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Article title: Geographical patterns in the size structure of European lake fish communities along abiotic and biotic gradients

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35 Running head: Size structure patterns of European lake fish communities

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37 Biosketch

38 The authors share an interest in studying the structure and function of European lake fish
39 communities.

40

41

42 Author contribution

43 ME & TM conceived the idea, all authors collected the data, ME analysed the data, and ME & TM led
44 the writing with support from all co-authors.

Aim To document geographical patterns of variation in the size structure of European lake fish communities along abiotic gradients and differences in fish community composition.

Location 356 European lakes

Methods Variation in the size structure of the fish communities was explored on a continental scale in relation to the location, morphometry, productivity and fish community composition of 356 lakes. Separate analyses were also conducted for lake subsets located in five ecoregions (Borealic Uplands/Tundra, Fenno-Scandian Shield, Central Plains, Western Plains, Western Highlands) and for lakes with different functional community classifications (cold-, cool-, warmwater fish communities).

Results

Geographical patterns of variation in the size structure of European lake fish communities could be clearly discerned along a temperature gradient for both the continental dataset (356 lakes) and the data subsets of smaller geographical dimension (ecoregions). We found systematic changes in fish community size structure across temperature gradients in correspondence with the dominant thermal fish guild. The majority of the lakes, mainly located in the warmer European lowlands, were dominated by eurythermic cool- and warmwater fish communities with small-sized individuals characterised by linear individual size distributions. Lakes located in cold regions and dominated by stenothermic coldwater salmonids with larger-sized individuals were characterised by unimodal or bimodal size distributions. The average size of cold-, cool- and warmwater fish communities changed uniformly along a temperature gradient.

Main conclusion

Patterns of variation in the size structure of European lake fish communities are consistent with the temperature-size rule. Temperature modifies fish community size structure uniformly within the thermal fish guilds and different ecoregions. Furthermore, our results indicate an increasing predictive power of temperature to explain variability in the size structure when moving from warm to cold geographical regions.

Keywords biogeography, body size, freshwater fish, functional classification, individual size distribution, temperature gradient, multi-mesh gillnet, temperature-size rule, thermal guild

Introduction

Species traits often vary substantially across geographical gradients (Gaston *et al.*, 2008). Among them, body size is of central importance because it directly relates to several ecological and physiological processes such as respiration, growth, maturation, reproduction and longevity (Blueweiss *et al.*, 1978; Calder, 1984). Geographical size clines are evident across multiple faunal taxa and have been observed in both terrestrial and aquatic environments (e.g. Olalla-Tárraga *et al.*, 2006; Blanck & Lamouroux, 2007). In most ectotherms an increase in developmental temperature leads to a decrease in adult body size (but see e.g. Atkinson, 1994; Willott & Hassall, 1998 for a reverse relationship), a phenomenon described as the temperature-size rule (Atkinson, 1994). However, there is no complete mechanistic understanding of this macroecological pattern and in fact several partially competing hypotheses exist on the occurrence of thermal size clines in ectotherms (Atkinson *et al.*, 2006; Walters & Hassall, 2006; Zuo *et al.*, 2012). For example, Atkinson *et al.* (2006) suggest that ectotherms grow to a smaller final body size at high temperatures to maintain their aerobic scope as oxygen concentrations decline with increasing temperature. In contrast, Zuo *et al.* (2012) propose different temperature sensitivities of development and growth during ontogeny, leading to smaller body sizes at higher temperatures as a result of lower somatic growth following earlier sexual maturity.

Despite these different explanations, the general pattern of smaller sizes in ectotherms at higher temperature seems to be universal (Gardner *et al.*, 2011) and particularly prevalent in usually strongly size-structured aquatic communities (Peters, 1983; Blanchard *et al.*, 2009, Ohlberger, 2013). Such substantial variation in body size has a significant effect across multiple levels of ecosystem organisation and determines the strength of predator-prey interactions, body-size abundance

relationships and energy fluxes in food webs (Emmerson & Raffaelli, 2004; Reuman & Cohen, 2005; White *et al.*, 2007). Analysing geographical patterns and variation of size structure in aquatic communities is therefore important for the identification and understanding of fundamental ecological and biogeographical processes. Furthermore, analysis of size structure may help to identify and predict the response of species, communities and ecosystems functioning relative to large-scale anthropogenic disturbances and environmental change (Petchey & Belgrano, 2010; Gardner *et al.*, 2011; Brose *et al.*, 2012).

Earlier studies on the size structure of freshwater fish communities have primarily used local presence-absence data combined with generalised location-independent data on maximum species-specific size from the scientific literature to analyse changes in species richness across size classes over large geographical scales (Lindsey, 1966; Knouft, 2004; Griffiths, 2012). Other studies have focused on selected species and have demonstrated variations in the size structure of fish populations across geographical gradients (Heibo *et al.*, 2005; Blanck & Lamouroux, 2007). These studies have shown that fish communities in warm environments typically consist of more small-sized species (Knouft, 2004; Griffiths, 2012), and individuals of the same species in cold environments are larger than conspecifics in warm environments (Blanck & Lamouroux, 2007; Jeppesen *et al.*, 2010).

Besides temperature, further evidence of abiotic and biotic predictors of fish community size structure has been obtained from several regional studies showing that differences in lake morphometry, lake productivity and functional fish community composition contribute to size differences (Jeppesen *et al.*, 2000; Jeppesen *et al.* 2010, Emmrich *et al.*, 2011). However, these studies did not cover large-scale geographical gradients (but see Holmgren & Appelberg, 2000 for a large-scale Swedish study) where different factors are likely to affect fish community size structure (Borcard *et al.*, 2004). In addition to changes in the abiotic environment along such broad geographical gradients, shifts in the taxonomic composition of freshwater fish communities (Griffiths,

2006; Reyjol *et al.*, 2007) may contribute to variation in their size structure, a topic that has only been marginally explored. Accordingly, it remains unresolved whether the great variability in the size structure of lake fish communities over large geographical gradients reflects the taxonomy-independent effect of simple temperature-size rules or whether it basically reflects fundamental shifts in taxonomic composition. To distinguish between these processes, the ideal approach would be based on empirically obtained specific data on fish communities from a large number of dispersed lakes instead of being based on generalised location-independent average species-specific size measures obtained from the scientific literature. However, such large and detailed datasets from lakes have previously not been available.

