Fish resource use and habitat coupling in lake ecosystems

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Abstract

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Mobile consumers frequently acquire and use resources from differing habitats. This habitat coupling can influence ecosystem function, stability, and structure. Mobile consumers such as freshwater lacustrine fish are known to couple littoral-benthic, pelagic, and terrestrial ecosystems. Studies have shown that some freshwater fish are strong couplers, while others remain relative resource specialists with studies demonstrating the relative use of terrestrial, littoral-benthic, and pelagic resources varying widely. This research leans into this variability and seeks to identify abiotic and biotic factors that control resource use and habitat coupling. The overarching questions woven through this research are: 1) What are the spatial patterns in resource use and habitat coupling by fish in lake ecosystems? 2) What are the abiotic (environmental) and biotic (consumer traits or community context) determinants of resource use and habitat coupling? In chapter 1, from a local perspective leveraging the simple food webs of stocked mountain lakes in the Cascade Range of western North America I address how different population sizes, along with the relative availability of illuminated benthic habitat and terrestrial influence, determine resource use by rainbow trout. After collecting data and samples 16 lakes, I used stable isotope mixing models to quantify proportional use of basal resources for each trout, then compositional regression analysis to identify how interactions between relative habitat availability and population abundance influence Rainbow Trout use of basal resources. My findings from this first study highlighted the importance of environmental and biological interactions as drivers of relative resource use in lake ecosystems. In chapter 2, with a global perspective, I considered the influence of environmental factors (mean annual temp, elevation, area, average depth, shoreline index), relative ^{15}N:^{14}N increase, and fish community species richness on habitat coupling by fishes worldwide. I also explored how morphological traits influence habitat coupling. Using dataset consisting of fish ^{13}C:^{12}C and ^{15}N:^{14}N I developed an index of habitat coupling for fish populations in lake communities around the world. Using Bayesian hierarchical and non-hierarchical beta regressions I estimated the effects of environmental context and morphological traits on habitat coupling by fishes. These results demonstrate high rates of habitat coupling among fishes globally and show increases in relative habitat coupling is slightly associated with decreases in mean annual temp and elevation, while other environmental context factors had little or no relationship to habitat coupling. Last, I found relative habitat coupling was associated with morphological traits, in particular traits related to locomotion. Overall, these studies highlight the prevalence of multiple resources supporting fish populations and the importance of studying, conserving, and protecting littoral habitat.

Table of Contents

List of Figures i

List of Tables..iv

1 Chapter 1 1

  1.1 Abstract..2

  1.2 Introduction 3

  1.3 Methods 6

    1.3.1 Study lakes 6

    1.3.2 Lake attributes and sample collection 7

    1.3.3 Resource use by Rainbow Trout 10

    1.3.4 Determinants of Rainbow Trout resource use..11

    1.3.5 Sensitivity analysis 13

  1.4 Results 14

    1.4.1 Lake food web structure...14

    1.4.2 Rainbow Trout resource use...15

    1.4.3 Determinants of Rainbow Trout resource use..16

    1.4.4 Sensitivity analysis 17

  1.5 Discussion..18

  1.6 Acknowledgements 26

  1.7 Literature cited...27

1.8 Tables....35

1.9 Figures....39

1.10 Chapter 1 Appendix 1....47

2 Chapter 2....55

2.1 Abstract....56

2.2 Introduction....57

2.3 Materials and methods....59

2.3.1 Data collected from literature....59

2.3.2 Habitat coupling....61

2.3.3 Lake attributes, species traits, and community characteristics....63

2.3.4 Statistical analysis....66

2.4 Results....69

2.5 Discussion....72

2.6 Acknowledgements....81

2.7 Literature cited....82

2.8 Figures....90

2.9 Chapter 2 Appendix 1....96

List of Figures

Figure 1.1 Study lakes (black points) are all located on the western slope of the Cascade Range in Washington, USA. The star in the inset indicates the approximate location of the study lakes relative to major cities. Rainbow Trout (Oncorhynchus mykiss Walbaum, 1792), primary producers, and data for bathymetry were collected from each lake. USFS = United States Forest Service. 39

Figure 1.2 Isotope biplots for Rainbow Trout (Oncorhynchus mykiss Walbaum, 1792) and primary producers collected in 16 lakes in Washington, USA. Mean values are shown for source pools of terrestrial (▲), pelagic (◆), and littoral (■) basal resources for each lake; error bars are 1 SD of the pooled mean of samples from each habitat. The darkest shaded area designates the outer area of the resource polygon drawn from source means, the medium shade encompasses 1 SD of mean source isotope ratios, and the lightest shade delineates 2 SD from source means. Units are per mil relative to international standards. Raw data from individual fish are shown as solid black points, whereas the same data corrected for N enrichment (4.3‰) are shown as hollow (brown in digital pdf) points (Trout corrected), which includes uncertainty (± 1.5‰). 40

Figure 1.3 Ternary diagrams displaying use of basal resources by Rainbow Trout (Oncorhynchus mykiss Walbaum, 1792) in 16 Washington, USA, lakes estimated from stable isotope mixing models (assumed N enrichment of 4.3 ± 1.5‰). Points are shaded by the littoral extent (LE, %) of the lake that fish were captured in, sized according to population abundance (PA, no. fish/h), and plotted according to proportional reliance on basal resources (colored axes). A.—Mean use of basal resources by trout in each lake. Highlighted are the lakes with the greatest mean use of terrestrial derived (Denny) and pelagic derived (Annette) resources as well as the lake with lowest mean use of littoral derived resources (Olallie). B.—Individual fish compositional use of basal resources...43

