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3   Article title: Geographical patterns in the size structure of European lake fish communities along

4   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.

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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.

45   **Aim** To document geographical patterns of variation in the size structure of European lake fish

46   communities along abiotic gradients and differences in fish community composition.

47   **Location** 356 European lakes

48   **Methods** Variation in the size structure of the fish communities was explored on a continental scale

49   in relation to the location, morphometry, productivity and fish community composition of 356 lakes.

50   Separate analyses were also conducted for lake subsets located in five ecoregions (Borealic

51   Uplands/Tundra, Fenno-Scandian Shield, Central Plains, Western Plains, Western Highlands) and for

52   lakes with different functional community classifications (cold-, cool-, warmwater fish communities).

53   **Results**

54   Geographical patterns of variation in the size structure of European lake fish communities could be

55   clearly discerned along a temperature gradient for both the continental dataset (356 lakes) and the

56   data subsets of smaller geographical dimension (ecoregions). We found systematic changes in fish

57   community size structure across temperature gradients in correspondence with the dominant

58   thermal fish guild. The majority of the lakes, mainly located in the warmer European lowlands, were

59   dominated by eurythermic cool- and warmwater fish communities with small-sized individuals

60   characterised by linear individual size distributions. Lakes located in cold regions and dominated by

61   stenothermic coldwater salmonids with larger-sized individuals were characterised by unimodal or

62   bimodal size distributions. The average size of cold-, cool- and warmwater fish communities changed

63   uniformly along a temperature gradient.

64   **Main conclusion**

65   Patterns of variation in the size structure of European lake fish communities are consistent with the

66   temperature-size rule. Temperature modifies fish community size structure uniformly within the

67   thermal fish guilds and different ecoregions. Furthermore, our results indicate an increasing

68   predictive power of temperature to explain variability in the size structure when moving from warm

69   to cold geographical regions.

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

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95 relationships and energy fluxes in food webs (Emmerson & Raffaelli, 2004; Reuman & Cohen, 2005;

96 White *et al.,* 2007). Analysing geographical patterns and variation of size structure in aquatic

97 communities is therefore important for the identification and understanding of fundamental

98 ecological and biogeographical processes. Furthermore, analysis of size structure may help to identify

99 and predict the response of species, communities and ecosystems functioning relative to large-scale

100 anthropogenic disturbances and environmental change (Petchey & Belgrano, 2010; Gardner *et al.,*

101 2011; Brose *et al.*, 2012).

102 Earlier studies on the size structure of freshwater fish communities have primarily used local

103 presence-absence data combined with generalised location-independent data on maximum species-

104 specific size from the scientific literature to analyse changes in species richness across size classes

105 over large geographical scales (Lindsey, 1966; Knouft, 2004; Griffiths, 2012). Other studies have

106 focused on selected species and have demonstrated variations in the size structure of fish

107 populations across geographical gradients (Heibo *et al.*, 2005; Blanck & Lamouroux, 2007). These

108 studies have shown that fish communities in warm environments typically consist of more small-

109 sized species (Knouft, 2004; Griffiths, 2012), and individuals of the same species in cold environments

110 are larger than conspecifics in warm environments (Blanck & Lamouroux, 2007; Jeppesen *et al.,*

111 2010).

112 Besides temperature, further evidence of abiotic and biotic predictors of fish community size

113 structure has been obtained from several regional studies showing that differences in lake

114 morphometry, lake productivity and functional fish community composition contribute to size

115 differences (Jeppesen *et al.,* 2000; Jeppesen *et al.* 2010, Emmrich *et al.,* 2011). However, these

116 studies did not cover large-scale geographical gradients (but see Holmgren & Appelberg, 2000 for a

117 large-scale Swedish study) where different factors are likely to affect fish community size structure

118 (Borcard *et al.*, 2004). In addition to changes in the abiotic environment along such broad

119 geographical gradients, shifts in the taxonomic composition of freshwater fish communities (Griffiths,

120   2006; Reyjol *et al*., 2007) may contribute to variation in their size structure, a topic that has only

121   been marginally explored. Accordingly, it remains unresolved whether the great variability in the size

122   structure of lake fish communities over large geographical gradients reflects the taxonomy-

123   independent effect of simple temperature-size rules or whether it basically reflects fundamental

124   shifts in taxonomic composition. To distinguish between these processes, the ideal approach would

125   be based on empirically obtained specific data on fish communities from a large number of dispersed

126   lakes instead of being based on generalised location-independent average species-specific size

127   measures obtained from the scientific literature. However, such large and detailed datasets from

128   lakes have previously not been available.

129   In this study, we moved beyond previous approaches in three directions. Firstly, we used a very

130   large-scale dataset on fish catches from 356 lakes located in eight European countries covering a

131   latitudinal gradient of 28.2°, a longitudinal gradient of 35.4° and an elevation gradient of 1201 m.

132   Fish communities were sampled with standardised multi-mesh gillnets and evaluated with respect to

133   species, individual body length and individual mass. Secondly, we analysed the effects of abiotic

134   predictors previously identified to influence the size structure of lake fish communities at small

135   regional scales within the broad geographical gradients covered by our dataset. Specifically, we

136   compared the slopes of non-taxonomic individual size distributions (ISD) (*sensu* size spectra, White *et*

137   *al.,* 2007) and the average size of individuals in the fish community along temperature gradients,

138   gradients of lake morphometry and variations in lake productivity. Thirdly, we merged the size

139   structure approach with taxonomic predictors characterising geographical patterns of species

140   richness, community composition and dominance of thermal guilds (Magnuson *et al*., 1979). All

141   analyses were performed in a hierarchical way by comparing the patterns and dominant predictors

142   between the total dataset and subsets defined by either smaller geographical extent or dominance of

143   certain functional classifications of fishes. By splitting the total dataset into subsets, we aimed to

144   elucidate responses of size structures at smaller spatial scales by reducing the contribution from the

145   overarching geographical gradient. In this way, we characterise the major patterns in size structures

146   of entire lake fish communities at a continental spatial scale and identify the primary drivers behind

147   these large-scale patterns.