In this study, we moved beyond previous approaches in three directions. Firstly, we used a very large-scale dataset on fish catches from 356 lakes located in eight European countries covering a latitudinal gradient of 28.2°, a longitudinal gradient of 35.4° and an elevation gradient of 1201 m. Fish communities were sampled with standardised multi-mesh gillnets and evaluated with respect to species, individual body length and individual mass. Secondly, we analysed the effects of abiotic predictors previously identified to influence the size structure of lake fish communities at small regional scales within the broad geographical gradients covered by our dataset. Specifically, we compared the slopes of non-taxonomic individual size distributions (ISD) (*sensu* size spectra, White *et al.*, 2007) and the average size of individuals in the fish community along temperature gradients, gradients of lake morphometry and variations in lake productivity. Thirdly, we merged the size structure approach with taxonomic predictors characterising geographical patterns of species richness, community composition and dominance of thermal guilds (Magnuson *et al.*, 1979). All analyses were performed in a hierarchical way by comparing the patterns and dominant predictors between the total dataset and subsets defined by either smaller geographical extent or dominance of certain functional classifications of fishes. By splitting the total dataset into subsets, we aimed to elucidate responses of size structures at smaller spatial scales by reducing the contribution from the overarching geographical gradient. In this way, we characterise the major patterns in size structures

of entire lake fish communities at a continental spatial scale and identify the primary drivers behind these large-scale patterns.

Methods

Fish data

In total, 356 lakes (317 natural lakes and 39 reservoirs) located in eight European countries (Fig. 1a) and representing nine ecoregions were sampled once between 1993 and 2010 using stratified random sampling with benthic multi-mesh gillnets (type NORDIC: length 30 m; height 1.5 m; 12 panels of 2.5 m each with bar mesh sizes between 5 and 55 mm knot to knot). Samplings were undertaken during late summer and early autumn with a pre-defined number of nets per lake set randomly in each depth stratum depending on lake area and depth (Appelberg *et al.*, 1995). Captured fish were identified to species level, measured (nearest cm total length) and weighed (nearest g fresh mass). Missing size measures were back-calculated using latitudinal-specific (5° latitude) and species-specific mass-length and length-mass relationships calculated from fish with complete information on individual length and fresh mass (Emmrich, unpublished). Due to the well established biased sampling efficiency of multi-mesh gillnets against very small fish (Prchalová *et al.*, 2009), individuals < 8 cm were omitted from the analysis to reduce the ‘noise’ of varying seasonal recruitment success and differences in sampling time. To account for possible effects of differences in taxonomic and functional fish community composition on size structure, all fish were classified according to their thermal preferences into cold-, cool and warmwater fish following Magnuson *et al.* (1979) (further details in Appendix S1 in Supporting Information).

Predictor variables

Five abiotic variables known to influence fish community size structure were selected. Because lake temperature was not available for most lakes, air temperature was used instead as it has been shown to be a reliable surrogate parameter for epilimnetic lake temperature (Livingstone & Lotter, 1998) and it has recently been used to study geographical patterns in European freshwater fishes (Brucet *et*

al., 2013; Edeline *et al.*, 2013). Temperature metrics of the lake's location were obtained from a climate model with a spatial resolution of 10' latitude/longitude and taking into account elevation differences (New *et al.*, 2002). This specific model has already been successfully used to study air temperature effects on lake fish communities (Argillier *et al.*, 2013; Brucet *et al.*, 2013). We selected average air temperature (averaged across monthly mean temperatures, range: -3.7-14.0 °C) and maximum monthly mean temperature (range: 7.4-23.1 °C) for use in our analyses. The temperature amplitude (difference between mean temperature in July and January) was used as a proxy for seasonality (range: 9.9-28.9 °C). Lake morphometry was characterised by area (range: 0.02-113 km²) and maximum depth (range: 1-190 m). Annual mean total phosphorus concentration (TP, range: 1-561 µg L⁻¹) was selected as a measure of lake productivity. TP was sampled seasonally (i.e., minimum four samples per year) usually in the year of fish sampling, although in the case of some Swedish lakes such measurements were taken up to three years before the fish sampling. For more details on the abiotic variables, see Appendix S2 in the Supporting Information.

Among the biotic variables of fish community composition, we selected local species numbers (richness, range: 1-15) for particular analysis. In addition, we characterised the relative dominance structure and species composition of fish communities by conducting a principle component analysis (PCA) derived with a Chord-transformed site-species matrix based on numerical abundance data. This unconstrained ordination allows the robust application of Euclidean distance-based PCA to zero-inflated datasets (Legendre & Gallagher, 2001) which are typical when many species are replaced across broad gradients of abiotic lake characteristics and geographical position. The Chord distance downweights the importance of rare species (Legendre & Gallagher, 2001), which is important for our data as the highly abundant species were also the ones with the strongest influence on the calculation of the size metrics. To further reduce the number of zeros in the site-species matrix, rare species caught in less than five lakes were removed from the analyses (details are found in Appendix S3 in Supporting Information). The site (lake) scores along the first two PCA axes were used as taxonomic descriptors of fish communities.

197 Size metrics

198 To cover different aspects of the size structure of lake fish communities, we selected three non-
199 taxonomic size metrics. We calculated average size (AS) as the geometric mean length (cm) of all
200 fishes caught per lake. Furthermore, we calculated individual size distributions (ISD) (*sensu* size
201 spectra, White *et al.*, 2007) which represent a frequency distribution of individual body sizes across
202 size classes irrespective of taxonomy (White *et al.*, 2007). ISDs may be characterised by
203 monotonically decreasing, unimodal or multimodal distributions (White *et al.*, 2007). Size groups
204 were based on \log_2 class intervals of fresh mass (g). Due to the omission of fish < 8 cm, the smallest
205 individuals of 1-8 g were summed in the first fresh mass class, and all fish > 4096 g were summed in
206 the last (11th) fresh mass class. Because ISDs were based on log-size classes, assumptions of
207 multiplicative log-normal error structures were better supported than additive normal error
208 structures. Consequently, log-linear ordinary least square (OLS) regressions were calculated (Xiao *et*
209 *al.*, 2011) by plotting the midpoint of each \log_2 fresh mass class against the \log_2 -transformed number
210 of individuals per size class. To improve between-lake comparability, regression slopes from the log-
211 linear models were initially calculated for all lakes, independently of whether nonlinear models
212 would have fitted better. To account for deviations from log-linear models, the determination
213 coefficient (R^2) of the regression lines was additionally considered in the subsequent analyses. In the
214 case of non-significant log-linear models, we explored whether size distributions were alternatively
215 better described by unimodal or multimodal models.

