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Density-dependent effects as key drivers of intraspecific size structure of six abundant fish species in lakes across Europe¹

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

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 along large-scale environmental gradients. We further analyzed the response of these three size metrics to environmental variables and to density-dependent effects, i.e., relative estimates of abundance (catch per unit effort, CPUE). 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 (*Perca fluviatilis*), roach (*Rutilus rutilus*), and ruffe (*Gymnocephalus cernuus*). Lake productivity (expressed as total phosphorus concentration) and lake depth were also predictors of size structure for four 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 when density dependence increases. This suggests that density dependence is a key driver of fish size structure.

Résumé : Nous avons étudié la structure de tailles des poissons en utilisant la taille moyenne, la diversité des tailles et la pente des distributions linéaires des tailles de six espèces communes de poissons européens sur des gradients environnementaux à large échelle. Nous avons ensuite analysé la réponse de ces trois métriques de tailles aux variables environnementales et à des mesures de densité-dépendances, i.e. estimations relatives de l'abondance (captures par unité d'effort, CPUE). Nous avons décelé des différences quant à l'importance des principales variables explicatives de la structure de taille entre les six espèces, mais le sens de la réponse était relativement comparable et cohérent pour la plupart des paramètres associés à la taille. La taille moyenne du corps présentait une relation négative avec la température pour la perche (*Perca fluviatilis*), le gardon (*Rutilus rutilus*) et la grémille (*Gymnocephalus cernuus*). La productivité du lac (représentée par la concentration de phosphore total) et la profondeur du lac étaient également des variables explicatives de la structure de tailles pour quatre des six espèces. En outre, nous avons constaté une forte densité dépendance de la structure de tailles de toutes les espèces qui se traduit par des tailles du corps moyennes et une diversité de tailles plus faibles, ainsi que des pentes plus grandes des distributions de tailles avec l'augmentation de la densité. Ces résultats donnent à penser que la densité dépendance est un facteur clé de la structure de tailles des poissons.

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 variations 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 being dominated by percids or salmonids (Persson et al. 1988; Bergman 1991), but also by intra- and inter-specific competition and perhaps reduced predation by piscivores (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 in 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

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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 the 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. 1999). 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 the 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). Because 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.

Materials 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-fish 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°N and 69.69°N and a longitudinal gradient between 10.17°E 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 (European Committee for Standardization (CEN) 2005; reports from Confederación Hidrográfica del Ebro (CHE) 2008–2012); the data were, therefore, comparable with data from 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 10 ecoregions along a latitudinal gradient between 40.81°N and 69.69°N (Fig. 1).

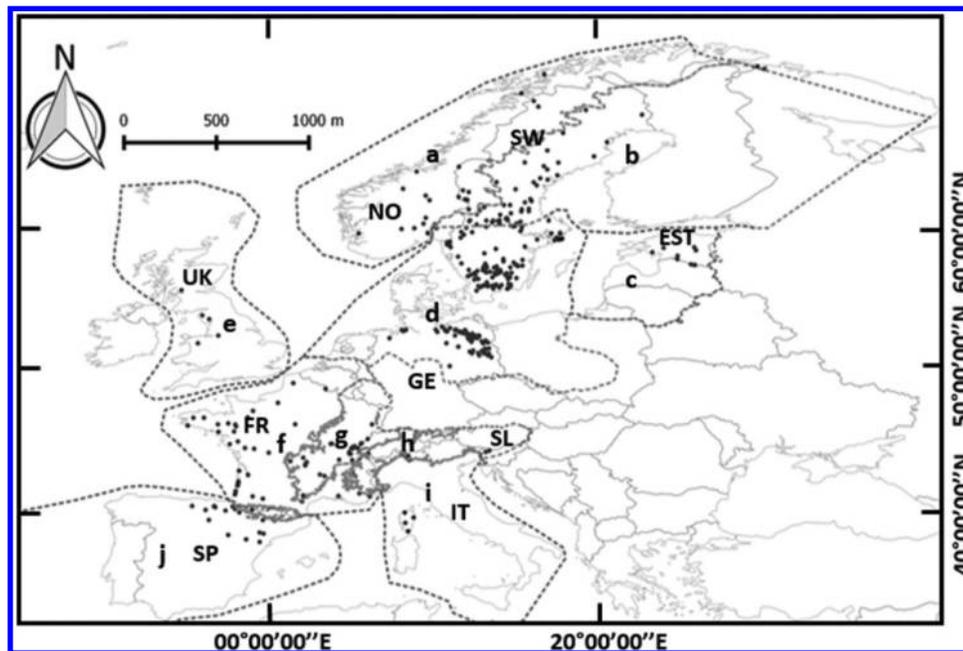
Sampling

All fish were caught in accordance with European Standard 14757 (CEN 2005) during late summer and early autumn using benthic multimesh 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 h overnight because gillnet catching is highly dependent on fish activity (Prchalová et al. 2009). To ensure comparable individual-fish 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 European Standard 14757 (CEN 2005). Fish catches were expressed as lake-specific 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 interannual 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 means \pm SD: 19.71 \pm 14.48, 8.34 \pm 3.07, and 0.73 \pm 0.32 for perch, roach, and ruffe, respectively, in the lake with highest variability). The exception was the perch population in the lake at the highest latitude: 1-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 centimetre) and fresh body mass (FM, nearest gram). 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. For more details, see Brucet et al. (2013).

