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Drivers of diet patterns in a globally distributed freshwater fish species

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Abstract

We analysed data of a globally distributed model organism (brown trout) in an attempt to understand relationships among biogeography, prey communities and climate on diet composition at regional spatial scales (Scandinavia), and thereafter explored whether diet patterns remained the same at global scales. At regional scales, we uncovered comprehensive patterns in diet composition among neighbouring freshwater ecoregions, with site-specific prey communities as the best predictor of the observed prey utilisation patterns. Thus, we posit that environmental gradients altering site-specific prey communities and consequently the trophic niche of the predator through bottom-up mechanisms are key in understanding spatial dietary patterns. Proximity was also important for the revealed biogeographic patterns at global scales. We suggest that geographic location (latitude and elevation) as a proxy of environmental heterogeneity is key at small spatial scales, and climate at global extents, to understand spatial dietary patterns. Our findings support the hypothesis that future shifts in prey communities due to climate change will strengthen biographical patterns in feeding of freshwater fishes, with consequences for invasiveness assessment and nature management and conservation.

Keywords: biogeographic patterns, climate change, freshwater ecoregions, global trophic ecology, macroecology, modelling

Introduction

Knowledge of the feeding habits of fish populations is essential to understand its ecological role in food webs and their potential carrying capacity, which, in turn, is critical for the development of conservation and management plans (Teixeira and Cortes 2006). Most studies of trophic ecology focus on a specific geographic area (e.g. Jensen et al. 2008; Trystram et al. 2017; Mumby et al. 2018), whereas studies that integrate multiple factors such as climatic conditions and geographic regions to assess biogeographic (spatial *sensu lato*) feeding patterns on global scales are rare (e.g. Clavero et al. 2003; Lozano et al. 2006; Rheingantz et al. 2017). Because both temporal and spatial variations in site-specific prey communities likely shape foraging and diet composition of aquatic predators (e.g. Rader 1997; Zhou et al. 2011; Baudrot et al. 2016, but see Van Ginderdeuren et al. 2014), biogeographic feeding patterns of animals can be strongly shaped by bottom-up mechanisms (i.e. through geographical differences in prey availability). Climatic conditions also have important influences on prey communities and predator–prey dynamics (e.g. Wilmers et al. 2007; Arbeiter et al. 2016). Thus, aquatic species that occupy a broad geographical range may be expected to show dietary differences that may reflect variation in environmental factors (e.g. Iriarte et al. 1990; Clavero et al. 2003; Papacostas and Freestone 2016). However, we know surprisingly little about how biogeography and predation can interact to influence trophic ecology and diet patterns of aquatic animals. This can be accomplished through comprehensive studies that consider feeding, prey communities and climate. Recent studies have highlighted the importance of climate seasonality for delineating biogeographic patterns in feeding of animals (Zhou et al. 2011; Rheingantz et al. 2017); demonstrating that diet breadth can be positively correlated with precipitation seasonality (Zhou et al. 2011) and temperature seasonality (Rheingantz et al.

2017) in mustelid species, but inversely correlated with latitude in temperate brachyuran crabs (Papacostas and Freestone 2016). Here, we empirically test the response of diet variation along biographical gradients of prey availability, climate and geographical location (latitude and elevation).

Most studies exploring biogeographic patterns in feeding of animals focus on homoeothermic animals (e.g. Clavero et al. 2003; Lozano et al. 2006; Rheingantz et al. 2017), whereas less attention have been paid to poikilotherm animals (Griffiths 1994; Budy et al. 2013; Papacostas and Freestone 2016; Sánchez-Hernández and Amundsen 2018). Ecological insights into the biogeographic patterns in feeding of aquatic predators have typically been reached by contrasting the spatial variation of piscivorous behaviour, where piscivory of both aquatic mammals and fishes is found to be more prevalent at higher latitudes (Griffiths 1994; Clavero et al. 2003). Among freshwater predators, brown trout (*Salmo trutta* Linnaeus, 1758) has a wide geographic distribution and has been considered as one of the world's most invasive species (Lowe et al. 2000; Lobón-Cerviá and Sanz 2017). Brown trout is a cold-water species widely studied, being indigenous to Europe, North Africa and western Asia, but has been successfully introduced in many countries outside its native range (Lobón-Cerviá and Sanz 2017 and references therein). This wide geographic distribution facilitates the use of brown trout as a model species to explore global patterns in trophic ecology. Indeed, Budy et al. (2013) observed little variation in the diet of brown trout among geographic areas, but they found more frequent switches to piscivory in exotic territories. Here, we explore the specific association of key environmental and ecological variables with the diet composition of brown trout, hypothesising that both climatic conditions related to geography and biogeographical

constraints on the distribution of prey species are prime determinants for the dietary niche. Although the successful disentangling of patterns in diet composition of animals partly may depend on the taxonomic resolution of prey identification, we expected that the diet composition of brown trout would show major biogeographic patterns related to aspects of both latitudinal gradients and site-specific prey communities. The identification of such patterns will allow us to address the relationship between diet composition and environmental variables from a global biogeographical perspective. Based on the above considerations, we hypothesised that (H1) the diet composition will be more similar among similar geographic areas (here freshwater ecoregions as defined by Abell et al. 2008) such as Mediterranean ecoregions located in different parts of the world, whereas larger differences should occur among non-similar regions or between native and exotic territories; and (H2) site-specific prey communities will be associated with foraging and diet composition (Baudrot et al. 2016), and consequently, biogeographic patterns in feeding. Also, spatial differences in inherent food preferences of species can be expected to lead patterns in feeding (e.g. Sanford et al. 2003). Additionally, we hypothesised that (H3) climate factors may be important for the development of biogeographic feeding patterns of brown trout via alterations of site-specific prey communities, thereby activating bottom-up mechanisms that may influence the trophic ecology of the model species. A greater understanding of how environmental variables (latitude, geographic region, altitude and seasonality of rainfall and temperature) and ecological opportunity (i.e. prey availability) are associated with diet utilisation is pivotal for a holistic understanding of trophic ecology of fishes. This is key to improve our ability to predict how aquatic animals may be capable of adapting their diets to different climate scenarios under the ongoing climate changes.

112

Methods

We explored dietary patterns using data for brown trout body size, prey community composition, climate, freshwater ecoregions and geographic coordinates (latitude and elevation) collected from 117 sampling events located across marked biogeographical gradients in Norway. Subsequently, we conducted a broad literature review compiling information from different regions of the species' global distribution to evaluate whether the revealed dietary patterns remain the same at global scale.

Norwegian dataset: regional approach

We utilised a unique dataset of fish diet composition and prey community composition from sampling in seven Norwegian rivers (Altaelva, Beiarelva, Gaula, Klubbvasselva, Litjvasselva, Stjørdalselva and Reisa) located between 63°N to 69.9°N. Brown trout and Atlantic salmon (*Salmo salar* Linnaeus, 1758) are the dominant species in the fish community of the studied rivers. Other fish species, such as Arctic charr [*Salvelinus alpinus* (Linnaeus, 1758)], European eel (*Anguilla anguilla*, Linnaeus, 1758), alpine bullhead (*Cottus poecilopus* Heckel, 1836), and three-spine stickleback (*Gasterosteus aculeatus* Linnaeus 1758), are also present in the river basins, but only sporadically found at the current study sites. The study included 117 sampling events between 1986 and 2004 implemented during the ice-free season (May–November, but mainly carried out in summer as indicated in Appendix 1). At each sampling event, we recorded geographical coordinates (altitude, latitude and longitude) and collected fish and benthic invertebrates.

In order to avoid confounding effects of maturation and migratory behaviour between migratory (i.e. anadromous) and resident individuals within populations (e.g. Lobón-Cerviá

and Sanz 2017), we focused the current study on small fishes. Accordingly, we collected brown trout in riffle stretches of the rivers using portable backpack electrofishing gear, including 10401 resident individuals (fork length range: 24-226 mm) in total. We visually determined the percentage of total fullness, ranging from empty (0%) to full (100%). Next, we identified and grouped each prey item in 15 categories of prey taxa: (i) Copepoda, (ii) benthic Crustacea, (iii) Mollusca, (iv) Diptera larvae, (v) Trichoptera larvae, (vi) Megaloptera larvae, (vii) Coleoptera (both larvae and adults), (viii) Heteroptera, (ix) Ephemeroptera nymphs, (x) Plecoptera nymphs, (xi) Odonata nymphs, (xii) other benthic invertebrates (mostly Hydracarina, Oligochaeta, Turbellaria, Hirudinea) (xiii) surface prey (terrestrial arthropods and emerged aquatic insects), (xiv) Urodela, and (xv) fish. We estimated the volumetric contribution of each prey category to the total stomach fullness according to Amundsen et al. (1996), where the sum of all prey categories of a stomach meets the visually determined total fullness. Finally, we estimated the diet composition at the population level using relative prey abundance ($A_i = (\sum S_i / \sum S_i) * 100$, where S_i is the stomach content composed of prey i , and S_i the total stomach content of all stomachs in the entire sample).

At each sampling event, we collected benthic invertebrates from riffles using a 0.15 m² Surber sampler (in 110 sampling events) or three parallel samples with kick-nets standardised by kicking for 3 minutes inside a metal frame defining 1.5×1.5 m of the bottom (in seven sampling events). We calculated relative abundance of benthic invertebrates according to the same taxonomic classifications as fish prey (see above). This enabled us to compare diet (stomach contents) and prey availability (benthic invertebrate communities) and study feeding selectivity of brown trout using Chesson's index:

$$S = \frac{d_i/b_i}{\sum_{j=1}^m d_j/b_j}, i = 1, \dots, m,$$

where d and b are the relative abundance of each prey category in the diet and in the benthic invertebrate community, respectively. This index varies from zero (complete avoidance) to one (complete preference).

We further quantified the Shannon-Wiener's diversity index as a proxy for the structural complexity of the benthic invertebrate community:

$$H' = -\sum p_i \log_{10} p_i$$

where p_i is the proportion of species i in the benthic invertebrate samples. Unfortunately, no information is available about drift patterns or magnitude of terrestrial subsidies into the studied rivers. It should be noted that benthic communities may reflect spatial differences in the drift compositions among riverine systems as there is a positive relationship between benthic and drift invertebrates (e.g. Sagar and Glova 1992; Siler et al. 2001; Shearer et al. 2003). Diptera (mainly Chironomidae), Ephemeroptera, Plecoptera and Trichoptera are commonly the most abundant drifting invertebrates over the ice-free season in Norwegian rivers (e.g. Johansen et al. 2000; Saltveit et al. 2001). Additionally, the contribution of terrestrial insects to the drift in Norwegian rivers may be very noteworthy from June to

October, with terrestrial insects being the largest drifting group in August (Johansen et al. 2000).

Due to a lack of information regarding climate data for all the different study sites, we used information from Worldclim (<http://www.worldclim.org/>) to obtain representative environmental variables to address the possible effects of climate on the diet patterns of the model organism. Worldclim provides 19 bioclimatic variables, including minimum, mean, and maximum air temperature and precipitation for 1960-1990 (Hijmans et al. 2005) at a spatial resolution of about 1 km². Although the climate data did not cover all the time period of the dietary data, we assumed Worldclim data were representative to explore climate effects on diet composition. In order to reduce the number of climate variables, and to avoid the likelihood of spurious correlations among them (Appendix 2), we selected seven climate variables likely to be a predictor of diet composition: (i) annual mean temperature, (ii) temperature seasonality (i.e. standard deviation*100), (iii) temperature annual range, (iv) max temperature of warmest month, (v) mean temperature of warmest quarter, (vi) annual precipitation and (vii) precipitation seasonality. We spatially matched climate data with fish data using the Point Sampling Tool plug-in of QGIS 2.16 (QGIS development team 2016).

For freshwater ecosystems, ecoregions have been delineated based on distributions and compositions of freshwater fish species (Abell et al. 2008). In this study, we assigned sampling sites to freshwater ecoregions on the basis of their coordinates to account for geographically-distinct assemblages of fish species (as a proxy of potential interspecific competition) and environmental conditions in the analyses.

The final dataset consisted of diet data (fifteen prey categories), body size (mean population values), prey availability data (benthic invertebrate fauna and Shannon-Wiener's diversity index), climate data (the above five selected variables), freshwater ecoregion, and geographical coordinates (altitude, latitude and longitude).