148   **Methods**

149   Fish data

150   In total, 356 lakes (317 natural lakes and 39 reservoirs) located in eight European countries (Fig. 1a)

151   and representing nine ecoregions were sampled once between 1993 and 2010 using stratified

152   random sampling with benthic multi-mesh gillnets (type NORDIC: length 30 m; height 1.5 m; 12

153   panels of 2.5 m each with bar mesh sizes between 5 and 55 mm knot to knot). Samplings were

154   undertaken during late summer and early autumn with a pre-defined number of nets per lake set

155   randomly in each depth stratum depending on lake area and depth (Appelberg *et al.*, 1995).

156   Captured fish were identified to species level, measured (nearest cm total length) and weighed

157   (nearest g fresh mass). Missing size measures were back-calculated using latitudinal-specific (5°

158   latitude) and species-specific mass-length and length-mass relationships calculated from fish with

159   complete information on individual length and fresh mass (Emmrich, unpublished). Due to the well

160   established biased sampling efficiency of multi-mesh gillnets against very small fish (Prchalová *et al.*,

161   2009), individuals < 8 cm were omitted from the analysis to reduce the 'noise' of varying seasonal

162   recruitment success and differences in sampling time. To account for possible effects of differences

163   in taxonomic and functional fish community composition on size structure, all fish were classified

164   according to their thermal preferences into cold-, cool and warmwater fish following Magnuson *et al.*

165   (1979) (further details in Appendix S1 in Supporting Information).

166   Predictor variables

167   Five abiotic variables known to influence fish community size structure were selected. Because lake

168   temperature was not available for most lakes, air temperature was used instead as it has been shown

169   to be a reliable surrogate parameter for epilimnetic lake temperature (Livingstone & Lotter, 1998)

170   and it has recently been used to study geographical patterns in European freshwater fishes (Brucet *et*

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171   *al.*, 2013; Edeline *et al.*, 2013). Temperature metrics of the lake's location were obtained from a

172   climate model with a spatial resolution of 10' latitude/longitude and taking into account elevation

173   differences (New *et al.*, 2002). This specific model has already been successfully used to study air

174   temperature effects on lake fish communities (Argillier *et al.*, 2013; Brucet *et al.*, 2013). We selected

175   average air temperature (averaged across monthly mean temperatures, range: -3.7-14.0 °C) and

176   maximum monthly mean temperature (range: 7.4-23.1 °C) for use in our analyses. The temperature

177   amplitude (difference between mean temperature in July and January) was used as a proxy for

178   seasonality (range: 9.9-28.9 °C). Lake morphometry was characterised by area (range: 0.02-113 km^2)

179   and maximum depth (range: 1-190 m). Annual mean total phosphorus concentration (TP, range: 1-

180   561 μg L^{-1}) was selected as a measure of lake productivity. TP was sampled seasonally (i.e., minimum

181   four samples per year) usually in the year of fish sampling, although in the case of some Swedish

182   lakes such measurements were taken up to three years before the fish sampling. For more details on

183   the abiotic variables, see Appendix S2 in the Supporting Information.

184   Among the biotic variables of fish community composition, we selected local species numbers

185   (richness, range: 1-15) for particular analysis. In addition, we characterised the relative dominance

186   structure and species composition of fish communities by conducting a principle component analysis

187   (PCA) derived with a Chord-transformed site-species matrix based on numerical abundance data.

188   This unconstrained ordination allows the robust application of Euclidean distance-based PCA to zero-

189   inflated datasets (Legendre & Gallagher, 2001) which are typical when many species are replaced

190   across broad gradients of abiotic lake characteristics and geographical position. The Chord distance

191   downweighs the importance of rare species (Legendre & Gallagher, 2001), which is important for our

192   data as the highly abundant species were also the ones with the strongest influence on the

193   calculation of the size metrics. To further reduce the number of zeros in the site-species matrix, rare

194   species caught in less than five lakes were removed from the analyses (details are found in Appendix

195   S3 in Supporting Information). The site (lake) scores along the first two PCA axes were used as

196   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

222   predictor to the total variation in each of the three size metrics. Interactions between predictors

223   were automatically included in the models via tree complexity. A Gaussian error distribution was

224   appropriate for the size metrics. The predictive performance of the BRT models was evaluated using

225   ten-fold cross-validation. Ten mutually exclusive data subsets were randomly selected and model

226   predictions were compared to the withheld proportion of the data. The optimal number of trees

227   which produced the lowest prediction error without model overfitting was identified testing tree

228   complexities of one and two (this accounts for no or one-way interactions), learning rates of 0.01,

229   0.005 and 0.001 and bag fractions of 0.5 and 0.75. The bag fraction determines the proportion of

230   data selected during each iteration process and introduces stochasticity which improves model

231   accuracy and reduces model overfitting (Friedman, 2002). The minimum limit to fit models was set to

232   1000 trees to reduce the contribution from single trees to the final model (Elith *et al*., 2008). BRT

233   analysis does not generate P-values, but the relative influence was used to estimate the significance

234   of each predictor influence (measuring how often a predictor variable is selected and testing the

235   strength of its influence on model improvement). Partial dependence plots were used to visualize the

236   effects of individual predictors on the response variables (size metrics) after accounting for the

237   average effects of all other predictors (Friedman, 2002).