Fish species selected

Species selection was hierarchically guided by the following requirements: (i) the species had to be present in a representative number of lakes (minimum 20 lakes; Table 1); and (ii) 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 error in size diversity estimation of approximately 30%.

Fig. 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), and UK. Ten ecoregions according to Illies (1978) are 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, and (j) Iberian Peninsula.



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 and 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 the 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-fish size measurements (Brucet et al. 2006; Quintana et al. 2008) for each lake following an integral formula:

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

where μ_2 is the Shannon size diversity index and ρ_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 calculating the pdf is by using a nonparametric Kernel estimation (Quintana et al. 2008). A kernel estimation is essentially a pdf, usually symmetric, with a dispersion that 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 are double standardised to (i) make the size data adimensional and (ii) make size data comparable with data from other studies whose samples are measured with different units,

e.g., 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 that 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 as 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 as 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 the \log_2 midpoint of size classes (axis x) and the \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 (Prchalová et al. 2009). Hence, 1 to 4 g fish (i.e., fish in the first year of life) were under-represented 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;

Table 1. Occurrences, countries, and ecoregions where the six fish species were sampled.

| 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 |

Note: 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), size diversity (μ), and slope of linear spectra \pm standard deviation are provided, with minimum and maximum values given in parentheses. Size range is 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, and (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, and (j) Iberian Peninsula.

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, for instance, for ruffe (size range of five 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 (Appendix A, Table A1): (1) total phosphorus concentration (hereafter TP, $\text{mg}\cdot\text{m}^{-3}$) as a surrogate of lake productivity, (2) maximum depth (m), and (3) lake area (ha) and excluded geographical position and instead used direct local climate data expressed as (4) maximum monthly mean air temperature ($^{\circ}\text{C}$), which was calculated using the climate Climatic Research Unit (CRU) model proposed by New et al. (2002). This specific model can obtain a spatial resolution of 10' latitude and (or) 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, CPUE_{intra}) and (6) the interspecific density-dependent effect (sum of CPUE of the other five potentially competing species, hereafter CPUE_{inter}). The sum of the six species in each lake was $82.2\% \pm 29.9\%$ (SD) of total CPUE, and hence intra- and inter-specific CPUE covered a 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 and (or) 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 indicated 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 (two or more distinct peaks) size distributions and hence deviated from linear size spectra. We only included linear slopes with significance $p < 0.10$. 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 Appendix A, 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

Table 2. Relative strength for each predictor represented by the beta coefficients with their positive or negative trends and the predicted variance (%) (in parentheses for predictors).

| Common name | Max. T (°C) | 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 bream | | 0.58** (13.15) | | | -0.65*** (27.12) | | 40.27 |
| 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 |

Note: 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 (°C); TP, total phosphorus (µg·L⁻¹); CPUEintra, intraspecific density-dependent effect; CPUEinter, interspecific density-dependent effect. Significance: no asterisk, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

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 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 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 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 among 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 et al. 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 (Appendix A, 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 (Appendix A, Table A1).

