## **ORIGINAL RESEARCH**



# Global investigation of lake habitat coupling by fishes

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## Abstract

Habitat coupling, where consumers acquire resources from different habitats, plays an important role in ecosystem functioning. In this study, we provide a global investigation of lake habitat coupling by freshwater fishes between littoral (nearshore) and pelagic (open water) zones and elucidate the extent to which magnitude of coupling varies according to environmental context and consumer traits. We consider the influence of lake factors (surface area, depth, shoreline complexity, and annual temperature), relative trophic position of consumers, fish community species richness, and fish morphological traits on habitat coupling by fishes. Using a worldwide dataset consisting of fish stable isotope values ( $\delta^{13}$ C and  $\delta^{15}$ N), we developed an index of habitat coupling, and used Bayesian hierarchical and non-hierarchical beta regressions to estimate the effects of environmental lake context and morphological traits on habitat coupling by fishes. Our results show high rates of habitat coupling among fishes globally with marked taxonomic differences in the magnitude and variation. Habitat coupling was higher in lower elevation lakes and in regions characterized by relatively colder climates, whereas other environmental context factors had little or no effects on habitat coupling. Furthermore, habitat coupling was associated with several locomotion and feeding traits, but independent from species maximum body length. Overall, we highlight the prevalence of multiple resources supporting fish populations and suggest future research identify implications to ecosystem functioning that may result from alterations to habitat coupling by fishes.

Keywords Consumer · Carbon · Littoral · Functional traits · Stable isotopes

# Introduction

Mobile consumers can connect or "couple" distinct habitats across both space and time through predation and grazing. Wide ranging examples of habitat coupling include Arctic polar bears *Ursus maritimus* linking water and solid ice energy pathways through predation on seals (Horton et al. 2009), red-necked grebes *Podiceps grisegena* using nutrients acquired in marine and freshwater habitats (Kloskowski et al. 2019), *Anolis* lizards integrating understory

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<sup>3</sup> Laboratoire Evolution & Diversité Biologique, UMR 5174 EDB, CNRS, Université Paul Sabatier, Toulouse, France and canopy food webs (Giery et al. 2013), and adult siscowet trout *Salvelinus namaycush siscowet* connecting benthic and pelagic energy sources in lakes (Gorman et al. 2012). The extent an organism couples distinct habitats has been shown to vary according to specific traits of the consumer (Edmunds et al. 2016; Keppeler et al. 2021), environmental conditions (Dolson et al. 2009; Eloranta et al. 2015), and interactions between suites of drivers (Tunney et al. 2018; Stiling et al. 2021).

Habitat coupling by mobile consumers has several important implications for ecosystem functioning (Rooney et al. 2006, 2008). For example, ecosystem structure, such as plant and animal assemblage or food chain length can be influenced by cross-habitat predation and foraging. The use of multiple habitats by herbivores can promote increased plant species richness within a foraging habitat (Takada et al. 2002) and diverse habitat use by predators can lead to food-chain length contraction within a community (Tunney et al. 2012). Additionally, ecosystem productivity may be enhanced when consumers integrate resources acquired in multiple habitats through the mobilization and transport of

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nutrients (Schindler and Scheuerell 2002; McIntyre et al. 2006). Coupling by consumers may also promote ecosystem stability, such as the maintenance of prey biomass through time supported by upper trophic level consumers switching between prey types in different habitats (Marklund et al. 2019). Despite the well-established implications of habitat coupling for ecosystems, our understanding of the environmental factors and consumer attributes influencing the degree of habitat coupling remains much less clear.

Habitat coupling is a result of consumer behavior, which is ultimately influenced through interactions with environmental conditions. Temperature and precipitation are two climatic variables that affect foraging behavior and resource availability (Burles et al. 2009; Irons et al. 2017). For instance, movement between marine and freshwater habitats by American alligators (Alligator mississippiensis) is influenced by climatic factors such as temperature and humidity, which affect osmoregulation (Nifong and Silliman 2017). Fish can optimize growth and survival by foraging where prey resources are maximized and then residing or digesting at temperatures where metabolic costs are minimized (Bevelhimer and Adams 1993); behaviors that are compromised by climate change (Ficke 2007). In addition to climate factors, habitat size and shape can influence consumer foraging behavior and resource use (Hayden et al. 2019). For example, in deep clear lakes where primary production can occur above and below the thermocline, zooplankton vertical diel migration leads to diets heavily reliant on subsurface derived autochthonous organic matter, contrasting patterns in turbid lakes where primary production and feeding is primarily above the mixed layer (Francis et al. 2011).