Figure 1.4 Ternary diagrams displaying predicted use of terrestrial, littoral–benthic, and pelagic derived resources by 200 mm Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) in the study lakes when littoral extent and population abundance vary. Orange points represent compositions expected within 100% littoral habitats; purple points represent compositions predicted with 40% littoral resource availability. Lines linking pairs of orange and purple points trace the range of compositions expected as littoral availability changes. Increasing line widths represent greater population abundance (PA). A.—Predicted compositions in low terrestrial loading (TL) circumstances (0.4/m). B.—Predicted range of compositions resulting from high TL conditions (3.4/m). Plotting predicted compositions of incrementally changing variables allows for visualizing the direction of compositional change owing to interaction terms in the model.........44

Figure 1.5 Pairwise Pearson correlations according to lake-wide estimates of relative use of (A) terrestrial, (B) pelagic, and (C) littoral–benthic derived resources based on alternative assumptions related to N and C enrichment due to trophic enrichment. The assumed mean and standard deviation of trophic enrichment is indicated for N and C for each alternative tested. 46

Figure 2.1. Each ● represents a study lake. Gray shading indicates one or more lake communities from that country are included in the dataset. 90

Figure 2.2. Boxplots represent the median and 1st and 3rd quantile. Sorted by mean habitat coupling values within colored groupings according to family. Species presented represents of a subset of 45 species that occur in 5% or more of the lakes within the dataset. 91

Figure 2.3. Posterior distributions of environmental condition as estimated by a Bayesian hierarchical beta regression ordered by posterior mean estimates. Shading indicates 95% credible interval. The x-axis indicates the effect of each scaled and centered parameter on habitat coupling. Samples included 496 populations in 100 lakes with varying intercepts according to species (45 species). 92

Figure 2.4. Distribution of habitat coupling according to categorical food acquisition traits. Grouped violin plots including light gray boxplots which represent the median and 1st and 3rd quantile values for habitat coupling according to group. Mean habitat coupling score overlaid as a dark bar. 93

Figure 2.5. Posterior distributions by morphological traits as estimated by a Bayesian non-hierarchical model ordered by trait category and posterior mean with include a shaded 95% credible interval. The x-axis indicates the effect of each scaled and centered parameter on habitat coupling. Grey is metabolism, blue locomotive traits, pink feeding traits. Model completed on 733 populations across 104 lakes. 94

Figure 2.6. Differing relationships between habitat coupling and environmental factors (depth, total area, mean annual temp, and fish species richness) among species observed in 10% or more of the study lakes (17 species). Colors are according to species. Depth is presented on a log scale, accounting for the majority of lakes being less than 100 m deep. 95

List of Tables

Table 1.1. Study lakes represented a range of bathymetries and had differing recommended stocking numbers and frequencies of Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) as decided by Washington State Department of Fish and Wildlife (retrieved from https://wdfw.wa.gov/fishing/locations/high-lakes on 3 January 2021). Our estimates of population abundance, littoral extent, and terrestrial loading are presented alongside the total captured Rainbow Trout from each study lake. 35

Table 1.2. Top 5 candidate models, listed in order of Akaike Information Criterion (AIC) values, relating the isometric log-transformed composition of Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) use of terrestrial, littoral, and pelagic derived resources to fish length (LEN, cm), lake population abundance (PA, no. fish/h), littoral extent (LE, %), terrestrial loading (TL, m), and interactions. Shown is the Pillai's trace statistic value from a Type II multivariate analysis of variance indicating predictor contribution to the model, with the corresponding *p*-value listed below each Pillai statistic. Bold values indicate $p < 0.05$. Model adjusted R^2 values are provided for an additional aspect of model comparison. 37

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1 Chapter 1

Population structure and habitat availability determine resource use by Rainbow Trout in high elevation lakes

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1.1 Abstract

Lake food webs are primarily fueled by energy from pelagic, littoral–benthic, and terrestrial habitats. Aquatic consumers acquire C from across these habitats in varying proportions, either directly or by way of consumer–prey transfers along energy pathways. Several factors, including relative habitat availability, allochthonous inputs, and population density, influence consumer use of various basal resources. However, the extent to which these factors interact to control resource use is not well understood. We used mountain lakes in the Cascade Range of western North America to address the question of how different population sizes, along with the relative availability of illuminated benthic habitat and terrestrial influence, determine resource use by Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792). We measured lake bathymetry, light attenuation, and fish catch/unit effort in 16 lakes and analyzed samples of Rainbow Trout muscle tissue, pelagic seston, littoral–benthic periphyton, and terrestrial vegetation for C and N stable isotope ratios. Stable isotope mixing models quantified proportional use of basal resources for each trout. Compositional regression analysis identified how interactions between relative habitat availability and population abundance influence Rainbow Trout use of basal resources. At low population abundance, we found low relative use of terrestrial derived resources with balanced relative use of pelagic and littoral–benthic derived resources. At high abundance, relative use of littoral–benthic derived resources was low, and relative use of terrestrial and pelagic derived resources varied according to habitat availability. Our findings highlight the importance of environmental and biological interactions when considering factors that influence relative resource use in lake ecosystems.

1.2 Introduction

Ecological resources, such as detritus, dissolved nutrients, and prey, regularly cross ecosystem boundaries (Polis et al. 1997). Consumers acquire C from different habitats either directly or indirectly from consumer–prey transfers along energy pathways (Lindeman 1942). The use of resources traversing these habitat interfaces influences species biomass, community structure, and food web stability (e.g., Nakano and Murakami 2001, Rooney et al. 2006, Gratton et al. 2008). Consequently, severing or altering habitat connections through environmental change or species invasions can alter ecosystem structure and function (Benjamin et al. 2011, Turschak et al. 2014). Growing evidence demonstrates that organisms in upper trophic levels can use multiple food web pathways to varying degrees (Vander Zanden et al. 2011, Vander Zanden and Vadeboncoeur 2020). Previous studies have examined the influence of physical factors in controlling proportional use of resources originating from different habitats (Dolson et al. 2009, Vander Zanden et al. 2011, Eloranta et al. 2015) and population level factors that affect consumer resource use (Svanbäck and Persson 2004, Svanbäck and Bolnick 2007).