Literature review: global approach

To complement the data from the sampled sites and cover a broader geographical territory than Norway, we performed an extensive literature review including worldwide studies on riverine brown trout to explore global patterns in feeding (a list of the data sources is found in Appendix 1). We used Web of Science® to search for studies using the key word “brown trout” in combination with “diet”, “feeding”, “river”, “juvenile”, “summer” and “*Salmo trutta*”. To match information from the primary data (i.e. the Norwegian sampling sites focussed on small fish sampled during the summer) and the published sources, and to avoid any bias from seasonal (e.g. Lagarrigue et al. 2002) and ontogenetic (e.g. Sánchez-Hernández and Cobo 2018 and references therein) variations in brown trout feeding, we delimited the literature review to include a comparable size range of fish and seasonal range of sampling. Thus, the literature used in this study met the following criteria: the source contained information about (1) summer feeding (summer including the period from summer solstice to autumnal equinox, i.e. from June to September and from December to March in the Northern and Southern Hemispheres, respectively); and (2) diet composition of small fish (i.e., we selected information from studies of fish with fork length <200 mm or age ≤ 2 years, but excluded first feeding fry). Because of the difficulties associated with the compilation of a global dataset with standardised methods for stomach contents

analysis, we assumed studies to be mutually comparable regardless of method. The literature review included different measures of diet composition based on relative prey abundance in stomachs (mainly numerical, constituting 63.9% of the total). Additionally, we did not include several studies because their data was not available (e.g. they only presented the diet information in figures). Hence, this literature review did not include all published studies to date, but still covers five continents, enabling us to test our hypotheses on a global scale.

In cases of missing records of geographical coordinates (altitude, latitude and longitude) of the study area in a literature source, we digitalised the coordinates based upon assessments of location information or maps provided in the source. We compiled climate data and freshwater ecoregion assignation following the same procedure as previously described, but information about prey community (benthic invertebrates) and brown trout body size was not available for all the literature sources. Therefore, we did not perform the prey availability, body size and selectivity analyses for the global database. Finally, we combined our own primary data matrix (Norway dataset) with the literature review to generate a global dataset covering prey abundances, geographical coordinates, climate and freshwater ecoregion from 275 sampling events (including the 117 sampling events from the regional approach) carried out in 60 watercourses from 16 countries and five continents spanning 40.6°S to 69.9°N (Fig. 1).

Statistics

We used R 3.4.2 (R Core Team 2017) for statistical analyses and graphical outputs. Shapiro–Wilk tests indicated non-normality in the data. We used variance inflation factors

(*VIF*) to detect multicollinearity (correlation between predictors) between geographical variables (altitude and latitude) and climatic variables. Zuur et al. (2010) recommended *VIF* < 3 as an indicator of low evidence for collinearity. Accordingly, variables with *VIF* > 3 were dropped in subsequent analyses.

We examined biogeographic patterns in diet composition using a hierarchical cluster analysis (i.e. dendrogram) with heatmaps through the “gplots” package (Warnes et al. 2016). We determined the optimal number of clusters using the “factoextra” package (Kassambara and Mundt 2017) based on the K-means method with 999 bootstrap replicates (Monte Carlo resampling simulation). We performed the clustering using the Manhattan dissimilarity measure and Ward’s clustering algorithm (Strauss and von Maltitz 2017). We ran two clustering approaches based on (i) prey composition to assign groups of systems with similar prey composition (i.e. including all sampling events for each approach: $n_{regional} = 117$ and $n_{global} = 275$), and (ii) freshwater ecoregions to account for a biogeographic association based on the global dataset (i.e. including the 18 studied freshwater ecoregions). The combination (dendrogram with heatmaps) provides a colour-scaled representation of the dataset arranging groups (here sampling events or freshwater ecoregions and diet composition) in a hierarchy based on the dissimilarity among them. Two types of information can be inferred from plots combining dendrograms and heatmaps: (i) the dendrogram shows the dissimilarity among sampling events or freshwater ecoregions, where nodes represent the result of the clustering calculation, and (ii) the heatmap is a colour-scaled representation of the diet composition, in terms of mean prey abundance values (%) of prey categories, for each freshwater ecoregion or sampling event.

We tested the association strength between prey categories and environmental variables using Pearson's rank correlation. This analysis allowed a preliminary examination of whether environmental variables are associated with diet composition. Using previously described methods (O'Gorman et al. 2016), we adopted Chesson's index in combination with Principal Coordinates Analysis (PCoA) and linear regression analyses to explore whether brown trout prefers to consume certain prey categories irrespective of environmental variables. We performed canonical correspondence analysis (CCA) using the "vegan" package (Oksanen et al. 2015) to examine the most important associations between diet data and environmental variables. In the resulting ordination diagram (CCA), groups of systems are represented by dots based on the identified hierarchical clustering with similar prey composition (hierarchical cluster analysis), using mean values for each identified group/cluster. Environmental variables are represented by arrows, with the length of the arrows indicating the importance of the variables. Additionally, we analysed the effect of environmental variables on the prey selectivity (PCoA) and diet composition (CCA) of brown trout using permutational multivariate analysis of variance (PERMANOVA) (O'Gorman et al. 2016).

In a first attempt to model the relation between diet and environmental conditions, we used the output of the nonmetric multidimensional scaling (NMDS) for a classification of groups of systems with similar prey composition (see first clustering described above). The rationale is that the NMDS scores express the variation in diet composition and reduce diet information to one dependent variable, which was then modelled as a function of environmental variables. NMDS is appropriate at compressing the distance relationships among objects into a few dimensions (two-dimensional ordination space), and especially

when it can be assumed that there is no linear response between the dependent variable and environmental variables (see Ramette 2007 for further details). We obtained the NMDS output (here scores for NMDS of axis 1 or NMDS1) using the package “vegan”. Because our data did not meet normality, and hence the assumptions for linear regression models (Zuur et al. 2009), we employed generalised additive models (*GAMs*) with the automatic estimation of the amount of smoothing (REML) using the “mgcv” package (Wood 2015). We used the NMDS scores as the dependent variable and environmental variables as smoothed variables in *GAM*. Secondly, we tested for environmental impact on diet composition by regressing each prey category separately (i.e. one model for each of the fifteen prey categories including all sampling events), and adjusting for biogeographical effects by adding freshwater ecoregion as a random intercept in the model using generalised additive mixed models (*GAMMs*) with the “mgcv” package. The random part contains components that allow for heterogeneity (Zuur et al. 2009). Thus, by introducing freshwater ecoregion as a random factor, we modelled between-ecoregion variation in diet composition resulting from variables not considered in the current study such as e.g. habitat characteristics (slope, river width, habitat heterogeneity), spatial inherent food preferences and intra- and interspecific competition. To account for spatial autocorrelation and altitude effects not captured by climatic variables, we included coordinates of points and altitude as smoothed terms. In addition, we addressed the status (native or exotic) of the populations in our global models by including this covariate as a smoothed term. We performed model selection in *GAMMs* by model comparison using the “MuMIn” package (Bartoń 2016). Using a model selection method (Burnham and Anderson 2002), we ranked the candidate models according to the Akaike information criterion (AIC) using a delta AIC threshold of 0 (i.e. the lowest AIC value and consequently the best model being the one with the lowest

AIC values). We visually inspected residuals of the final selected models for deviations from normality and heteroscedasticity (see Supporting information). We visually assessed the possible evidence of spatial correlation in residuals with the *bubble* function using the “sp” package (Pebesma and Bivand 2005) to examine if residuals showed a clear pattern with biogeography.

Results

Norwegian dataset: regional approach

Diptera (mean = 21.4%), Ephemeroptera (mean = 20.9%), surface prey (mean = 17.6%), Trichoptera (mean = 15.9%) and Plecoptera (mean = 15.2%) emerged as the primary dietary components of brown trout, with substantial variations within these taxa among sampling events (Fig. 2). Other prey categories were barely used as food, especially Heteroptera (mean = 0.04%), Megaloptera (mean = 0.07%) and Copepoda (mean = 0.19%), which were only consumed in two, three and eight populations, respectively. We identified five clusters with similar prey composition (Fig. 3), showing a great similarity dependence of Ephemeroptera, Plecoptera, surface prey, Diptera and Trichoptera (from first to fifth clusters, respectively; Fig. 4). The detailed differences in diets among the various clusters can be seen in Fig. 4.

All climatic variables were dropped in subsequent analyses because strong multicollinearity was found with annual mean temperature ($VIF = 2326.09$), temperature seasonality ($VIF = 62282.49$), temperature annual range ($VIF = 74818.01$), max temperature of warmest month ($VIF = 5717.73$), mean temperature of warmest quarter ($VIF = 4098.22$), annual precipitation ($VIF = 15.18$) and precipitation seasonality ($VIF = 48.72$). The dietary

contribution of Diptera and Ephemeroptera was positively associated with their abundance in the environment ($r = 0.31$; $p < 0.001$ and $r = 0.37$; $p < 0.001$, respectively), whereas piscivory increased with latitude ($r = 0.22$; $p = 0.016$) and decreased with elevation ($r = -0.19$; $p = 0.034$) (see Appendix 3.1 for identified significant correlations). According to the PCoA, elevation was strongly related with feeding selectivity of brown trout (PERMANOVA; $p = 0.005$). There was also a significant interaction between elevation and latitude (PERMANOVA; $p = 0.003$) and latitude and Shannon-Wiener's index (PERMANOVA; $p = 0.001$). However, linear regression analysis indicated that brown trout ate some prey categories irrespective of environmental variables (Appendix 3.2), although with some exceptions such as Trichoptera (negatively linked to elevation), Coleoptera (positively linked to elevation) and the category "other benthic invertebrates" (negatively linked to latitude, but positively with elevation) (Fig. 5). The structure of the available prey community (measured as prey diversity) and latitude emerged as the most important environmental variables in the CCA ordination to understand the brown trout prey composition, with different associations (positive or negative) for each prey category (see Fig. 6). However, only latitude was statistically related with prey categories (PERMANOVA; $p = 0.020$).

The NMDS output (NMDS1, understood as scores expressing the variation in diet composition) increased with increasing prey diversity (Fig. 7 and Appendix 3.3). The smoothness of the curve showed an inverse quadratic association between diet composition and latitude. Models (GAMMs) for each prey category highlighted the importance of prey community composition (i.e. Crustacea, Mollusca, Diptera, Ephemeroptera and "other benthic invertebrates") on the diet composition of brown trout (Table 1). Additionally, there

was a strong support for the best models to include geographical coordinates (present in five out of thirteen models) and body size (present in four out of thirteen models) as main effects. We observed a negative (Copepoda and Diptera) and positive (Trichoptera and Fish) allometry. According to the residuals, no evidence for violation of model assumptions were observed for the primary dietary components, but models seemed not to be reliable for uncommon prey categories such as Copepoda, Crustacea, Mollusca, Megaloptera and Heteroptera (Appendix 3.4). Taking Ephemeroptera as example, prey abundance and geographical coordinates emerged as the key variables to understand geographical patterns in the consumption of this food resource by brown trout (see Table 1 for variables with a significant impact on each prey category). Spatial patterns can be established for some prey categories; for example, residuals for “other benthic invertebrates” tended to be lowest in northern Norway, with brown trout barely feeding on them in this region (Appendix 3.5).

Literature review: global approach

The diet composition of brown trout showed large spatial variations (Fig. 2 and Appendix 4.1). Ephemeroptera, Diptera, Trichoptera, Plecoptera and surface prey emerged as primary dietary components contributing $88.3\% \pm 16.1$ to the diet (mean $\pm$ SD), with substantial variations among those taxa. We observed invasiveness (statistically higher abundance in exotic compared to native territories) only for three prey categories (Mollusca, Coleoptera and Ephemeroptera; Appendix 4.2). We revealed two distinct clusters of freshwater ecoregions relating to diet similarity (Fig. 8). One cluster (in blue) included freshwater ecoregions of the Iberian Peninsula (Western Iberia and Eastern Iberia), North America (Colorado and Middle Missouri), New Zealand and central Europe (Dniester–Lower Danube), whereas the other (in red) comprised a larger number of freshwater ecoregions

mostly located in western and northern Europe and the southern part of South America. The low abundance of surface prey and the high abundance of Ephemeroptera in one cluster (blue) seem to be responsible of the clustering. In the resulting dendrogram, proximity appears to be important for the revealed biogeographic patterns as high similarity in diet composition frequently was found among neighbouring freshwater ecoregions (e.g. Northern Baltic Drainages, Barents Sea Drainages and Central and Western Europe). However, high similarity in diet composition was also found between some pairs of distantly located freshwater ecoregions like e.g. Northern Baltic Drainages v. Valdivian Lakes, and Cantabric Coast–Languedoc v. South Andean Pacific Slopes (Fig. 8). The detailed differences in diets between the two identified clusters of the global approach can be seen in Fig. 4.

