zander and a negative one only for perch. Zander is the largest species in our study and greater proportions of large individuals were found in larger lakes, probably as a result of higher niche availability, reducing competition and providing habitats to more different age (size) classes (Persson 1983).

Besides abiotic predictors, we found strong density dependence of size structure for almost all species, which corroborates the substantial changes in growth rates when fish compete for food resources (Byström and García-Berthou 1999). However, interspecific density-dependent effects were weaker predictors than the intraspecific density-dependent effects (Table 2). According to our results, disproportionally more small than large fish are added at higher population densities, as reflected by lower mean body size, fewer size classes (i.e. lower size diversity) and steeper slopes (i.e. higher proportions of small fish). An exception is the pattern of roach populations whose size diversity and slope of linear spectra responded positively to the interspecific density, indicating wider size distributions and greater proportions of larger individuals when roach coexist with one or more of the other five species. Large roach coexisting with many competitors (i.e., high CPUEinter) were found primarily in shallow productive lakes. In these lakes, growth of roach is stimulated by utilisation of unique diet components, mainly cyanobacteria and detritus, which cannot be used by other competing species such as perch (Persson and Greenberg 1990; Bergman and Greenberg 1994). Because density and growth rates in fish are usually negatively correlated (Lorenzen and Enberg 2001), the positive correlation between CPUEinter and the size metrics of roach may in turn suggest a decrease of growth rates and hence recruitment of the competing species that exploit the same resource less efficiently (in our study reflected by a reduction in the mean body size of perch and ruffe). Although we do not have the age structure of each population to corroborate recruitment dynamics, our result is similar to those from an empirical experiment with roach, perch and ruffe (Bergman and Greenberg 1994), showing decreased abundance of perch because they were competitively sandwiched between planktivorous (i.e. roach) and benthivorous (i.e. ruffe) species. Our analysis included only one year of survey in each lake and thus did not capture the inter-annual recruitment variability that may affect the size structure. Some European studies give examples of high between-year fluctuations of recruitment on perch (Tolonen et al 2003) or roach and other cyprinids (e.g. Mills & Mann 1995; Kahl et al. 2008). In contrast, studies of Swedish lakes from which results of multiple years of sampling are available indicated a relatively low between-year variation in recruitment for perch and roach (Holmgren 2013; Holmgren 2014). As an example, the mean size of the dominant species perch, roach and ruffe sampled for more than twenty years in four Swedish lakes show relatively low variability, which may reflect a relatively constant annual recruitment, except for perch at the highest latitude in the dataset (Lake Jutsajaure, Fig. A5). On the other hand, our study expands a large-scale data set and recruitment variability may be integrated in part with the latitudinal gradient.

The increased abundance of small size classes at higher population densities may reflect a decline in growth rates (stunted growth) at high fish densities. Stunted growth of fish population as a result of density-dependent effects is a common phenomenon (Sandheinrich and Hubert 1984; Ylikarjula et al. 2000), which may contribute to the overall pattern observed in our analysis. This is theoretically included in both the Beverton-Holt (1957) and Ricker (1954) stock recruitment curves predicting lower recruitment when fish reproduction exceeds the carrying capacity of the system. If stunted populations exhibit extremely slow growth and early maturity in lakes with higher fish densities, then a systematic downward shift of slopes is plausible. An example is the temporal study of the vendace population in a Swedish lake (Hamrin and Persson 1986) where stunting of older age classes was ascribed to competitive superiority of small fish relative to larger conspecifics due to their lower metabolic requirements and foraging energetics. Alternatively, the density dependence of the slopes of linear size spectra may be considered a mathematical artifact. Normally, there is a negative correlation between the intercept and the slope of linear size spectra (Gómez-Canchong et al. 2013) and the intercept strongly correlates with the total abundance of fish (Sprules and Munawar 1986). Therefore, higher abundances may result in steeper slopes. However, it has to be mentioned that mean size (as based on fish mass) and size diversity (as based on fish length) also showed density-dependent effects, which suggests that steeper slopes at higher densities represent ecological effects.

We found weakly important, but significant interactions between CPUEintra*TP and CPUEintra*Depth as predictors of size diversity, but only in perch. The interactions suggest that the negative effect of density on size diversity of perch was strongest in shallow lakes at high TP in which perch is outcompeted by the large roach because the availability of benthic diet for perch is low (Persson and Greenberg, 1990). In turn, perch grow better in deep lakes at low TP because availability of benthic macroinvertebrates as preferred diet of perch of intermediate size is high under these conditions (Persson 1983). These results show that lake morphometry, productivity, fish density and growth can be strongly linked in some species. Nevertheless, significant interactions of CPUE with TP and lake depth were found only for one size metric and one fish species.

The present study is the first to compare congruence in intraspecific variability in the size structure of European fish species along a continental gradient, and our results indicate that density-dependent effects are a key driver of fish size structure. However, more research is needed to unravel the variation in the slope of linear size spectra in relation to density dependence, for example by studying the temporal evolution of the slope in lakes showing interannual variations in fish densities. In contrast, substantial differences in the size structure of populations between lakes were only marginally affected by environmental variables, except for temperature. Our study indicates that the size structure of the selected species cannot be used as unequivocal indicator of environmental changes, which contrasts the consistency at community level found by Emmrich et al. (2014). Unfortunately, the intraspecific variation in size structure cannot be directly translated into a defined life history strategy along the triangular scheme (Winemiller and Rose 1992), which contrasts the review by Heibo et al. (2005) for perch populations. Therefore, finding approaches which approximate life history from size variables also routinely measured in fish monitoring may be a major step to improve the programmes for managing and monitoring inland waters in the face of the ongoing global climate change.

Acknowledgments

This work was partially supported by the WISER project (Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery) funded by the European Union under the 7th Framework Programme, Theme 6 (Environment including Climate Change, contract no. 226273). Data from Spanish reservoirs were obtained through projects funded by Confederación Hidrográfica del Ebro (CHE). We thank Thomas Boll for efficiently providing the environmental variables for some of the lakes. We also thank the lecturer and the participants in the workshop “Scientific Writing” at the Leibniz-institute of Freshwater Ecology and Inland Fisheries for helpful discussions at an early stage of the manuscript. KH was supported by the Swedish Environmental Protection Agency (Dnr 10/179) and the Swedish Agency for Marine and Water Management through a contract for the research programme WATERS. EJ, CA and TLL were further supported by the MARS project (Managing Aquatic ecosystems and water Resources under multiple Stress) funded under the 7th EU Framework Programme, Theme 6 (Environment including Climate Change, contract no. 603378). SB’s contribution was supported by the Marie Curie

Intra European Fellowship no. 330249 (CLIMBING). We are grateful to three anonymous reviewers, the Editor, Brian Shutter and Henrique Giacomini for valuable suggestions.

References

Allen, C.R., Garmestani, A.S., Havlicek, T.D., Marquet, P.A., Peterson, G.D., Restrepo, C., Stow, C.A. and Weeks, B.E. 2006. Patterns in body mass distributions: sifting among alternative hypotheses. Ecol. Lett. **9**: 630-643. doi: 10.1111/j.1461-0248.2006.00902.x.

Argillier, C., Causse, S., Gevrey, M., Pedron, S., De Bortoli, J., Brucet, S., Emmrich, M., Jeppesen, E., Lauridsen, T., Mehner, T., Olin, M., Rask, M., Volta, P., Winfield, I.J., Kelly, F., Krause, T., Palm, A., and Holmgren, K. 2013. Development of a fish-based index to assess the eutrophication status of European lakes. Hydrobiologia. **704**(1): 193-211. doi: 10.1007/s10750-012-1282-y.

Appelberg, M., Berger, H.M., Hesthagen, T., Kleiven, E., Kurkulahti, M., Raitaniemi, J., and Rask, M. 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Poll. **85**: 401-406.

Akaike, H. 1974. A new look at the statistical model identification. IEEE. Trans. Autom. Control. **19**: 716-723.

Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? Adv. Ecol. Res. **3**: 1-58. doi: 10.1016/S0065-2504(08)60212-3.