Consumers acquiring resources from multiple habitats are a ubiquitous feature of lake ecosystems (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). The energy base of lake food webs is supported by primary production occurring in pelagic (open water), littoral–benthic (submerged, illuminated lake bottom), and terrestrial (watershed draining to the lake) habitats (sensu Solomon et al. 2011). Consumer use of basal resources from these different habitats fluctuates widely. For example, terrestrial reliance by zooplankton in north temperate lakes ranges from inconsequential (2%) to substantial (49%) (Berggren et al. 2014). Whole lake additions of carbonate labeled with elevated ratios of $^{13}C/^{12}C$ point to substantial reliance (22–

55%) on terrestrial C by lake zooplankton (Pace et al. 2004), whereas other studies suggest zooplankton use of terrestrial C is minimal (Francis et al. 2011, Vlah et al. 2018). Estimates of benthic resource use by fish in north temperate lakes, according to diet and stable isotope data, range between 43 and 65% (Vander Zanden and Vadeboncoeur 2002), and a review of lakes from across the world showed that fish varied from complete subsistence on (100%) to absolute independence (0%) from littoral–benthic derived C (Vander Zanden et al. 2011).

Physical factors, including the light environment, nutrient regimes, organic C inputs from the surrounding watershed, and habitat complexity (shoreline morphometry), are considered primary drivers of basal resource availability in lakes (Fee 1979, Carpenter 1983, Vadeboncoeur et al. 2008, 2014, Althouse et al. 2014, Devlin et al. 2016), but the relative availability of basal resources does not always determine relative use by organisms. Some evidence points to consumer resource use being associated with resource availability. For example, Bartels et al. (2016) reported that dissolved organic C (DOC) concentration was positively associated with increased fish use of pelagic resources, possibly caused by higher DOC leading to reduced littoral–benthic primary production (Karlsson et al. 2009) or because low oxygen depressed the zoobenthos prey population (Craig 2015). Similarly, increased zooplankton use of terrestrial resources was linked to reduced availability of macrophyte organic matter in a boreal lake (Grosbois et al. 2017). Smelt (*Retropinna retropinna* Richardson, 1848) and Common Bully (*Gobiomorphus cotidianus* McDowall, 1975) relied on pelagic resources that paralleled phytoplankton and zooplankton abundance, which in turn tracked with seasonal light and nutrient changes in New Zealand lakes (Stewart et al. 2017). By contrast, zooplankton in large montane lakes used less terrestrial derived C than did zooplankton in lowland lakes despite comparable terrestrial C availability, possibly because of more available labile littoral–benthic derived algal resources alongside the terrestrial organic matter (Vlah et al. 2018). In a set of temperate lakes exhibiting a range of littoral habitat availabilities, Lake Trout (*Salvelinus namaycush* Walbaum, 1792) populations relied less on littoral–benthic derived C in lakes with greater spatial extents of littoral habitat (Dolson et al. 2009). In this case, although lakes with highly sinuous shorelines had more littoral habitat, the water temperature of these areas exceeded the thermal tolerance of individuals during the summer, pointing to the potential for the interactive effects of abiotic (physical environmental conditions) and biotic factors (thermal tolerance) to shape lake-level resource use in response to fluctuating resource availability (Dolson et al. 2009).

Biotic factors, such as population abundance or community structure, can act as determinants of resource use. For example, increased population density of Three-spine Sticklebacks (*Gasterosteus aculeatus* Linnaeus, 1758) led to intraspecific competition that drove individuals within the population to consume previously under-used benthic and pelagic prey. Additionally, changes to community structure through the introduction of Smallmouth Bass (*Micropterus dolomieu* Lacepède, 1802) and Rock Bass (*Ambloplites rupestris* Rafinesque, 1817) in lakes of Ontario, Canada, drove native populations of Lake Trout to shift toward pelagic prey of lower trophic levels (Vander Zanden et al. 1999).

This study examined how relative habitat size—and its inferred influence on basal resource availability—interacted with consumer densities to influence among-lake variation in resource use. We build on a growing understanding of relative resource availability in lakes (Vadeboncoeur et al. 2008, 2014, Althouse et al. 2014, Devlin et al. 2016) and advances in measuring consumer use of resources derived from distinct habitats (Solomon et al. 2011, Detmer and Lewis 2019). After ascertaining gradients in population abundance, littoral habitat extent, and terrestrial loading among a suite of lakes, we 1) quantified the proportional use of littoral–benthic, pelagic, and terrestrial C by Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792), the only fish species present; and 2) identified shifts in use associated with physical and biological factors and their interactions. We addressed these questions in high elevation environments of the Cascade Range in Washington, USA, where lake ecosystems are embedded in relatively undisturbed catchments and share physio-climatic characteristics. The study lakes differ with regard to both lake morphometry-defining littoral habitat availability and catchment characteristics influencing terrestrially derived organic matter transport, both referenced as indices of resource availability. They also have dissimilar past stocking histories that have contributed to different relative abundances of Rainbow Trout. Results from this study help anticipate the implications of climate-driven littoral habitat loss and variable fish stocking practices common to these lakes.

1.3 Methods

1.3.1 Study lakes

The study focused on 16 high elevation lakes (953–1372 m a.s.l.) located on the western slope of the Cascade Range, Washington, USA. All lakes are within the Mt Baker Snoqualmie National Forest managed by the United States Forest Service; 13 lakes are located within designated wilderness, and the other 3 are within 5 km of the wilderness boundary (Fig. 1.1). The study lake watersheds are generally characterized by exposed plutonic and metamorphic rocks and dominated by forests of large coniferous trees (e.g., western red cedar, Douglas fir, western hemlock). With the exception of 2 lakes (Upper and Lower Melakwa), the catchments of all study lakes have forest cover >70%. The climate is wet and cool, with 1.5 to 6.4 m of precipitation annually and a temperature range of –5 to 23°C. Study lakes ranged in surface area (0.007–0.242 km^2) and maximum depth (4–70 m) and are characterized by intact shorelines with low convolution (shoreline development index 1.1–1.7). In addition, all lakes were historically fishless because of natural barriers prohibiting fish passage. The lakes selected for this study have been stocked with Rainbow Trout as a part of Washington Department of Fish and Wildlife's High Lakes recreational fishery (Table 1 [at of manuscript]). We selected lakes to have populations of Rainbow Trout and no other fish species, although we discovered Brown Trout (*Salmo trutta* Linnaeus, 1758) in 4 lakes at low abundances.