Multicollinearity was found between geographical variables and temperature seasonality, temperature annual range, max temperature of warmest month and mean temperature of warmest quarter ($VIF = 18.97, 15.33, 10.93$ and 9.20 , respectively), but not for annual mean temperature, annual precipitation and precipitation seasonality ($VIF = 2.96, 1.74$ and 1.04 , respectively). The dietary contribution of Diptera was positively associated with elevation ($r = 0.27; p < 0.001$) and Plecoptera with latitude ($r = 0.29; p < 0.001$), whereas Crustacea, Mollusca and Odonata were more related to annual mean temperature ($r = 0.29; p < 0.001, r = 0.29; p < 0.001$ and $r = 0.28; p < 0.001$, respectively) (Appendix 4.3). The CCA, performed according to the assigned groups of systems with similar prey composition (see Appendix 4.4), showed that precipitation seasonality and annual mean temperature emerged as the most important environmental variables to understand the brown trout prey composition at the global scale, with annual mean temperature having just

a slight effect on prey composition (PERMANOVA; $p = 0.050$). The association (positive or negative) were different for each prey category according to the environmental variables (Appendix 4.5).

All included environmental variables were associated with diet composition in GAMs (Appendix 4.6). In most cases no clear patterns were identified, the NMDS output tended to decrease with increasing annual mean temperature and precipitation seasonality, but increased with elevation. We identified temperature (annual mean temperature, present in eight out of fifteen models) as a key driver to understand diet patterns of brown trout (Table 2). For example, annual mean temperature had a significant negative association with the utilisation of Copepoda and Plecoptera, but a positive association with Crustacea and Mollusca. On the other hand, invasion status (native/exotic) received little support in our models (present in three out of fifteen models). According to the residuals, models for the primary dietary components captured the patterns in the data quite well and seem to be reliable despite a small amount of spatial autocorrelation in the residuals (Appendix 4.7). Spatial patterns can be established for some prey categories; for example, the highest residuals for Mollusca were located in the north of Iberian Peninsula and south of France (Cantabric Coast–Languedoc), with the relative abundance of Mollusca being highest in this region (Appendix 4.8).

Discussion

Our study provides a novel test to the prediction that environmental factors related to biogeography can be important for determining broad-scale patterns in feeding of freshwater fish species. Our findings are consistent with this prediction, documenting the

significance of site-specific prey community differences and environmental gradients related to temperature in underpinning broad-scale feeding patterns. Although the importance of site-specific prey communities and predator body size (as a proxy of ontogenetic mechanisms) was only tested and demonstrated at the regional scale (here represented by the Norwegian dataset), we confirmed that the importance of abiotic factors related with diet patterns can vary between the regional and global scale. Geographic location (latitude and elevation) was a reliable predictor at the regional level, whereas temperature *per se* (i.e. annual mean temperature) seemed to be more important at the global scale. Still, temperature needs to be acknowledged at the regional level, as we observed a strong multicollinearity between geographical and climatic variables. The influence of abiotic factors driving patterns in feeding can vary between a regional (here Norway) and a global scale, which is a matter that should be taken into consideration in future studies.

Our first hypothesis predicting that the diet composition would be more similar among comparable geographic areas (here freshwater ecoregions as defined by Abell et al. 2008) was partially supported. We identified compelling patterns in feeding among neighbouring freshwater ecoregions. This was exemplified when the Norwegian dataset is framed in a global framework, as brown trout populations inhabiting freshwater regions of Scandinavia showed similar diet compositions. Also, this similarity among nearby freshwater ecoregions was observed in South America and between British Isles and northern Europe (see Fig. 8). We accept the view that the importance of abiotic environmental conditions varies across a range of scales (from regional to global extents), with environmental heterogeneity (e.g. water quality, topography or land use) being more important at small

spatial scales, but climate at global extents (e.g. Stein et al. 2014 and references therein). In this study, variability of environmental variables is expected to be weaker at smaller spatial scales (here among neighbouring freshwater ecoregions) than at global scales (here among distant freshwater ecoregions). Thus, proximity, and thereby similarity in environmental conditions and aquatic invertebrate communities, may be a significant feature shaping the establishment of regional dietary patterns of brown trout as well as in other animal species with a broad geographic distribution. There are also ecological and environmental factors other than proximity which may be responsible for geographical diet patterns, given that high similarity in diet composition was found between some distantly located geographic regions. These factors include site-specific prey availability, ontogenetic mechanisms and factors not explored in the present study such as habitat heterogeneity, inter- and intraspecific competition and intrinsic features of the brown trout populations (e.g., evolutionary differences in food preferences and selection of the primary dietary components).

The identification of dietary patterns across larger spatial scales using freshwater ecoregions may be less accurate or incongruent in some cases as large differences in environmental variables may hamper broadscale dietary patterns. This can be exemplified from this study with the observed similarity between Europe (central and western) and South America (Patagonia), but not to Iberia. The observed similarities/dissimilarities between freshwater ecoregions of North America is another example; we identified similarity of freshwater ecoregions of North America (Colorado and Middle Missouri) with New Zealand and Iberia, but not with Laurentian Great Lakes (North America). From a simplistic perspective, this suggests that Abell et al. (2008)'s regionalisation, based on the

similarity of fish composition (as a proxy of interspecific competition), is not a reliable predictor to establish biogeographic patterns in feeding of freshwater fish species. On the other hand, climatic domains linked to broad geographic zones are probably responsible of large-scale patterns among distant freshwater ecoregions. Taking the above-mentioned example among Europe (central and western), South America (Patagonia), and Iberia; we posit that climate-latitude analogies among these geographic zones are the key responsible of such dietary patterns, with environmental heterogeneity most likely being more similar between Patagonia and central and western of Europe than with Iberia. Hence, our findings support the view that latitude (as a proxy of climate-related geographical variability) can be a key predictor of diet patterns in animals (e.g. Clavero et al. 2003; Lozano et al. 2006; Zhou et al. 2011; Papacostas and Freestone 2016). However, we identified that this association was not linear, as previously assumed. Additionally, some freshwater ecoregions are big, and locations within the same freshwater ecoregion may largely differ in environmental conditions (e.g. meso- and macro-scale environmental variables), competitive interactions and prey composition, and consequently in diet patterns. Thus, the same ecoregion can vary in its degree of homogeneity (ecoregion heterogeneity) regarding meaningful habitat and/or landscape-scale environmental variables (e.g. Hughes et al. 1994; Giakoumi et al. 2013), which may hinder the delineation of patterns (here feeding) related to ecoregion boundary. Yet, we confirmed that diet composition may converge geographically at larger scales; for example, there are similarities in the observed diet compositions between northern Europe and South America. That said, our expectation that the diet composition is related with environmental and ecological conditions resulting in large-scale biogeographic patterns is supported, with climate-related geographical variability being responsible for such patterns.

518

519 This is also in agreement with Budy et al. (2013), who provided evidence of similarity in
520 the diet of brown trout among geographic regions. Budy et al. (2013) observed that diets of
521 brown trout in native habitats (Spain, Norway, Denmark) are dominated by invertebrates,
522 whereas the proportion of piscivory is higher outside the natural native range (United States
523 and New Zealand). Our findings do not support this view because piscivory was similar
524 between native and exotic territories, but also tended to be higher in freshwater ecoregions
525 of Scandinavia and northwest Russia than in the other studied freshwater ecoregions.
526 Instead, we identified that non-native populations consumed a higher proportion of
527 Mollusca, Coleoptera and Ephemeroptera. Thus, our results indicate that riverine brown
528 trout could not function as an apex predator throughout the distribution range. As a caveat,
529 caution should be exercised regarding this conclusion because our analyses did not include
530 large brown trout. Our study also demonstrates that the diet composition may be notably
531 different among distant freshwater ecoregions or regions belonging to different continents.
532 That said, the explanation of dietary patterns across larger spatial scales need to be placed
533 into a broader context taking into account climatic domains and environmental
534 heterogeneity (e.g. Hughes et al. 1994; Giakoumi et al. 2013; Stein et al. 2014). We suggest
535 that geographic location (latitude and elevation) as a proxy of environmental heterogeneity
536 is more important at smaller spatial scales, and climate at global extents, to understand
537 spatial patterns in feeding of aquatic organisms.

538

539 Our second hypothesis (site-specific prey communities will be associated with the diet
540 composition and biogeographic patterns in feeding) was partially supported. We argue that
541 variations in the diet of freshwater fish species can largely be explained by differences in

prey communities among geographic areas, suggesting the presence of bottom-up mechanisms directly affecting the trophic niche of the predator. Differences in prey communities based on environmental gradients lead to direct consequences for the niche use of brown trout. This premise is supported by the selectivity analyses indicating brown trout consumed specific prey resources (e.g. Ephemeroptera, Diptera or Plecoptera) irrespective of water temperature, altitude, or other environmental variables, although with some minor exceptions for a few other prey categories. We posit that patterns of diet composition are caused by differences in the importance of some groups within the available prey community. In fact, we identified five prey categories (Ephemeroptera, Diptera, Trichoptera, Plecoptera and surface prey) as the primary dietary components for brown trout, and these may also constitute the principal food resources inducing consistent biogeographic patterns in prey utilisation. These key dietary components of brown trout are abundant and widely found in riverine systems across the globe (Balian et al. 2008), often constituting important energy sources for fish (Cobo et al. 2000). However, the conclusion of this study about the importance of site-specific prey communities on biogeographic patterns in feeding should be treated with caution as it relies on a specific geographic zone (Norway), and more studies would be needed to corroborate or refute this at larger spatial scales.

Our third hypothesis (climatic factors may be responsible for the development of biogeographic feeding patterns of the model species) was only partially supported, likely because the effects of climate seem to be masked by the strong impact of the site-specific prey community compositions. Still, temperature gradients need to be acknowledged to understand the establishment of global biogeographic patterns in trophic ecology of brown

trout; most likely, because the distribution and abundance patterns of many aquatic insects, particularly those with narrower temperature limits for survival than brown trout, are highly linked to water temperature (e.g. Jeffree and Jeffree 1994; Bhowmik and Schäfer 2015). Our study provides novel insights into the importance of site-specific prey communities and temperature as key factors for the establishment and understanding of biogeographic patterns in the feeding of freshwater fish species. Previous studies have exemplified the influence of temperature on foraging habits of fish (O’Gorman et al. 2016) and temperature seasonality on the diet breadth of otters (Rheingantz et al. 2017) and on the proportion of fruit in the diet of monkeys (Coleman and Hill 2014). Similarly, our study supports the view that temperature and rainfall seasonality (i.e. climate-related seasonal differences among regions) are predictors of the diet composition of freshwater fish species. For example, the availability of pulsed terrestrial resources occurs primarily during summer, when aquatic invertebrate biomass usually is low (Nakano and Murakami 2001). Thus, diet patterns might change with seasonality, but always in line with considerations about climate-related geographical variability as exposed earlier.

This study also reveals an inverse association between mean annual temperature and the global dietary contribution of Copepoda, Ephemeroptera and Plecoptera, whereas there was a positive association with Crustacea, Mollusca, Megaloptera and Urodela. Concerning the primary dietary components of brown trout, different consequences of global warming are expected; Ephemeroptera, Diptera, Trichoptera and Plecoptera being negatively affected (Li et al. 2014; Bhowmik and Schäfer 2015) and surface prey being positively affected (Hannesdóttir et al. 2013; O’Gorman 2016). Moreover, stream insect communities are expected to become more homogeneous under global warming (Li et al. 2014), a fact that

would lead to more consistent patterns in trophic ecology of fish species with important consequences for niche utilisation and resource partitioning by competing consumers (e.g. Schoener 1974). Climate-driven diet changes are thus likely to lead biogeographical patterns and increasing importance of terrestrial subsidies in the future.

To conclude, our results highlight the importance of a multiscale perspective for a complete understanding of the environmental factors delineating diet patterns in freshwater fish species. We outlined how diet composition and biogeographic patterns in feeding of freshwater fish species can be explained by site-specific prey community structures and environmental gradients related to temperature via a bottom-up mechanism. Given that diversity loss will occur globally within many aquatic macroinvertebrate taxa under global warming, future climate-driven changes in the prey community structure through homogenisation are likely to strengthen biogeographic patterns in feeding (i.e. similar diets irrespective of local region), with possible consequences for invasiveness assessment and nature management and conservation.

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Figure legends

Fig. 1. World map showing the location of the sampling sites used in this study (brown trout feeding) and annual mean temperature ($^{\circ}\text{C}$).

Fig. 2. Abundance (%) of the primary dietary components for brown trout (Ephemeroptera, Diptera, Trichoptera, Plecoptera and surface prey). Data are displayed regionally (Norway, including 117 sampling events) and globally (including 275 sampling events). Dots overlaying each other indicate several sampling sites. Further details on the abundance of the remaining eleven ten categories (Copepoda, Crustacea, Mollusca, Megaloptera, Coleoptera, Heteroptera, Odonata, other benthic invertebrates, Urodela and fish) are presented in supporting information (Appendix 4.1).