238   In addition to the continental BRT analysis, patterns in AS were separately analysed for lake subsets.

239   To account for possible spatial non-independence in our lake dataset, we tested whether similar

240   abiotic variables account for variation in fish community size structure across smaller geographical

241   units with more consistent climates and a more homogeneous distribution of lakes. We selected five

242   ecoregions (after Illies, 1978) with a sufficiently large number of lakes for analysis: Borealic

243   Uplands/Tundra (n = 40 lakes), Fenno-Scandian Shield (n = 48), Central Plains (n = 179), Western

244   Highlands (n = 27) and Western Plains (n = 38) (Fig. 2b). The lakes not classified into lake subsets

245   were located in the ecoregions Alps (n = 6), Baltic Province (n = 8), Great Britain (n = 5) and

246   Italy/Corsica/Malta (n = 5). Additionally, we classified the lakes into three groups according to the

247   dominant thermal guild in their fish community composition based on the PCA results (cold-, cool- or

248 warmwater fish, cf. Results). A classification of our dataset into three clusters was statistically

249 verified using the Caliński criterion (Caliński & Harabasz, 1974) which determines a finite set of

250 clusters to best describe the dataset according to lake fish community similarity by maximising the

251 intra-cluster similarity and minimising the inter-cluster similarity. K-means partitioning was then used

252 to assign the lakes to one of the three clusters representing a dominant thermal fish guild.

253 Differences in AS in the lake subsets (ecoregions and thermal guilds) were tested using Welch's

254 analysis of variance (ANOVA) followed by Dunnett-Tukey-Kramer test for pairwise multiple

255 comparisons adjusted for unequal variances and sample sizes. Furthermore, general linear models

256 (LMs) were calculated to model trends in AS in the lake subsets along abiotic gradients and thermal

257 fish communities (Table 2). Model selection (only main effects were included in the initial full

258 models) was based on Akaike's Information Criterion (AIC) using a backwards variable selection

259 procedure. A Gaussian link function was appropriate for all models. Conditional plots were selected

260 to show the effect of significant abiotic variables on the response (AS), holding all other predictor

261 variables constant at their median values. Statistical analyses were performed in R (R Development

262 Core Team 2012) version 2.15 using the packages vegan (Oksanen *et al.*, 2012) and gbm (Ridgeway,

263 2012) plus codes provided by Elith *et al.* (2008) and Xiao *et al.* (2011).

264 **Results**

265 Fish community composition

266 A total of 54 fish species was caught by the benthic multi-mesh gillnets in 356 European lakes

267 (Appendices S1 & S3). Thirty species were caught in more than four lakes. Perch (*Perca fluviatilis* L.)

268 and roach [*Rutilus rutilus* (L.)] dominated the overall catch (Appendix S1). The first two PCA axes of

269 fish community ordination explained 64.1% of the variability. Axis 1 (40.2%) discriminated perch-

270 dominated lakes (Pearson's r = 0.76) from roach-dominated lakes (r = -0.63). Roach-dominated lakes

271 were additionally characterised by relatively high abundances of bream [*Abramis brama* (L.), r = -

272 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

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298   PCA axis 1 (separation between cool- and warmwater dominated fish communities) was consistently

299   weak across the size metrics (RI ≤ 5.5 %, Table 1).

300   The largest AS was observed in fish communities inhabiting relatively cold areas (lowest maximum

301   temperature). These lakes with large fish were also deep, and the fish communities were dominated

302   by few species, mainly stenothermic coldwater salmonids (brown trout, Arctic charr; Fig. 3a,

303   Appendix S 4a). The smallest AS was observed in warm and shallow, mainly lowland lakes with more

304   diverse fish communities dominated by eurythermic coolwater and warmwater species (mainly perch

305   and roach; Fig. 3a, Appendix S 4a). The slope of the ISDs increased (i.e. became less negative) with

306   decreasing maximum temperature. Smaller lakes dominated by a few coldwater salmonid species

307   had the flattest slopes (Fig. 3b, Appendix S 4b). The lowest R^2 indicating nonlinear ISDs were

308   observed in salmonid-dominated lakes with low species richness which are located in areas with low

309   temperature and less pronounced seasonality (amplitude temperature, Fig. 3c, Appendix S 4c).

310   Lake subsets defined by geography and functional fish community guilds

311   The AS differed significantly across ecoregions (Welch ANOVA: $F_{4, 81.3}$ = 18.9; P < 0.001). Lake fish

312   communities of colder (high latitude, high elevation) ecoregions (Borealic Uplands/Tundra, Fenno-

313   Scandian Shield, Western Highlands) were characterised by significantly (P < 0.001) larger AS (16.9,

314   14.7 and 15.3 cm, respectively) than the warmer European lowland ecoregions Central Plains (AS =

315   13.0 cm) and Western Plains (AS = 13.2 cm). However, AS responded similarly to abiotic gradients

316   related to the thermal environment of the fish (temperature, lake depth) within all ecoregions. Fish

317   size increased significantly with decreasing temperature and increasing lake depth (Table 2, Fig. 4).