1.3.2 Lake attributes and sample collection

Field sampling occurred from June to August 2018. To create bathymetric maps for each lake, we surveyed lake depth with an ECHOMAP™ Plus 43Cv and a Cv20TM Transducer (Garmin®, Schaffhausen, Switzerland) in parallel and perpendicular 10- to 20-m transects and marked the lake perimeter with a GPS unit at 5- to 10-m intervals. If the lake perimeter was not walkable, we traced it from the world imagery basemap in ArcMap (version 10.6.1; Esri™, Redlands, California). We delineated watershed area by determining flow direction and flow accumulation for each lake based on digital elevation models. At the deepest part of each lake, we recorded vertical profiles of temperature, dissolved oxygen, and light intensity by deploying a YSI EXO2 (Yellow Springs Instruments, Yellow Springs, Ohio) equipped with a thermometer, optical dissolved oxygen sensor, and an attached HOBO® MX2202 Pendant Temperature/Light Data Logger (Onset®, Bourne, Massachusetts). We used light intensity vertical profiles for each lake to calculate the light attenuation coefficient (k_d) by taking the slope of the relationship between depth and the natural log of the measured light intensity. We used k_d to determine the littoral extent, which we defined as the portion of the lake surface area below which ≥1% of the surface light reached the littoral–benthic habitat. We used a volume-based drainage ratio (watershed area divided by the lake volume, including additional upstream lake volumes when relevant) as an index of terrestrial loading to capture the landscape influence on terrestrially derived organic matter transported to the study lakes (Planas et al. 2001, Sobek et al. 2007, Cremona et al. 2019). Drainage ratio is positively correlated with the flux of allochthonous C into lakes (Cremona et al. 2019). Drainage ratio is also associated with DOC concentration in lakes, although the direction of this relationship can vary (Sobek et al. 2007). For high elevation lakes, the drainage ratio–DOC relationship has been reported to be negative (Seekell et al. 2014) because of high flushing rates (Cremona et al. 2019).

We collected samples of primary producers from pelagic, littoral–benthic, and terrestrial habitats. We gathered pelagic seston from 2 depths (0.5 m and the depth of each lake's dissolved O_2 maximum) at the lake center, and we passed these samples through a 62-µm mesh screen to remove large zooplankton. We collected benthic (attached) periphyton by scrubbing 4 rocks found at 0.5 m depth in the littoral zone in purified water, which we then poured through a 500-µm mesh screen to remove sand and macroinvertebrates. After coarse filtering, we concentrated samples of seston and periphyton on ashed 0.7-µm quartz fiber (QM-A) filters (Whatman, Maidstone, United Kingdom), stored them in tin foil, and froze them in the field using liquid N.

At each lake, we gathered living and dead leaves and needles from the dominant deciduous shrub and conifer vegetation.

We captured Rainbow Trout for muscle tissue samples and to estimate fish population relative abundance and size structure. With relatively few prey species available (including no heterospecific prey fish), omnivorous Rainbow Trout in Washington high lakes are thought to primarily consume zooplankton and terrestrial and littoral–benthic invertebrates (Pfeifer et al. 2001). We set a monofilament gillnet (50 m long × 2 m deep) composed of 8 panels of different mesh sizes ranging from 19 to 64 mm perpendicular to shore, from shallow to deep water, in proximity to large woody debris, in a standardized manner consistent among all lakes. With the exception of the 2 Tuscohatchie Out-In Pot lakes, sampling included at least 1 overnight set. We euthanized captured fish with exsanguination, measured total body length (mm), and froze them on dry ice in the field. Fish capture was approved by the University of Washington Office of Animal Welfare and carried out according to Institutional Animal Care and Use Committee Protocol #4332-02. We cut 1 cm^2 of dorsal muscle tissue from each fish after thawing in the laboratory. Catch/unit effort, calculated as total fish captured divided by net deployment time, served as an index of relative population abundance (Hubert and Fabrizio 2007, Pope et al. 2010, Alexander et al. 2015). In using catch/unit effort, our goal was to provide an accurate ranking of relative fish abundance given that we sampled with identical gear, during the same season, and in locations with similar low structural complexity (Pope et al. 2010).

We completed bulk C and N stable isotope analysis on fish and primary producer samples at the University of Washington, Seattle. We freeze-dried all samples in a BenchTop™ SLC (VirTis, Gardiner, New York) for 48 h, then homogenized them with a ball mill. We packed between 0.330 and 0.350 mg of non-lipid-corrected fish dorsal muscle tissue or 0.999 to 2.021 mg of primary producer material into tin capsules, then analyzed these samples using an Elemental Analyzer (NA 2500; CE Instruments, Wigan, United Kingdom) interfaced with a Delta V Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts) referenced to 2 glutamic acid standards and Bristol Bay Sockeye Salmon (*Oncorhynchus nerka* Walbaum, 1792). We recorded stable isotope ratios in delta notation as ‰ vs Vienna Pee Dee Belemnite for C and ‰ vs air for N. We completed stable isotope analysis in triplicate on 3 random fish samples and 6 random primary producer samples to estimate sample precision; the mean standard deviation of analytical replicates was 0.15‰ for $\delta^{15}N$ and 0.17‰ for $\delta^{13}C$.