Fig 3. A. Hierarchical cluster analysis with heatmaps on diet composition of brown trout associated with sampling events for the regional approach (Norway dataset). The five dashed squares show the optimal number of clusters (also indicated by different colours). Urodela and Odonata were not found in the stomach contents. B. Based on hierarchical clustering, the five main clusters mapped for each freshwater ecoregion. The numbers are references to the ecoregion ID given in Abell et al. (2008): Northern Baltic Drainages (405), Northern Baltic Drainages (406) and Barents Sea Drainages (407). Dots overlaying each other indicate several sampling sites.

Fig. 4. Violin plots showing the distribution of the data (percentage of abundance of different prey categories of brown trout) and its probability density. Data are displayed regionally (R, including 117 sampling events in Norgay) and globally (G, including 275

sampling events). The clusters for each approach (regional and global) are represented with a number and include the same colour as Fig. 3 and Fig. 8. The boxplot within each violin plot indicates the median and the interquartile range with the 95% confidence interval for the median. R = regional and G = global.

Fig. 5. Selectivity (Chesson's index) in the feeding of brown trout on the statistically significant prey categories (see Appendix 3.2 for linear regression statistics) for the regional approach (Norway dataset). Note that Chesson's index is based on proportional data, so no units are displayed. Significant linear trends with 95% confidence limits are shown.

Fig. 6. Canonical correspondence analysis (CCA) plot based on diet composition and environmental variables (latitude, elevation and Shannon-Wiener's diversity index) for the regional approach (Norway dataset). The five groups correspond with the identified clusters of Fig. 3.

Fig. 7. Generalised additive models (*GAMs*) explaining the association between diet composition (NMDS1) of brown trout and the environmental variables for the regional approach (Norway dataset). Observed data (open circles) and fitted values to the smoothing curve (red line) with 95% confidence bands (broken black line). Shannon and Latitude were only significant predictors.

Fig. 8. A. Hierarchical cluster analysis with heatmaps on global diet composition of brown trout associated with freshwater ecoregions. The dendrogram shows the dissimilarity in diet composition of brown trout among freshwater ecoregions. The heatmap is a colour-scaled

830 representation of the diet composition of brown trout for each freshwater ecoregion. B.
831 Based on hierarchical clustering, the two main clusters (blue and red) mapped for each
832 freshwater ecoregion. The numbers are references to the ecoregion ID given in Abell et al.
833 (2008): Laurentian Great Lakes (116), Colorado (130), Middle Missouri (143), South
834 Andean Pacific Slopes (341), Patagonia (348), Valdivian Lakes (349), Northern British
835 Isles (402), Cantabric Coast–Languedoc (403), Central and Western Europe (404),
836 Northern Baltic Drainages (405), Northern Baltic Drainages (406), Barents Sea Drainages
837 (407), Lake Onega–Lake Ladoga (409), Western Iberia (412), Eastern Iberia (414),
838 Dniester–Lower Danube (418), Western Transcaucasia (433) and New Zealand (811).
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Tables

Table 1. Summary table of the best model simulations for each prey category according to AIC values for the regional approach (Norway dataset). The parametric coefficients with significance values are given for each variable. Body size (mean values), prey diversity (Shannon = Shannon's diversity index) and prey abundance. Prey abundance refers to the specific relative prey abundance for each prey category (i.e. Trichoptera, Ephemeroptera, Plecoptera, etc). $***p < 0.001$, $**p < 0.01$ and $*p < 0.05$. Some prey categories (Odonata and Urodela) were not found in the stomach contents and no information about prey abundance was available for surface prey and fish (NA). Significant effect of the smooth term (+).

Variable	Intercept	Predictor variables			Smooth terms		Model fit R^2 (adjusted)
		Body size	Shannon	Prey abundance	Geographical coordinates	Elevation	
Copepoda	1.406**	-0.015**	—	—	—	+***	0.12
Crustacea	0.019	—	—	0.122***	—	+*	0.11
Mollusca	0.050	—	—	0.436***	—	—	0.19
Diptera	32.218***	-0.258***	—	0.279***	—	—	0.16
Trichoptera	1.279	0.211***	—	—	+**	—	0.19
Megaloptera	0.065	—	—	—	—	+**	0.05
Coleoptera	1.217	—	—	—	—	+	0.03
Heteroptera	-0.081	—	—	0.095	—	—	0.01
Ephemeroptera	13.517***	—	—	0.215**	+***	—	0.29
Plecoptera	13.160***	—	—	0.156	+**	—	0.10
Other benthos	8.430**	—	-4.571*	0.366***	+*	—	0.19
Surface prey	17.635	—	—	NA	+***	—	0.29
Fish	-2.545*	0.041**	—	NA	+***	+***	0.24

Table 2. Summary table of the best model simulations for each prey category according to AIC values for the global approach (worldwide dataset). The parametric coefficients with significance values are given for each variable. Annual mean temperature (BIO1), annual precipitation (BIO12) and precipitation seasonality (BIO15). *** $p < 0.001$, ** $p < 0.01$ and * $p < 0.05$. Significant effect of the smooth term (+).

Variable	Intercept	Predictor variables			Smooth terms			Model fit
		BIO1	BIO12	BIO15	Geographical coordinates	Elevation	Status (native/exotic)	R^2 (adjusted)
Copepoda	5.549*	-0.104***	-0.005***	0.247***	–	–	–	0.09
Crustacea	4.825	0.109*	–	-0.260	***	–	–	0.44
Mollusca	3.998	–	0.002**	-0.175***	–	***	***	0.35
Diptera	18.795*	–	–	–	–	***	+	0.08
Trichoptera	82.572	–	–	0.286	***	–	***	0.30
Megaloptera	0.287	0.001	–	–	–	–	–	0.01
Coleoptera	3.669**	–	–	-0.067	–	–	–	0.01
Heteroptera	-0.227	–	–	0.014*	–	–	–	0.01
Ephemeroptera	22.798***	-0.043	0.006	–	–	–	–	0.04
Plecoptera	3.206	-0.101***	0.009***	–	–	–	–	0.16
Odonata	-0.681***	0.002	–	0.027***	+	–	–	0.23
Other benthos	-1.014	–	0.003	–	–	–	–	0.09
Surface prey	17.330***	–	–	–	***	–	–	0.31
Urodela	-0.003*	0.001	–	0.001	–	–	–	0.02
Fish	0.899**	-0.006	–	–	–	–	–	0.01

Fig. 1. World map showing the location of the sampling sites used in this study (brown trout feeding) and annual mean temperature (°C).

94x57mm (300 x 300 DPI)

Fig. 2. Abundance (%) of the primary dietary components for brown trout (Ephemeroptera, Diptera, Trichoptera, Plecoptera and surface prey). Data are displayed regionally (Norway, including 117 sampling events) and globally (including 275 sampling events). Dots overlaying each other indicate several sampling sites. Further details on the abundance of the remaining eleven ten categories (Copepoda, Crustacea, Mollusca, Megaloptera, Coleoptera, Heteroptera, Odonata, other benthic invertebrates, Urodela and fish) are presented in supporting information (Appendix S4.1).

137x168mm (300 x 300 DPI)

Fig 3. A. Hierarchical cluster analysis with heatmaps on diet composition of brown trout associated with sampling events for the regional approach (Norway dataset). The five dashed squares show the optimal number of clusters (also indicated by different colours). Urodela and Odonata were not found in the stomach contents. B. Based on hierarchical clustering, the five main clusters mapped for each freshwater ecoregion. The numbers are references to the ecoregion ID given in Abell et al. (2008): Northern Baltic Drainages (405), Northern Baltic Drainages (406) and Barents Sea Drainages (407). Dots overlaying each other indicate several sampling sites.

206x282mm (300 x 300 DPI)

Fig. 4. Violin plots showing the distribution of the data (percentage of abundance of different prey categories of brown trout) and its probability density. Data are displayed regionally (R, including 117 sampling events in Norgay) and globally (G, including 275 sampling events). The clusters for each approach (regional and global) are represented with a number and include the same colour as Fig. 3 and Fig. 8. The boxplot within each violin plot indicates the median and the interquartile range with the 95% confidence interval for the median. R = regional and G = global.

191x93mm (300 x 300 DPI)

Fig. 5. Selectivity (Chesson's index) in the feeding of brown trout on the statistically significant prey categories (see Appendix S3.2 for linear regression statistics) for the regional approach (Norway dataset). Note that Chesson's index is based on proportional data, so no units are displayed. Significant linear trends with 95% confidence limits are shown.

121x148mm (300 x 300 DPI)

Fig. 6. Canonical correspondence analysis (CCA) plot based on diet composition and environmental variables (latitude, elevation and Shannon-Wiener’s diversity index) for the regional approach (Norway dataset). The five groups correspond with the identified clusters of Fig. 3.

122x97mm (300 x 300 DPI)

Fig. 7. Generalised additive models (GAMs) explaining the association between diet composition (NMDS1) of brown trout and the environmental variables for the regional approach (Norway dataset). Observed data (open circles) and fitted values to the smoothing curve (red line) with 95% confidence bands (broken black line). Shannon and Latitude were only significant predictors.

90x173mm (300 x 300 DPI)

Fig. 8. A. Hierarchical cluster analysis with heatmaps on global diet composition of brown trout associated with freshwater ecoregions. The dendrogram shows the dissimilarity in diet composition of brown trout among freshwater ecoregions. The heatmap is a colour-scaled representation of the diet composition of brown trout for each freshwater ecoregion. B. Based on hierarchical clustering, the two main clusters (blue and red) mapped for each freshwater ecoregion. The numbers are references to the ecoregion ID given in Abell et al. (2008): Laurentian Great Lakes (116), Colorado (130), Middle Missouri (143), South Andean Pacific Slopes (341), Patagonia (348), Valdivian Lakes (349), Northern British Isles (402), Cantabric Coast-Languedoc (403), Central and Western Europe (404), Northern Baltic Drainages (405), Northern Baltic Drainages (406), Barents Sea Drainages (407), Lake Onega-Lake Ladoga (409), Western Iberia (412), Eastern Iberia (414), Dniester-Lower Danube (418), Western Transcaucasia (433) and New Zealand (811).

Appendix material to 'Drivers of diet patterns in a globally distributed freshwater fish species'

Javier Sánchez-Hernández, Anders G. Finstad, Jo Vegar Arnekleiv, Gaute Kjærstad and Per-Arne Amundsen

List of items in the appendix material:

-Appendix 1. Information about the sampling sites from the Norwegian water courses and the literature review (including the full reference list).

-Appendix 2. Correlation among the bioclim variables.

-Appendix 3. Extended output and additional analyses focus on Norway (regional approach), including residual plots for the modelling (both generalised additive models – *GAMs* and generalised additive mixed models – *GAMMs*).

3.1: Correlation plot.

3.2: Brown trout selectivity (*PCoA* and linear regression analysis).

3.3: Generalised additive models (*GAMs*).

3.4: Residual structure (*GAMMs*).

3.5: Spatial correlation (*GAMMs*).

-Appendix 4. Extended output and additional analyses for the global approach (worldwide), including residual plots for the modelling (both generalised additive models – *GAMs* and generalised additive mixed models – *GAMMs*).

4.1: Prey abundance (%).

4.2: Differences in prey abundance (%) between native and exotic populations.

4.3: Correlation plot.

4.4: Hierarchical cluster analysis.

4.5: Canonical correspondence analysis (*CCA*).

4.6: Generalised additive models (*GAMs*).

4.7: Residual structure (*GAMMs*).

4.8: Spatial correlation (*GAMMs*).

-Appendix 1. Information about the sampling sites from the Norwegian water courses and the literature review (including the full reference list).

This appendix includes information about the sampling sites from the Norwegian water courses (Table A1) and the literature review (Table A2).

Table A1. Information about the sampling sites from the Norwegian water courses (regional approach).