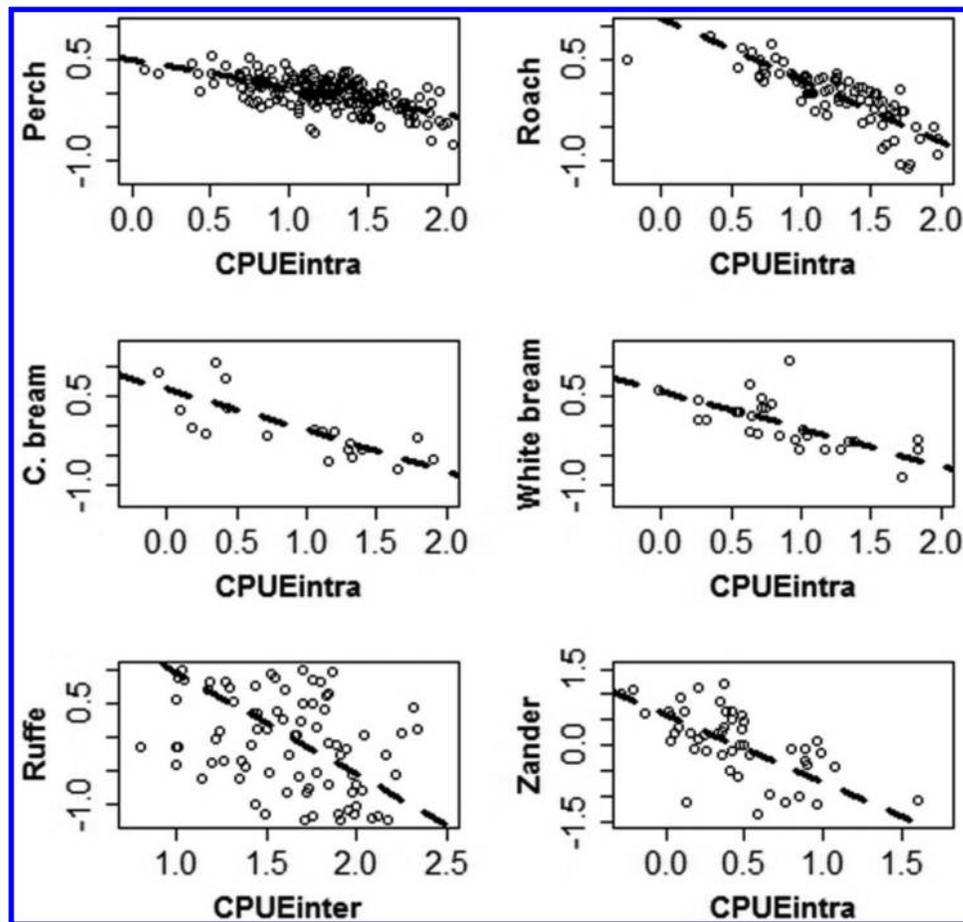
Zander had the highest number of size classes, from the smallest (1st class, 4–8 g) to the largest size class (11th class, 4096–8192 g), whereas ruffe sizes covered only five classes (maximum 5th class, 64–128 g). The proportion of lakes in which fish populations exhibited linear size spectra was relatively high for perch (62.9%), ruffe (46.9%), and white bream (41.7%). In contrast, nonlinear ($p > 0.10$) size distributions dominated in common bream, zander, and roach populations (nonsignificant 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; Appendix A, 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 °C; Table 2; Appendix A, 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; Appendix A, Fig. A4).

Lake productivity (TP) affected size metrics for five of the six species (Table 2; Appendix A, Figs. A2, A3, and A4). 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 µg·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.

Fig. 2. Significant partial residual plots selected according to the highest beta coefficients in density-dependent effects: y axes represent size metrics, and x axes represent the density-dependent predictor (i.e., CPUE_{intra} and CPUE_{inter}). CPUE_{intra}, CPUE of the focal species; CPUE_{inter}, sum of CPUE of the other five potentially competing species. For perch, roach, white bream, and common bream (c. bream): slope vs CPUE_{intra}; for ruffe: mean size vs CPUE_{inter}; for zander: size diversity vs CPUE_{intra}.



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; Appendix A, Fig. A3). The slope of the linear spectra for perch became significantly steeper with increasing lake area (Table 2; Fig. A3). There were also some relationships between lake area and mean size, with smaller sizes being observed for ruffe and larger sizes for white bream in larger lakes (Table 2; Appendix A, Fig. A2).

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; Appendix A, Figs. A2, A3, and A4). Particularly, lower mean size and steeper slopes (i.e., greater relative abundance of small-sized individuals) occurred at higher CPUE_{intra} for five and four, respectively, of the six species (Table 2). Additionally, a negative response of size diversity to CPUE_{intra} was found for three species (Table 2; Fig. 2; Appendix A, Fig. A4). In contrast, there was a weaker and less consistent effect for CPUE_{inter} (mean beta coefficients for CPUE_{intra} and CPUE_{inter}: 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 CPUE_{inter} (Table 2; Appendix A, Figs. A2 and A3). In contrast, CPUE_{inter} 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; Appendix A, Figs. A3 and A4). Finally, interactions terms were not significant ($p > 0.05$) except CPUE_{intra} ×

TP and CPUE_{intra} × Depth for the size diversity of perch ($p \leq 0.001$ and $p \leq 0.01$, respectively).