318   Size patterns of fish communities in the Western Highlands did not respond significantly to any

319   abiotic variable, probably due to the relatively small sample size (n = 27 lakes). However, trends of

320   change in average size were comparable to the patterns observed in the other ecoregions, i.e., an

321   increase in average size with decreasing temperature (results not shown). The predictive power of

322   the GLM's indicated an increasing importance of temperature variables in explaining the variability in

323   the size structure of fish communities in northern (cold) ecoregions (Table 2). Compared with the

324   continental BRT analysis (356 lakes), lake productivity did not predict variability in the size structure

325   of fish communities at the ecoregion scale.

326   Average size also differed significantly between fish communities dominated by the three thermal

327   guilds (Welch ANOVA: $F_{2,\,48.9}$ = 24.4; P < 0.001). Fish size was significantly (all pairwise comparisons: P

328   < 0.001) larger in species-poor communities dominated by coldwater fishes (18.8 cm) than the AS of

329   the more diverse coolwater (14.2 cm) and warmwater dominated fish communities (13.0 cm).

330   Furthermore, AS of all thermal fish guilds significantly increased with decreasing temperature (Table

331   2, Fig. 5). Variability in size structure explained by temperature was highest for coldwater fish

332   communities (Table 2).

333   **Discussion**

334   Our results demonstrate a dominant effect of temperature on the size structure of entire lake fish

335   communities. Average and maximum air temperatures were the strongest predictors of the average

336   size and slope of non-taxonomic individual size distributions. These results were consistently found

337   for both the continental dataset (356 lakes) and the lake subsets defined according to ecoregion or

338   functional dominance structure of fish communities with respect to thermal guilds. Temperature

339   modifies the size of fishes within the thermal guilds and the corresponding ecoregions. Cold-, cool-

340   and warmwater fishes become bigger with decreasing temperature, a pattern that is consistent with

341   the temperature-size rule and which has been observed for the majority of ectothermic species

342   (Atkinson, 1994).

343   It is well known that environmental temperature modifies the species richness and taxonomic

344   composition of lake fish communities (Irz *et al*. 2007; Jeppesen *et al.*, 2012). However, our results

345   demonstrate that in addition there are systematic changes in fish community composition across

346   temperature gradients in correspondence with the dominant thermal fish guilds which

347   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

374   demonstrated a gradient of omnivory in freshwater fishes along a temperature gradient indicating

375   high omnivory (low predator abundances) in warmwater fish communities which further explains the

376   dominance of juvenile small-sized fishes in warm- and coolwater fish communities. However,

377   because we did not age the fish, a possible effect of temperature on the age structure of populations

378   could not be verified. We can also not exclude the possibility that abundances of small fish in

379   salmonid-dominated lakes were underestimated where lakes were connected to rivers. Juvenile

380   brown trout and Arctic charr regularly occupy lotic river habitats before they return as larger-sized

381   adults to the lake (Klemetsen *et al.,* 2003).

382   According to earlier studies, the dominant fish species of lakes in the European lowlands are the

383   coolwater species perch and the warmwater species roach (Mehner *et al.*, 2005; 2007). This general

384   pattern was well depicted by the first PCA axis on fish community composition, which discriminated

385   perch-dominated from roach-dominated lakes. The switch in the dominance of the thermal guild

386   within the ecoregions is here caused by lake morphometry, in particular lake depth. Deep and

387   stratified lakes are inhabited by coolwater species, whereas the warmwater cyprinids dominate in

388   shallow and polymictic lakes (Mehner *et al.*, 2005). However, the change between roach and perch

389   dominance did not correspond to strong variability of any size metric. Both the average size of perch

390   and roach populations in the dataset (mean total length perch: 12.8 cm; roach: 13.6 cm) and their

391   size distributions (two sample Kolmogorov-Smirnov test: $D = 0.15$, $P = 0.58$) were very similar. The

392   small average size and the steep ISD slopes indicated that small fishes dominated these communities.

393   In addition to the taxonomy-related changes in size structure across the temperature gradient, we

394   observed an increase in fish size with decreasing environmental temperature despite relatively

395   homogeneous fish community compositions. This gives further evidence for intraspecific size clines

396   of fish populations (cf. Blanck & Lamouroux, 2007). Temperature effects on body size have been

397   shown for many aquatic organisms including freshwater fish (Daufresne *et al.*, 2009; Edeline *et al.*,

398   2013). An increase in the relative proportion of large fish within populations and a larger average fish

399   community size (AS) were observed with decreasing temperature and less seasonality. This pattern

400   was also consistently found in our study within ecoregions and within groups of lakes dominated by

401   the different thermal guilds, and it hence supports the temperature-size rule (Atkinson, 1994) which

402   describes the phenotypically plastic response of body size of ectothermic species to their

403   environmental temperature. Individuals in colder environments mature as larger adults and live

404   longer than individuals in warm environments (Blanck & Lamouroux, 2007). In turn, fish mortality

405   rates are higher at high temperatures (Pauly, 1980), resulting in on average smaller fishes. Although

406   environmental temperature was the main predictor accounting for differences in fish community size

407   structure in our study, total variation explained by the statistical models was always < 50%. This

408   indicates that other predictors not included here might also be important. Edeline *et al*. (2013)

409   recently showed that biotic interactions such as competition and predation had a negative effect on

410   the body size of river fish communities, particularly at higher temperatures. Such a pattern is also

411   indirectly supported by our data on lake fish communities. Our general linear models indicated

412   increasing importance (i.e., more explained variability) of abiotic descriptors for size structure

413   towards colder environments. In northern ecoregions such as the Borealic Uplands/Tundra, the

414   temperature variables explained almost twice as much the variability of the fish community size

415   structure as they did for lake fish communities found in warm, southern ecoregions such as the

416   Western Plains (Table 2). This trend was also evident in the dominant thermal fish guilds. Variation in

417   the size structure of coldwater-dominated fish assemblages was strongly explained by temperature

418   variables, whereas the amount of variability explained by temperature was low in case of warmwater

419   fish communities. This statistical pattern supports the results of Edeline *et al*. (2013) that abiotic

420   influences on fish community size structure are weaker at higher temperatures.