Code	River	Country	Freshwater ecoregion	Latitude	Longitude	Elevation (m)	Date	Sample size (n)	Mean length (mm)	Shannon index (benthos)	Dominant prey	Cluster
1	Altaelva	Norway	407	69.91	23.28	12	02/05/1994	9	81.9	1.01	Ephemeroptera	1
2	Altaelva	Norway	407	69.91	23.28	12	10/09/1996	14	78.3	1.22	Plecoptera	2
3	Altaelva	Norway	407	69.91	23.28	12	12/08/1996	8	54.8	0.86	Diptera	4
4	Altaelva	Norway	407	69.91	23.28	12	15/08/1994	5	80.4	1.49	Diptera	4
5	Altaelva	Norway	407	69.91	23.28	12	21/09/2001	5	74.2	1.72	Diptera	4
6	Altaelva	Norway	407	69.91	23.28	13	26/07/1995	5	99.3	1.48	Diptera	4
7	Beiarelva	Norway	405	67.00	14.62	7	04/09/1990	119	74.9	1.22	Trichoptera	5
8	Beiarelva	Norway	405	67.00	14.62	7	04/10/1990	24	84.7	1.07	Ephemeroptera	2
9	Beiarelva	Norway	405	66.84	14.67	119	04/10/1990	26	88.7	1.10	Ephemeroptera	5
10	Beiarelva	Norway	405	66.78	14.60	117	04/10/1990	28	104.3	1.02	Ephemeroptera	1
11	Beiarelva	Norway	405	66.78	14.60	117	05/08/1990	89	82.5	1.01	Trichoptera	4
12	Beiarelva	Norway	405	66.84	14.67	119	05/09/1990	107	78.5	0.99	Trichoptera	5
13	Beiarelva	Norway	405	67.00	14.62	7	06/06/1990	27	88.9	1.61	Ephemeroptera	1
14	Beiarelva	Norway	405	67.00	14.62	7	06/08/1990	95	73.0	1.48	Trichoptera	5
15	Beiarelva	Norway	405	67.00	14.62	7	08/09/1992	135	63.1	1.49	Plecoptera	5
16	Beiarelva	Norway	405	66.84	14.67	119	08/09/1992	105	62.5	1.19	Diptera	5
17	Beiarelva	Norway	405	66.78	14.60	117	09/09/1992	81	61.3	1.21	Ephemeroptera	1
18	Beiarelva	Norway	405	67.00	14.62	7	13/08/1991	115	71.9	1.35	Diptera	5
19	Beiarelva	Norway	405	66.78	14.60	117	13/08/1991	9	45.8	0.89	Diptera	4
20	Beiarelva	Norway	405	66.84	14.67	119	14/08/1991	108	71.8	1.26	Diptera	4
21	Beiarelva	Norway	405	66.78	14.60	117	14/08/1991	120	76.6	0.89	Diptera	4
22	Beiarelva	Norway	405	66.84	14.67	119	17/10/1989	145	90.7	1.34	Ephemeroptera	2
23	Beiarelva	Norway	405	67.00	14.62	7	18/10/1989	134	81.7	1.44	Ephemeroptera	1
24	Beiarelva	Norway	405	66.78	14.60	117	18/10/1989	91	91.8	0.52	Ephemeroptera	1
25	Beiarelva	Norway	405	66.84	14.67	119	19/08/1992	79	63.6	1.05	Diptera	5
26	Beiarelva	Norway	405	67.00	14.62	7	20/08/1992	138	63.6	1.08	Diptera	4
27	Beiarelva	Norway	405	66.78	14.60	117	20/08/1992	101	60.4	0.77	Ephemeroptera	5
28	Beiarelva	Norway	405	67.00	14.62	7	21/04/1990	102	72.9	1.02	Plecoptera	2
29	Beiarelva	Norway	405	66.84	14.67	119	21/04/1990	88	92.7	1.19	Plecoptera	2
30	Beiarelva	Norway	405	66.78	14.60	117	22/04/1990	64	100.5	0.00	Plecoptera	2
31	Beiarelva	Norway	405	67.00	14.62	7	23/06/1992	66	62.9	1.40	Ephemeroptera	1
32	Beiarelva	Norway	405	66.84	14.67	119	23/06/1992	26	62.5	1.49	Ephemeroptera	1
33	Beiarelva	Norway	405	66.78	14.60	117	23/06/1992	20	62.3	1.29	Ephemeroptera	1
34	Beiarelva	Norway	405	67.00	14.62	7	24/04/1991	33	83.8	1.04	Ephemeroptera	1
35	Beiarelva	Norway	405	66.84	14.67	119	24/04/1991	34	100.7	1.09	Ephemeroptera	2
36	Beiarelva	Norway	405	66.78	14.60	117	24/04/1991	49	95.8	0.90	Plecoptera	2
37	Beiarelva	Norway	405	67.00	14.62	7	26/04/1989	96	68.9	0.96	Plecoptera	4
38	Beiarelva	Norway	405	66.84	14.67	119	26/04/1989	67	88.5	1.26	Trichoptera	5
39	Beiarelva	Norway	405	66.78	14.60	117	26/04/1989	48	98.4	1.11	Plecoptera	2
40	Beiarelva	Norway	405	66.84	14.67	119	29/04/1992	59	87.5	1.12	Plecoptera	2
41	Beiarelva	Norway	405	66.78	14.60	117	29/04/1992	42	99.1	1.31	Ephemeroptera	2
42	Beiarelva	Norway	405	66.78	14.60	117	29/07/1989	82	88.5	1.24	Ephemeroptera	5
43	Beiarelva	Norway	405	67.00	14.62	7	30/04/1992	52	64.5	1.12	Plecoptera	2
44	Beiarelva	Norway	405	67.00	14.62	7	30/07/1989	113	81.2	0.94	Ephemeroptera	5
45	Beiarelva	Norway	405	66.78	14.60	117	31/07/1989	17	68.6	1.24	Ephemeroptera	4
46	Gaula	Norway	405	63.05	10.30	64	20/10/1989	17	46.9	0.39	Surface prey	3
47	Gaula	Norway	405	63.06	10.30	199	20/10/1989	5	47.1	1.21	Surface prey	3
48	Gaula	Norway	405	63.05	10.30	64	25/08/1988	8	69.0	1.42	Diptera	4
49	Gaula	Norway	405	63.06	10.30	199	25/08/1988	5	66.4	1.37	Surface prey	3
50	Gaula	Norway	405	63.05	10.30	64	29/08/1989	18	44.6	1.05	Diptera	4
51	Gaula	Norway	405	63.06	10.30	199	29/08/1989	10	44.9	1.75	Surface prey	4
52	Gaula	Norway	405	63.05	10.30	64	30/06/1988	12	59.1	1.89	Ephemeroptera	5
53	Gaula	Norway	405	63.06	10.30	199	30/06/1988	10	40.2	1.86	Ephemeroptera	4
54	Klubbvasselva	Norway	406	65.70	13.20	74	03/10/1990	20	97.6	1.22	Ephemeroptera	5
55	Klubbvasselva	Norway	406	65.72	13.19	168	03/10/1990	68	83.5	0.83	Plecoptera	2
56	Klubbvasselva	Norway	406	65.70	13.20	74	04/08/1988	11	87.4	1.78	Other benthos	5
57	Klubbvasselva	Norway	406	65.70	13.20	106	04/08/1988	54	86.9	1.56	Surface prey	5
58	Klubbvasselva	Norway	406	65.71	13.20	149	04/08/1988	16	48.7	1.86	Surface prey	4
59	Klubbvasselva	Norway	406	65.72	13.19	146	05/08/1988	12	86.2	1.61	Surface prey	3
60	Klubbvasselva	Norway	406	65.72	13.19	168	05/08/1988	62	61.6	1.48	Diptera	4
61	Klubbvasselva	Norway	406	65.70	13.20	74	08/06/1990	9	70.2	1.15	Plecoptera	2
62	Klubbvasselva	Norway	406	65.72	13.19	168	08/06/1990	21	57.3	1.36	Plecoptera	2
63	Klubbvasselva	Norway	406	65.70	13.20	74	08/08/1991	6	104.1	1.52	Surface prey	3
64	Klubbvasselva	Norway	406	65.70	13.20	106	08/08/1991	47	81.8	1.52	Diptera	4

65	Klubbvasselva	Norway	406	65.71	13.20	149	09/08/1991	24	51.3	1.62	Diptera	4
66	Klubbvasselva	Norway	406	65.72	13.19	146	09/08/1991	33	48.2	1.48	Diptera	4
67	Klubbvasselva	Norway	406	65.70	13.20	74	10/08/1989	16	64.3	1.96	Surface prey	5
68	Klubbvasselva	Norway	406	65.70	13.20	106	10/08/1989	11	86.6	1.87	Surface prey	3
69	Klubbvasselva	Norway	406	65.72	13.19	146	10/08/1992	11	89.2	0.65	Ephemeroptera	5
70	Klubbvasselva	Norway	406	65.72	13.19	168	10/08/1992	51	96.1	1.22	Diptera	4
71	Klubbvasselva	Norway	406	65.72	13.19	146	11/08/1989	5	59.9	1.81	Surface prey	3
72	Klubbvasselva	Norway	406	65.72	13.19	168	11/08/1989	47	60.2	1.78	Ephemeroptera	5
73	Klubbvasselva	Norway	406	65.70	13.20	74	11/08/1992	6	98.7	1.49	Surface prey	5
74	Klubbvasselva	Norway	406	65.70	13.20	106	11/08/1992	30	93.9	1.50	Diptera	5
75	Klubbvasselva	Norway	406	65.70	13.20	74	12/10/1989	14	82.3	1.10	Trichoptera	5
76	Klubbvasselva	Norway	406	65.72	13.19	168	12/10/1989	26	55.7	1.39	Trichoptera	5
77	Klubbvasselva	Norway	406	65.70	13.20	74	14/10/1992	17	95.3	1.44	Trichoptera	5
78	Klubbvasselva	Norway	406	65.72	13.19	168	14/10/1992	33	96.4	1.08	Plecoptera	2
79	Klubbvasselva	Norway	406	65.70	13.20	74	15/08/1990	14	85.6	1.52	Other benthos	5
80	Klubbvasselva	Norway	406	65.70	13.20	106	15/08/1990	29	88.3	1.52	Diptera	5
81	Klubbvasselva	Norway	406	65.70	13.20	74	15/10/1991	19	93.2	1.22	Ephemeroptera	1
82	Klubbvasselva	Norway	406	65.72	13.19	168	15/10/1991	28	103.8	0.99	Plecoptera	2
83	Klubbvasselva	Norway	406	65.71	13.20	149	16/08/1990	7	68.3	1.62	Diptera	5
84	Klubbvasselva	Norway	406	65.72	13.19	146	16/08/1990	14	77.0	1.74	Surface prey	3
85	Klubbvasselva	Norway	406	65.70	13.20	74	25/06/1991	6	96.7	1.29	Trichoptera	5
86	Klubbvasselva	Norway	406	65.72	13.19	168	25/06/1991	7	91.4	1.59	Trichoptera	4
87	Klubbvasselva	Norway	406	65.70	13.20	74	25/06/1992	11	89.2	1.63	Ephemeroptera	5
88	Klubbvasselva	Norway	406	65.72	13.19	168	25/06/1992	21	86.6	1.51	Ephemeroptera	5
89	Litjvasselva	Norway	406	65.55	13.65	352	03/08/1988	8	90.3	1.30	Surface prey	3
90	Litjvasselva	Norway	406	65.58	13.74	468	05/09/1990	5	84.6	0.80	Plecoptera	2
91	Litjvasselva	Norway	406	65.58	13.74	438	06/08/1991	19	79.7	1.24	Diptera	4
92	Litjvasselva	Norway	406	65.55	13.65	352	07/08/1991	88	71.0	1.59	Diptera	4
93	Litjvasselva	Norway	406	65.58	13.74	438	08/08/1989	6	128.5	0.90	Diptera	4
94	Litjvasselva	Norway	406	65.58	13.74	468	08/08/1989	5	125.0	1.07	Surface prey	3
95	Litjvasselva	Norway	406	65.53	13.61	233	09/08/1989	9	135.5	1.95	Ephemeroptera	5
96	Litjvasselva	Norway	406	65.55	13.65	352	09/08/1989	16	114.9	1.78	Ephemeroptera	5
97	Litjvasselva	Norway	406	65.58	13.74	438	10/08/1992	5	106.4	1.54	Surface prey	5
98	Litjvasselva	Norway	406	65.58	13.74	468	10/08/1992	9	125.6	1.64	Trichoptera	5
99	Litjvasselva	Norway	406	65.58	13.74	468	11/10/1989	5	148.2	0.62	Trichoptera	5
100	Litjvasselva	Norway	406	65.58	13.74	438	13/08/1990	6	78.6	1.33	Diptera	4
101	Litjvasselva	Norway	406	65.58	13.74	468	13/08/1990	7	119.4	0.77	Diptera	4
102	Litjvasselva	Norway	406	65.58	13.74	468	14/06/1990	5	144.8	1.41	Trichoptera	4
103	Litjvasselva	Norway	406	65.55	13.65	352	14/08/1990	97	63.1	0.91	Ephemeroptera	1
104	Litjvasselva	Norway	406	65.58	13.74	468	15/10/1992	5	118.4	1.57	Plecoptera	2
105	Litjvasselva	Norway	406	65.58	13.74	468	16/10/1991	22	101.1	0.90	Plecoptera	2
106	Litjvasselva	Norway	406	65.58	13.74	468	26/06/1991	8	109.6	1.77	Plecoptera	2
107	Litjvasselva	Norway	406	65.58	13.74	468	26/06/1992	9	97.2	1.81	Plecoptera	2
108	Litjvasselva	Norway	406	65.55	13.65	352	29/07/1986	9	39.2	1.48	Diptera	5
109	Reisa	Norway	407	69.74	21.10	6	August-2004	29	44.4	1.14	Surface prey	3
110	Reisa	Norway	407	69.75	21.10	10	August-2004	54	83.4	1.40	Trichoptera	5
111	Reisa	Norway	407	69.76	21.03	3	August-2004	34	82.6	1.22	Trichoptera	5
112	Reisa	Norway	407	69.57	21.30	79	August-2004	68	71.8	1.08	Trichoptera	5
113	Reisa	Norway	407	69.72	21.21	15	August-2004	64	75.2	1.15	Surface prey	3
114	Reisa	Norway	407	69.65	21.30	49	August-2004	6	82.0	1.24	Surface prey	3
115	Reisa	Norway	407	69.75	21.07	6	August-2004	5	48.7	1.26	Diptera	4
116	Stjørdalselva	Norway	405	63.45	10.91	6	09/09/2003	5	124.5	1.04	Trichoptera	5
117	Stjørdalselva	Norway	405	63.45	10.91	6	11/09/2003	7	58.5	1.57	Surface prey	3

Table A2. Information about the sampling sites from the literature review (global approach). *Juveniles (<200 mm) without length measure.