216 Data analyses

217 Continental patterns (356 lakes) in the size metrics were modelled along gradients of abiotic lake
218 characteristics and differences in fish community composition using boosted regression tree (BRT)
219 analysis. BRT analysis is a predictive technique which combines boosting algorithms with regression
220 trees and considers nonlinear response-predictor relationships as well as interactions between
221 predictors (Friedman, 2002; De'ath, 2007). BRTs were applied to estimate the contribution of each

predictor to the total variation in each of the three size metrics. Interactions between predictors were automatically included in the models via tree complexity. A Gaussian error distribution was appropriate for the size metrics. The predictive performance of the BRT models was evaluated using ten-fold cross-validation. Ten mutually exclusive data subsets were randomly selected and model predictions were compared to the withheld proportion of the data. The optimal number of trees which produced the lowest prediction error without model overfitting was identified testing tree complexities of one and two (this accounts for no or one-way interactions), learning rates of 0.01, 0.005 and 0.001 and bag fractions of 0.5 and 0.75. The bag fraction determines the proportion of data selected during each iteration process and introduces stochasticity which improves model accuracy and reduces model overfitting (Friedman, 2002). The minimum limit to fit models was set to 1000 trees to reduce the contribution from single trees to the final model (Elith *et al.*, 2008). BRT analysis does not generate P-values, but the relative influence was used to estimate the significance of each predictor influence (measuring how often a predictor variable is selected and testing the strength of its influence on model improvement). Partial dependence plots were used to visualize the effects of individual predictors on the response variables (size metrics) after accounting for the average effects of all other predictors (Friedman, 2002).

In addition to the continental BRT analysis, patterns in AS were separately analysed for lake subsets. To account for possible spatial non-independence in our lake dataset, we tested whether similar abiotic variables account for variation in fish community size structure across smaller geographical units with more consistent climates and a more homogeneous distribution of lakes. We selected five ecoregions (after Illies, 1978) with a sufficiently large number of lakes for analysis: Borealic Uplands/Tundra (n = 40 lakes), Fenno-Scandian Shield (n = 48), Central Plains (n = 179), Western Highlands (n = 27) and Western Plains (n = 38) (Fig. 2b). The lakes not classified into lake subsets were located in the ecoregions Alps (n = 6), Baltic Province (n = 8), Great Britain (n = 5) and Italy/Corsica/Malta (n = 5). Additionally, we classified the lakes into three groups according to the dominant thermal guild in their fish community composition based on the PCA results (cold-, cool- or

warmwater fish, cf. Results). A classification of our dataset into three clusters was statistically verified using the Caliński criterion (Caliński & Harabasz, 1974) which determines a finite set of clusters to best describe the dataset according to lake fish community similarity by maximising the intra-cluster similarity and minimising the inter-cluster similarity. K-means partitioning was then used to assign the lakes to one of the three clusters representing a dominant thermal fish guild. Differences in AS in the lake subsets (ecoregions and thermal guilds) were tested using Welch's analysis of variance (ANOVA) followed by Dunnett-Tukey-Kramer test for pairwise multiple comparisons adjusted for unequal variances and sample sizes. Furthermore, general linear models (LMs) were calculated to model trends in AS in the lake subsets along abiotic gradients and thermal fish communities (Table 2). Model selection (only main effects were included in the initial full models) was based on Akaike's Information Criterion (AIC) using a backwards variable selection procedure. A Gaussian link function was appropriate for all models. Conditional plots were selected to show the effect of significant abiotic variables on the response (AS), holding all other predictor variables constant at their median values. Statistical analyses were performed in R (R Development Core Team 2012) version 2.15 using the packages *vegan* (Oksanen *et al.*, 2012) and *gbm* (Ridgeway, 2012) plus codes provided by Elith *et al.* (2008) and Xiao *et al.* (2011).

Results

Fish community composition

A total of 54 fish species was caught by the benthic multi-mesh gillnets in 356 European lakes (Appendices S1 & S3). Thirty species were caught in more than four lakes. Perch (*Perca fluviatilis* L.) and roach [*Rutilus rutilus* (L.)] dominated the overall catch (Appendix S1). The first two PCA axes of fish community ordination explained 64.1% of the variability. Axis 1 (40.2%) discriminated perch-dominated lakes (Pearson's $r = 0.76$) from roach-dominated lakes ($r = -0.63$). Roach-dominated lakes were additionally characterised by relatively high abundances of bream [*Abramis brama* (L.), $r = -0.11$] and white bream [*Blicca bjoerkna* (L.), $r = -0.10$]. Therefore, all negative lake scores along the

first PCA axis represent fish communities dominated by eurythermic warmwater cyprinids, whereas the positive lake scores along this axis represent fish communities dominated by eurythermic coolwater perch. The second PCA axis (23.9%) discriminated salmonid-dominated lakes characterised by stenothermic coldwater species such as brown trout (*Salmo trutta* L., $r = -0.70$) and Arctic charr (*Salvelinus* spp., $r = -0.53$) from lakes dominated by eurythermic roach ($r = 0.35$) and perch ($r = 0.29$). Other species were less important in the ordination (all $r < 0.1$, Appendix S1). According to PCA and K-means partitioning, we distinguished three fish community types: coldwater fish (7 species) were numerically dominant in 5.6% of the lakes, coolwater fish (5 species) were dominant in 47.5% of the lakes, and warmwater fish (18 species) were dominant in 46.9% of the lakes.

Continental dataset (356 lakes)

Average size (AS) of fish across all lakes was 13.9 ± 2.7 cm (SD). Fish catches from 332 lakes could be characterised by significantly linear ($P < 0.05$) ISDs, which indicates a monotonically decreasing size-frequency pattern (Fig. 2a). The slopes of the OLS regression lines of these lakes averaged -0.74 (95% CI = -0.75 to -0.72 ; range -1.24 to -0.02). Mean R^2 of these regression models was 0.76 ± 0.21 (SD). Size structures of fish communities for which linear ISDs were non-significant were better fitted by quadratic models with either unimodal ($n = 17$, Fig. 2b) or multimodal ISDs, typically shaped by two peaks ($n = 7$, Fig. 2c).

Final BRT models were run with a learning rate of 0.001 (AS) and 0.005 (slope and R^2 of ISD), a bag fraction of 0.75 and a tree complexity of two (i.e. one-way interactions between the predictors were included). Optimal tree number ranged between 1650 and 3150. Percentages of deviance explained by the models were 30.2% (AS), 46.0% (slope ISD) and 42.9% (R^2). The relative influence (RI) of the predictors differed among the size metrics (Table 1). The functions fitted to the BRT models were highly variable and revealed linear and curvilinear patterns (Fig. 3). Scores to PCA axis 2 (separation between cold- and cool-/warmwater dominated fish communities) and maximum temperature had the highest RI in the BRT models ($> 20\%$, Table 1). The relative influence of lake productivity (TP) and

PCA axis 1 (separation between cool- and warmwater dominated fish communities) was consistently weak across the size metrics ($RI \leq 5.5\%$, Table 1).