421   Although our study lakes covered a large gradient in productivity from ultra-oligotrophic to

422   hypertrophic, lake productivity did not significantly explain the variability in the size structure of lake

423   fish communities. This finding seems to contrast with results from earlier regional studies in which

424   correspondence between the size structure of multi-species communities along gradients of lake

425 productivity has been documented (Jeppesen *et al.*, 2000; Emmrich *et al.*, 2011). However, lake

426 productivity and lake temperature both co-vary with lake depth. Shallow (warm) lakes are typically

427 more nutrient-rich than colder, stratified lakes (Nõges, 2009). Fish densities increase in number and

428 biomass with increasing lake productivity, causing a reduction in average size due to density-

429 dependent food limitation (Jeppesen *et al.*, 2010, Brucet *et al*., 2013). This effect becomes obvious

430 only if fish communities in lakes with comparable depth and at comparable climatic conditions are

431 compared along a productivity gradient (cf. Brucet *et al*., 2013). At any broader scales of comparison,

432 effects of variation in trophic status are covered by temperature variations which affect size

433 structure in the same direction. Therefore, the subtle response of fish size to local predictors in

434 regional studies is relativised when shifts in lake fish community size structure are considered across

435 large geographical scales.

436 Conclusions

437 Temperature modifies the size structure of lake fishes via two processes. Local temperature

438 determines which thermal guild dominates in the fish community. Indirectly, these changes in

439 functional dominance structure along a temperature gradient also induce taxonomy-related changes

440 in size structure from a few large species in the coldwater guild towards many small species in the

441 cool- and warmwater guilds. Clines in the size structure of entire lake fish communities are consistent

442 with the temperature-size rule which implies smaller size with increasing temperature for the

443 majority of ectothermic species. The pattern holds true for large and smaller (i.e., ecoregions)

444 geographical scales as well as for all thermal fish guilds including cold-, cool- and warmwater fish

445 communities. Our results indicate an increasing importance of temperature for the size structure of

446 lake fish communities in cold environments.

459

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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	%
Borealic 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

629   Figure 1. (a):Geographical distribution of the 356 lakes across eight European countries (grey-

630   coloured) where fish communities were sampled with benthic multi-mesh gillnets. Letters indicate

631   position of three lakes for which individual size distributions are shown in Figure 2. (b): Ecoregions,

632   defined according to Illies (1978), with five lake subsets analysed separately: Borealic

633   Uplands/Tundra (1), Fenno-Scandian Shield (2), Central Plains (3), Western Highlands (4), Western

634   Plains (5).

635   Figure 2. Examples of individual size distributions ($\log_2$ midpoints of fresh mass in g vs. $\log_2$ numbers)

636   of fish communities from three European lakes (cf. Figure 1) showing monotonically decreasing (a),

637   unimodal (b) and multimodal (c) distributions. The distribution shown in (a) is characteristic for cool-

638   and warmwater dominated fish communities while those shown in (b) and (c) are characteristic for

639   communities dominated by cool- and coldwater fishes.

640   Figure 3. Partial dependence plots showing the three most influential predictor variables according to

641   the boosted regression tree analysis on the fitted function (centred around the mean) of average size

642   (a) and slope (b) and R^2 (c) of the individual size distributions (ISD). Rug plots on the top horizontal

643   axes indicate the distributions of the predictor variables, in deciles. Percentage values indicate the

644   relative importance of the predictor variables in the boosted regression tree analyses. Axis 2 PCA:

645   Discrimination between cold- and cool-/warmwater dominated fish communities.

646   Figure 4. Changes in average size of European lake fish communities in five ecoregions along air

647   temperature and lake depth gradients. Only significant variables in the general linear models are

648   shown. Plots show the partial residuals (points), prediction line and the 95% confidence interval (grey

649   area). Rug plots indicate the distribution of the response and explanatory variables.

650   Figure 5. Trends in average size of European lake fish communities with numerical dominance of

651   cold- (a), cool- (b) and warmwater fish (c). Only significant variables in the general linear models are

652   shown. Plots show the partial residuals (points), prediction line and the 95% confidence interval (grey