Code	River	Country	Freshwater ecoregion	Latitude	Longitude	Elevation (m)	Sample size (n)	Max length (cm)	Mean length (cm)	Dominant prey	Source
1	Allt a Choire Dhuibh	UK	402	57.16	-3.61	500	NA	*	*	Surface prey	Bridcut (2000)
2	Allt Bheadhair	UK	402	57.19	-3.62	380	NA	*	*	Diptera	Bridcut (2000)
3	Allt Bheadhair	UK	402	57.19	-3.62	380	NA	*	*	Diptera	Bridcut (2000)
4	Aullóns	Spain	403	43.23	-8.89	10	17	17.6	*	Surface prey	Sánchez-Hernández (2009)
5	Aullóns	Spain	403	43.23	-8.89	10	2	9.4	*	Diptera	Sánchez-Hernández (2009)
6	Ansjöån	Sweden	406	63.00	16.08	246	NA	*	*	Ephemeroptera	Degerman et al (2000)
7	Ansjöån	Sweden	406	63.00	16.08	246	NA	*	*	Surface prey	Degerman et al (2000)
8	Black Brows Beck	UK	404	54.32	-3.01	69	12	*	*	Crustacea	McCormack (1962)
9	Black Brows Beck	UK	404	54.32	-3.01	69	20	*	*	Ephemeroptera	McCormack (1962)
10	Black Brows Beck	UK	404	54.32	-3.01	69	10	*	*	Surface prey	McCormack (1962)
11	Black Brows Beck	UK	404	54.32	-3.01	69	13	*	*	Ephemeroptera	McCormack (1962)
12	Black Brows Beck	UK	404	54.32	-3.01	69	9	*	*	Crustacea	McCormack (1962)
13	Black Brows Beck	UK	404	54.32	-3.01	69	33	*	*	Ephemeroptera	McCormack (1962)
14	Black Brows Beck	UK	404	54.32	-3.01	69	8	*	*	Trichoptera	McCormack (1962)
15	Black Brows Beck	UK	404	54.32	-3.01	69	15	*	*	Surface prey	McCormack (1962)
16	Black Brows Beck	UK	404	54.32	-3.01	69	39	*	*	Ephemeroptera	McCormack (1962)
17	Black Brows Beck	UK	404	54.32	-3.01	69	8	*	*	Diptera	McCormack (1962)
18	Black Brows Beck	UK	404	54.32	-3.01	69	24	*	*	Diptera	McCormack (1962)
19	Black Brows Beck	UK	404	54.32	-3.01	69	91	*	*	Diptera	McCormack (1962)
20	Black Brows Beck	UK	404	54.32	-3.01	69	55	*	*	Diptera	McCormack (1962)
21	Black Brows Beck	UK	404	54.32	-3.01	69	38	*	*	Diptera	McCormack (1962)

22	Black Brows Beck	UK	404	54.32	-3.01	69	44	*	*	Diptera	McCormack (1962)
23	Bol'shaya Uya	Russia	409	61.57	35.57	33	NA	20	*	Surface prey	Shustov et al. (2008)
24	Bueno	Chile	349	40.38	-73.00	26	33	13	*	Plecoptera	Arisemendi et al. (2012)
25	Chillán	Chile	341	36.63	-72.31	62	20	*	*	Diptera	Berrios et al. (2002)
26	Coruh	Turkey	433	40.82	41.66	553	NA	8.9	*	Trichoptera	Becer Ozvarol et al. (2011)
27	Coruh	Turkey	433	40.82	41.66	553	NA	11.9	*	Trichoptera	Becer Ozvarol et al. (2011)
28	Coruh	Turkey	433	40.82	41.66	553	NA	14.9	*	Surface prey	Becer Ozvarol et al. (2011)
29	Coruh	Turkey	433	40.82	41.66	553	NA	5.9	*	Diptera	Becer Ozvarol et al. (2011)
30	Dalgety	New Zealand	811	44.32	170.58	857	10	3	*	Diptera	Fochney (1988)
31	Douglas Creek	USA	143	41.08	-106.30	2230	24	5.8	*	Ephemeroptera	Hubert et al. (1993)
32	Douglas Creek	USA	143	41.12	-106.25	2600	23	5	*	Ephemeroptera	Hubert et al. (1993)
33	Douglas Creek	USA	143	41.12	-106.25	2600	26	3.9	*	Ephemeroptera	Hubert et al. (1993)
34	Douglas Creek	USA	143	41.08	-106.30	2230	22	4.2	*	Ephemeroptera	Hubert et al. (1993)
35	Douglas Creek	USA	143	41.19	-106.27	2840	25	4.1	*	Diptera	Hubert et al. (1993)
36	Douglas Creek	USA	143	41.08	-106.30	2230	13	2.9	*	Diptera	Hubert et al. (1993)
37	Douglas Creek	USA	143	41.19	-106.27	2840	40	3.4	*	Diptera	Hubert et al. (1993)
38	Douglas Creek	USA	143	41.12	-106.25	2600	29	2.8	*	Diptera	Hubert et al. (1993)
39	Douglas Creek	USA	143	41.19	-106.27	2840	29	2.3	*	Diptera	Hubert et al. (1993)
40	Endrick system	UK	402	56.05	-4.42	18	NA	15	*	Surface prey	Maitland (1965)
41	Endrick system	UK	402	56.05	-4.42	18	NA	*	*	Surface prey	Maitland (1965)
42	Erro	Spain	414	43.00	-1.40	810	41	9.7	*	Ephemeroptera	Oscoz et al. (2005)
43	Estibère	France	403	42.84	0.19	2050	28	17	*	Ephemeroptera	Elliott (1973)
44	Estibère	France	403	42.84	0.19	2050	22	17	*	Ephemeroptera	Elliott (1973)
45	Estibère	France	403	42.84	0.19	2050	12	17	*	Diptera	Elliott (1973)
46	Estibère	France	403	42.84	0.19	2050	12	17	*	Diptera	Elliott (1973)
47	Forss	UK	402	58.44	-3.67	134	30	*	6.1	Ephemeroptera	Frost (1950)
48	Furelos	Spain	403	42.87	-8.02	411	20	17	*	Surface prey	Sánchez-Hernández (2009)
49	Furelos	Spain	403	42.87	-8.02	411	37	8.7	*	Diptera	Sánchez-Hernández (2009)
50	Grout Brook	USA	116	42.76	-76.27	267	18	7.4	*	Surface prey	Johnson and McKenna (2015)
51	Grout Brook	USA	116	42.76	-76.27	267	20	7.8	*	Crustacea	Johnson and McKenna (2015)
52	Grout Brook	USA	116	42.76	-76.27	267	14	8.4	*	Trichoptera	Johnson and McKenna (2015)
53	Grout Brook	USA	116	42.76	-76.27	267	18	7.2	*	Surface prey	Johnson and McKenna (2015)
54	Grout Brook	USA	116	42.76	-76.27	267	16	7.5	*	Coleoptera	Johnson and McKenna (2015)
55	Grout Brook	USA	116	42.76	-76.27	267	18	7.9	*	Surface prey	Johnson and McKenna (2015)
56	Inгла	Spain	414	42.34	1.78	1140	19	9.6	*	Diptera	Montori et al. (2006)
57	King's Well Beck	UK	404	54.57	-2.59	148	16	*	*	Ephemeroptera	McCormack (1962)
58	King's Well Beck	UK	404	54.57	-2.59	148	19	*	*	Ephemeroptera	McCormack (1962)
59	King's Well Beck	UK	404	54.57	-2.59	148	17	*	*	Ephemeroptera	McCormack (1962)
60	King's Well Beck	UK	404	54.57	-2.59	148	9	*	*	Coleoptera	McCormack (1962)
61	King's Well Beck	UK	404	54.57	-2.59	148	13	*	*	Ephemeroptera	McCormack (1962)
62	King's Well Beck	UK	404	54.57	-2.59	148	11	*	*	Ephemeroptera	McCormack (1962)
63	King's Well Beck	UK	404	54.57	-2.59	148	23	*	*	Ephemeroptera	McCormack (1962)
64	King's Well Beck	UK	404	54.57	-2.59	148	11	*	*	Ephemeroptera	McCormack (1962)
65	King's Well Beck	UK	404	54.57	-2.59	148	10	*	*	Ephemeroptera	McCormack (1962)
66	King's Well Beck	UK	404	54.57	-2.59	148	8	*	*	Ephemeroptera	McCormack (1962)
67	King's Well Beck	UK	404	54.57	-2.59	148	35	*	*	Diptera	McCormack (1962)
68	King's Well Beck	UK	404	54.57	-2.59	148	14	*	*	Diptera	McCormack (1962)
69	King's Well Beck	UK	404	54.57	-2.59	148	11	*	*	Diptera	McCormack (1962)
70	King's Well Beck	UK	404	54.57	-2.59	148	63	*	*	Diptera	McCormack (1962)
71	Kuusinkijoki	Finland	407	66.24	29.71	151	47	*	12.2	Trichoptera	Kreivi et al. (1999)
72	Kuusinkijoki	Finland	407	66.24	29.71	151	77	*	6.2	Trichoptera	Kreivi et al. (1999)
73	Kuusinkijoki	Finland	407	66.24	29.71	151	79	*	6.8	Ephemeroptera	Kreivi et al. (1999)
74	Kuusinkijoki	Finland	407	66.24	29.71	151	78	*	7	Ephemeroptera	Kreivi et al. (1999)
75	Kuusinkijoki	Finland	407	66.24	29.71	151	35	*	11	Trichoptera	Kreivi et al. (1999)
76	Kuusinkijoki	Finland	407	66.24	29.71	151	41	*	8.3	Ephemeroptera	Kreivi et al. (1999)
77	Kuusinkijoki	Finland	407	66.24	29.71	151	54	*	5.4	Ephemeroptera	Kreivi et al. (1999)
78	Kuusinkijoki	Finland	407	66.24	29.71	151	42	*	9.6	Diptera	Kreivi et al. (1999)
79	Kuusinkijoki	Finland	407	66.24	29.71	151	40	*	11.1	Diptera	Kreivi et al. (1999)
80	Kuusinkijoki	Finland	407	66.24	29.71	151	80	*	4	Diptera	Kreivi et al. (1999)
81	Ladra	Spain	412	43.15	-7.69	395	31	8.8	*	Diptera	Sánchez-Hernández et al. (2011)
82	Larraun	Spain	414	42.91	-1.84	430	NA	*	*	Ephemeroptera	Oscoz et al. (2000)
83	Larraun	Spain	414	42.96	-1.83	472	185	11	*	Ephemeroptera	Oscoz et al. (2008)
84	Larraun	Spain	414	42.96	-1.83	472	185	11	*	Ephemeroptera	Oscoz et al. (2008)
85	Larraun	Spain	414	42.96	-1.83	472	185	11	*	Crustacea	Oscoz et al. (2008)
86	Lengüelle	Spain	403	42.98	-8.46	164	12	13.9	*	Diptera	Sánchez-Hernández (2009)
87	Lengüelle	Spain	403	42.98	-8.46	164	6	7.2	*	Diptera	Sánchez-Hernández (2009)
88	Lissuraga	France	403	43.28	-1.61	133	NA	*	*	Mollusca	Neveu and Thibault (1977)
89	Lissuraga	France	403	43.28	-1.61	133	NA	*	*	Ephemeroptera	Neveu and Thibault (1977)
90	Lissuraga	France	403	43.28	-1.61	133	NA	*	*	Ephemeroptera	Neveu and Thibault (1977)
91	Lissuraga	France	403	43.28	-1.61	133	NA	*	*	Ephemeroptera	Neveu and Thibault (1977)
92	Llico	Chile	349	41.18	-73.69	10	67	13	*	Surface prey	Arisemendi et al. (2012)
93	Lopuszanka	Poland	404	49.47	20.13	565	6	*	6.2	Trichoptera	Witkowski et al. (1994)
94	Lopuszanka	Poland	404	49.47	20.13	565	5	*	9.5	Surface prey	Witkowski et al. (1994)
95	Nethy	UK	402	57.23	-3.62	300	75	*	*	Surface prey	Bridcut (2000)
96	Orzega	Russia	409	61.57	35.57	33	NA	20	*	Surface prey	Shustov et al. (2008)
97	Pescado	Chile	349	41.28	-72.73	214	164	13	*	Ephemeroptera	Arisemendi et al. (2012)
98	Pichi leufu	Argentina	348	40.61	-70.66	590	79	15	*	Ephemeroptera	Ferriz (1993)
99	Pigüefía	Spain	403	43.35	-6.20	93	23	10	*	Diptera	Suarez et al. (1988)
100	Pigüefía	Spain	403	43.35	-6.20	93	20	15	*	Diptera	Suarez et al. (1988)
101	Pulonga	Russia	407	66.55	39.69	166	32	*	3.5	Surface prey	Yevsin and Ivanov (1979)
102	Rakaia	New Zealand	811	43.75	172.04	103	36	10	*	Ephemeroptera	Sagar and Eldon (1983)
103	Rensjön	Sweden	406	68.02	19.83	481	11	*	*	Copepoda	Nilsson (1957)