Belk, M.C., and Houston, D.D. 2002. Bergmann ’ s Rule in Ectotherms : A Test Using Freshwater Fishes. Am. Nat. **160**(6): 803-808.

Belsley, D. A., Kuh, E. & Welsch, R. E. (1980). Regression Diagnostics: Identifying Influential Data and Sources of Collinearity. New York: John Wiley. doi: 10.1002/0471725153.

Bergmann, C. 1847. Über die Verhaltnisse der Warmeökonomie der Thiere zu ihrer Grosse. Gottinger Studien. **3**: 595-708.

Bergman, E. 1991. Changes in abundance of two percids, Perca fluviatilis and Gymnocephalus cernuus, along a productivity gradient: feeding strategies and competitive abilities. Can. J. Fish. Aquat. Sci. **48**(4): 536-545. doi: 10.1139/f91-068

Bergman, E., and Greenberg, L.A. 1994. Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. Ecology. **75**(5): 1233–1245. doi: 10.2307/1937449.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations, fishery investigations series II, Volume XIX, Ministry of Agriculture, Fisheries and Food.

Blanck, A., and Lamouroux, N. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. J. Biogeogr. **34**: 862-875. doi: 10.1111/j.1365-2699.2006.01654.x.

Brucet, S., Boix, D., López-Flores, R., Badosa, A., and Quintana, X.D. 2006. Size and species diversity of zooplankton communities in fluctuating Mediterranean salt marshes. Estuar. Coast. Shelf. S. **67**: 424-432. doi: 10.1016/j.ecss.2005.11.016.

Brucet, S., Boix, D., Quintana, X.D., Quintana, Jensen, E., Nathansen, W., Trochine, C., Meerhoff, M., Gascón, S. and Jeppesen E. 2010. Factors influencing zooplankton size structure at contrasting temperatures in coastal shallow lakes: Implications for effects of climate change. **55**(4):1697-1711. doi:10.4319/lo.2010.55.4.1697.

Brucet, S., Pédron, S., Mehner, T., Lauridsen, T.L., Argillier, C., Winfield, I.J., Volta, P., Emmrich, M., Hesthagen, T., Holmgren, K., Benejam, L., Kelly, F., Krause, T., Palm, A., Rask, M., and Jeppesen, E. 2013. Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures. Freshw. Biol. **58**(9): 1779-1793. doi: 10.1111/fwb.12167.

Byström, P., and García-Berthou, E. 1999. Dependent growth and size specific competitive interactions in young fish. Oikos. **86**(2): 217-232. doi: 10.2307/3546440.

CEN. 2005. Water quality – sampling of fish with multi-mesh gillnets. European standard. European Committee for Standardization. Ref. No. EN 14757:2005.

Confederación Hidrográfica del Ebro. 2018-2012. Estudios censales de peces en la Cuenca Hidrográfica del Ebro. Ministerio de Agricultura, Alimentación y Medio Ambiente, Gobierno de España.

Edeline, E., Lacroix, G., Delire, C., Poulet, N., and Legendre, S. 2013. Ecological emergence of thermal clines in body size. Glob. Chang. Biol. **19**: 3062-3068. doi: 10.1111/gcb.12299.

Emmrich, M., Brucet, S., Ritterbusch, D., and Mehner, T. 2011. Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use. Freshw. Biol. **56**(11): 2316-2333. doi: 10.1111/j.1365-2427.2011.02658.x.

Emmrich, M., Winfield, I.J., Guillard, J., Rustadbakken, A., Vergès, C., Volta, P., Jeppesen, E., Lauridsen, T.L., Brucet, S., Holmgren, K., Argillier, C., and Mehner, T. 2012. Strong correspondence between gillnet catch per unit effort and hydroacoustically derived fish biomass in stratified lakes. Freshw. Biol. **57**(12): 2436-2448. doi: 10.1111/fwb.12022.

Emmrich, M., Pédron, S., Brucet, S., Winfield, I.J., Jeppesen, E., Volta, P., Argillier, C., Lauridsen, T.L., Holmgren, K., Hesthagen, T., and Mehner, T. 2014. Geographical patterns in the body-size structure of European lake fish assemblages along abiotic and biotic gradients. J. Biogeogr. 42: 2221-2233. doi: 10.1111/jbi.12366.

Fletcher, T.D. 2012. QuantPsyc: Quantitative Psychology Tools. R package version 1.5. http://CRAN.R-project.org/package=QuantPsyc.

Fox, J., and Weisberg, S. 2011. An R Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.

García-Berthou, E. 1999. Spatial heterogeneity in roach (Rutilus rutilus) diet among contrasting basins within a lake. Arch. Hydrobiol. **146**(2): 239-256.

Gómez-Canchong, P., Blanco, J.M., and Quiñones, R. a. 2013. On the use of biomass size spectra linear adjustments to design ecosystem indicators. Sci. Mar. **77**(2): 257-268. doi: 10.3989/scimar.03708.22A.

Hamrin, S.F., and Persson, L. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos. **47**(2): 223-232. doi: 10.2307/3566049.

Heibo, E., Magnhagen, C., and Vøllestad, L.A. 2005. Latitudinal variation in life-history traits in Eurasian Perch. Ecology. **86**(12): 3377-3386. doi: 10.1890/04-1620.

Holmgren, K. 1999. Between-year variation in community structure and biomass-size distributions of benthic lake fish communities. J. Fish. Biol. **55**: 535-552. doi: 10.1111/j.1095 8649.1999.tb00698.x

Holmgren, K. 2013. Betydelse av fiskens ålder vid bedömning av fiskfaunans status. Aqua reports 2013:5. Sveriges lantbruksuniversitet, Drottningholm (in Swedish with English summary).

Holmgren, K. 2014. Challenges in assessing biological recovery from acidification in Swedish lakes. AMBIO. **43**: 19-29. doi: 10.1007/s13280-014-0559-y.

Holmgren, K., and Appelberg, M. 2000. Size structure of benthic freshwater fish communities in relation to environmental gradients. J. Fish Biol. **57**(5): 1312-1330. doi: 10.1111/j.1095-8649.2000.tb00489.x.

Illies, J. 1978. Limnofauna Europaea. Gustav Fisher. Stuttgart, Germany.

Jennings, S., Pinnegar, J., Polunin, N., and Warr, K. 2002. Linking size-based and trophic analyses of benthic community structure. Mar. Ecol. Prog. Ser. **226**: 77-85. doi: 10.3354/meps226077.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., and Landkildehus, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes : changes along a phosphorus gradient. Freshw. Biol. **45**(2): 201-218. doi: 10.1046/j.1365-2427.2000.00675.x.

Jeppesen, E., Meerhoff, M., Holmgren, K., González-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S. a. J., Meester, L., Søndergaard, M., Lauridsen, T.L., Bjerring, R., Conde-Porcuna, J.M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H.J., Liu, Z., Balayla, D., and Lazzaro, X. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia. **646**(1): 73-90. doi: 10.1007/s10750-010-0171-5.

Jeppesen E., T. Mehner, I. J. Winfield, K. Kangur, J. Sarvala, D. Gerdeaux, M. Rask, H. J. Malmquist, K. Holmgren, P. Volta, S. Romo, R. Eckmann, A. Sandström, S. Blanco, A. Kangur, H. R. Stabo, M. Tarvainen, A.-M. Ventelä, M. Søndergaard, T. L. Lauridsen and M. Meerhoff. 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. Hydrobiologia. **694**(1): 1-39. doi: 10.1007/s10750-012-1182-1.

Kahl, U., S. Hülsmann, R.J. Radke and J. Benndorf. 2008. The impact of water level fluctuations on the year class strength of roach: implications for fish stock management. Limnologica **38**: 258-268. doi:10.1016/j.limno.2008.06.006.

Kindt, R. & Coe, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi.

Knouft, J.H. 2004. Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. Oecologia. **139**(3): 408-417. doi: 10.1007/s00442-004-1510-x.

Lammens, E.H.R.R., Frank-Landman, A., McGillavry, P.J. and Vlink, B. 1992. The role of predation and competition in determining the distribution of common bream, roach and white bream in Dutch eutrophic lakes. Environ. Biol. Fishes. **33**: 195-205.