Consumer traits, such as those associated with foraging and resource acquisition, may be a strong determinant of habitat coupling. Body size has historically been considered a major organizing force in food webs, with larger consumers hypothesized to occupy higher trophic positions, however, this structure varies among ecosystem types (e.g., Kopf et al. 2021). Closely linked with body size, organisms with greater mobility tend to have greater opportunities to access different macrohabitats and prey types, thereby promoting habitat coupling (Vander Zanden and Vadeboncoeur 2002). Additionally, greater cognitive ability, as measured by larger relative brain size, may be associated with increased habitat coupling suggesting creativity or decision making are necessary for using resources from multiple habitats (Edmunds et al. 2016). Finally, traits associated with visual acuity have been shown to relate to foraging behavior and resource use (Tunney et al. 2018).

The occurrence of distinct littoral-benthic (hereafter "littoral") and pelagic habitats, along with diverse consumer assemblages of fishes, make freshwater lakes a valuable context to explore drivers of habitat coupling (Vander Zanden and Vadeboncoeur 2002). Fish exhibit considerable reliance on littoral derived resources, likely due to high rates of primary production along lake edge habitats promoting prey availability and diversity (Vadeboncoeur et al. 2011; Vander Zanden et al. 2011). While fish species and communities consistently couple resources from both pelagic and littoral habitats (Schindler and Scheuerell 2002), the factors that drive variability in coupling are less understood. Here we provide a global assessment of habitat coupling by lake fish species including the identification of environmental and consumer attribute factors that contextualize the extent of resources derived from multiple habitats. Our study leverages the diverse taxonomy of freshwater fishes by first using  $\delta^{13}$ C values to quantify littoral-pelagic habitat coupling for fish populations around the globe. Next, we assess differences in habitat coupling estimates among fish species and variability within species, and relate environmental (climatic and geomorphic) and community context factors to habitat coupling. Last, we identify fish morphology and food acquisition traits associated with habitat coupling. We expect body size and mobility to relate to greater magnitudes in habitat coupling. Results from this investigation highlight the importance of protecting inter-connected lake habitats and the species that forge these linkages in a rapidly changing world.

# **Materials and methods**

## Fish community stable isotope data compilation

We augmented a previously compiled dataset of fish community bulk <sup>13</sup>C:<sup>12</sup>C and <sup>15</sup>N:<sup>14</sup>N (Sagouis et al. 2015; Pool et al. 2016; Comte et al. 2016, 2017) for the period 1995-2013 to include new literature published 2014 through 2020. We searched the Institute of Scientific Information (ISI; Thomson Reuters) Web of Science online database using the following search terms: "TS = (isotope\* AND fish\* AND carbon AND nitrogen) AND TS = (lake\* OR reservoir\*), Indexes = SCI-EXPANDED, SSCI, A&HCI, ESCI Timespan = 2014 - 2020." Google Scholar search terms were: "all the words: isotope, fish, C, N; at least one word: lake, reservoir; and dates: 2014-now", where now is December 2020. Individual lake fish communities were considered as the fish species for which stable isotope values were provided along with a statement in the methods indicating the captured species were representative of the fish community. We included the lake communities that consisted of four or more fish species. Populations are mean stable isotope values of all individuals of the same species captured from a lake. If more than one set of isotope values were recorded for a single lake (e.g., differing seasons, years, or studies) we retained only one