1.3.3 Resource use by Rainbow Trout

For each fish (j) from each lake (i), we estimated the composition of proportional use of basal resources ($comp_{ij}$) by a 10,000 iteration (k) Monte Carlo simulation using stable isotope mixing models (Phillips and Gregg 2001). For each iteration within each Monte Carlo simulation, a stable isotope mixing model composed of 3 equations with 3 unknown parameters was solved algebraically. The 3 unknown values to be solved, φT, φP, and φL, represent the portion of consumer biomass fixed by primary production in T = terrestrial, P = pelagic, and L = littoral–benthic habitats. The known values within the equations are: 1) the C- and N-stable isotope ratios of each source category (leaves, seston, periphyton) taken from normal distributions of the lake specific means and standard deviations of $\delta^{13}C$ and $\delta^{15}N$, 2) the N trophic enrichment factor ($\Delta^{15}N$) taken from a normally distributed mean and standard deviation (we used 4.3 ± 1.5‰ [Bunn et al. 2013] as our estimate of trophic enrichment between algae and omnivorous fish, a value selected because it accounts for variation in discrimination according to trophic position), 3) the individual fish (*j*) from lake (*i*) N- and C-stable isotope ratios, and 4) the value of 1 representing the sum of the portions.

$$\varphi T_{ijk} + \varphi P_{ijk} + \varphi L_{ijk} = 1 \quad \text{(Eq. 1)}$$

$$\varphi T_{ijk}(\delta^{13}C_{leaves_i}) + \varphi P_{ijk}(\delta^{13}C_{seston_i}) + \varphi L_{ijk}(\delta^{13}C_{periphyton_i}) = \delta^{13}C_{fish_{ij}} \quad \text{(Eq. 2)}$$

$$\varphi T_{ijk}(\delta^{15}N_{leaves_i}) + \varphi P_{ijk}(\delta^{15}N_{seston_i}) + \varphi L_{ijk}(\delta^{15}N_{periphyton_i}) = \delta^{15}N_{fish_{ij}} - \Delta^{15}N_{ijk}$$

(Eq.3)

After the completion of the Monte Carlo simulation, we removed iterations that resulted in the mixture falling outside of the resource polygon for each fish (i.e., iterations that produced irrational source portions such as <0 or >1; Table S1), then we calculated proportional use of each resource by taking the mean and variance of the remaining Monte Carlo simulation iterations. Together, the respective non-negative values for proportional use of terrestrial, pelagic, and littoral–benthic derived resources were a composition represented as a vector of 3 components that summed to 1, expressed as $comp_{ij} = [\overline{\varphi T_{ij}}, \overline{\varphi P_{ij}}, \overline{\varphi L_{ij}}]$.

1.3.4 Determinants of Rainbow Trout resource use

We performed a regression analysis with the compositions of proportional resource use ($comp_{ij}$) for each fish as the response variable and the fish's body length and metrics associated with the lake each fish was captured in (littoral extent, population abundance, and terrestrial loading), including 2-way (littoral extent and population abundance, littoral extent and terrestrial loading, population abundance and terrestrial loading) and higher-order (littoral extent, population abundance, and terrestrial loading) interactions, as predictors variables. Owing to the compositional nature of our response data (3 portions that summed to 1), we first transformed $comp_{ij}$ using an isometric log-ratio (ilr) transformation to create a pair of ilr coordinates (van den Boogaart and Tolosana-Delgado 2013). We then regressed the ilr coordinates as a multivariate multiple regression, visually inspecting residuals to confirm normal error distribution and homogenous error structure(van den Boogaart and Tolosana-Delgado 2013). After confirming the data met multivariate assumptions of normality according to Doornik–Hansen's test (Doornik and Hansen 2008), parameters within the candidate models were assessed with a Type II multivariate analysis of variance. We ranked our candidate models using Akaike Information Criterion (AIC) to evaluate the relative support (given the data) for each model. We also calculated the difference between the lowest approximating model AIC value and all remaining model values (ΔAIC), considering models within 2 AIC units as the same rank (Burnham et al. 2002). We considered the 3 models with the lowest AIC when identifying parameters with explanatory power. The coefficients of these models conveyed little meaning because the response variables were ilr coordinates; therefore, it was necessary to use direct visualization to describe the relationships between predictors and response variables (van den Boogaart and Tolosana-Delgado 2013). We used the best fit model to calculate predicted ilr coordinates for fish of 3 size classes (100, 200, 300 mm total body length) across a range of possible littoral extent and population abundance values according to low (25th quantile, 0.4/m) and high (75th quantile, 3.4/m) terrestrial loading. Then we transformed the predicted ilr coordinates back into compositions and plotted them using ternary diagrams for explanatory interpretation of the model coefficients. All analyses were conducted in R (version 3.6.2 and 4.0.3; R Project for Statistical Computing, Vienna, Austria) with use of the *tidyverse* (1.3.0 Wickham et al. 2019), *MASS* (7.3-53.1; Venables and Riley 2002), *MVN* (5.8; Korkmaz et al. 2014), *car* (3.0-10; Fox and Weisberg 2019), *faraway* (1.0.7 ; Faraway 2016), *MuMIn* (1.43.17; Bartoń 2020), *compositions* (2.0-1; van den Boogaart et al. 2021), *broom* (0.7.6; Robinson et al. 2021), *patchwork* (1.1.1; Pedersen 2020), *ggtern* (3.3.0; Hamilton and Ferry 2018), *corrplot* (0.84; Wei et al. 2017), and *magick* (2.6.0; Ooms 2021) packages.