The largest AS was observed in fish communities inhabiting relatively cold areas (lowest maximum temperature). These lakes with large fish were also deep, and the fish communities were dominated by few species, mainly stenothermic coldwater salmonids (brown trout, Arctic charr; Fig. 3a, Appendix S 4a). The smallest AS was observed in warm and shallow, mainly lowland lakes with more diverse fish communities dominated by eurythermic coolwater and warmwater species (mainly perch and roach; Fig. 3a, Appendix S 4a). The slope of the ISDs increased (i.e. became less negative) with decreasing maximum temperature. Smaller lakes dominated by a few coldwater salmonid species had the flattest slopes (Fig. 3b, Appendix S 4b). The lowest R^2 indicating nonlinear ISDs were observed in salmonid-dominated lakes with low species richness which are located in areas with low temperature and less pronounced seasonality (amplitude temperature, Fig. 3c, Appendix S 4c).

Lake subsets defined by geography and functional fish community guilds

The AS differed significantly across ecoregions (Welch ANOVA: $F_{4, 81.3} = 18.9$; $P < 0.001$). Lake fish communities of colder (high latitude, high elevation) ecoregions (Borealic Uplands/Tundra, Fennoscandian Shield, Western Highlands) were characterised by significantly ($P < 0.001$) larger AS (16.9, 14.7 and 15.3 cm, respectively) than the warmer European lowland ecoregions Central Plains (AS = 13.0 cm) and Western Plains (AS = 13.2 cm). However, AS responded similarly to abiotic gradients related to the thermal environment of the fish (temperature, lake depth) within all ecoregions. Fish size increased significantly with decreasing temperature and increasing lake depth (Table 2, Fig. 4). Size patterns of fish communities in the Western Highlands did not respond significantly to any abiotic variable, probably due to the relatively small sample size ($n = 27$ lakes). However, trends of change in average size were comparable to the patterns observed in the other ecoregions, i.e., an increase in average size with decreasing temperature (results not shown). The predictive power of the GLM's indicated an increasing importance of temperature variables in explaining the variability in

the size structure of fish communities in northern (cold) ecoregions (Table 2). Compared with the continental BRT analysis (356 lakes), lake productivity did not predict variability in the size structure of fish communities at the ecoregion scale.

Average size also differed significantly between fish communities dominated by the three thermal guilds (Welch ANOVA: $F_{2, 48.9} = 24.4$; $P < 0.001$). Fish size was significantly (all pairwise comparisons: $P < 0.001$) larger in species-poor communities dominated by coldwater fishes (18.8 cm) than the AS of the more diverse coolwater (14.2 cm) and warmwater dominated fish communities (13.0 cm). Furthermore, AS of all thermal fish guilds significantly increased with decreasing temperature (Table 2, Fig. 5). Variability in size structure explained by temperature was highest for coldwater fish communities (Table 2).

Discussion

Our results demonstrate a dominant effect of temperature on the size structure of entire lake fish communities. Average and maximum air temperatures were the strongest predictors of the average size and slope of non-taxonomic individual size distributions. These results were consistently found for both the continental dataset (356 lakes) and the lake subsets defined according to ecoregion or functional dominance structure of fish communities with respect to thermal guilds. Temperature modifies the size of fishes within the thermal guilds and the corresponding ecoregions. Cold-, cool- and warmwater fishes become bigger with decreasing temperature, a pattern that is consistent with the temperature-size rule and which has been observed for the majority of ectothermic species (Atkinson, 1994).

It is well known that environmental temperature modifies the species richness and taxonomic composition of lake fish communities (Irz *et al.* 2007; Jeppesen *et al.*, 2012). However, our results demonstrate that in addition there are systematic changes in fish community composition across temperature gradients in correspondence with the dominant thermal fish guilds which fundamentally alter size structures. The richer cool- and warmwater fish communities at warmer

temperatures were dominated by small-sized species and characterised by linear individual size distributions. In contrast, the less rich lake fish communities dominated by coldwater species were characterised by high proportions of large fish (brown trout, Arctic charr) and unimodal or bimodal individual size distributions. The brown trout and Arctic charr populations were characterised by similar size structures (two sample Kolmogorov Smirnov Test: $D = 0.23$, $P = 0.13$) and were dominated by larger-sized fish and lower abundances of small-sized juvenile individuals (cf. L'Abée-Lund *et al.*, 1992). Generally, salmonids are species that mature late, have high fecundity and large sizes due to an equilibrium life history strategy (Winemiller & Rose, 1992). In contrast, warm- and coolwater cyprinids and percids (mainly perch) are characterised by early maturity, lower fecundity and smaller size (Vila-Gispert & Moreno-Amich, 2002) following a periodic life history strategy which allows adult fish to survive suboptimal environmental conditions such as reduced food availability during winter (Winemiller & Rose, 1992). Accordingly, the major change in average size and individual size distributions of lake fish communities from coldwater to cool- and warmwater communities is attributable to a significant switch in life history from the equilibrium to the period type.

More than 90% of the lakes, primarily located in the European lowlands (Central Plains, Western Plains, Fenno-Scandian Shield), were dominated by small-sized cool- and warmwater fishes such as perch and/or roach. The smaller average size as compared to the coldwater fish communities can be due to either the occurrence of many small-sized species or the high abundances of juvenile fishes (> 8 cm here) (Daufresne *et al.*, 2009). Small-sized species typically inhabit the warmer, shallow near-shore lake zones and may be underestimated in benthic multi-mesh gillnet catches as applied in our study (Diekmann *et al.*, 2005). However, local richness was higher in warm- and coolwater communities than in the lakes dominated by coldwater species (cf. Brucet *et al.*, 2013) and many warmwater species are small-sized cyprinids. We suggest that the dominance of small fish sizes in these lakes is caused by high juvenile abundances due to the different life-history strategies of warm- and coolwater fishes compared to coldwater fishes. Gonza'lez-Bergonzoni *et al.* (2012) have recently

demonstrated a gradient of omnivory in freshwater fishes along a temperature gradient indicating high omnivory (low predator abundances) in warmwater fish communities which further explains the dominance of juvenile small-sized fishes in warm- and coolwater fish communities. However, because we did not age the fish, a possible effect of temperature on the age structure of populations could not be verified. We can also not exclude the possibility that abundances of small fish in salmonid-dominated lakes were underestimated where lakes were connected to rivers. Juvenile brown trout and Arctic charr regularly occupy lotic river habitats before they return as larger-sized adults to the lake (Klemetsen *et al.*, 2003).