set of records. For studies that sampled both wet and dry season, we included the wet season values in our analysis which best correspond to estimates of total lake area; when multiple sampling events occurred, we included the most comprehensive (greatest number of fish species); for remaining replicate sampling events, we used the most recent. When available, we also extracted values for end member taxa such as snails, attached algae, or periphyton reflecting littoral primary production or zooplankton, phytoplankton, pelagic bivalve, or seston representative of pelagic primary production. Fish species names were harmonized according to current and accepted taxonomy using the taxize package in R (Chamberlain and Szöcs 2013). When populations were not reported to the species level, the values were recorded as genus\_sp. The complete dataset consists of 112 lakes with fish community stable isotope data. Twenty lakes include non-fish end member taxon data (Fig. 1, Table ESM2). Fish communities in these globally distributed lakes range from 4 to 22 fish species (average 8.3 species) with differences in  $\delta^{13}$ C fish minimums and maximus averaging 5.7% (range 2.3-11.4%, Fig. ESM2B). There are 107 fish species observed in the 20-lake subset. Owing to an inability to obtain environmental or climate data, we dropped 8 lakes from subsequent analysis. The final dataset contained 82 published studies reporting stable isotope data for 972 populations, comprising 237 fish species in 104 lakes located in 22 countries spanning North America, South America, Europe, Africa, Asia, and Oceania (Fig. 1). Species richness among the 104 study lakes ranged from 4 to 44 (mean 9.3). Differences in  $\delta^{13}$ C fish minima and maxima averaged 5.6% (range 1.4-10.9%).

#### Indices of habitat coupling

In 20 studies that reported  ${}^{13}C{}^{12}C$  for pelagic and littoral end member taxa as well as fishes, we estimated littoral resource use ( $\varphi$ ) for each population in two ways. First, following Vander Zanden and Vadeboncoeur (2002), the proportion of C derived from littoral habitats for the population was calculated as:

$$\varphi_{pop} = \frac{\delta^{13} C_{pop} - \delta^{13} C_{pel\_end}}{\delta^{13} C_{lit\_end} - \delta^{13} C_{pel\_end}}$$
(1)

where  $\delta^{I3}C_{pop}$  is the mean <sup>13</sup>C:<sup>12</sup>C ratios of the population and  $\delta^{I3}C_{pel_{end}}$  and  $\delta^{I3}C_{lit_{end}}$  are lake specific pelagic and littoral end members.

Second, we designated the greatest  $\delta^{13}C$  population value  $(\delta_{13}C_{pop_max})$  as a littoral end member value and the lowest  $\delta^{13}C$  population value  $(\delta_{13}C_{pop_min})$  as a pelagic end member, and then calculated littoral resource use for each fish population as:

$$\varphi \prime_{pop} = \frac{\delta^{13} C_{pop} - \delta^{13} C_{pop\_min}}{\delta^{13} C_{pop\_max} - \delta^{13} C_{pop\_min}}$$
(2)

The estimates of littoral resource use between the two methods were similar (Pearson's R = 0.60, ESM1). This approach estimated that some fish populations were fully reliant (1) and completely non-reliant (0) on littoral resources, which was not reflected in the results using non-fish end member taxa. We then tested a simple adjustment to capture as many lakes as possible including those that did not report end member values. Based on our observations



**Fig. 1** Geographical distribution of the studied lakes. Each circle and square represent a lake. Lakes with fish and end member C isotope data (black; n=20) were used to estimate littoral reliance for all lakes

in the study (circles; n=104) allowing inclusion of lakes with fish isotope data but not baseline data (blue; n=92). Gray shading indicates countries with lakes included in the dataset

(ESM1), we designated stand-in end member terms that were adjusted to be lower than the  $\delta^{13}$ C value of the most depleted fish population within the community, and greater than the  $\delta^{13}$ C value for the most enriched fish population according to the absolute value of the mean differences observed between the two approaches (mean pelagic difference,  $adj_{pel} = 1.55 \%$ ; mean littoral difference,  $adj_{lit} = 2.54 \%$ ). This was calculated as:

$$\varphi \mathcal{U}_{pop} = \frac{\delta^{13} C_{pop} - (\delta^{13} C_{pop\_min} - adj_{pel})}{(\delta^{13} C_{pop\_max} + adj_{lit}) - (\delta^{13} C_{pop\_min} - adj_{pel})}$$
(3)

We compared the estimates of littoral resource use between Eq. 1 and Eq. 3 in order to validate Eq. 3 as an alternative approach to estimating littoral resource use by fish populations in lakes for use when published studies did not include end member data (ESM1). We then estimated littoral resource use for all fish populations using Eq. 3.