1.3.5 Sensitivity analysis

We developed compositions of proportional resource use by using the same Monte Carlo simulation approach described above but with alternative assumptions regarding N and C trophic enrichment and uncertainty to determine the influence of different trophic enrichment assumptions on compositional regression analysis results. In all, we tested 12 alternatives, each consisting of a different combination of values regarding N and C trophic enrichment and uncertainty between primary producers and fish. We tested 2 different N trophic enrichment values, 4.3‰, estimated to be the distance between algae and omnivorous fish (Bunn et al. 2013), and 6.8‰, determined by assigning Rainbow Trout a trophic level of 3 and applying a 3.4‰ estimate/trophic level >1 (Post 2002). We assigned a trophic level of 3 to the Rainbow Trout given the lack of smaller prey fish in the study lakes. For each N value, we tested 3 different levels of uncertainty surrounding enrichment. We used ±1.5‰ to reflect the calculated uncertainty between algae and omnivorous fish (Bunn et al. 2013), ±0.22‰, a Rainbow Trout-specific value derived from McCutchan et al. (2003), and ±0‰, which assumed all Rainbow

Trout muscle tissue was similarly enriched with no variation. We tested 2 alternatives for C. First, we considered no C trophic enrichment (Solomon et al. 2011), then tested a trout-specific trophic enrichment value between trout chow and Rainbow Trout of $\Delta^{13}C$ of 1.9 ± 0.51‰ (McCutchan et al. 2003). We calculated the mean composition of the Rainbow Trout from each lake under each alternative set of trophic enrichment assumptions to determine pairwise correlation between alternatives. We also refit and reranked compositional linear regression models and then compared model results within and among the alternative sets of assumptions.

1.4 Results

1.4.1 Lake food web structure

There were differences in littoral extent, terrestrial loading (as estimated by drainage ratio), population abundance (as estimated by catch/unit effort), and isotopic variability among the lakes. Littoral extent ranged from 39 to 100%, terrestrial loading varied from 0.3 to 45.4/m, and population abundance spanned 0.05 to 4.6 fish/h (Table 1). The C-stable isotope ratio of periphyton averaged across all lakes was 3.7‰ higher than that of seston and 6.7‰ higher than that of terrestrial vegetation (periphyton: –23.7‰, seston: –27.4‰, terrestrial: –30.4‰). However, there was a substantial effect of lake on primary producer C values confirming the importance of analyzing the data using lake-specific stable isotope mixing models (terrestrial: $F_{15,45} = 2.18$, $p = 0.022$, pelagic: $F_{15,16} = 3.48$, $p = 0.009$, and littoral–benthic: $F_{15,48} = 6.60$, $p < 0.001$). The N-stable isotope ratio of pelagic seston averaged across all lakes was 4.4‰ higher than that of periphyton and 8.1‰ higher than that of terrestrial vegetation (seston: 3.8‰, periphyton: –0.7‰, terrestrial: –4.3‰). We also found a substantial effect of lake on periphyton N-stable isotope ratios ($F_{15,48} = 2.04$, $p = 0.031$), but terrestrial and pelagic primary producers showed little difference in N isotope ratios across lakes (terrestrial: $F_{15,45} = 1.54$, $p = 0.131$, pelagic: $F_{15,16} = 2.12$, $p = 0.073$). Rainbow Trout C isotope ratios were always within the range of the basal resources contributing to each lake food web (fish $\delta^{13}C$ values ranged between –32.2 and –24.2‰). The N-stable isotope ratios of fish were consistently enriched relative to the basal resources contributing to the food web and ranged from 4.6 to 6.7‰ (Fig. 1.2).

1.4.2 Rainbow Trout resource use

Trout use of basal resources based on 3 source isotope mixing models varied among and within the lakes. Based on an assumed N enrichment of 4.3 ± 1.5‰ (Bunn et al. 2013), overall trout use of resources was relatively balanced with slightly more use of pelagic derived resources and the remaining use split between littoral and terrestrial resources (Fig. 1.3A, B). Within each lake, the mean proportional contributions from habitat sources to trout biomass ranged from 0.11 to 0.42 (littoral–benthic resources), 0.26 to 0.64 (pelagic resources), and 0.13 to 0.42 (terrestrial resources) (Fig. 1.3A). Mean basal resource use by fish captured in Denny Lake tended more toward terrestrial resources relative to all other lakes, and mean use by trout in Annette Lake tended toward pelagic derived resources (Fig. 1.3A). Compared to other lakes, trout in Olallie Lake relied the least on littoral–benthic derived resources (Fig. 1.3A). Among all fish in all lakes, individual consumer use of littoral–benthic derived resources ranged from 0.08 to 0.63, pelagic from 0.17 to 0.74, and terrestrial from 0.08 to 0.65 (Fig. 1.3B). Within a lake, individual fish varied in their use of resources. As an example, although all individual fish in Denny Lake relied minimally on pelagic resources, some individuals tended toward heavy terrestrial resource use and others used more littoral resources. Unlike the trout in Denny Lake, all individuals in Kulla Kulla Lake relied minimally on terrestrial derived resources, whereas use of pelagic resources was more variable, ranging from 36 to 61%.

1.4.3 Determinants of Rainbow Trout resource use

Fish use of littoral, pelagic, and terrestrial resources varied as a function of littoral extent, fish length, relative population abundance, and interactions between littoral extent and relative population abundance and between terrestrial influence and littoral extent, as determined by Pillai's trace statistics with $p < 0.05$ in the 3 candidate models with the lowest AIC (Table 2 [at end of manuscript]). Interaction between relative population abundance and littoral extent explained the most variability observed in the resource use compositions for the top 3 candidate models (Pillai's trace statistic is 0.30–0.29 for top models). Visual inspection of observed vs fitted values demonstrated adequate fit with an overall R^2 of 0.36 for the best model (Table 2). We examined how average fish (length 200 mm) use of basal resources changed as a function of littoral extent and relative population abundance by using the best fit model to generate ilr coordinates, which we transformed into predictions of consumer resource use and plotted on ternary diagrams. The ternary diagrams demonstrate that when littoral extent is high (orange points, Fig. 1.4A, B), resource use is relatively similar among fish regardless of relative population abundance (line thickness within Fig. 1.4A, B) or terrestrial loading (location of orange points in Fig. 1.4A compared to B); in this case, proportional use of basal resources is balanced between littoral and pelagic use with low terrestrial reliance (assumed N enrichment is

4.3 ± 1.5‰). But when littoral extent is low (purple points, Fig. 1.4A, B), increasing relative population abundance leads to either higher terrestrial resource use when terrestrial loading is low or a balance of pelagic and terrestrial use when terrestrial loading is high (Fig. 1.4A, B). Likewise, at low relative population abundance (thin lines in Fig. 1.4A, B), resource use is relatively similar, balanced between littoral and pelagic resources regardless of littoral extent or terrestrial loading. As relative population abundance increases, the models suggest that littoral extent becomes more influential on determining resource use (thick lines in Fig. 1.4A, B). Alongside trends related to relative population abundance, littoral extent, and terrestrial loading as drivers of relative resource use, we observed that the relative use of pelagic resources tended to increase with fish body length (determined by comparison of prediction plots with fish lengths of 100, 200, and 300 mm; Fig. S1).