According to earlier studies, the dominant fish species of lakes in the European lowlands are the coolwater species perch and the warmwater species roach (Mehner *et al.*, 2005; 2007). This general pattern was well depicted by the first PCA axis on fish community composition, which discriminated perch-dominated from roach-dominated lakes. The switch in the dominance of the thermal guild within the ecoregions is here caused by lake morphometry, in particular lake depth. Deep and stratified lakes are inhabited by coolwater species, whereas the warmwater cyprinids dominate in shallow and polymictic lakes (Mehner *et al.*, 2005). However, the change between roach and perch dominance did not correspond to strong variability of any size metric. Both the average size of perch and roach populations in the dataset (mean total length perch: 12.8 cm; roach: 13.6 cm) and their size distributions (two sample Kolmogorov-Smirnov test: $D = 0.15$, $P = 0.58$) were very similar. The small average size and the steep ISD slopes indicated that small fishes dominated these communities.

In addition to the taxonomy-related changes in size structure across the temperature gradient, we observed an increase in fish size with decreasing environmental temperature despite relatively homogeneous fish community compositions. This gives further evidence for intraspecific size clines of fish populations (cf. Blanck & Lamouroux, 2007). Temperature effects on body size have been shown for many aquatic organisms including freshwater fish (Daufresne *et al.*, 2009; Edeline *et al.*, 2013). An increase in the relative proportion of large fish within populations and a larger average fish

community size (AS) were observed with decreasing temperature and less seasonality. This pattern was also consistently found in our study within ecoregions and within groups of lakes dominated by the different thermal guilds, and it hence supports the temperature-size rule (Atkinson, 1994) which describes the phenotypically plastic response of body size of ectothermic species to their environmental temperature. Individuals in colder environments mature as larger adults and live longer than individuals in warm environments (Blanck & Lamouroux, 2007). In turn, fish mortality rates are higher at high temperatures (Pauly, 1980), resulting in on average smaller fishes. Although environmental temperature was the main predictor accounting for differences in fish community size structure in our study, total variation explained by the statistical models was always < 50%. This indicates that other predictors not included here might also be important. Edeline *et al.* (2013) recently showed that biotic interactions such as competition and predation had a negative effect on the body size of river fish communities, particularly at higher temperatures. Such a pattern is also indirectly supported by our data on lake fish communities. Our general linear models indicated increasing importance (i.e., more explained variability) of abiotic descriptors for size structure towards colder environments. In northern ecoregions such as the Borealic Uplands/Tundra, the temperature variables explained almost twice as much the variability of the fish community size structure as they did for lake fish communities found in warm, southern ecoregions such as the Western Plains (Table 2). This trend was also evident in the dominant thermal fish guilds. Variation in the size structure of coldwater-dominated fish assemblages was strongly explained by temperature variables, whereas the amount of variability explained by temperature was low in case of warmwater fish communities. This statistical pattern supports the results of Edeline *et al.* (2013) that abiotic influences on fish community size structure are weaker at higher temperatures.

Although our study lakes covered a large gradient in productivity from ultra-oligotrophic to hypertrophic, lake productivity did not significantly explain the variability in the size structure of lake fish communities. This finding seems to contrast with results from earlier regional studies in which correspondence between the size structure of multi-species communities along gradients of lake

productivity has been documented (Jeppesen *et al.*, 2000; Emmrich *et al.*, 2011). However, lake productivity and lake temperature both co-vary with lake depth. Shallow (warm) lakes are typically more nutrient-rich than colder, stratified lakes (Nöges, 2009). Fish densities increase in number and biomass with increasing lake productivity, causing a reduction in average size due to density-dependent food limitation (Jeppesen *et al.*, 2010, Brucet *et al.*, 2013). This effect becomes obvious only if fish communities in lakes with comparable depth and at comparable climatic conditions are compared along a productivity gradient (cf. Brucet *et al.*, 2013). At any broader scales of comparison, effects of variation in trophic status are covered by temperature variations which affect size structure in the same direction. Therefore, the subtle response of fish size to local predictors in regional studies is relativised when shifts in lake fish community size structure are considered across large geographical scales.

Conclusions

Temperature modifies the size structure of lake fishes via two processes. Local temperature determines which thermal guild dominates in the fish community. Indirectly, these changes in functional dominance structure along a temperature gradient also induce taxonomy-related changes in size structure from a few large species in the coldwater guild towards many small species in the cool- and warmwater guilds. Clines in the size structure of entire lake fish communities are consistent with the temperature-size rule which implies smaller size with increasing temperature for the majority of ectothermic species. The pattern holds true for large and smaller (i.e., ecoregions) geographical scales as well as for all thermal fish guilds including cold-, cool- and warmwater fish communities. Our results indicate an increasing importance of temperature for the size structure of lake fish communities in cold environments.

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607

608 Additional Supporting Information may be found in the online version of this article
609
610 Appendix S1 List of fish species, their thermal guild, abundance and frequency of occurrence
611 Appendix S2. Predictor variables of the 356 European lakes.
612 Appendix S 3. List of fish species occurring in less than four of the 356 lakes
613 Appendix S 4: Plots showing the two strongest pair-wise interactions in the boosted regression tree
614 model for the size metrics
615 Appendix S 5: Geographical positions of the 356 lakes, their species richness and size characteristics
616 of their fish communities
617

618 Table 1. Relative influence (%) of the abiotic and biotic predictor variables in the boosted regression
619 tree models on average size (AS) and slope and determination coefficient (R^2) of the individual size
620 distributions from 356 European lakes.

Predictor	AS	Slope	R^2
T_{\max}	28.0	20.3	20.6
T_{mean}	4.8	7.2	5.6
T_{amp}	4.7	5.9	13.3
Area	4.3	16.1	11.3
Maximum depth	10.1	8.7	4.6
Total phosphorus	1.2	3.9	2.3
Species number	8.1	14.5	10.8
PCA axis 1	2.9	1.9	5.4
PCA axis 2	35.9	21.5	26.2

621 Axis 1: Discrimination between cool- and warmwater dominated fish communities

622 Axis 2: Discrimination between cold- and cool-/warmwater dominated fish communities

623

624 Table 2. Significant abiotic variables (air temperature and lake depth) affecting average size of lake
 625 fish communities. Given are the number of lakes(n) included in the general linear models, the
 626 Akaike's Information Criterion (AIC), the t-statistics (t), significance (P) and variability explained by
 627 the model (%).