Loder, N., Blackburn, T.M. and Gaston, K.J. 1997. The slippery slope: Towards an understanding of the body size frequency distribution. Oikos. **78**: 195-201. doi: 10.2307/3545817.

Lorenzen, K. and Enberg, K. 2001. Density-dependent growth as a key mechanism in the regulation of the fish populations: evidence from among-population comparisons. Proceedings of the Royal Society. 269: 49-54. doi: 10.1098/rspb.2001.1853.

Mehner, T. 2010. No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes. Limnol. Oceanogr. **55**(1): 203-213. doi: 10.4319/lo.2010.55.1.0203.

Mehner, T., Diekmann, M., Brämick, U. and Lemcke, R. 2005. Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. Fresh. Biol. **50**: 70-85. doi: 10.1111/j.1365-2427.2004.01294.x

Mims, M.C., and Olden, J.D. 2012. Life history theory predicts fish assemblage response to hydrologic regimes. Ecology. **93**(1): 35-45. doi: 10.1890/11-0370.1.

Mills, C.A. and R.H. Mann. 1985. Environmentally-influenced fluctuations in year-class strength and their implications for management. Journal of Fish Biology **27** (Supplement A): 209-226. doi: 10.1111/j.1095-8649.1985.tb03243.x.

Nagelkerke, L.A.J., and Sibbing, F.A. 1996. Efficiency of feeding on zebra mussel (*Dreissena polymorpha*) by common bream (*Abramis brama*), white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*): the effects of morphology and behavior. Can. J. Fish. Aquat. Sci. **53**(12): 2847-2861.

New, M., Lister, D., Hulme, M., and Makin, I. 2002. A high-resolution data set of surface climate over global land areas. Clim. Res. **21**: 1-25.

Olin, M., Rask, M., Ruuhijärvi, J., Kurkilahti, M., Ala-Opas, P., and Ylönen, O. 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. J. Fish. Biol. **60**(3): 593-612. doi: 10.1006/jfbi.2002.1876.

Persson, A., and Hansson, L.A. 1999. Diet shift in fish following competitive release. Can. J. Fish. Aquat. Sci. **56**(1): 70-78. doi: 10.1139/f98-141.

Persson, L. 1983. Effects of intra- and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. Oikos. **41**(1): 126-132. doi: 10.2307/3544354.

Persson, L. 1987. Competition-induced switch in young of the year perch, *Perca fluviatilis*: an experimental test of resource limitation. Env. Biol. Fish. **19**(3): 235-239. doi: 10.1007/BF00005353.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. In Size Structured Populations, Ecology and Evolution (Ebenmann, B. and Persson, L., eds). Berlin: Springer. pp. 203-218.

Persson, L., and Greenberg, L.A. 1990. Juvenile competitive bottlenecks : the perch (*Perca fluviatilis*) - roach (*Rutilus Rutilus*) interaction. Ecology. **71**(1): 44-56. doi: 10.2307/1940246.

Persson, L., Diehl, S., Johansson, L., Andersson, G., and Hamrin, S.F. 1991. Shifts in fish communities along the productivity gradient of temperate lakes – patterns and the importance of size-structured interactions. J. Fish. Biol. **38**: 281-293. doi: 10.1111/j.1095-8649.1991.tb03114.x.

Tolonen, A., J. Lappalainen and E. Pulliainen. 2003. Seasonal growth and year class strength variations of perch near the northern limits of its distribution range. Journal of Fish Biology **63**: 176-186. doi: 10.1046/j.1095-8649.2003.00141.x.

Prchalová, M., Kubečka, J., Říha, M., Mrkvička, T., Vašek, M., Jůza, T., Kratochvíl, M., Peterka, J., Draštík, V. and Křížek, J. 2009. Size selectivity of standardized multimesh gillnets in sampling coarse European species. Fish. Res. **96**: 51-57. doi: 10.1016/j.fishres.2008.09.017.

Quintana, X.D., Brucet, S., Boix, D., López-flores, R., Gascón, S., Badosa, A., and Sala, J. 2008. A nonparametric method for the measurement of size diversity with emphasis on data standardization. Limnol. Oceanogr. Methods. **6**: 75-86. doi: 10.4319/lom.2008.6.75.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. http://www.R-project.org.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board. Can. 11(5): 559-623. doi: 10.1139/f54-039.

Rudstam, L.G., Magnuson, J.J. and Tonn, W M. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. **41**(8):1252-1255. doi: 10.1139/f84-151.

Sandheinrich, M.B., and Hubert, W.A. 1984. Intraspecific resource partitioning by yellow perch, *Perca flavescens*, in a stratified lake. Can. J. Fish. Aquat. Sci. **41**(12): 1745-1752. doi: 10.1139/f84-215.

Schulmberger, O., and Élie, P. 2008. Poissons des lacs naturels français - Ecologie des espèces et évolution des peuplements. Quae editor. 212 pp.

Sprules, W.G., and Munawar, M. 1986. Plankton size Spectra in relation to ecosystem productivity, size, and perturbation. Can. J. Fish. Aquat. Sci. **43**(9): 1789-1794. doi: 10.1139/f86-222.

Trebilco, R., Baum, J.K., Salomon, A.K., and Dulvy, N.K. 2013. Ecosystem ecology: size-based constraints on the pyramids of life. Trends Ecol. Evol. **28**(7): 423-431. doi: 10.1016/j.tree.2013.03.008.

Vander Zanden, M.J., Shuter, B.J., Lester, N. and Rasmussen, J.B. 1999. Patterns of food chain length in lakes: a stable isotope study. Am. Nat. **154**(4):406-416. doi: 10.1086/303250.

Venables, W.N., and Ripley, B.D. 2002. Modern Applied Statistics with S, fourth ed. Springer, New York.

Volta, P., Jeppesen, E., Mehner, T., Emmrich, M., Campi, B., Sala, P., Winfield, I. 2013. The population biology and life history traits of Eurasian ruffe (Gymnocephalus cernua) introduced to eutrophic and oligotrophic lakes in northern Italy. J. Limnol. **72**(2): 280-290.

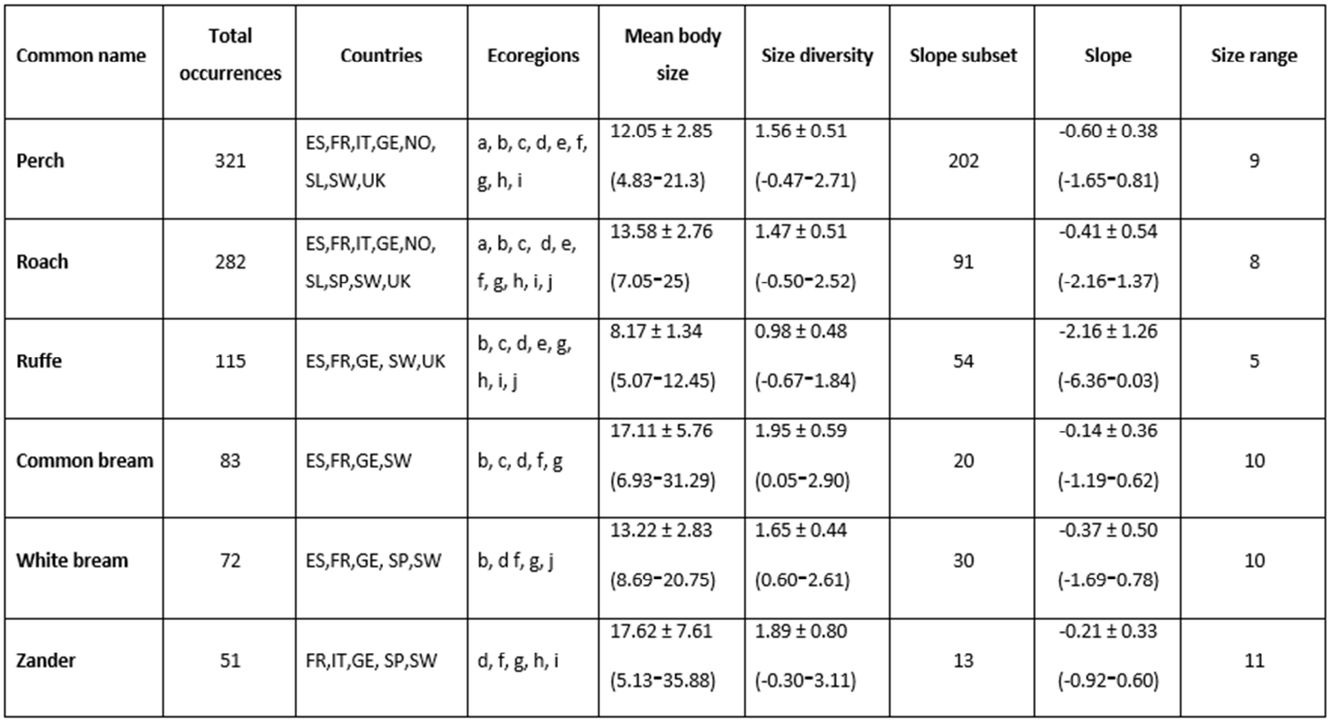
Winemiller, K.O., and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implication for population regulation. Can. J. Fish. Aquat. Sci. **49**(10): 2196-2218. doi: 10.1139/f92-242.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A., and Warren, P.H. 2005. Body size in ecological networks. Trends Ecol. Evol. **20**(7): 402-409. doi: 10.1016/j.tree.2005.04.005.