1.4.4 Sensitivity analysis

Individual consumer estimates of proportional use of littoral–benthic, pelagic, and terrestrial resources differed depending on assumptions of trophic enrichment. However, the estimated compositions remained highly correlated between the alternatives (Fig. 1.5A–C). Larger values for N enrichment ($\Delta^{15}N$ = 6.8‰ compared with $\Delta^{15}N$ = 4.3‰) slightly increased estimates of terrestrial resource use and reduced estimates of pelagic resource use; similarly, alternatives tested with C enrichment ($\Delta^{13}C$ of 1.9 ± 0.51‰) estimated lower use of littoral–benthic resources and greater terrestrial and pelagic resource use compared to alternatives with no C enrichment. Littoral–benthic resource use was the least correlated between the alternatives with corrections of $\Delta^{15}N$ = 4.3‰ and $\Delta^{13}C$ = 1.9‰ compared with $\Delta^{15}N$ = 6.8‰ and $\Delta^{13}C$ = 0‰ (Fig.

1.5C). Monte Carlo simulations with reduced uncertainty for N enrichment (no uncertainty and ±0.22‰), when compared to simulations with the highest uncertainty (±1.5‰), resulted in a slightly expanded range of values for proportional use of littoral–benthic, pelagic, and terrestrial resources among the trout.

Although proportional use of basal resources differed depending on the enrichment assumptions used in each alternative, compositional regression analysis results were robust to assumptions of trophic enrichment. Regardless of the assumed trophic enrichment values used in the stable isotope mixing models, all subsequent highest ranked linear models identified littoral extent and the interaction between littoral extent and relative population abundance as important drivers of proportional use of basal resources. In addition, the interaction between littoral extent and relative population abundance consistently surfaced as contributing the most to the models' explanatory power, with Pillai's trace statistics ranging from 0.21 to 0.43 for models with the lowest AIC (Table S2).

1.5 Discussion

By leveraging the relative simplicity of a single fish species system of lakes (i.e., previously fishless mountain lakes stocked with Rainbow Trout), we demonstrate that consumer population abundance can modulate the manner in which physical habitat conditions influence consumer resource use. This work highlights the importance of interactions between abiotic and biotic factors as determinants of relative use of terrestrial, littoral, and pelagic resources. In exploring our results, we also present potential mechanisms driving our predicted resource use.

Overall, we suggest that increased understanding of how populations, species, or communities respond to, and interact with, changes in the physical environment will aid in understanding the implications of future environmental change for lake ecosystems.

Our study demonstrates that interactions between littoral habitat availability and population abundance influence Rainbow Trout use of basal resources in high elevation lakes. We found that resource use was relatively balanced between littoral and pelagic sources, with low terrestrial reliance, regardless of littoral habitat availability at low population abundance. However, as abundance increased, leading to presumed greater intraspecific competition, habitat structure became more influential, shifting resource use toward terrestrial or pelagic resources in lakes with low littoral extent. These results suggest the heightened importance of biotic factors, specifically modulated by fish abundance, as a determinant of resource use in Rainbow Trout when littoral habitat is more limited.

We found that pelagic resource use by trout increased with the loading of terrestrial material from the watershed as inferred by the drainage ratio. Terrestrial loading of allochthonous material includes both C and nutrient inputs, which can support pelagic primary production and promote zooplankton production (Pace et al. 2004, Kelly et al. 2016, Rivera Vasconcelos et al. 2018). Evidence suggests that in oligotrophic lakes additional terrestrial inputs supply nutrients that promote phytoplankton that serve as a food resource for zooplankton (Kissman et al. 2017), which could explain increased Rainbow Trout use of pelagic resources in lakes with high terrestrial loading when relative population abundance is high. Another potential mechanism linking increased terrestrial inputs and increased pelagic resource use may be shading of littoral–benthic habitat by terrestrial dissolved organic matter. Nutrients not taken up by benthic algae could then be used by pelagic primary producers (Vasconcelos et al. 2016). However, light attenuation patterns in our lakes do not appear to support this explanation. Overall, the mechanism responsible for our observation of increased pelagic resource use with increased terrestrial loading remains uncertain. We encourage further exploration into when, and how, the arrival of terrestrially derived materials to recipient waterbodies impacts the resources available to and used by biota.

We found evidence that low terrestrial inputs alongside low littoral extent and high population abundance leads to increased use of terrestrially derived resources relative to other resources. It is common for aquatic consumers to be supported by littoral–benthic primary production in highly oligotrophic lakes, possibly because plankton productivity is insufficient to support planktivorous food webs (Sierszen et al. 2003). One possible explanation for increased use of terrestrially derived resources at high population abundance, even in lakes with lower terrestrial loading, may be that as trout population abundance increases beyond what the littoral–benthic pathways can support, trout, as salmonids with flexible diets (Vander Zanden et al. 2000, Robillard et al. 2011), shift to alternative resources. In high elevation lakes, the only alternative may be to forage for terrestrial insects and benthic macroinvertebrates that consume detritus (Mehner et al. 2016).