Discussion

Our results showed some differences 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). Temperature effect is probably masked by the strong density-dependent effect, which was not considered in the community-wide analyses. Thus, our results suggest that, at least at the 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 (Appendix A, Figs. A2 and A4). Studies in Swedish lakes have shown that roach populations may attain >20 cm and >100 g already in their fourth 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 antipredation 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 Élie 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 Bruce et al. (2013) found a decrease in the mean body size of fish in lakes with increasing TP. Our results at the species level partially contrast these findings: 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 $\mu\text{g TP}\cdot\text{L}^{-1}$) and Lake Schwielochsee (260 $\mu\text{g TP}\cdot\text{L}^{-1}$). 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 the 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 was found 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, disproportionately more small fish 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 in that 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 CPUE_{inter}) was 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 CPUE_{inter} 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 interannual 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 and Mann 1985; 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, 2014). As an example, the mean size of the dominant species perch, roach, and ruffe sampled for more than 20 years in four Swedish lakes shows relatively low variability, which may reflect a relatively constant annual recruitment, except for perch at the highest latitude in the dataset (Lake Jutsajaure; Appendix A, 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 a fish population as a result of density-dependent effects is a common phenomenon (Sandheinrich and Hubert 1984; Ylikarjula et al. 1999), which may contribute to the overall pattern observed in our analysis. This is theoretically included in both the Beverton–Holt (Beverton and 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) in which 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 weak but significant interactions between CPUE_{intra} × TP and CPUE_{intra} × 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 pre-

ferred diet of perch of intermediate size is high under these conditions (Persson 1983). These results show that lake morphometry, productivity, and fish density and growth can be strongly linked in some species. Nevertheless, significant interactions of CPU 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 intra-specific 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 an unequivocal indicator of environmental changes, which contrasts the consistency at the 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 that approximate life history from size variables also routinely measured in fish monitoring may be a major step to improving the programmes for managing and monitoring inland waters in the face of the ongoing global climate change.

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Appendix A

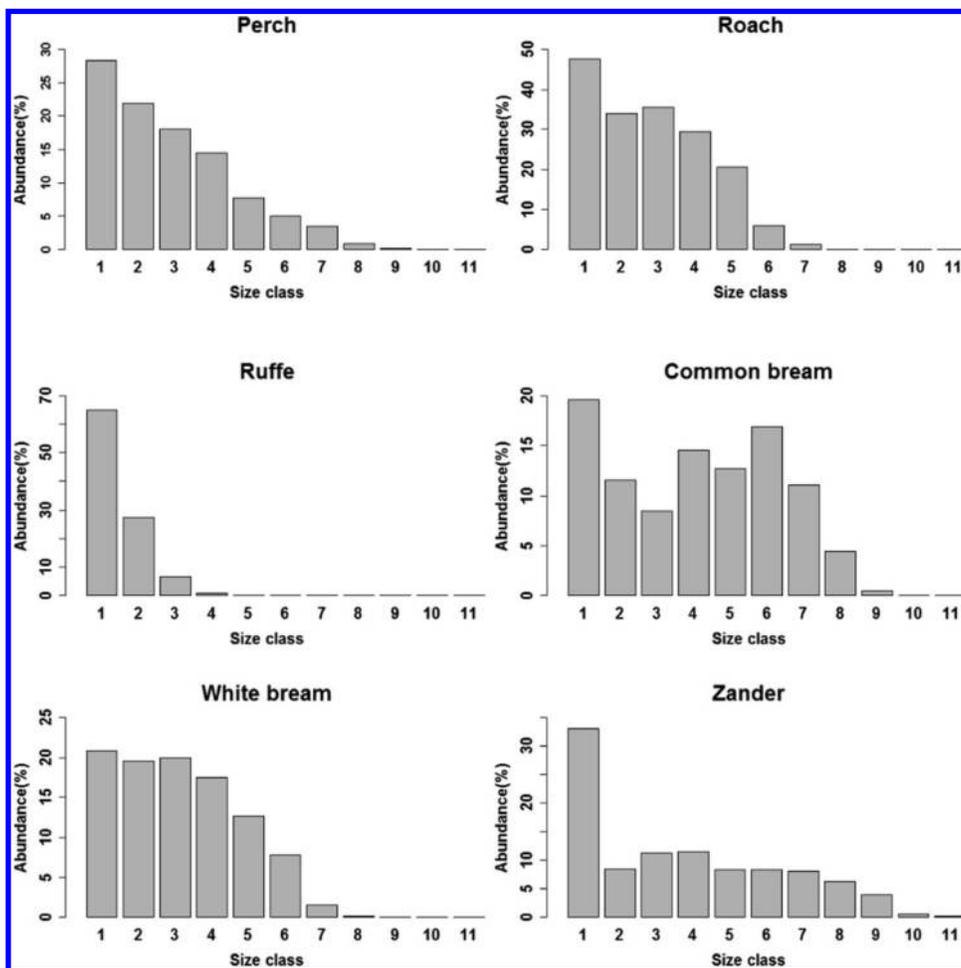
Table A1 and Figs. A1–A5 appear on the following pages.