104	Rensjön	Sweden	406	68.02	19.83	481	23	*	*	Copepoda	Nilsson (1957)
105	Rensjön	Sweden	406	68.02	19.83	481	7	*	*	Ephemeroptera	Nilsson (1957)
106	Rensjön	Sweden	406	68.02	19.83	481	8	*	*	Surface prey	Nilsson (1957)
107	Rensjön	Sweden	406	68.02	19.83	481	19	*	*	Copepoda	Nilsson (1957)
108	Rensjön	Sweden	406	68.02	19.83	481	7	*	*	Ephemeroptera	Nilsson (1957)
109	Rensjön	Sweden	406	68.02	19.83	481	22	*	*	Diptera	Nilsson (1957)
110	Rensjön	Sweden	406	68.02	19.83	481	18	*	*	Diptera	Nilsson (1957)
111	Rensjön	Sweden	406	68.02	19.83	481	12	*	*	Diptera	Nilsson (1957)
112	Riobo	Spain	403	42.75	-8.42	65	15	*	6.6	Ephemeroptera	Santamarina (1993)
113	Rois	Spain	403	42.77	-8.66	75	32	17.4	*	Surface prey	Sánchez-Hernández (2009)
114	Santa Lucia	Spain	403	42.85	-8.51	143	24	16.9	*	Surface prey	Sánchez-Hernández (2009)
115	Sar	Spain	403	42.78	-8.66	70	26	18.5	*	Diptera	Sánchez-Hernández (2009)
116	Shag	New Zealand	811	45.45	170.69	237	30	8.4	*	Ephemeroptera	Sagar and Glova (1995)
117	Shag	New Zealand	811	45.45	170.69	237	30	8.2	*	Trichoptera	Sagar and Glova (1995)
118	Shag	New Zealand	811	45.45	170.69	237	30	8.9	*	Trichoptera	Sagar and Glova (1995)
119	Shipot	Ukraine	418	48.74	22.84	391	15	13	*	Ephemeroptera	Kruzhylina and Didenko (2011)
120	Snällersödsån	Sweden	406	56.02	13.42	91	NA	12.5	*	Surface prey	Greenberg and Dahl (1998)
121	Snällersödsån	Sweden	406	56.02	13.42	91	NA	12.5	*	Surface prey	Greenberg and Dahl (1998)
122	Snällersödsån	Sweden	406	56.02	13.42	91	NA	12.5	*	Surface prey	Greenberg and Dahl (1998)
123	Snällersödsån	Sweden	406	56.02	13.42	91	NA	12.5	*	Crustacea	Greenberg and Dahl (1998)
124	Snällersödsån	Sweden	406	56.02	13.42	91	NA	12.5	*	Crustacea	Greenberg and Dahl (1998)
125	Snällersödsån	Sweden	406	56.02	13.42	91	NA	12.5	*	Crustacea	Greenberg and Dahl (1998)
126	Stampen	Sweden	406	55.67	13.22	9	17	*	*	Crustacea	Otto (1976)
127	Stampen	Sweden	406	55.70	13.14	8	5	*	*	Surface prey	Otto (1976)
128	Sundtjärnsbäcken	Sweden	406	59.57	12.34	188	24	*	7.9	Other benthos	Eros et al. (2012)
129	Sundtjärnsbäcken	Sweden	406	59.57	12.34	188	17	*	7.9	Other benthos	Eros et al. (2012)
130	Sundtjärnsbäcken	Sweden	406	59.57	12.34	188	22	*	7.9	Diptera	Eros et al. (2012)
131	Tambre	Spain	403	42.99	-8.31	302	26	16.6	*	Surface prey	Sánchez-Hernández (2009)
132	The Bright Angel Creek	USA	130	36.10	-112.10	765	NA	15	*	Ephemeroptera	Whiting et al. (2014)
133	Tornes	Spain	412	40.32	-5.49	1051	18	7.8	*	Ephemeroptera	Sanchez-Hernandez and Cobo (2012)
134	Tornes	Spain	412	40.32	-5.49	1051	18	18.5	*	Ephemeroptera	Sanchez-Hernandez and Cobo (2012)
135	Traba	Spain	403	42.79	-8.86	25	16	16.7	*	Diptera	Sánchez-Hernández (2009)
136	Ucero	Spain	412	41.68	-3.05	938	NA	*	*	Ephemeroptera	Montañes and Lobón-Cerviá (1986)
137	Ucero	Spain	412	41.68	-3.05	938	NA	*	*	Diptera	Montañes and Lobón-Cerviá (1986)
138	Ulla	Spain	403	42.79	-8.34	67	21	8.1	*	Diptera	Sánchez-Hernández et al. (2013)
139	Wakapuaka	New Zealand	811	41.23	173.40	62	30	11.5	*	Ephemeroptera	Sagar and Glova (1995)
140	Wakapuaka	New Zealand	811	41.23	173.40	62	29	10.9	*	Trichoptera	Sagar and Glova (1995)
141	Walla Brook	UK	404	50.57	-3.93	349	330	*	6	Crustacea	Horton (1961)
142	Walla Brook	UK	404	50.58	-3.88	348	20	12	*	Other benthos	Elliott (1967)
143	Walla Brook	UK	404	50.58	-3.88	348	4	7	*	Ephemeroptera	Elliott (1967)
144	Walla Brook	UK	404	50.58	-3.88	348	20	12	*	Plecoptera	Elliott (1967)
145	Walla Brook	UK	404	50.58	-3.88	348	8	7	*	Trichoptera	Elliott (1967)
146	Weydon Burn	New Zealand	811	45.65	168.19	319	95	10.6	*	Ephemeroptera	Glova et al. (1992)
147	Weydon Burn	New Zealand	811	45.65	168.19	319	109	9.7	*	Ephemeroptera	Glova et al. (1992)
148	Wolosaty	Poland	404	49.14	22.67	620	5	*	*	Trichoptera	Kukua and Bylak (2007)

Data sources: full reference list used in this study for the review of literature

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Appendix 2. Correlation among the bioclim variables.

Correlations were calculated with the Spearman correlation method. A correlation matrix plot was produced using the R package “corrplot” (Wei 2012). The correlation matrix plot is shown for the regional (Norway) and global approach (Fig. B1) including all bioclim variables (Table B1).

Wei, T. 2012. Package ‘corrplot’: correlation plot. R Foundation for Statistical Computing, Vienna. Available at: <https://cran.r-project.org/web/packages/corrplot/index.html> [accessed 19 July 2018].

Fig. B1. Correlation matrix plot among bioclim variables for the regional (left) and global approach (right). In this matrix significant correlations are only shown (blank = no significant coefficient). [Colour online]

Table B1. Bioclim variables included in the correlation matrix plots.

Variable	Definition	Variable	Definition
BIO1	Annual Mean Temperature	BIO11	Mean Temperature of Coldest Quarter
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	BIO12	Annual Precipitation
BIO3	Isothermality (BIO2/BIO7) (*100)	BIO13	Precipitation of Wettest Month
BIO4	Temperature Seasonality (standard deviation *100)	BIO14	Precipitation of Driest Month
BIO5	Max Temperature of Warmest Month	BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO6	Min Temperature of Coldest Month	BIO16	Precipitation of Wettest Quarter
BIO7	Temperature Annual Range (BIO5-BIO6)	BIO17	Precipitation of Driest Quarter
BIO8	Mean Temperature of Wettest Quarter	BIO18	Precipitation of Warmest Quarter
BIO9	Mean Temperature of Driest Quarter	BIO19	Precipitation of Coldest Quarter
BIO10	Mean Temperature of Warmest Quarter		

Appendix 3. Extended output and additional analyses focus on Norway (regional approach), including residual plots for the modelling (both generalised additive models – *GAMs* and generalised additive mixed models – *GAMMs*).

-3.1: Correlation plot

Correlations were calculated with the Spearman correlation method. A correlation matrix plot was produced using the R package “corrplot” (Wei 2012). Fig. C1 shows the correlations between prey categories and environmental variables at the regional level.

Wei, T. 2012. Package ‘corrplot’: correlation plot. R Foundation for Statistical Computing, Vienna. Available at: <https://cran.r-project.org/web/packages/corrplot/index.html> [accessed 19 July 2018].

Fig. C1. Correlation matrix plot between prey categories and environmental variables at the regional level. In this matrix significant correlations are only shown (blank = no significant coefficient). Annual mean temperature (BIO1), temperature seasonality (BIO4), temperature annual range (BIO7), annual precipitation (BIO12) and precipitation seasonality (BIO15). Some prey categories (Odonata and Urodela) were not found in the stomach contents. [Colour online]

3.2: Brown trout selectivity:

-Principal Coordinates Analysis (PCoA)

Principal Coordinates Analysis (PCoA) was performed using the “vegan” package (Oksanen et al. 2015). PCoA was based on a Euclidean resemblance matrix (Fig. C2).

Oksanen, J, Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., ... Wagner, H. 2015. Vegan: community ecology package. R package version 2.3-0. Available at: <https://cran.r-project.org/web/packages/vegan/index.html> [accessed 19 July 2018].

Fig. C2. Principal Coordinates Analysis (PCoA) plot based on brown trout selectivity and environmental variables [latitude, elevation and Shannon-Wiener’s diversity index]. [Colour online]

-Linear regression analysis

Linear regression analysis indicated that brown trout ate some prey categories irrespective of environmental variables (Table C1).

Table C1. Linear regression statistics for selectivity of brown trout feeding on prey categories. No models for Copepoda, Heteroptera and Megaloptera are given because the low number of locations restricted it. Statistically significant differences ($P<0.05$) are marked in bold.

	Intercept	Slope	<i>t</i>	<i>p</i>	Intercept	Slope	<i>t</i>	<i>p</i>
		Latitude				Elevation		
Crustacea	0.095	-0.001	-0.719	0.473	0.004	0.001	0.177	0.86
Mollusca	-0.204	0.003	1.055	0.294	0.010	0.001	0.394	0.694
Diptera	-0.068	0.003	0.248	0.805	0.164	-0.001	-1.476	0.143
Trichoptera	-1.049	0.022	1.242	0.217	0.488	-0.001	-2.38	0.019
Coleoptera	0.690	-0.010	-1.036	0.302	0.005	0.001	3.846	<0.001
Ephemeroptera	0.977	-0.013	-1.450	0.150	0.110	-0.001	-0.654	0.514
Plecoptera	-0.013	0.018	1.450	0.150	0.179	-0.001	-0.727	0.469
Other benthic	1.409	-0.020	-2.030	0.045	0.061	0.001	2.950	0.004
		Shannon						
Crustacea	0.011	-0.005	-0.607	0.545				
Mollusca	0.018	-0.005	-0.379	0.705				
Diptera	0.025	0.085	1.523	0.130				
Trichoptera	0.560	-0.109	-1.347	0.181				
Coleoptera	0.039	0.009	0.206	0.837				
Ephemeroptera	0.004	0.075	1.824	0.071				
Plecoptera	0.166	-0.002	-0.031	0.975				
Other benthic	0.136	-0.022	-0.494	0.622				

-3.3: Generalised additive models (GAMs)

Generalised additive models (GAMs) were performed using the automatic estimation of the amount of smoothing with REML in the “mgcv” package (Wood 2015). Significant outcomes were found for latitude and Shannon index (Table C2) without finding evidence of violation of the model assumptions (Fig. C3).