Ecoregion	n	AIC	Significant variables	t	P	%
Boreal Uplands/Tundra	40	210.32	Ave temp	-4.19	<0.001	31.61
Fenno-Scandian Shield	48	198.60	Max depth	2.23	0.03	27.02
			Max temp	-3.69	<0.001	
Central Plains	179	659.47	Max depth	2.38	0.02	18.50
			Max temp	-3.63	<0.001	
Western Plains	36	160.16	Ave temp	-2.42	0.02	17.80
Western Highlands	27	---	---	---	---	---
Thermal fish guild						
Coldwater	20	122.00	Ave temp	-2.12	0.04	27.80
Coolwater	169	717.96	Max temp	-3.42	<0.001	19.60
Warmwater	167	704.60	Ave temp	-2.62	0.009	17.80
			Amp temp	-3.08	0.002	

628

Figure 1. (a): Geographical distribution of the 356 lakes across eight European countries (grey-coloured) where fish communities were sampled with benthic multi-mesh gillnets. Letters indicate position of three lakes for which individual size distributions are shown in Figure 2. (b): Ecoregions, defined according to Illies (1978), with five lake subsets analysed separately: Borealic Uplands/Tundra (1), Fenno-Scandian Shield (2), Central Plains (3), Western Highlands (4), Western Plains (5).

Figure 2. Examples of individual size distributions (\log_2 midpoints of fresh mass in g vs. \log_2 numbers) of fish communities from three European lakes (cf. Figure 1) showing monotonically decreasing (a), unimodal (b) and multimodal (c) distributions. The distribution shown in (a) is characteristic for cool- and warmwater dominated fish communities while those shown in (b) and (c) are characteristic for communities dominated by cool- and coldwater fishes.

Figure 3. Partial dependence plots showing the three most influential predictor variables according to the boosted regression tree analysis on the fitted function (centred around the mean) of average size (a) and slope (b) and R^2 (c) of the individual size distributions (ISD). Rug plots on the top horizontal axes indicate the distributions of the predictor variables, in deciles. Percentage values indicate the relative importance of the predictor variables in the boosted regression tree analyses. Axis 2 PCA: Discrimination between cold- and cool-/warmwater dominated fish communities.

Figure 4. Changes in average size of European lake fish communities in five ecoregions along air temperature and lake depth gradients. Only significant variables in the general linear models are shown. Plots show the partial residuals (points), prediction line and the 95% confidence interval (grey area). Rug plots indicate the distribution of the response and explanatory variables.

Figure 5. Trends in average size of European lake fish communities with numerical dominance of cold- (a), cool- (b) and warmwater fish (c). Only significant variables in the general linear models are

shown. Plots show the partial residuals (points), prediction line and the 95% confidence interval (grey area). Rug plots indicate the distribution of average fish community size and air temperature metrics.

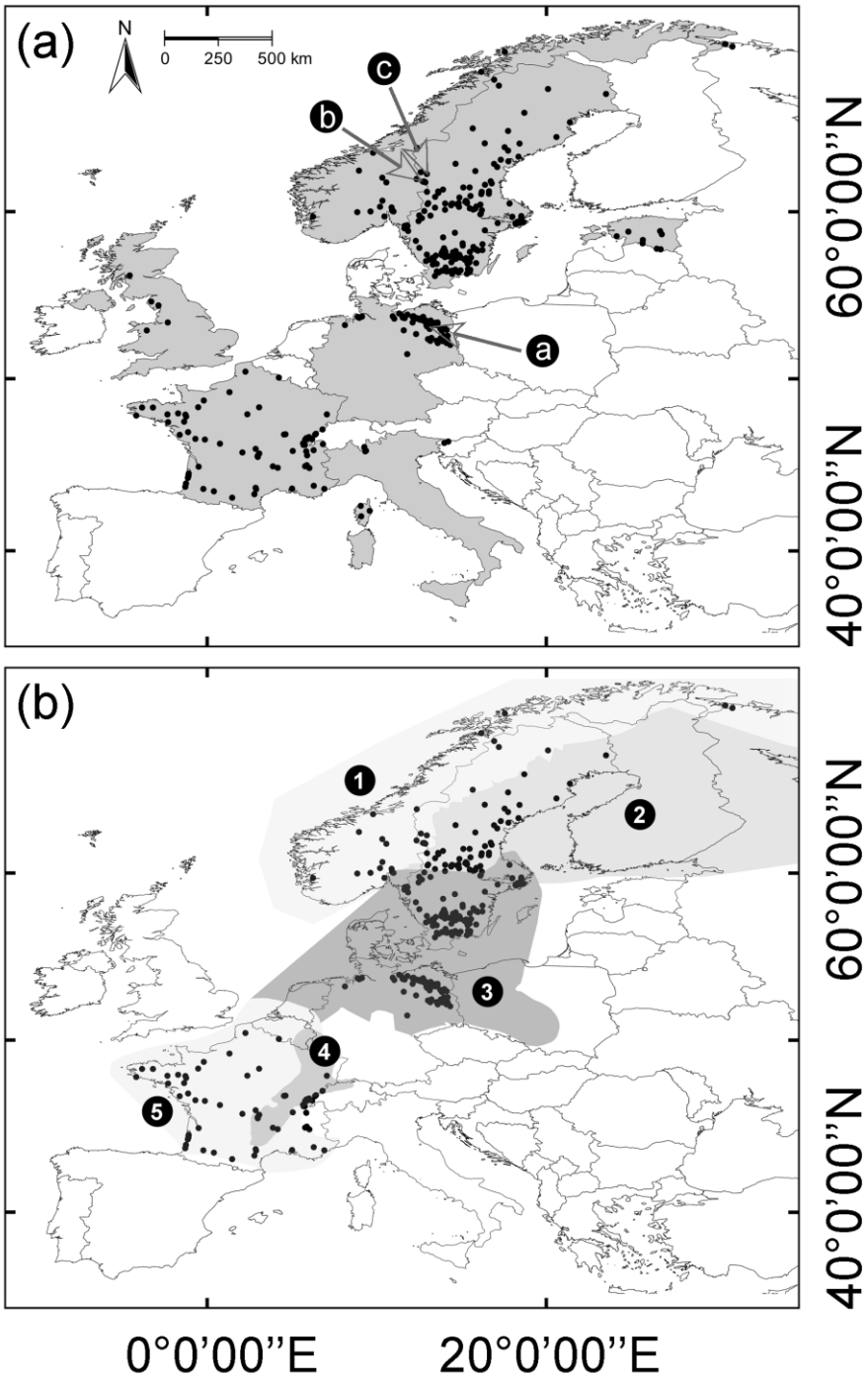
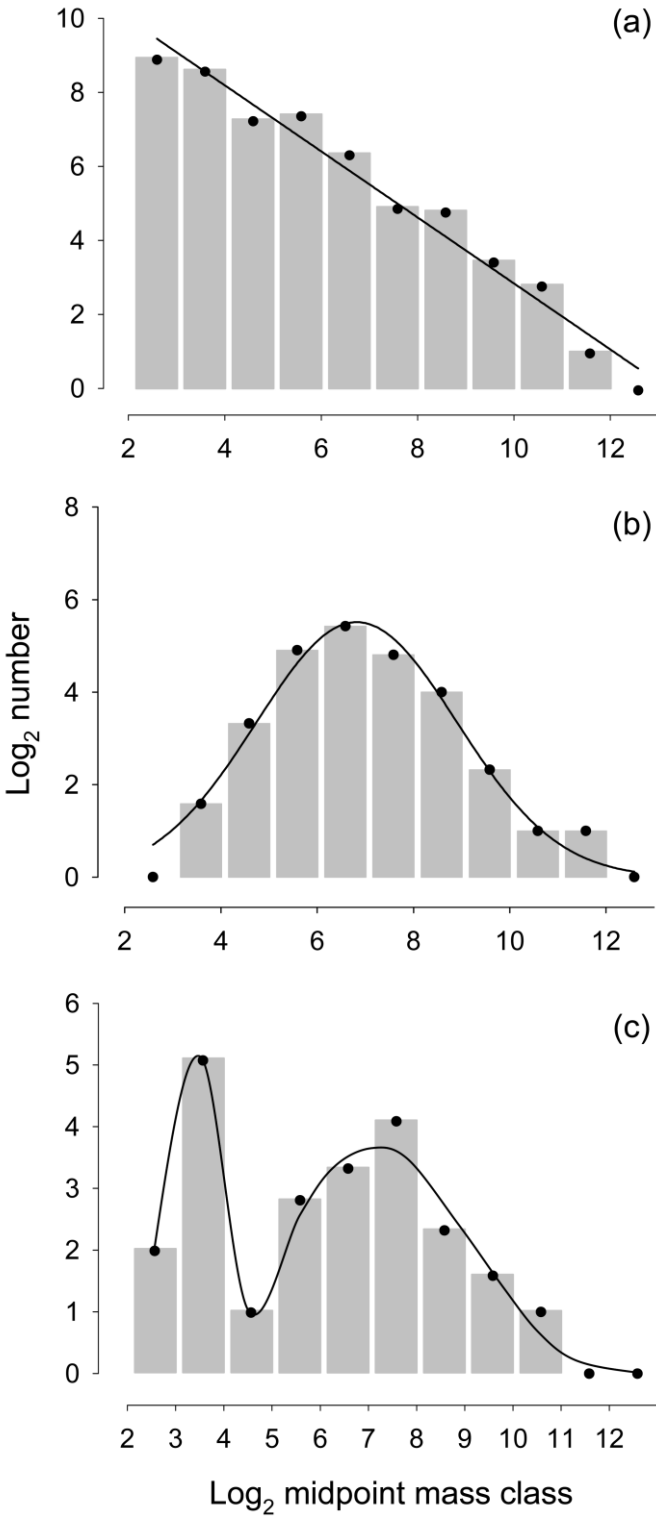