Table A1. Minimum, maximum, and arithmetic mean (in parentheses) of all environmental predictors for each species.

| Common name | Max.T (°C) | 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) | 3–330 (64.09) | 0.24–113 (5.24) | 1.2–100 (14.48) |
| White bream | 14.6–23.1 (17.83) | 2–561 (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) |

Note: Max.T, maximum temperature (°C); TP, total phosphorus (µg·L⁻¹).

Fig. A1. Frequency distributions based on all individuals for each species for all lakes accumulated together: x axis, fresh mass by a log₂ scale; y axis, relative frequencies (%) for each size class. Note the different scales on the y axis.



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Fig. 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. Max.T, maximum temperature (°C); TotalP, total phosphorus concentration ($\mu\text{g}\cdot\text{L}^{-1}$); Area, lake area (ha); Depth, maximum lake depth (m); CPUEintra, catch per unit effort of the focal species; CPUEinter, sum of CPUE of the other five potentially competing species; c. bream, common bream. (Fig. A2 is concluded on the next page.)

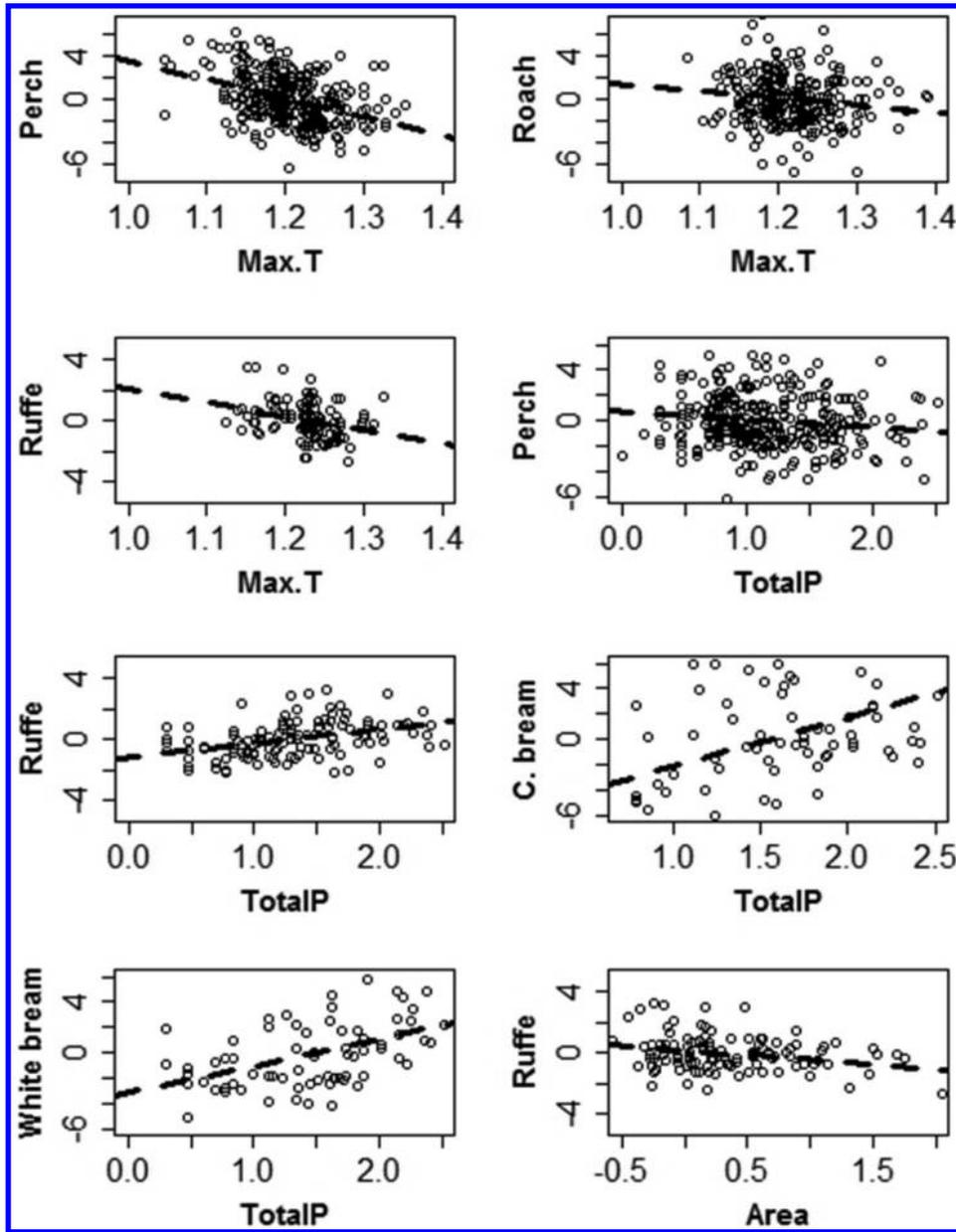
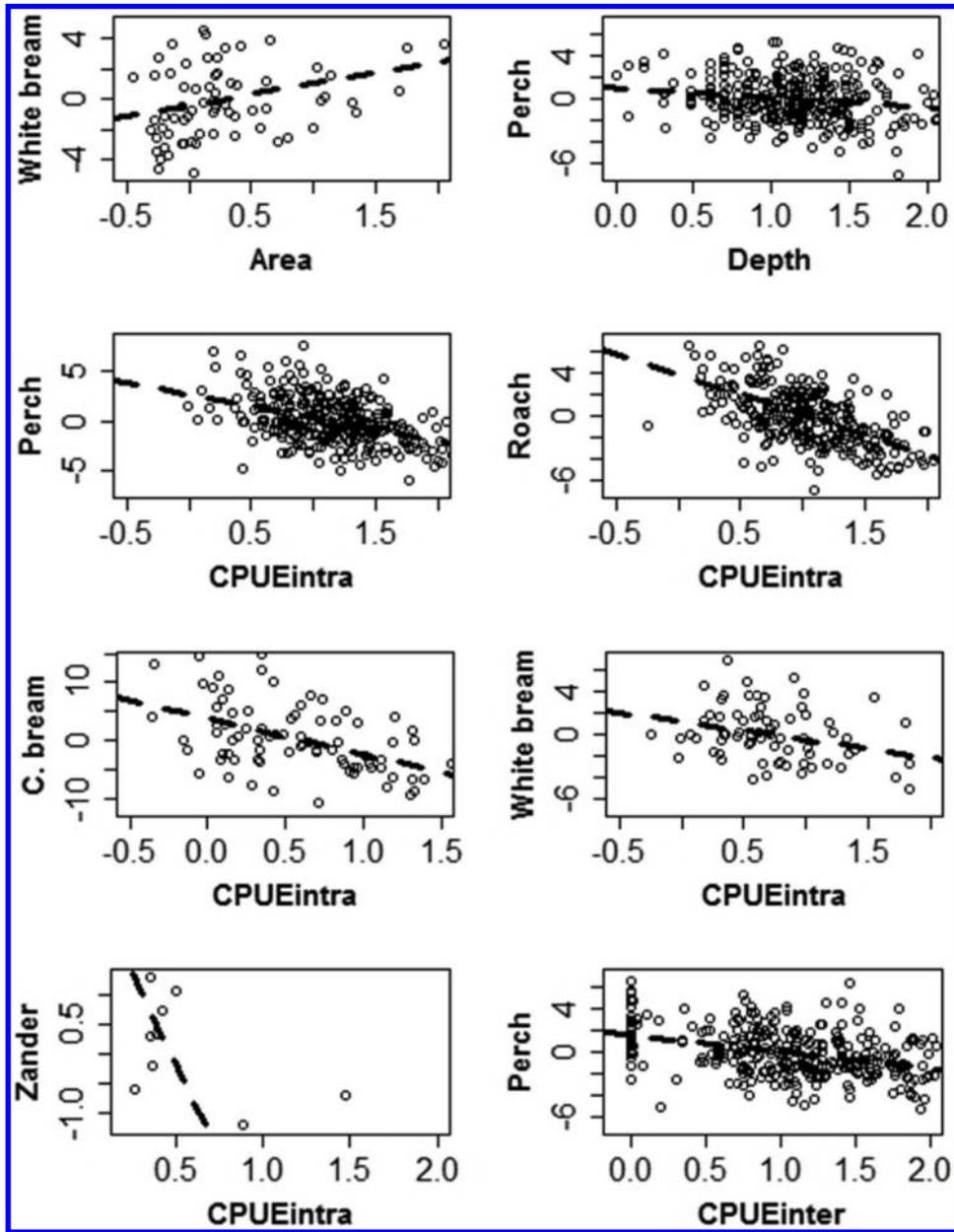


Fig. A2 (concluded).



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Fig. 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. See caption of Fig. A2 for explanation of predictor abbreviations.