653   area). Rug plots indicate the distribution of average fish community size and air temperature metrics.
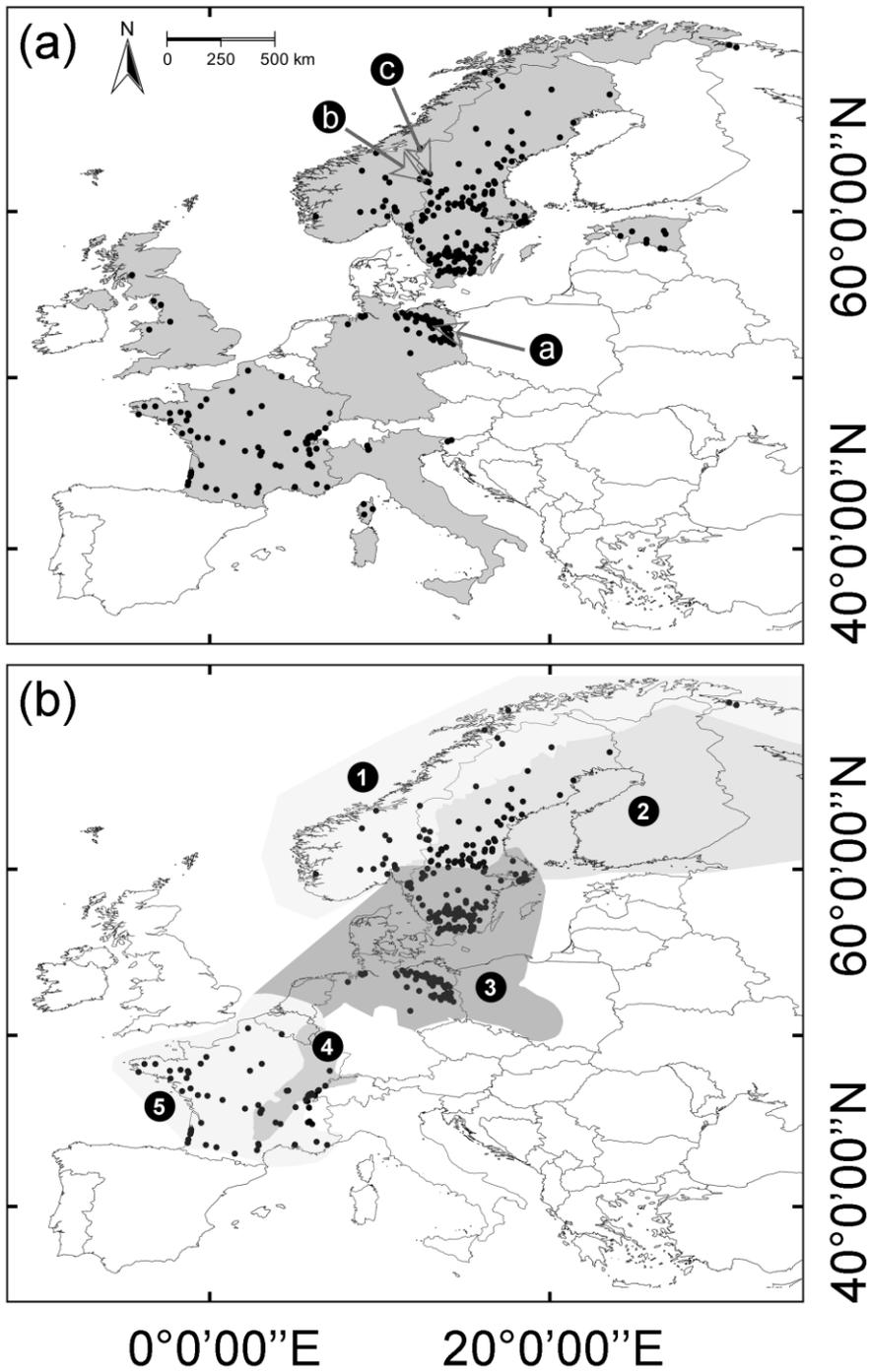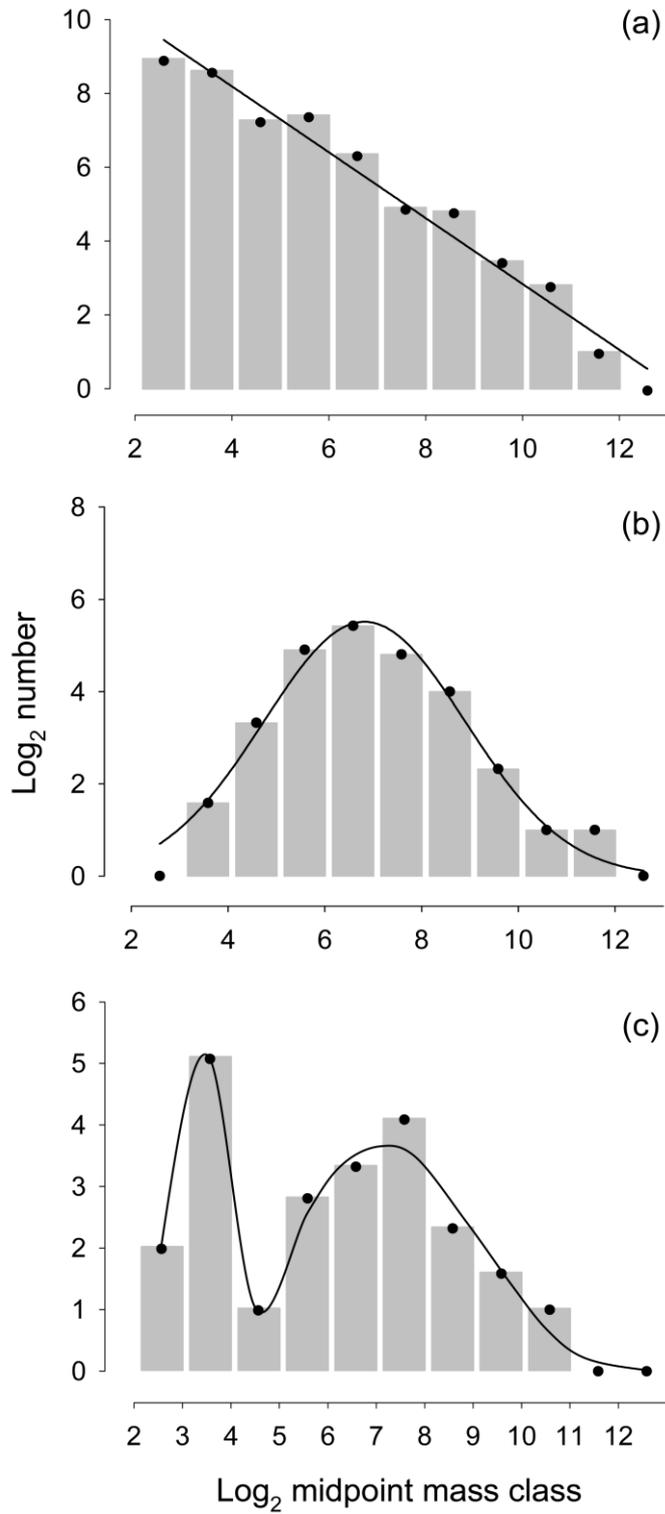