Figure 1

657



658

659 Figure 2

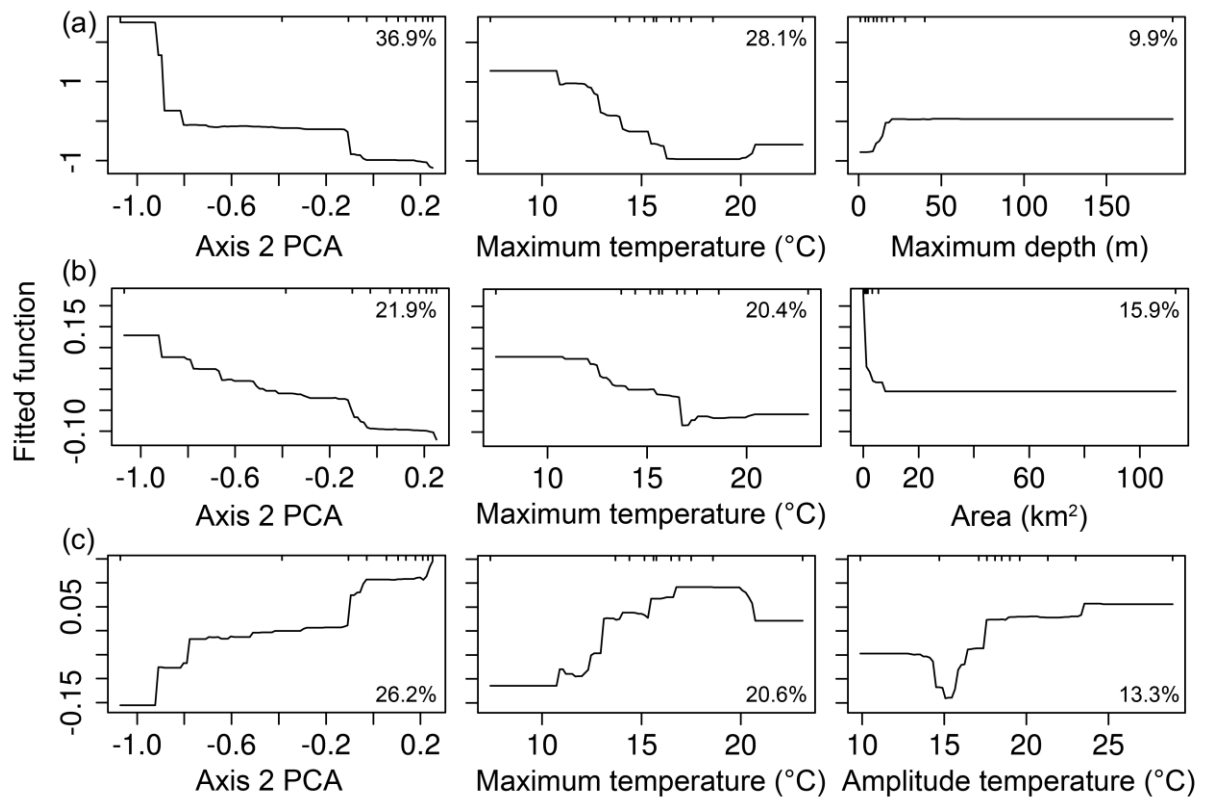
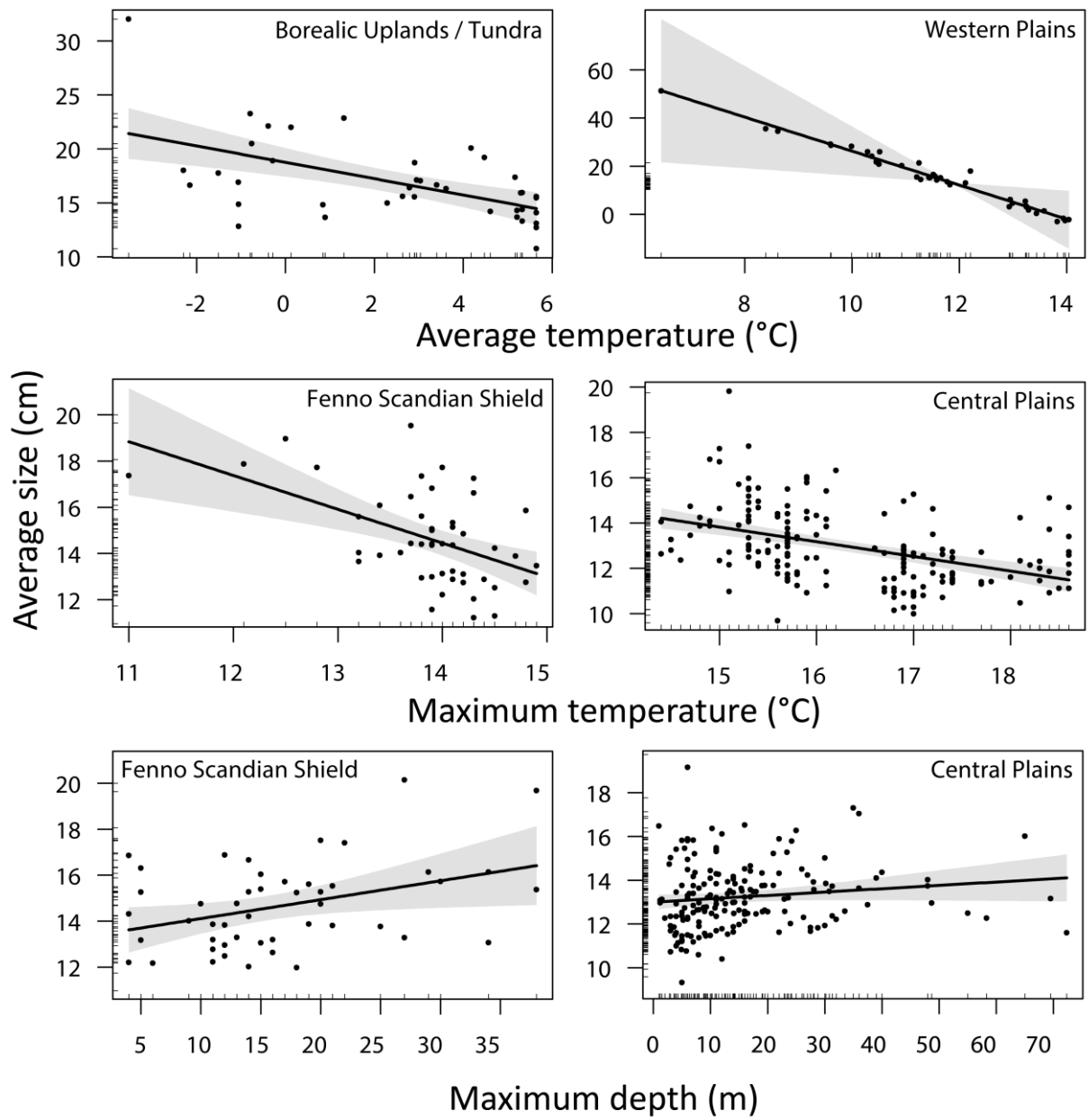