We then estimated the degree of habitat coupling for each fish population in each lake by taking the proportion littoral use and converting it to a scaled coupling score (Y; Eq. 4) ranging from 0–1 where 0 represents a population purely reliant on either littoral or pelagic derived resources, and 1 represents a population equally coupling littoral and pelagic derived resources (high coupling sensu Tunney et al. 2018).

$$Y_{pop} = \frac{0.5 - |\varphi''_{pop} - 0.5|}{0.5} \tag{4}$$

The accuracy of the scaled coupling score estimate is primarily sensitive to the extent that the  $\delta^{13}$ C range of the fish community is centrally located within the true, but unknown, end member  $\delta^{13}$ C range (ESM1). These values may differ slightly from estimates of habitat coupling reported in the literature due to our exclusive use of fish community carbon isotope values.

# Lake attributes, species traits, and community characteristics

We obtained physical attributes and summarized climatic conditions for each lake to test for their association with overall habitat coupling. Using publicly available databases, we collated data on mean depth, shoreline development index (a measure of shoreline irregularity relative to a perfect circle, hereafter shoreline complexity index), lake elevation (HydroLAKES: Messager et al. 2016), and surface area (Global Lake area, Climate, and Population dataset [GLCP]: Meyer et al. 2020). We used total water area from the GLCP to ensure lake surface area estimates included seasonal high waters, when applicable, mirroring our use of wet season fish community data. The climatic variables, mean annual temperature and total annual accumulated precipitation, as estimated for each lake's watershed in 2015, were also acquired from the GLCP (Meyer et al. 2020). We included all lakes smaller than 500 km<sup>2</sup> (Alin and Johnson 2007) and were limited to lakes greater than 0.1 km<sup>2</sup> (cutoff for inclusion for HydroLAKES and GLCP).

Species-specific morphological traits were also considered as covariates (Manjarrés-Hernández et al. 2021; Brosse et al. 2021). Body morphometry traits associated with locomotion consisted of body elongation, body lateral shape, pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling (Brosse et al. 2021). Body morphometry traits associated with feeding included vertical eye position, relative eye size, oral gape position, and relative maxillary length (Brosse et al. 2021). Fish size, frequently associated with metabolism, was represented by maximum body length (Brosse et al. 2021). Finally, trophic guild encompassed five categories—primary consumer, secondary consumer, toppredator, omnivorous and detritivorous—and three habitats—pelagic, benthopelagic and benthic- was assigned to each species (Manjarrés-Hernández et al. 2021).

Species richness for each lake community was calculated as the sum of unique species recorded in the stable isotope dataset for each lake. We calculated isotopic evenness using the IDiversity R function from Cucherousset and Villéger (2015) for each community to determine whether most species are using a similar range of  $\delta^{13}$ C (scores towards 0) or whether species  $\delta^{13}$ C are evenly distributed within the range of values used by the community (scores towards 1). Relative trophic position was estimated according to the relative change in  ${}^{15}N$ :  ${}^{14}N$  ratios ( $\Delta N$ ) calculated as the difference in  $\delta^{15}N$  % between the minimum  $\delta^{15}N$  found in the fish community and the  $\delta^{15}$ N value of the population (Eq. 5). We opted to use change in isotope value,  $\Delta N$ , rather than calculate a specific trophic position because it represents the relative trophic position within the fish community as opposed to overall trophic position relative to the base of the food web.

$$\Delta N_{pop} = \delta^{15} N_{pop} - \delta^{15} N_{pop\_min} \tag{5}$$

### **Statistical analysis**

We used a Bayesian hierarchical beta regression to estimate the association between lake environmental characteristics and habitat coupling by freshwater fishes (Model 1). We fit a beta distribution to habitat coupling ( $Y_{pop}$ ) to account for the response variable being constrained between 0 and 1 (Ferrari and Cribari-Neto 2004). The predictors variables in the model were scaled and centered (Schielzeth 2010) and comprised of local community characteristics ( $\Delta N$ , richness, isotopic evenness), lake physical features (mean depth, elevation, shoreline complexity, surface area) and climatic elements (temperature and precipitation) as fixed effects. Predictor variables showed weak correlations (Pearson's R, -0.24-0.49). We accounted for observations that occur in populations of the same species by allowing intercepts to differ among species as random effects (McElreath 2020). We included species found in  $\geq 5\%$ of the communities, resulting in an examination of 496 populations, comprising 45 species in 100 lakes. Models were implemented in the Stan computational framework (http://mc-stan. org/) accessed with the brms package in R (Bürkner 2017). We accepted the default Student's t priors (positive values only, mean of 0, standard deviation of 2.5, and 3 degrees of freedom) for intercept and species effects standard deviations due to lack of information about these parameters. Similarly, the Beta-regression specific precision parameter theta ( $\theta$ ) included the default Gamma prior (shape term of 0.01 and a scaling term of 0.01) and uninformative flat priors for each  $\beta$ . Models were sampled using a Hamiltonian Monte-Carlo algorithm, the No-U-Turn Sampler. We ran all models with four chains and 5000 iterations, of which the first 1000 were discarded. We report median values of numerically generated posterior samples with two-tailed 95% Bayesian credible intervals for parameters associated with our predictor variables.