Wysujack, K., and Mehner, T. 2002. Comparison of losses of planktivorous fish by predation and seine-fishing in a lake undergoing long-term biomanipulation. Freshw. Biol. **47**(12): 2425-2434. doi: 10.1046/j.1365-2427.2002.00994.x.

Ylikarjula, J., Heino, M., and Dieckmann, U. 2000. Ecology and adaptation of stunted growth in fish. Evol. Ecol. **13**(5): 433-453. doi: 10.1023/A:1006755702230.

Table 1. Occurrences, countries and ecoregions where the six fish species were sampled. Total occurrence represents the lakes with at least 25 individuals per species in the catch. The slope subset is comprised of those lakes for which the significance of the linear regression of size spectra was p<0.1. Mean body size (cm), slope of linear spectra and size diversity (μ) ± standard deviation are given in brackets showing minimum and maximum values. Size range: the maximum number of $\log_2$ size classes. Nine countries: (ES) Estonia, (FR) France, (IT) Italy, (GE) Germany, (NO) Norway, (SL) Slovenia, (SP) Spain, (SW) Sweden, (UK) UK. Ten ecoregions ordered from north to south: (a) Borealic Uplands, (b) Fennoscandian Shield, (c) Baltic Province, (d) Central Plains, (e) Great Britain, (f) Western Plains, (g) Western Highlands, (h) Alps, (i) Italy Corsica Malta, (j) Iberian Peninsula.



Common name	Total occurrences	Countries	Ecoregions	Mean body size	Size diversity	Slope subset	Slope	Size range
Perch	321	ES,FR,IT,GE,NO, SL,SW,UK	a, b, c, d, e, f, g, h, i	12.05 ± 2.85 (4.83-21.3)	1.56 ± 0.51 (-0.47-2.71)	202	-0.60 ± 0.38 (-1.65-0.81)	9
Roach	282	ES,FR,IT,GE,NO, SL,SP,SW,UK	a, b, c, d, e, f, g, h, i, j	13.58 ± 2.76 (7.05-25)	1.47 ± 0.51 (-0.50-2.52)	91	-0.41 ± 0.54 (-2.16-1.37)	8
Ruffe	115	ES,FR,GE, SW,UK	b, c, d, e, g, h, i, j	8.17 ± 1.34 (5.07-12.45)	0.98 ± 0.48 (-0.67-1.84)	54	-2.16 ± 1.26 (-6.36-0.03)	5
Common bream	83	ES,FR,GE,SW	b, c, d, f, g	17.11 ± 5.76 (6.93-31.29)	1.95 ± 0.59 (0.05-2.90)	20	-0.14 ± 0.36 (-1.19-0.62)	10
White bream	72	ES,FR,GE, SP,SW	b, d f, g, j	13.22 ± 2.83 (8.69-20.75)	1.65 ± 0.44 (0.60-2.61)	30	-0.37 ± 0.50 (-1.69-0.78)	10
Zander	51	FR,IT,GE, SP,SW	d, f, g, h, i	17.62 ± 7.61 (5.13-35.88)	1.89 ± 0.80 (-0.30-3.11)	13	-0.21 ± 0.33 (-0.92-0.60)	11

Table 2. Relative strength for each predictor represented by the beta coefficients with their positive or negative trends and the predicted variance (%) (in brackets) For each species, significant predictors selected by the automatic stepwise model are given. A measure of model fitting is also shown: predicted deviance (%). Max.T. (maximum temperature, ºC) and TP (total phosphorus, µg L^{-1}). CPUEintra (intraspecific density-dependent effect) and CPUEinter (interspecific density-dependent effect). No asterisk: *P*>0.05; *: *P*<0.05; **: *P*<0.01; ***: *P*<0.001

Common name	**Max. T. (ºC)**	**TP (µg L^{-1})**	**Area (ha)**	**Depth (m)**	**CPUEintra**	**CPUEinter**	**Predicted variance (%)**
				MEAN SIZE			
Perch	-0.29***(15.92)	-0.09*(4.63)		-0.11*(<1)	-0.32***(13.95)	-0.29***(14.85)	50.12
Roach	-0.11*(4.45)				-0.54***(26.38)		30.83
Ruffe	-0.26**(7.19)	0.34***(7.35)	-0.26*(4.50)			-0.43***(9.85)	28.89
Common bream		0.30*(3.19)			-0.56***(18.52)		21.71
White bream		0.45***(13.54)	0.32*(7.00)		-0.28*(3.63)		24.17
Zander					-0.38***(26.84)		26.84
				SLOPE			
Perch			-0.14**(4.01)		-0.59***(38.26)		42.27
Roach					-0.83***(47.26)	0.2*(7.64)	54.90
Ruffe		0.41**(11.00)				-0.42**(11.00)	22.00
Common bream					-0.88**(43.63)		43.63
White		0.58**(13.15)			-0.65***(27.12)		40.27

bream							
Zander	-0.54**(13.75)			0.56**(23.68)		-0.41**(51.51)	88.94
SIZE DIVERSITY							
Perch		-0.17*(2.45)		0.13*(2.69)	-0.33***(10.27)		15.41
Roach	0.19**(2.40)	-0.18**(3.56)	0.13*(4.72)	0.26***(8.05)		0.12*(<1)	19.67
Ruffe				0.51***(27.59)			27.59
Common bream					-0.28***(8.00)		8.00
White bream	0.28**(10.15)						10.15
Zander					-0.75***(55.88)		55.88

Figures

Figure 1. Geographical distribution of study lakes across nine European countries: Estonia (EST), France (FR), Italy (IT), Germany (GE), Norway (NO), Slovenia (SL), Spain (SP), Sweden (SW), UK. Ten ecoregions according to Illies (1978) were separated by dotted lines: (a) Borealic Uplands, (b) Fennoscandian Shield, (c) Baltic Province, (d) Central Plains, (e) Great Britain, (f) Western Plains, (g) Western Highlands, (h) Alps, (i) Italy Corsica Malta, (j) Iberian Peninsula.

Figure 2. Significant partial residual plots selected according to the highest beta coefficients in density-dependent effects. Y axis represents size metrics and x axis the density-dependent predictor (i.e. CPUEintra and CPUEinter). CPUEintra, CPUE of the focal species; CPUEinter, sum of CPUE of the other five potentially competing species. For perch, roach, white bream and common bream: *Slope vs CPUEintra*. For ruffe: *Mean Size vs CPUEinter*. For zander: *Size Diversity vs CPUEintra.*

Figure 1.