Figure 3



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663 Figure 4

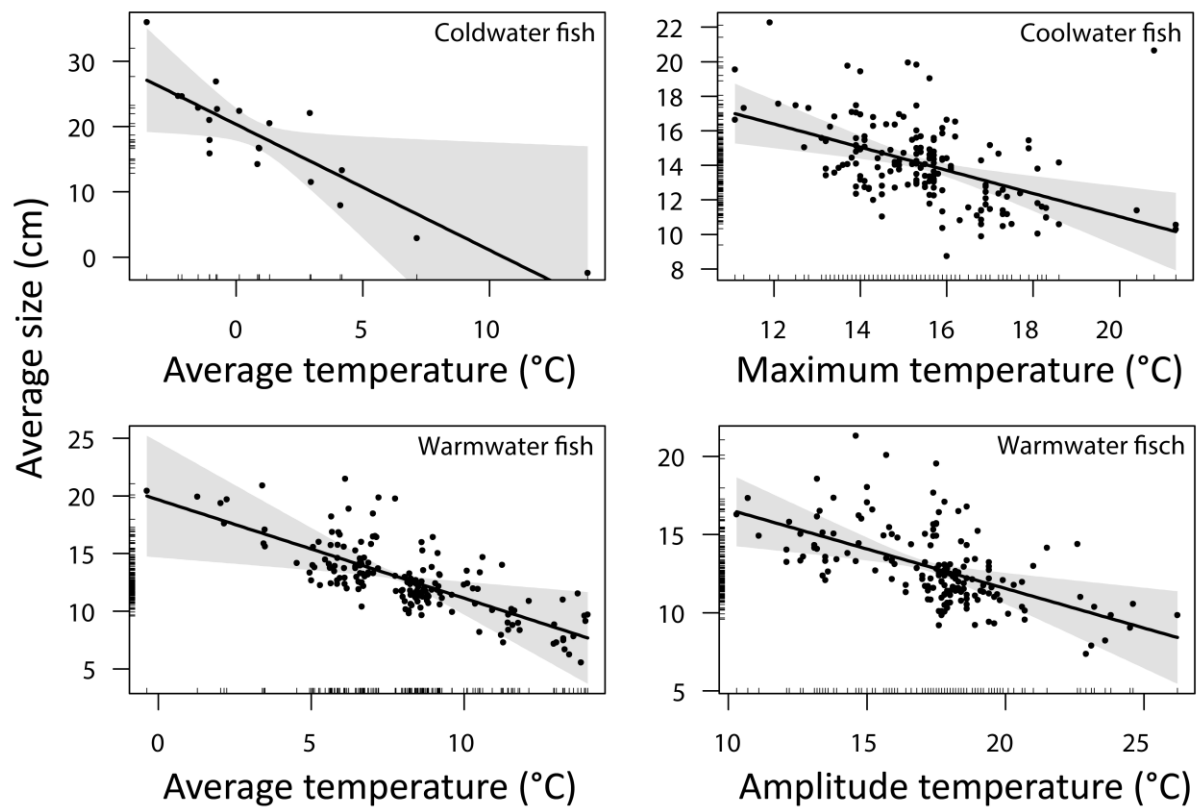


Figure 5