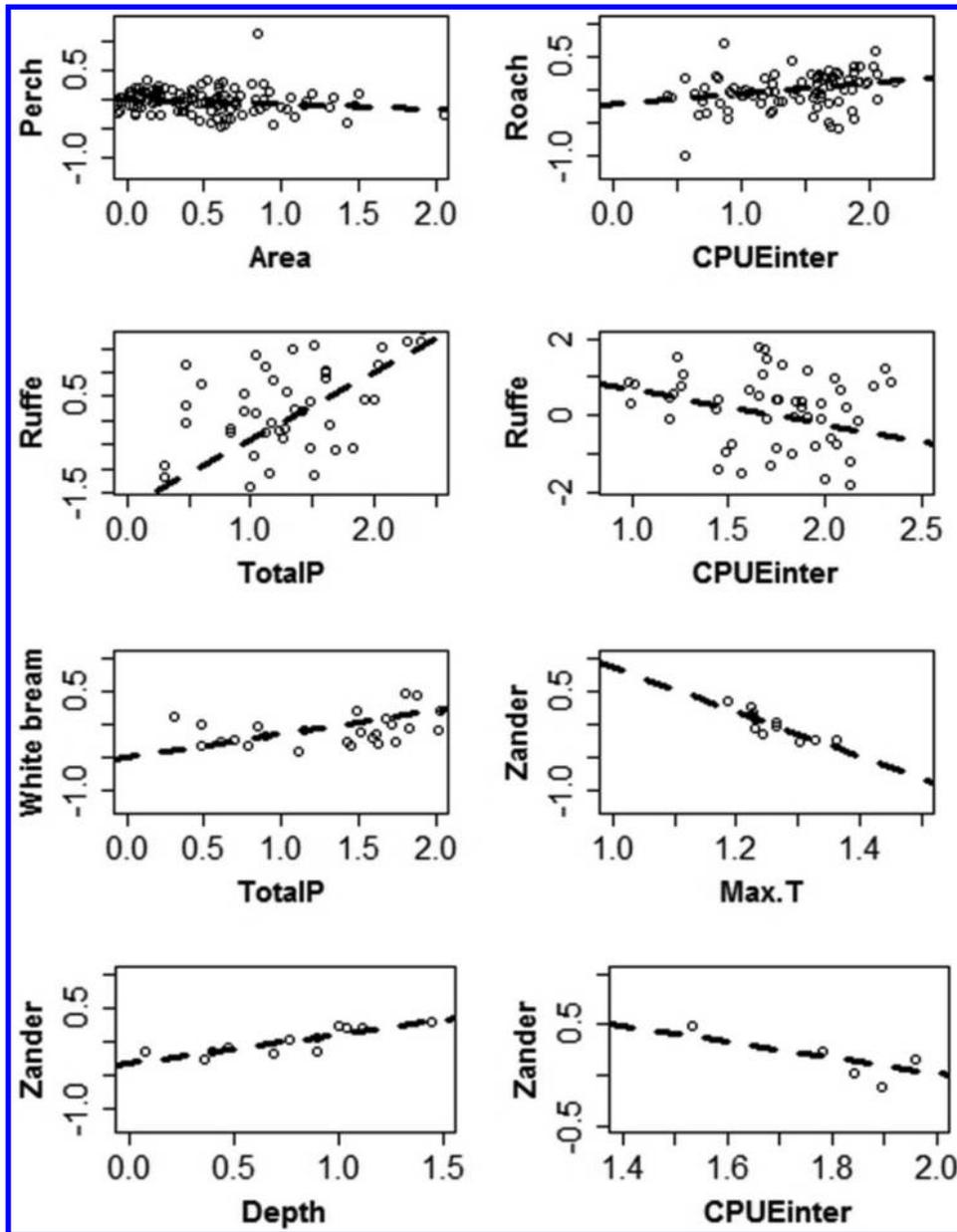


Fig. A4. Partial residual plots for each species between the size metric diversity (y axis) and the climatic, morphometric, productivity, and density-dependent predictors (x axis) included in the final model. See caption of Fig. A2 for explanation of predictor abbreviations. (Fig. A4 is concluded on the next page.)