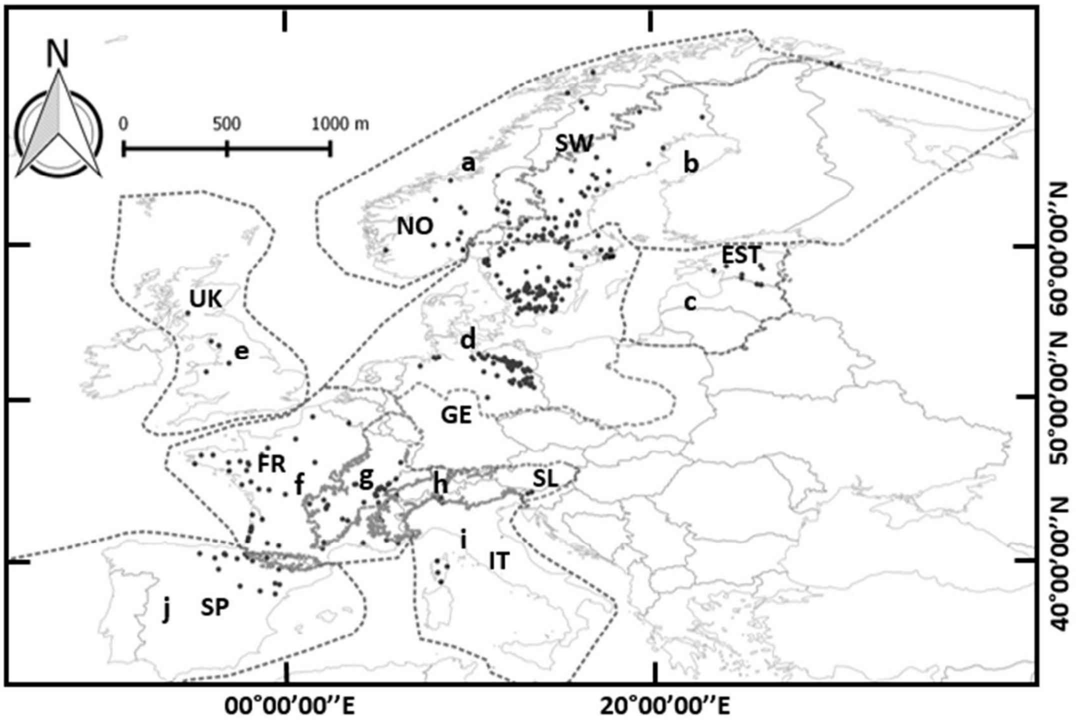
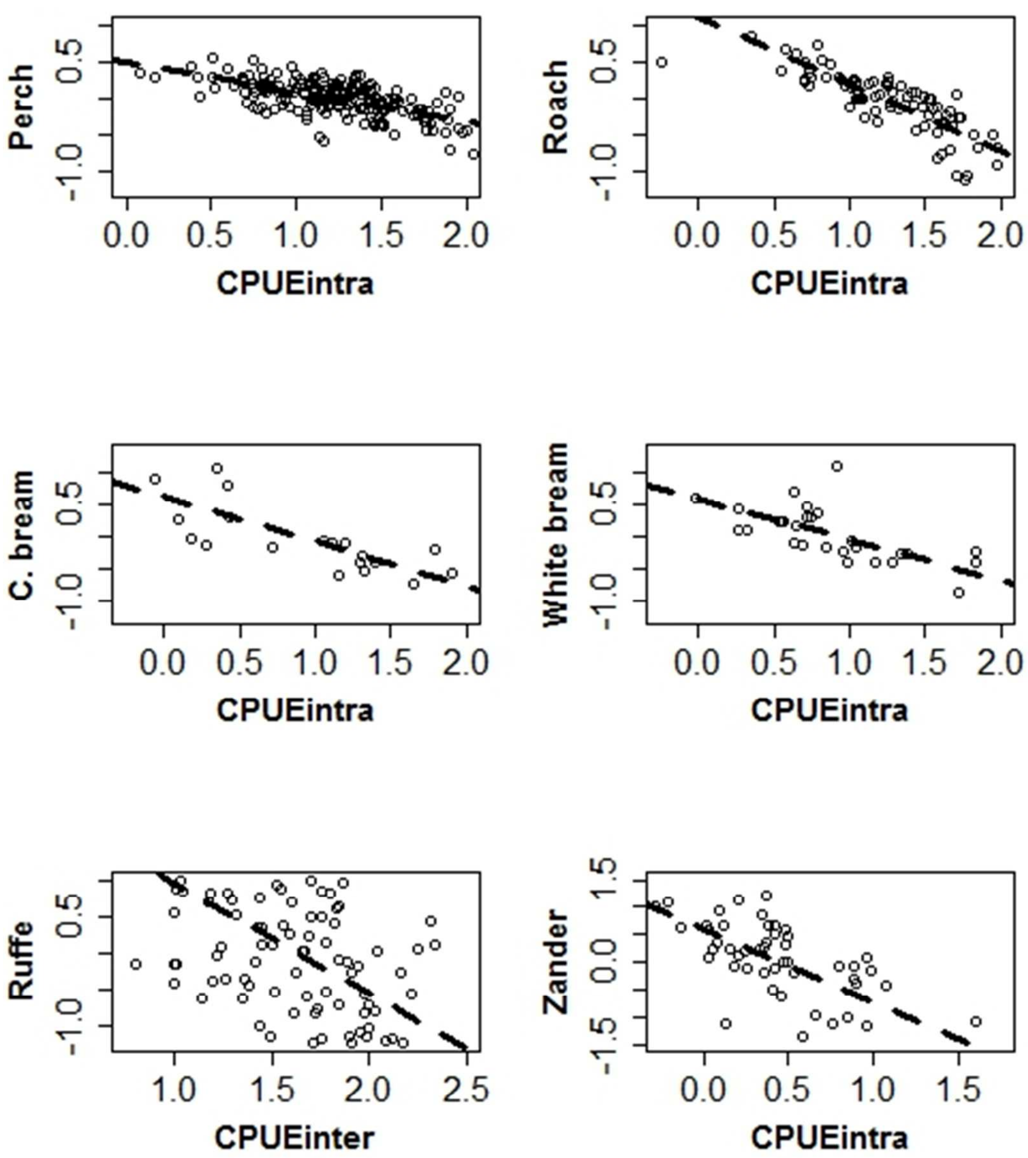

N
0
500
1000 m
a
b
c
d
e
f
g
h
i
j
NO
SW
EST
UK
GE
FR
SL
IT
SP
00°00'00''E
20°00'00''E
60°00'00''N
50°00'00''N
40°00'00''N

Figure 2.


Perch
0.5
-1.0
0.0 0.5 1.0 1.5 2.0
CPUEintra
Roach
0.5
-1.0
0.0 0.5 1.0 1.5 2.0
CPUEintra
C. bream
0.5
-1.0
0.0 0.5 1.0 1.5 2.0
CPUEintra
White bream
0.5
-1.0
0.0 0.5 1.0 1.5 2.0
CPUEintra
Ruffe
0.5
-1.0
1.0 1.5 2.0 2.5
CPUEinter
Zander
1.5
0.0
-1.5
0.0 0.5 1.0 1.5
CPUEintra

Appendix

Table A1. Minimum, maximum and arithmetic mean (in brackets) of all environmental predictors for each species. Max.T. is maximum temperature (ºC) and TP is total phosphorus (µg L^{-1}).

Common name	Max.T. (ºC)	TP (µg L^{-1})	Area (ha)	Depth (m)
Perch	11.1-23.1 (16.15)	1-330 (25.72)	0.02-113 (3.11)	1-190 (20.53)
Roach	12.1-24.6 (16.5)	1-561 (33.27)	0.06-6478 (35.71)	1-135 (18.88)
Ruffe	13.3-21.2 (17.03)	2-330 (44.39)	0.06-113 (5.57)	1.2-190 (23.12)
Common bream	14.2-21.9 (17.59)	3-[illegible]0 (64.09)	0.24-113 (5.24)	1.2-100 (14.48)
White bream	14.6-23.1 (17.83)	2-56[illegible] (76.17)	0.36-927 (31.53)	1.2-69.5 (16.01)
Zander	14.5-24.6 (18.76)	6-330 (82.8)	0.44-6478 (199.02)	1.2-100 (16.99)

Figure A1. Frequency distributions based on all individuals for each species for all lakes accumulated together. X axes represented fresh mass by a log2 scale and y axes represent the relative frequencies (%) for each size class. Note the different scales on the y axis.