**Model 1.** Bayesian hierarchical beta regression. The response variable  $(Y_{ij})$  is a habitat coupling score of a fish population (*i*) of a species (*j*).  $Y_{ij}$  is assumed to be derived from the beta function and related to 1)  $p_{ij}$  via the logit link function and linear predictors consisting of the overall intercept ( $\alpha$ ), species specific intercepts ( $\alpha_j$ ) and the sum all 9 (*k*) environmental predictor parameters ( $\beta$ ) times the *i* \* *k* matrix (*X*) of environmental values associated with each population and 2)  $\theta$ , the Beta distribution precision parameter.

 $Y_{ij} \sim Beta(p_{ij}, \theta)$   $logit(p_{ij}) = \alpha + \alpha_j + \sum_{k=1}^{9} \beta_k * X_{ik}$   $\alpha \sim Student.t_3(0, 2.5)$   $\alpha_j \sim Normal(0, \sigma_{\alpha})$   $\beta_k \sim Normal(0, \sigma_k)$   $\sigma_{\alpha} \sim Student.t_3^+(0, 2.5)$   $\sigma_k \sim Student.t_3^+(0, 2.5)$ 

$$\theta \sim Gamma(0.1, 0.1)$$

We used Bayesian (non-hierarchical) beta regression (Model 2) to estimate the extent that fish traits are related to

habitat coupling. For this analysis, by examining all populations for whom we had trait data, we considered 733 populations consisting of 195 species in 104 lakes. With the logit transformed habitat coupling for each population we tested five traits related to locomotion, four traits related to feeding, and one trait related to metabolism (body length).

**Model 2.** Bayesian beta regression. The response variable  $(Y_i)$  is a habitat coupling score of a fish population (i).  $Y_i$  is assumed to be derived from the beta function and related to 1)  $p_i$  via the logit link function and linear predictors consisting of the overall intercept  $(\alpha)$  and the sum all 10 (k) trait predictor parameters  $(\beta)$  times the i \* k matrix (X) of trait values associated with each population and 2)  $\theta$ , the Beta distribution precision parameter.

$$Y_i \sim Beta(p_i, \theta)$$

$$logit(p_i) = \alpha + \sum_{k=1}^{10} \beta_k * X_{ik}$$

 $\alpha \sim Student.t_3(0, 2.5)$ 

 $\beta_k \sim Normal(0, \sigma_k)$ 

 $\sigma_k \sim Student.t_3^+(0, 2.5)$ 

$$\theta \sim Gamma(0.1, 0.1)$$

We used a one-way analysis of variance (ANOVA) to determine differences in habit coupling among categorical traits associated with fish populations. We first compared categories associated with feeding habitat consisting of benthivorous, benthopelagic, and pelagic. Owing to unequal variances among the categorical trophic guilds (detritivorous, omnivorous, primary consumer, secondary consumer, and top-predator), we completed a Welch Corrected ANOVA followed by Games-Howell post hoc comparisons between groups.

Last, for the more frequently occurring species in the dataset ( $\geq 10\%$  of the lakes), we quantified species-specific relationships between environmental factors and habitat coupling by completing linear regression and plotting relationships between factors and responses according to species.

# Results

Fish populations consistently used resources derived from both the littoral and pelagic habitats and displayed widely ranging habitat coupling scores (Fig. 2). Overall, the average coupling score of fishes was  $0.68 \pm 0.22$  with individual population coupling scores ranging from 0.21 to 1.00. Median coupling value for all populations was 0.71 and most populations (75%) had coupling scores greater than 0.5. Fish species and families exhibit broad differences in habitat coupling (Fig. 2). Differences between families include high variability in mean species coupling among Salmonidae and Cyprinidae, but relatively consistent middle range values (0.5–0.65) for Centrarchidae and Catostomidae. Percidae primarily consisted of species that were high couplers.