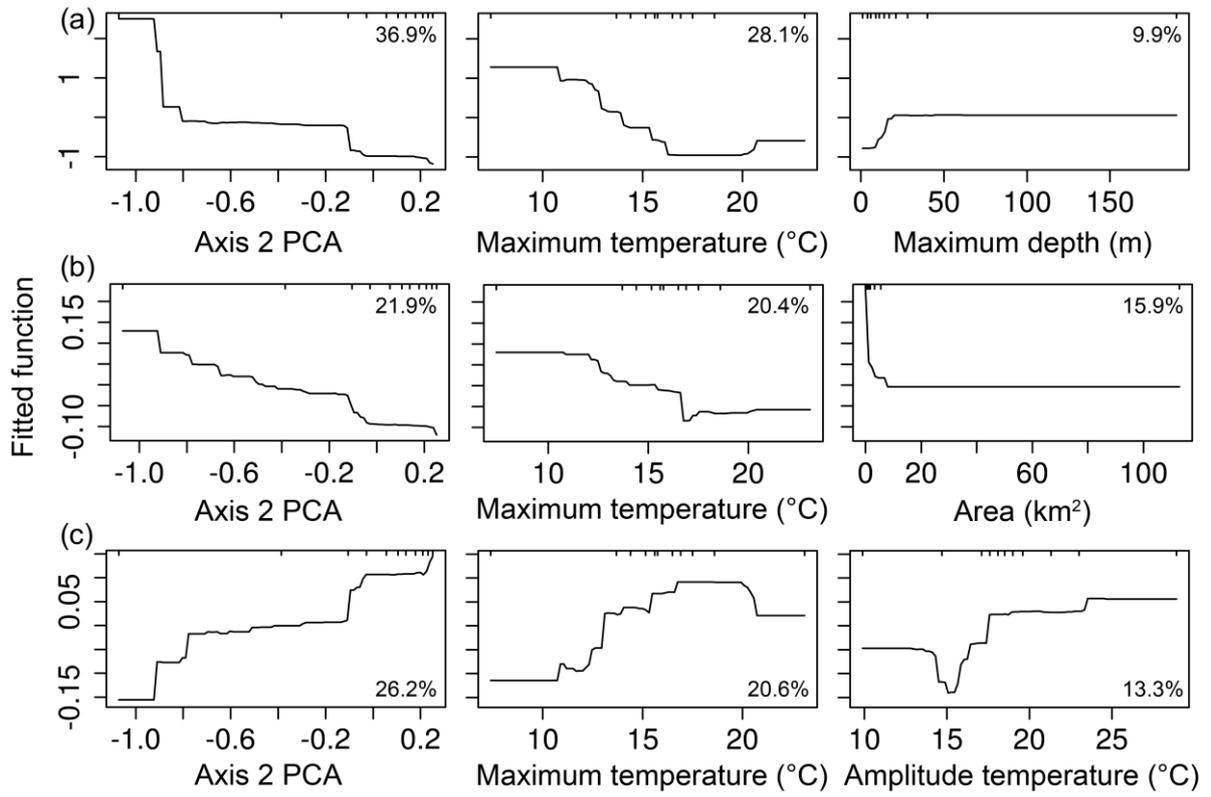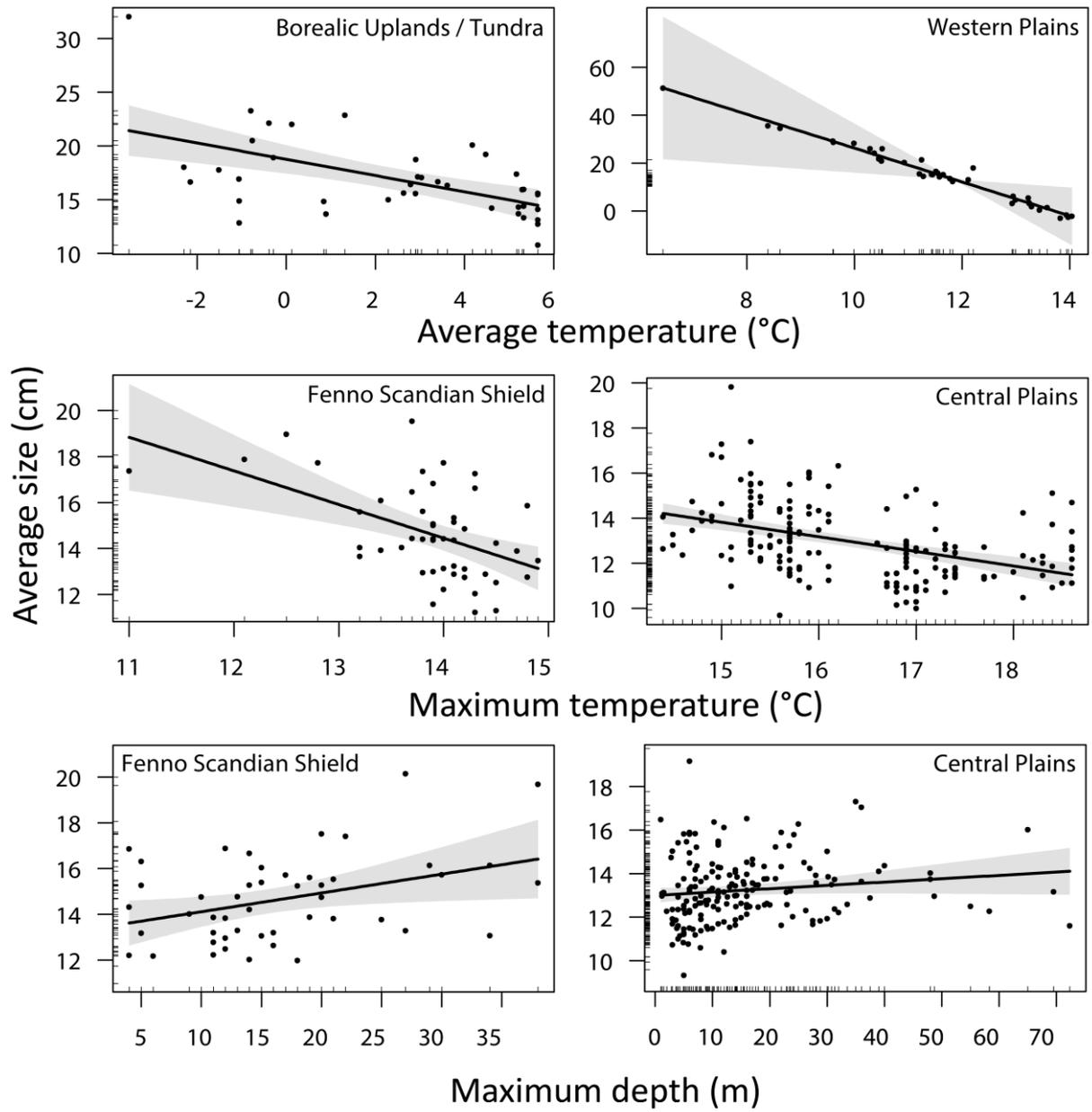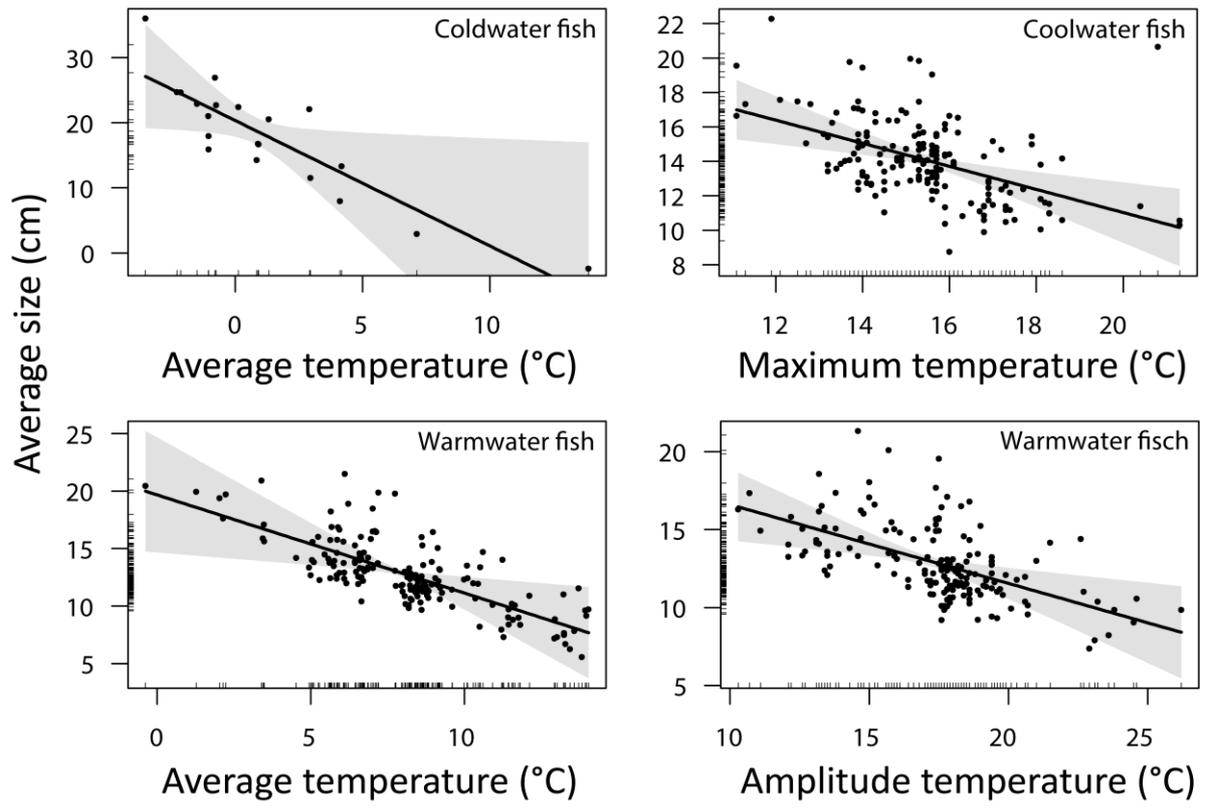

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655   Figure 1

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Figure 4

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665   Figure 5