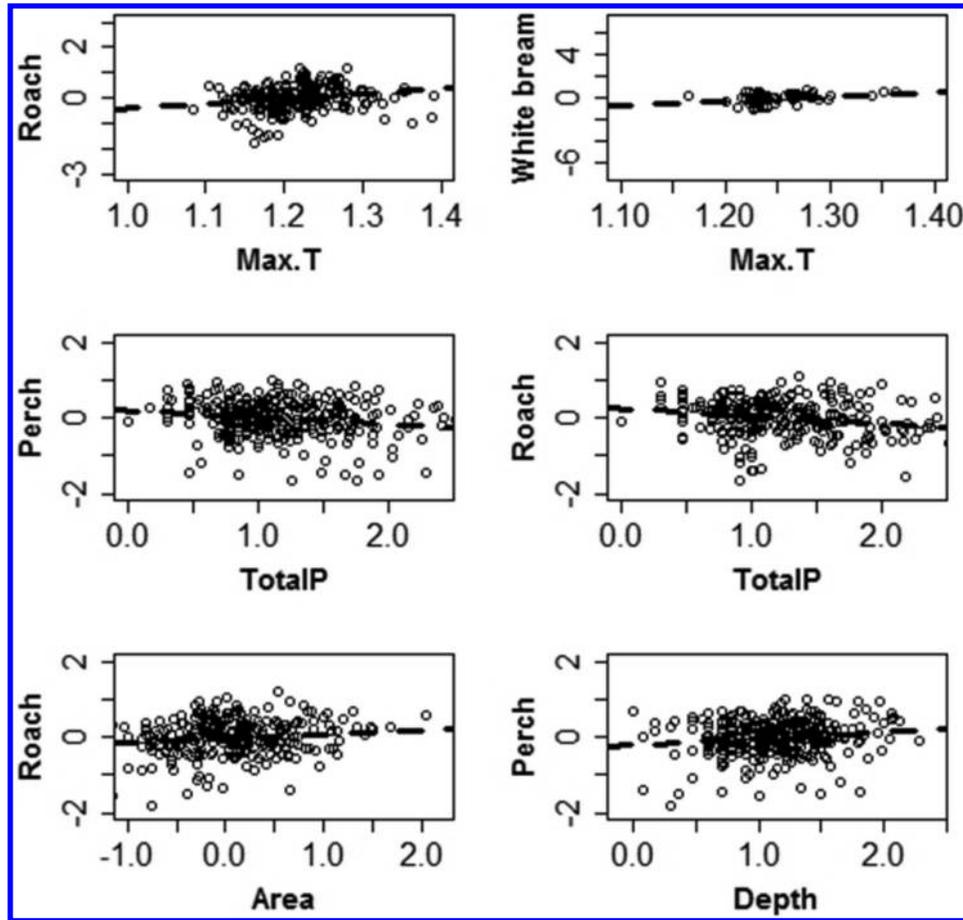


Fig. A4 (concluded).

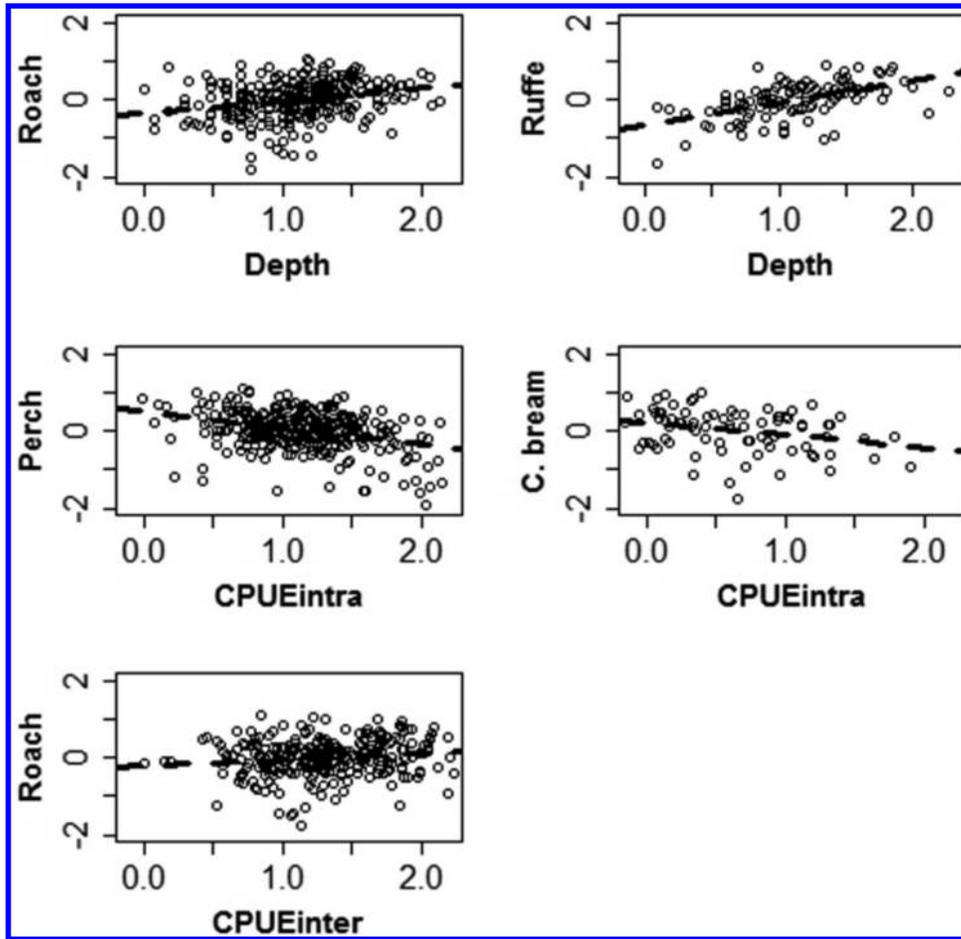


Fig. A5. Between-year variation of the geometric mean length for perch, roach, and ruffe in some Swedish lakes: x axis, mean length (expressed in mm); y axis, sampling year.