Within species, inter-population variability in habitat coupling was high. For example, coupling scores among populations of walleye (*Sander vitreus*) ranged narrowly from 0.77 to 0.93, whereas cisco (*Coregonus artedi*) displayed a much greater difference among populations which ranged from 0.21 to 0.97. Species with wide ranging coupling scores include several salmonids (*Salmonidae*) such as cisco, arctic char (*Salvelinus alpinus*), bull trout (*Salvelinus confluentus*), cutthroat trout (*Oncorhynchus clarkii*), and lake trout (*Salvelinus namaycush*). Species with the lowest variance in



**Fig. 2** Habitat coupling among the studied fish species and families (n=496 populations). Boxplots represent the median and 1st and 3rd quantile. Whiskers are min/max within 1.5 the interquartile range.

Dots are values outside 1.5 the interquartile range. Species were sorted by mean habitat coupling values within colored groupings according to family coupling included highfin catfish (*Neoarius berneyi*), North African catfish (*Clarias gariepinus*), and sockeye salmon (*Oncorhynchus nerka*), in addition to walleye.

Of the environmental factors we considered, the primary lake attributes related to habitat coupling of fishes included both physical and climatic elements, although the



**Fig. 3** Posterior distributions of environmental conditions as estimated by a Bayesian hierarchical beta regression ordered by posterior mean estimates (n = 496 populations). Shading indicates 95% credible interval. The x-axis indicates the effect of each scaled and centered parameter on habitat coupling

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95% credible interval of all predictors tested included zero (Fig. 3). Temperature and elevation had the strongest association with decreases in habitat coupling with posterior probability median estimates were -0.09 (95% highest posterior density credible interval, -0.21-0.02) and -0.09 (95% highest posterior density credible interval, -0.19-0.01), respectively. Increases in isotopic evenness and shoreline complexity index had an association with increased species coupling (posterior probability estimates of and 0.06 [-0.02-0.15] and 0.04 [-0.07-0.16]). Increases in  $\Delta N$  (0.02 [-0.09-0.12]), precipitation (0.01 [-0.09-0.11]), mean depth (0.01 [-0.09-0.10]), surface area (-0.02 [-0.13-0.09]), and richness (-0.04 [-0.15-0.08]) exhibited low association with habitat coupling.

Fish populations grouped according to categorical food acquisition strategies (i.e., trophic guild and primary feeding habitat) showed little associated with habitat coupling. Although there were only marginal differences in habitat coupling between omnivorous species, primary consumers, and secondary consumers, we found that detritivorous fishes displayed significantly lower habitat coupling compared to all other trophic guilds (post hoc Games-Howell p < 0.05) (Fig. 4). Habitat coupling did not significantly differ between categories of feeding habitats (ANOVA  $F_{2,115}=2.2$ , p=0.11), although species that feed primarily in the pelagic environment coupled slightly less (0.62) than either benthivorous (0.69) and benthopelagic (0.68) populations.

Species-level habitat coupling showed strong associations with morphological traits describing feeding habit and locomotion. Three of the five locomotion traits had effect sizes

**Fig. 4** Distribution of habitat coupling according to categorical trophic guild (n = 812 populations). Boxplots represent the median and 1st and 3rd quantile values for habitat coupling according to group overlaid with points indicating fish populations



different from zero: pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling (Fig. 5). Of the four feeding traits, only oral gape position had a statistically credible association with habitat coupling (Fig. 5). There was little evidence of any associations between habitat coupling and maximum body size (Fig. 5).

Lastly, habitat coupling varied as a function of environmental factors in species-specific ways (Fig. 6). Slope relationships between scaled coupling against average lake depth or lake surface area ranged from neutral to strongly positive and strongly negative depending on species (Fig. 6A, B). We observed similar patterns with species richness, with some species demonstrating lower coupling and others higher coupling as the lakes that they inhabit include more fish species (Fig. 6C). By contrast, the majority of the species exhibited decreased coupling as mean annual temperature increases (Fig. 6D).