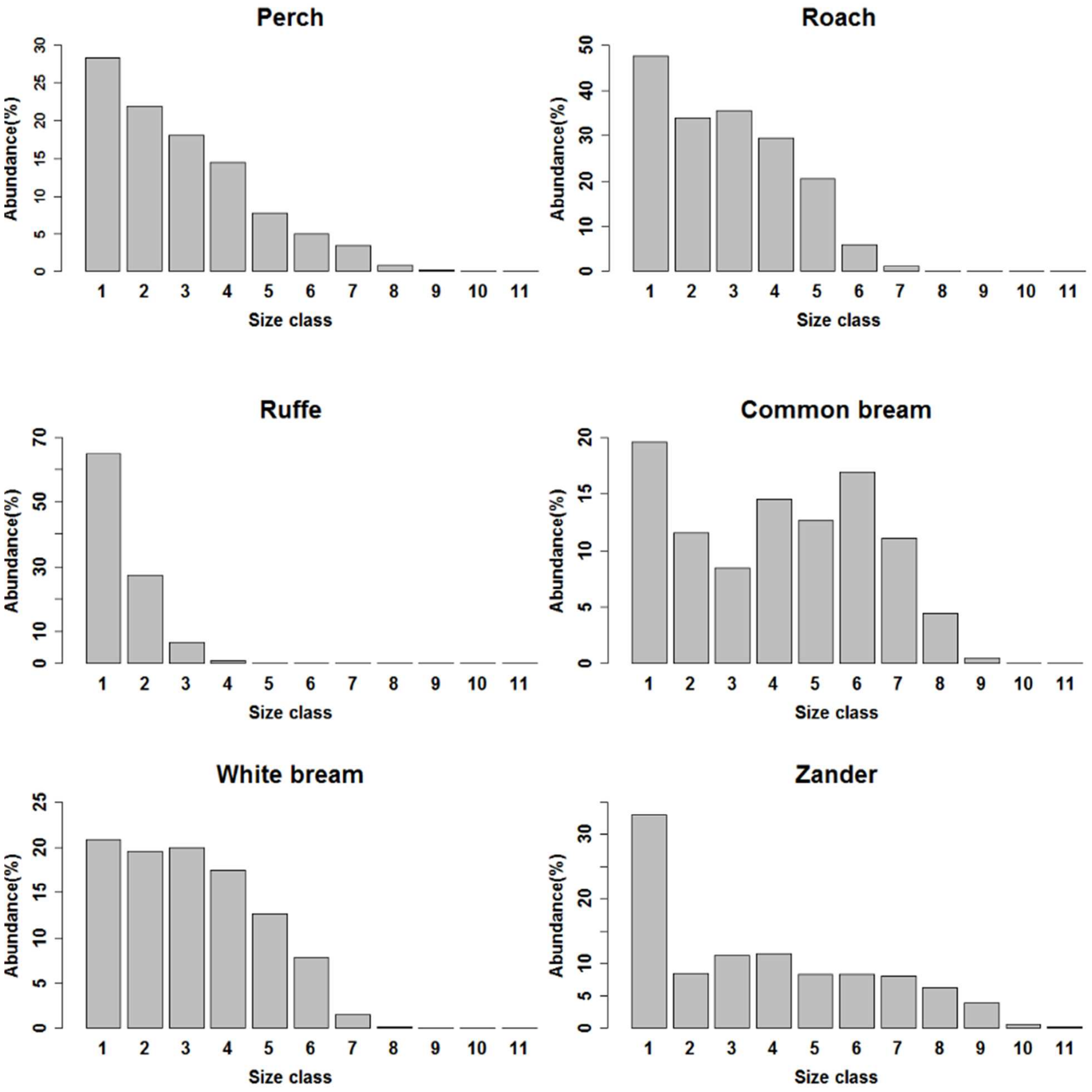
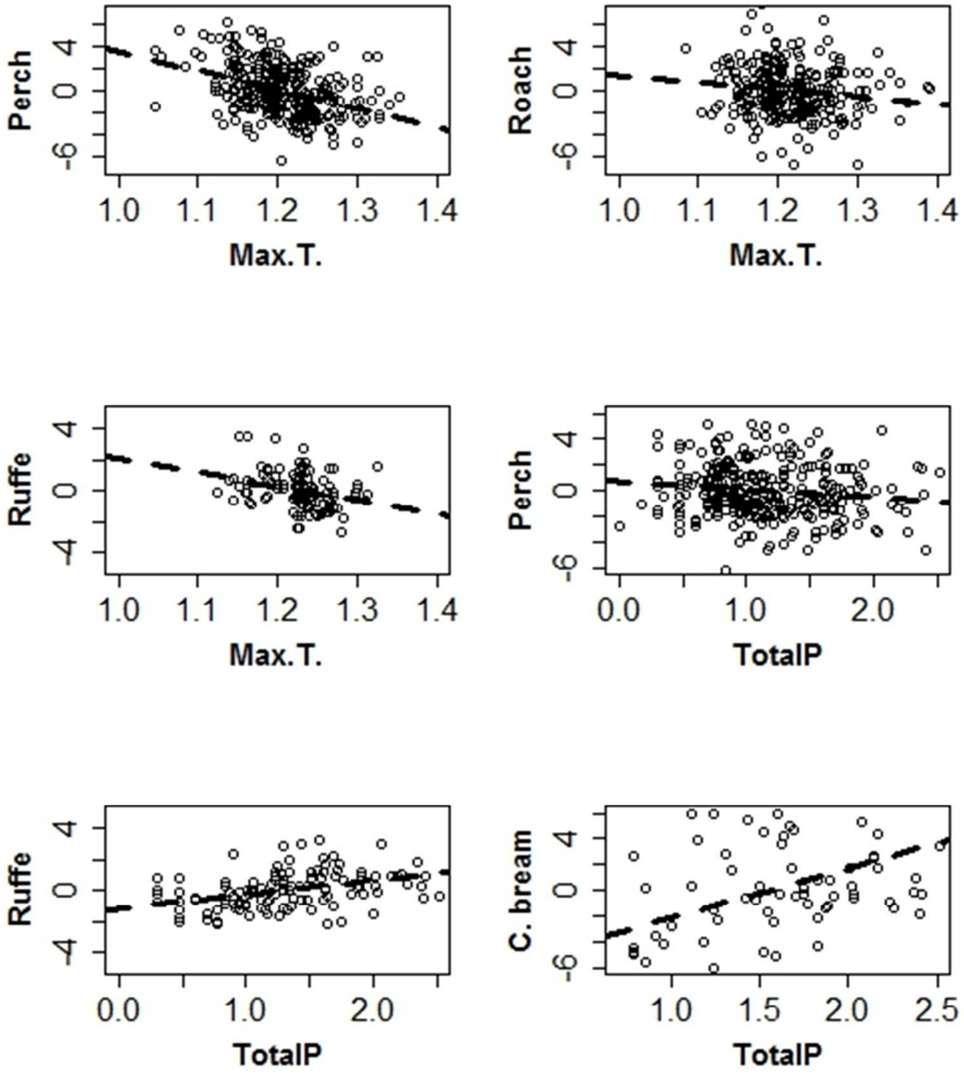
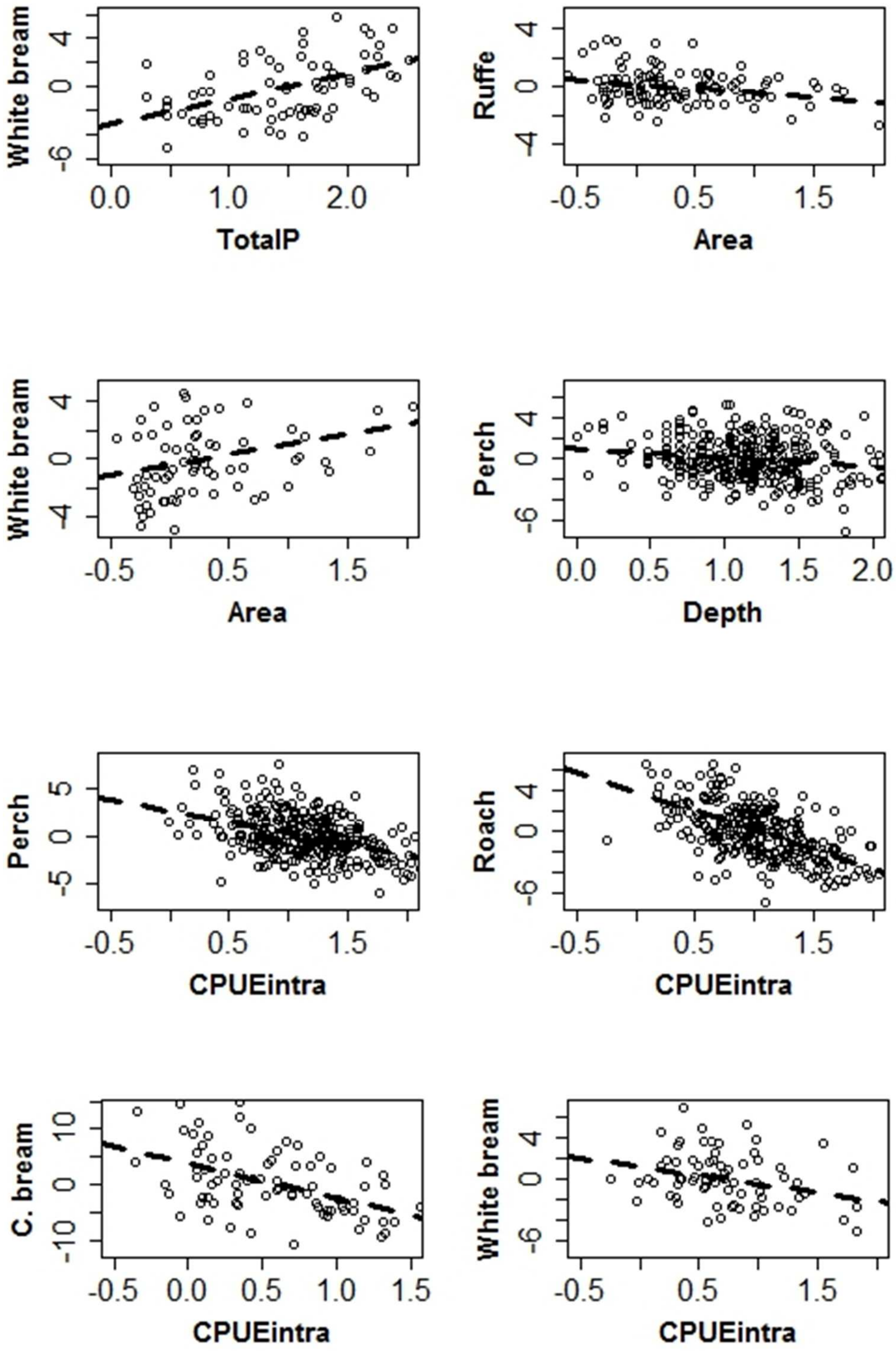