Wood, S.N. 2015. Package ‘mgcv’. Available at: <https://cran.r-project.org/web/packages/mgcv/index.html> [accessed 19 July 2018].

Table C2. Summary of generalised additive models (GAMs) explaining the variation in diet composition (PCA1) over environmental variables (latitude, elevation and Shannon-Wiener’s index). Statistically significant differences ($P < 0.05$) are marked in bold. Climatic variables were not included in the models because of assumptions of collinearity with elevation and latitude.

	Smooth terms		Model significance	
	<i>F</i>	<i>P</i>	R^2 (adjusted)	Deviance explained (%)
Latitude	5.37	<0.001	0.29	31
Elevation	0.04	0.842	0.01	0.1
Shannon	0.93	0.003	0.07	7.4

Fig. C3. Residual plot of the best model explaining the variation in diet composition over environmental variables. [Colour online]

-3.4: Residual structure (*GAMMs*)

Generalised additive mixed models (*GAMMs*) were performed with the “mgcv” package (Wood 2015). Additionally, model selection was done by model comparison using the “MuMIn” package (Bartoń 2016). Some prey categories (Odonata and Urodela) were not found in the stomach contents. The residual structure of the best model simulations for each prey category was assessed is shown in Fig. C4.

Bartoń, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. Available at: <https://CRAN.R-project.org/package=MuMIn> [accessed 19 July 2018].

Wood, S.N. 2015. Package ‘mgcv’. Available at: <https://cran.r-project.org/web/packages/mgcv/index.html> [accessed 19 July 2018].

Fig. C4. Residual structure of the best model simulations for each prey category was assessed. [Colour online]

QQ-plot was used to assess normality (if the points are in a line, normality can be assumed). Homogeneity was tested plotting residuals versus predicted values (the variance should be homogenous across the predicted values of the model). Spatial autocorrelation was tested using the autocorrelation function (ACF), the horizontal axis shows the time lags and the vertical axis the correlation with the dotted line representing the 95% confidence bands. Thus, residuals usually are theoretically assumed to have an ACF that has correlation = 0 for all lags. Additionally, we have estimated semivariance, which provides a measure of spatial correlation between points at different distances. Points closer to one another are more likely to be similar if observations in our dataset are spatially correlated.

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-3.5: Spatial correlation (GAMMs)

Evidence of spatial correlation was assessed with the *bubble* function using the “sp” package (Pebesma and Bivand 2005) to examine if residuals showed a clear residual pattern with biogeography (Fig. C5). Some prey categories (Odonata and Urodela) were not found in the stomach contents.

Pebesma, E.J. & Bivand, R.S. 2005. Classes and methods for spatial data in R. R News 5: 9–13.

Fig. C5. Evidence of spatial correlation at the regional level. [Colour online]

Appendix 4. Extended output and additional analyses for the global approach (worldwide), including residual plots for the modelling (both generalised additive models – *GAMs* and generalised additive mixed models – *GAMMs*).

-4.1: Prey abundance (%)

The diet composition of brown trout showed large spatial variations (Fig. D1).

Fig. D1. Abundance (%) of the dietary components for brown trout. Data are displayed by sampling sites for each prey category. [Colour online]

-4.2: Differences in prey abundance (%) between native and exotic populations

Prey abundance in exotic and native territories identifying density of probability (i.e. probability density function) and the interquartile range covering 95% of the data distribution using “yarr” package (Phillips 2017). We observed invasiveness (statistically higher abundance in exotic compared to native territories) only for three prey categories (Mollusca, Coleoptera and Ephemeroptera) (Fig. D2 and Table D1).

Phillips, N. 2017. yarr: A Companion to the e-Book "YaRrr!: The Pirate's Guide to R".

R package version 0.1.5. <https://CRAN.R-project.org/package=yarr>

Fig. D2. Abundance (%) of the dietary components for brown trout according to exotic and native territories. [Colour online]

Table D1. Mean values ($\pm$ SE) of prey abundance in exotic and native territories with pairwise comparisons according to nonparametric Mann-Whitney-Wilcoxon test for two independent groups of samples. Significant values are marked in bold.

	Mean $\pm$ SE		Pairwise comparisons		Mean $\pm$ SE		Pairwise comparisons
	Native	Exotic			Native	Exotic	
Copepoda	1.02 $\pm$ 0.45	0.26 $\pm$ 0.18	W = 1667, p = 0.175	Ephemeroptera	23.02 $\pm$ 1.31	34.79 $\pm$ 6.20	W = 1234.5, p = 0.041
Crustacea	3.57 $\pm$ 0.63	1.96 $\pm$ 0.89	W = 1648.5, p = 0.463	Plecoptera	8.75 $\pm$ 0.81	4.52 $\pm$ 2.76	W = 2376, p = 0.055
Mollusca	0.77 $\pm$ 0.26	0.90 $\pm$ 0.35	W = 1205, p = 0.001	Odonata	0.06 $\pm$ 0.03	0.62 $\pm$ 0.47	W = 1634, p = 0.071
Diptera	24.28 $\pm$ 1.33	23.40 $\pm$ 4.68	W = 1772, p = 0.856	Other benthos	4.06 $\pm$ 0.47	0.36 $\pm$ 0.21	W = 2346.5, p = 0.053
Trichoptera	14.25 $\pm$ 0.96	20.64 $\pm$ 4.56	W = 1374, p = 0.118	Surface prey	17.72 $\pm$ 1.25	10.15 $\pm$ 3.74	W = 2220.5, p = 0.175
Megaloptera	0.05 $\pm$ 0.03	—	—	Urodelia	0.01 $\pm$ 0.001	—	—
Coleoptera	1.75 $\pm$ 0.39	2.30 $\pm$ 0.88	W = 1136, p = 0.001	Fish	0.59 $\pm$ 0.18	0.03 $\pm$ 0.03	W = 1940, p = 0.497
Heteroptera	0.12 $\pm$ 0.06	0.07 $\pm$ 0.56	W = 1654, p = 0.118				

-4.3: Correlation plot

Correlations were calculated with the Spearman correlation method. A correlation matrix plot was produced using the R package “corrplot” (Wei 2012). Fig. D3 shows the correlations between prey categories and environmental variables at the global scale.

Wei, T. 2012. Package ‘corrplot’: correlation plot. R Foundation for Statistical Computing, Vienna. Available at: <https://cran.r-project.org/web/packages/corrplot/index.html> [accessed 19 July 2018].

Fig. D3. Correlation matrix plot between prey categories and environmental variables at the global scale. In this matrix significant correlations are only shown (blank = no significant coefficient). Annual mean temperature (BIO1), temperature seasonality (BIO4), temperature annual range (BIO7), annual precipitation (BIO12) and precipitation seasonality (BIO15). [Colour online]

-4.4: Hierarchical cluster analysis

Hierarchical cluster analysis was performed with the “gplots” package (Warnes et al. 2016), and the optimal number of clusters was determined using the package “factoextra” (Kassambara and Mundt 2017) for R. Fig. D4 represents the hierarchical cluster analysis with heatmaps on diet composition of brown trout associated with sampling events.

Warnes, G.R., Bolker, B., Bonebakker, L., Gentleman, R., Liaw, W.H.A., Lumley, T., ... Venables, B. 2016. Package ‘gplots’. Available at: <https://cran.r-project.org/web/packages/gplots/index.html> [accessed 19 July 2018].

Kassambara, A. & Mundt, F. 2017. Package ‘factoextra’. Available at: <https://cran.r-project.org/web/packages/factoextra/index.html> [accessed 19 July 2018].

Fig. D4. Hierarchical cluster analysis with heatmaps on diet composition of brown trout associated with sampling events. The nine dashed squares show the optimal number of clusters (also indicated by different colours). [Colour online]

-4.5: Canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA) was performed using the “vegan” package (Oksanen et al. 2015). Precipitation seasonality and annual mean temperature emerged as the most important environmental variables to understand the brown trout prey composition at the global scale (Fig. D5).

Oksanen, J, Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., ... Wagner, H. 2015. Vegan: community ecology package. R package version 2.3-0. Available at: <https://cran.r-project.org/web/packages/vegan/index.html> [accessed 19 July 2018].

Fig. D5. Canonical correspondence analysis (CCA) plot based on diet composition and environmental variables (latitude, elevation, annual mean temperature - BIO1, annual precipitation - BIO12 and precipitation seasonality - BIO15). In the ordination plot, the length of the arrow is a measure of the importance of the variable, and the arrow heads point in the direction of increasing influence. Temperature seasonality (BIO4) and temperature annual range (BIO7) were not included in the CCA because of assumptions of collinearity with elevation and latitude. The nine groups correspond with the identified clusters of Appendix S4.4 (see Fig. D4). [Colour online]

-4.6: Generalised additive models (GAMs)

Generalised additive models (GAMs) were performed using the “mgcv” package (Wood 2015). All included environmental variables were associated with diet composition in GAMs (Table D2). Residuals of the final selected models for deviations from normality and heteroscedasticity are shown in Fig. D6. In most cases no clear patterns were identified, the NMDS output tended to decrease with increasing annual mean temperature and precipitation seasonality (Fig. D7).

Wood, S.N. 2015. Package ‘mgcv’. Available at: <https://cran.r-project.org/web/packages/mgcv/index.html> [accessed 19 July 2018].

Table D2. Summary of generalised additive models (GAMs) explaining the variation in diet composition (PCA1) over environmental variables (annual mean temperature - BIO1, annual precipitation - BIO12 and precipitation seasonality - BIO15, latitude and elevation). Statistically significant differences ($P<0.05$) are marked in bold. Temperature seasonality (BIO4) and temperature annual range (BIO7) were not included in the models because of assumptions of collinearity with elevation and latitude.

Fig. D6. Residual plot of the best model explaining the variation in diet composition over environmental variables. [Colour online]

Fig. D7. Generalised additive models (GAMs) explaining the association between diet composition (NMDS1) of brown trout and the environmental variables for the global approach. Observed data (open circles) and fitted values to the smoothing curve (red line) with 95% confidence bands (broken black line). [Colour online]

-4.7: Residual structure (GAMMs)

Generalised additive mixed models (GAMMs) were performed with the “mgcv” package (Wood 2015). Additionally, model selection was done by model comparison using the “MuMIn” package (Bartoń 2016). The residual structure of the best model simulations for each prey category was assessed is shown in Fig. D8.

QQ-plot was used to assess normality (if the points are in a line, normality can be assumed). Homogeneity was tested plotting residuals versus predicted values (the variance should be homogenous across the predicted values of the model). Spatial autocorrelation was tested using the autocorrelation function (ACF), the horizontal axis shows the time lags and the vertical axis the correlation with the dotted line representing the 95% confidence bands. Thus, residuals usually are theoretically assumed to have an ACF that has correlation = 0 for all lags. Additionally, we have estimated semivariance, which provides a measure of spatial correlation between points at different distances. Points closer to one another are more likely to be similar if observations in our dataset are spatially correlated.

Bartoń, K. 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. Available at: <https://CRAN.R-project.org/package=MuMIn> [accessed 19 July 2018].

Wood, S.N. 2015. Package ‘mgcv’. Available at: <https://cran.r-project.org/web/packages/mgcv/index.html> [accessed 19 July 2018].

Fig. D8. Residual structure of the best model simulations for each prey category was assessed. [Colour online]

-4.8: Spatial correlation (GAMMs)

Evidence of spatial correlation was assessed with the *bubble* function using the “sp” package (Pebesma and Bivand, 2005) to examine if residuals showed a clear residual pattern with biogeography. Spatial patterns can be established for some prey categories; for example, the highest residuals for Mollusca were located in the north of Iberian Peninsula and south of France (Cantabric Coast–Languedoc), with the relative abundance of Mollusca being highest in this region (Fig. D9).

Pebesma, E.J. & Bivand, R.S. 2005. Classes and methods for spatial data in R. R News 5: 9–13.

Fig. D9. Evidence of spatial correlation at the global scale. [Colour online]