# Discussion

Our global investigation demonstrates that the vast majority of fish species are strong habitat couplers, reflecting the dual utilization of littoral and pelagic derived resources and highlighting the interconnected nature of lake food webs (Vadeboncoeur et al. 2002). Several species exhibited high inter-population variability in habitat coupling across their range. Habitat coupling varied taxonomically and was found to be influenced by both environmental context and mediated by morphological traits related to consumer feeding and mobility.

Magnitude and variability in species habitat coupling varied taxonomically. Suckers (Catostomidae) and basses and sunfishes (Centrarchidae) are found to be consistent (low inter-population variability) moderate habitat couplers (median scores between 0.5 and 0.75), whereas species of perches (Percidae) were predominantly strong habitat couplers (median values > 0.75, Fig. 2). As an example, walleye, found to be a strong coupler, have been previously shown to occupy both pelagic and littoral habitats, with maximum coupling occurring in lakes with low visibility (Tunney et al. 2018). The moderate-high coupling scores for yellow and European Perch are also expected given these species are considered ontogenetic trophic generalist switching frequently between piscivorous, zooplanktivorous and benthivorous feeding styles even as adults (Linzmaier et al. 2018). Other examples of high couplers include Berney's catfish (Neoarius berneyi) and northern pikeminnow (Ptychocheilus oregonensis); both species exhibit flexible diets and consume foods derived from multiple habitats (McIntyre et al. 2006; Pusey et al. 2020). Finally, species classified as detritivorous, such as those in the genus Potamorhina (Potamorhina altamazonica, P. latior, P. pristigaster), demonstrated relatively low habitat coupling coinciding with their dependence on detrital pathways.

Salmonids (Family: Salmonidae) exhibited high variability in habitat coupling. For example, European whitefish (*Coregonus lavaretus*), sockeye salmon, and cisco had

**Fig. 5** Posterior distributions of morphological traits as estimated by a Bayesian non-hierarchical model ordered by trait category and posterior mean width (n = 733 populations). Shading indicates 95% credible interval. The x-axis indicates the effect of each scaled and centered parameter on habitat coupling. Teal are traits related to mobility, pink are traits related to feeding habits, and gray indicates body length as a surrogate of metabolism





**Fig. 6** Relationships between habitat coupling and environmental factors (depth, surface area, mean annual temperature, and fish species richness) differ among the 17 species observed in 10% or more of the

low median coupling values compared to all other species. Although the metric doesn't differentiate between littoral or pelagic derived resource use, extensive research from the Laurentian Great Lakes point to the heavy reliance of cisco on pelagic resources, being predominantly zooplanktivorous (Gatch et al. 2021). Similarly, diet studies on landlocked kokanee (lacustrine Oncorhynchus nerka) provide support for their planktivorous tendencies primarily consuming pelagic resources (Schoen et al. 2015). Arctic char exhibited high variances in habitat coupling; supported by past studies reporting the highly flexible diet of this species (Gregersen et al. 2006). Not only do Arctic char exhibit flexible diets, subpopulations of Arctic char display differing body forms associated with differing diet preferences or available resources (Woods et al. 2013). In summary, broad differences in mean species average habitat coupling and differences in variance around coupling reflect the high diversity of diets in Salmonidae.

Environmental conditions affecting habitat coupling by fishes include both local-scale physical factors and regional

study lakes. Colors are according to species. Depth is presented on a log scale, accounting for the majority of lakes being less than 100 m deep

climatic factors. The strong relationship between increased mean annual temperature and decreased habitat coupling may be a result of some species such as lake trout utilizing deep cold water habitats for refuge in warmer climates, thereby shifting towards increased pelagic resource use (Guzzo et al. 2017). In addition, mean annual temperature increase and decreased habitat coupling could reflect increased littoral resource use in more tropical ecosystems (Lopes et al. 2015). The relationship between increased elevation and decreased coupling may reflect a similar trend, except in this case, oligotrophic high elevation lakes being fueled primarily by attached algae and littoral primary production with little pelagic primary production (Loria et al. 2020). The negative relationship between lake surface area and increased coupling reflects observations in large systems where food webs may be more compartmentalized, with some species shifting towards primarily pelagic resource use (Tunney et al. 2012).