Figure A2. Partial residual plots for each species between the size metric mean body size (y axis) and the climatic, morphometric, productivity and density-dependent predictors (x axis) included in the final model.




White bream
-6
0
4
0.0
1.0
2.0
TotalP
Ruffe
-4
0
4
-0.5
0.5
1.5
Area
White bream
-4
0
4
-0.5
0.5
1.5
Area
Perch
-6
0
4
0.0
0.5
1.0
1.5
2.0
Depth
Perch
-5
0
5
-0.5
0.5
1.5
CPUEintra
Roach
-6
0
4
-0.5
0.5
1.5
CPUEintra
C. bream
-10
0
10
-0.5
0.0
0.5
1.0
1.5
CPUEintra
White bream
-6
0
4
-0.5
0.5
1.5
CPUEintra

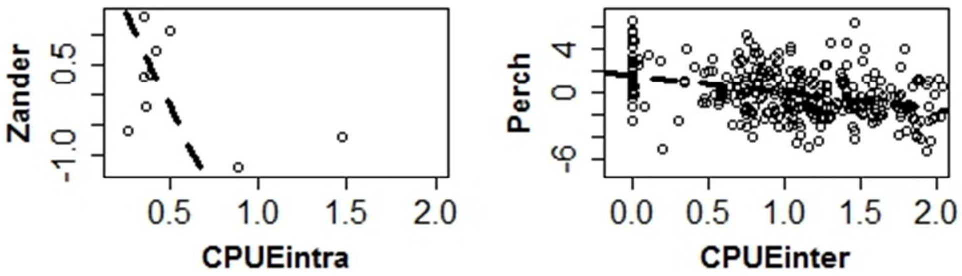

Zander
-1.0
0.5
0.5
1.0
1.5
2.0
CPUEintra
Perch
-6
0
4
0.0
0.5
1.0
1.5
2.0
CPUEinter

Figure A3. Partial residual plots for each species between the size metric slope (y axis) and the climatic, morphometric, productivity and density-dependent predictors (x axis) included in the final model.