Morphological fish traits related to locomotion and feeding were the strongest related to habitat coupling. Pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling—traits shown to relate to swimming and propulsion efficiency (Villéger et al. 2017; Brosse et al. 2021) were tightly associated with habitat coupling. Traits describing feeding morphology were also correlated with habitat coupling. Together, traits related to mobility and feeding reflect the ability of fishes to access and exploit multiple habitats. Had we found the opposite, then we might speculate that mobility plays a large role in non-feeding aspects of fish life history (e.g., predator avoidance or reproductive migration).

We found little evidence for an association between species-level body size and habitat coupling, which contrasts with theory and recent literature demonstrating larger body size increases marine-terrestrial habitat coupling (Rooney et al. 2008; Keppeler et al. 2021). Although body size is expected to be positively associated with coupling, our findings highlight the nuanced relationship between body size and trophic position for freshwater fishes given that many large bodied species are non-carnivorous (Keppeler et al. 2020). Trophic position and, in turn, coupling by fishes may be associated with other functional traits not included here (e.g., maxillary jaw length; Kopf et al. 2021).

The categorical functional trait trophic guild, which is related to trophic position, was moderately associated with habitat coupling. Fishes classified as top predators, omnivores, and secondary consumers are generally littoralpelagic couplers whereas detritivores ranked low on the coupler spectrum. This finding is consistent with the lack of relation with body size, as many large-bodied freshwater fish are also detritivores (e.g., catfishes). We also found that primary consumers coupled slightly less than fish in higher trophic levels, which again aligns with food web theory (Rooney et al. 2008). Little differences in overall habitat coupling between fish grouped according to preferred feeding habitat (benthic, benthopelagic, or pelagic) were observed, although the median coupling score for pelagic species were the lowest; a result consistent with pelagic species using primarily open-water resources in larger lakes. Not only did we not find statistical differences in coupling among most classifications, but the wide variances also match similar findings suggesting that several differing energy sources can support fishes within the same feeding habitat or trophic guild classification (Lopes et al. 2015).

For a subset of species, the importance of coupled pelagic and littoral resources to consumers varied according to environmental gradients including lake surface area and mean depth. For example, lake trout has been shown to decrease coupling as lake area increases, owing to increased exclusive pelagic foraging (Tunney et al. 2012). Similarly, cisco (*Coregonus artedi*) increased coupling in deeper and larger lakes. On the other hand, common carp (*Cyprinus carpio*) appeared to couple habitats consistently, relatively

unaffected by environmental context. Therefore, these results suggest that divergent changes in resource use and habitat coupling among species challenge our ability to predict the effects of environmental changes at the community level.

This study highlights the need for continued understanding of the magnitude and causes of uncertainty associated with methodologies that estimate resource use and habitat coupling within aquatic food webs. Building on thoughtfully timed and located community data collection (Syväranta et al. 2006), the comparison of the carbon isotope values of essential (non-synthesized) amino acids among aquatic community members may help illuminate the fluxes of molecules through aquatic food webs (Whiteman et al. 2019). Detailed understanding of source contributions to diet can further help quantify uncertainty associated with assumptions made while estimating resource use and, by extension, habitat coupling.

In conclusion, numerous species of freshwater fishes display a heavy reliance on both pelagic and littoral derived resources. Human-induced environmental changes such as near shore habitat loss and water level fluctuations may destabilize linkages between littoral and pelagic habitats with profound effects on lake ecosystem functioning that remain to be quantified (Evtimova and Donohue 2016). There is also evidence that individual fish or groups of fish (sub-populations) within the same population use differing habitat and resources leading to intra-population compartmentalization within food-webs (Bolnick et al. 2003). Exciting opportunities exist to merge topics of food web theory and ecosystem function to reveal mechanisms of how and when ecosystems respond adaptively to a change in climate or environment (McMeans et al. 2016). This study takes an initial, broad-scale look at drivers of habitat coupling, leaving ample opportunity to further explore how environmental drivers and individual traits help determine species coupling and the implications for the stability, structure, and productivity of freshwater ecosystems.

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Author contribution statement RRS, GWH, and JDO conceived the study. JC, SB, and RRS compiled the dataset. RRS analyzed the data. All wrote the manuscript.

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**Data availability** The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

**Code availability** The R code used during the current study is available from the corresponding author on reasonable request.

# Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This article does not contain any studies with human participants or animals performed by any of the authors.

Consent to participate Not applicable.

Consent for publication Not applicable.

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