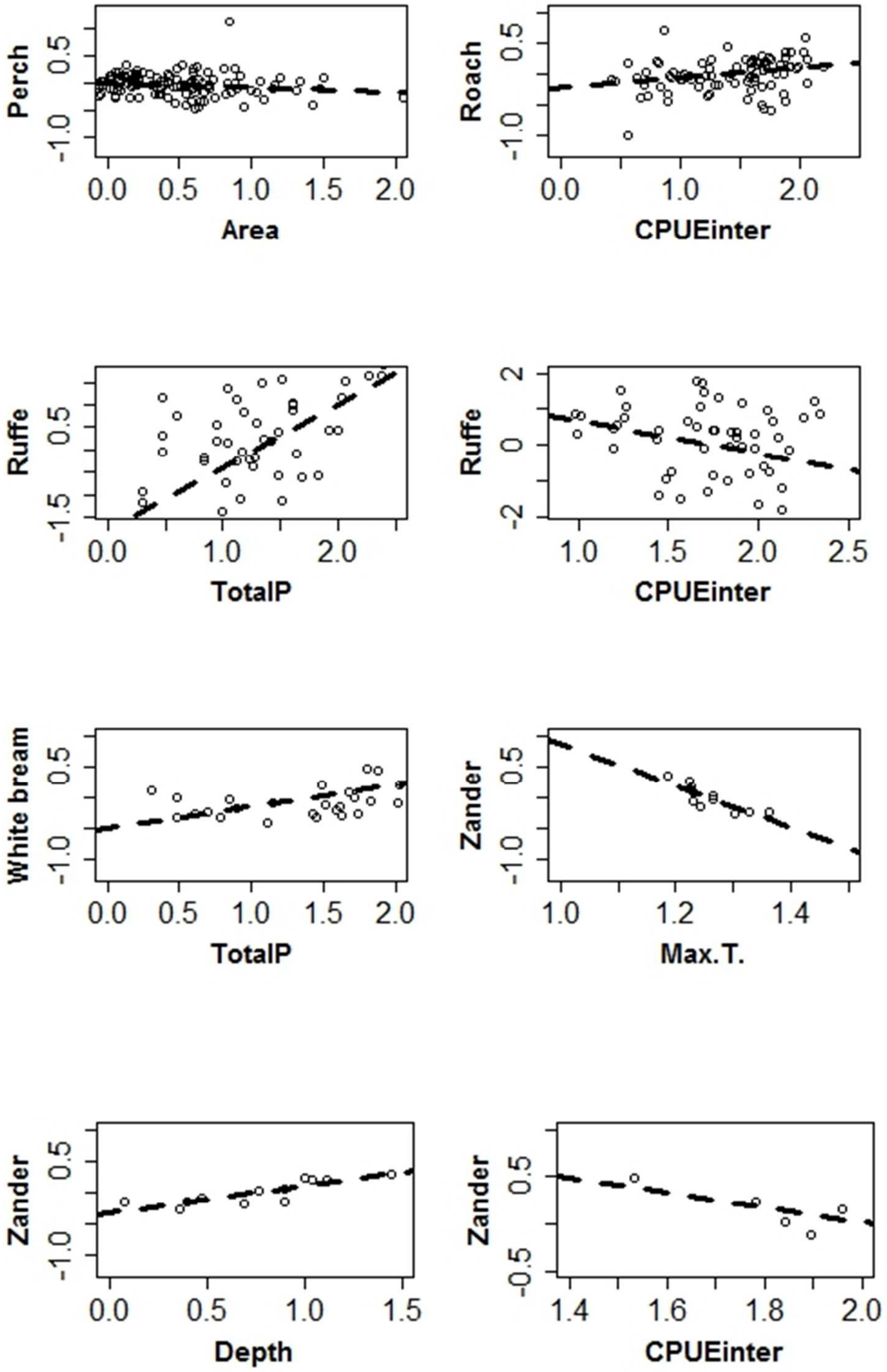
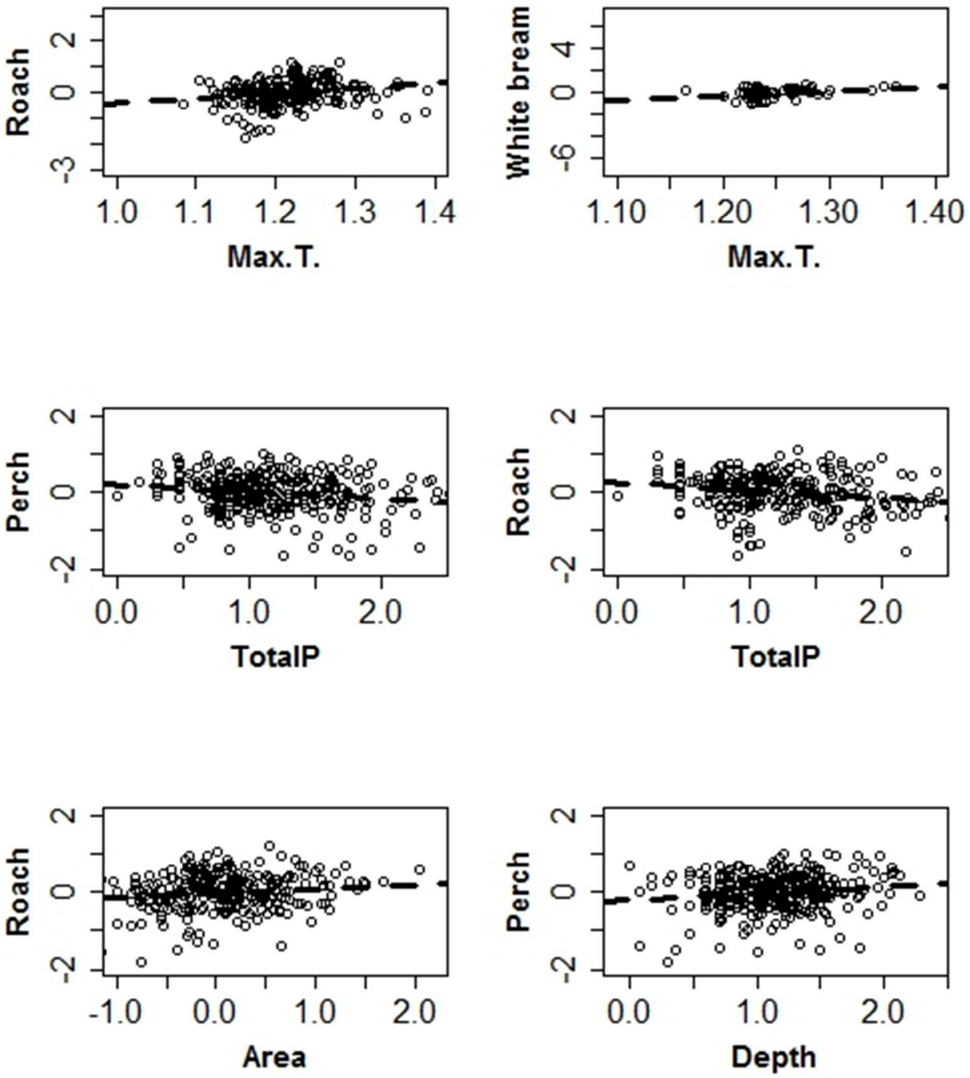


Figure A4. Partial residual plots for each species between the size metric diversity (y axis) and the climatic, morphometric, productivity and density-dependent predictors (x axis) included in the final model.



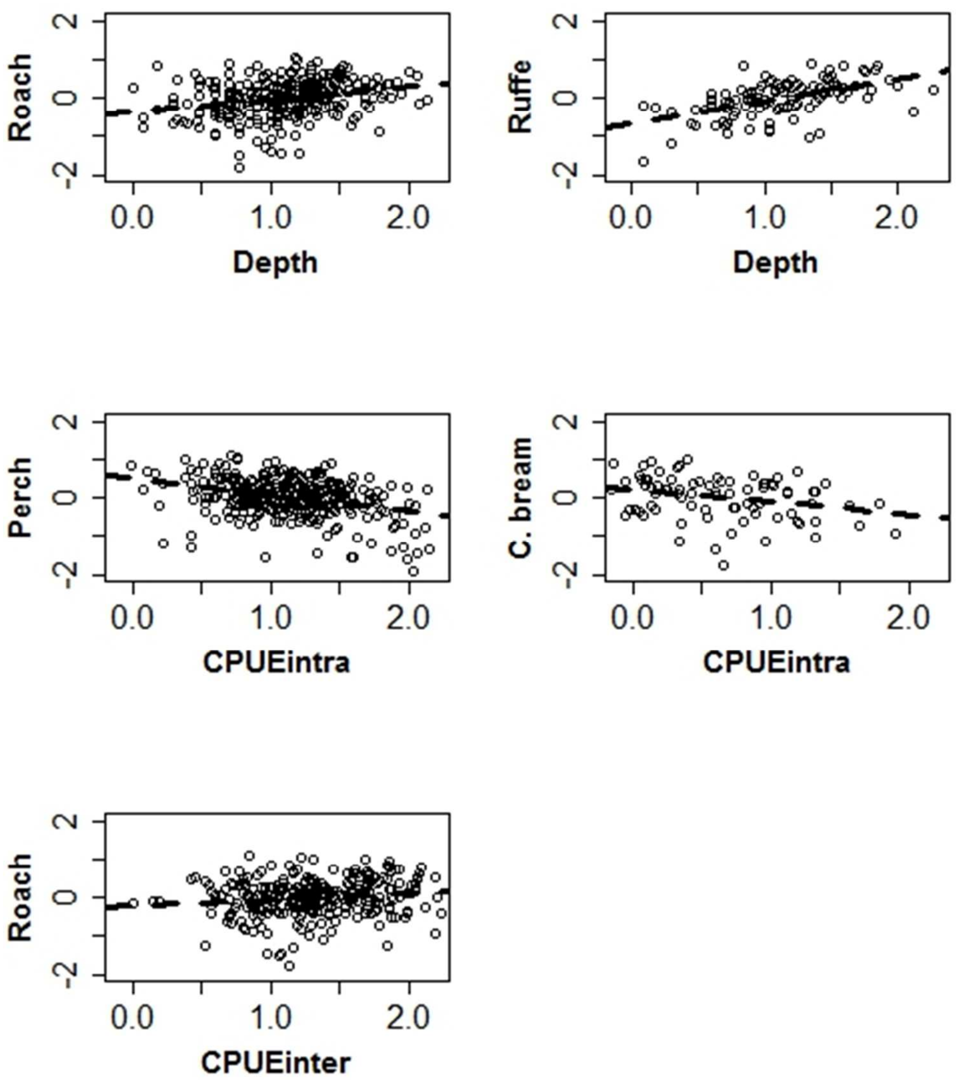

Roach
Depth
Ruffe
Depth
Perch
CPUEintra
C. bream
CPUEintra
Roach
CPUEinter
2
0
-2
0.0
1.0
2.0

Figure A5. Between-year variation of the geometric mean length (mm) for perch, roach and ruffe in some Swedish lakes. X axis is the mean length expressed in mm and Y axis is the sampling year.