An increased use of terrestrially derived resources when terrestrial loading is low and increased use of pelagic resources when terrestrial loading is high (with low littoral extent and high population abundance) may reflect increasing drainage ratio being associated with low DOC concentration due to high flushing rates in mountain lakes (Seekell et al. 2014, Cremona et al. 2019). Testing this hypothesis in our study lakes is not possible because of lack of data.

Nonetheless, increased pelagic resource use when the amount of allochthonous material entering the lake is thought to be high may be related to increased hydrologic flushing rates and reduced DOC concentration, limiting the terrestrial subsidies available to consumers. By contrast, if we assume that low terrestrial loading is associated with relatively higher DOC in our lakes, then the mechanism for increased terrestrial resource use at high relative population abundance may be a reflection of terrestrially derived C supporting zooplankton via bacterial pathways (Berggren et al. 2010), although evidence points to zooplankton use of terrestrial detritus as being minimal (Francis et al. 2011, Brett et al. 2017). Without zooplankton data and other primary consumer data from these lakes, the mechanisms behind these findings remain unclear. However, our findings confirm the importance of considering lakes as lake-catchment complexes that integrate terrestrial and aquatic processes (Toporowska et al. 2018).

We found evidence that increased use of pelagic derived resources occurs with increased fish body length. Rainbow Trout are known to undergo ontogenetic diet shifts (Lattuca et al. 2008), and in this case, the greater portion of pelagic derived resources observed with increased trout body size is likely a reflection of increased off-shore foraging and consumption of pelagic prey. As our study system did not have pelagic forage fish or some other intermediate fish prey, we did not associate increased consumption of pelagic resources with increasing trout trophic position. Our observation is supported by other studies that demonstrate ontogenetic shifts in salmonids do not always include an increase in trophic position (Vander Zanden et al. 2000).

Evidence for the importance of interactions between biotic and abiotic factors influencing relative use of basal resources extends beyond what we have highlighted for Rainbow Trout. For example, temperature (Dolson et al. 2009, Guzzo et al. 2017) is an environmental condition that influences relative use of resources when conditions exceed the thermal tolerance for Lake Trout. Increased DOC in the water column of lakes had contrasting effects on resource use by different species: Tunney et al. (2018) showed that Walleye (*Sander vitreus* Mitchill, 1818) increased use of benthic resources when DOC was elevated, whereas other studies indicated Eurasian Perch (*Perca fluviatilis* Linnaeus, 1758) and other fish species showed the opposite pattern (Karlsson et al. 2009, Bartels et al. 2016). These divergent responses to DOC between species are explained in part by their differing visual acuities: Walleye, unlike Eurasian Perch, are effective predators in the low light conditions resulting from high DOC (Tunney et al. 2018). Additionally, subgroups of Eurasian Perch within a single waterbody used substantially different ratios of pelagic:littoral derived resources, emphasizing that intraspecific trait variability can influence resource acquisition (Marklund et al. 2019). Our study expands on this work to demonstrate that littoral habitat availability interacts with presumed intraspecific competition associated with population abundance to drive relative use of basal resources.

Fish species richness commonly increases with lake surface area (Jackson et al. 2001), which makes it challenging to separate the effects of biotic interactions from the effects of population size and habitat availability on consumer resource use. However, our study lakes were historically fishless because of natural barriers prior to being stocked with Rainbow Trout, thereby providing an opportunity to control for the species diversity–area relationship. When examining several lakes of increasing area, but relatively low Rainbow Trout abundances, we observed similar ratios of resource use regardless of lake size or relative habitat availability. Our findings, which occurred in the context of a single fish system, dovetail with the observations of Eloranta et al. (2015) who reported increased pelagic resource use by Arctic Charr (*Salvelinus* *alpinus* Linnaeus, 1758) in relation to lake size in a context that included changes in fish species richness and relative fish species proportions. Together these observations highlight the challenge, and importance, of teasing apart how fish population abundance, fish assemblage composition, and relative resource availability interact to influence how consumers use differing resource pathways.

We expect that basal resource use by Rainbow Trout in high elevation lakes expresses linkages to both climate-driven littoral habitat alterations and stocking regimes that influence population size. In the North Cascades, changes in climate are expected to include decreased snowpack and increased summer evaporation (Raymond et al. 2014), which can lead to lower water levels in mountain lakes (Moser et al. 2019). Littoral zones are drastically altered as lake water levels decline, where the associated downslope shift of littoral zones reduces riparian linkages and the availability of littoral structure (Lake 2011). These alterations can cause changes to population structure, increase predation rates, and intensify intra- and interspecific competition among fish species (Sass et al. 2006, Gaeta et al. 2014, Glassic and Gaeta 2019). Our study predicts that climate-driven reductions in littoral habitat will lead to increased use of terrestrial and pelagic resources. Furthermore, fish-stocking practices that increase population abundances, either directly or as a result of reduced lake volumes, are expected to contribute to even greater use of terrestrially derived resources by Rainbow Trout.

Each of the lakes we surveyed is part of a managed high-lakes fishery, meaning that annual decisions about stocking directly influence Rainbow Trout population abundance. We observed that, regardless of relative resource availability, stocked Rainbow Trout consume adequate resources to maintain biomass, including when resource flow pathways vary or are altered (Hayden et al. 2019). Omnivorous taxa like Rainbow Trout may impact the abundance of prey organisms, leading to changes in lower trophic community structure. Although we do not have evidence of community-level impacts in our study system, it is common to see fish introductions alter zooplankton assemblages and impact amphibian populations in mountain lakes (Liss et al. 1998, Knapp et al. 2001, Knapp 2005). Changes to lower trophic level populations can have implications even for adjacent ecosystems, particularly if aquatic exports from lakes to the surrounding terrestrial ecosystem are diminished as a result of trout introductions (Matthews et al. 2002, Epanchin et al. 2010). Our study points to the relevance of considering lake morphometry and watershed attributes, in particular littoral extent, when making annual decisions about stocking levels.

Results of stable isotope mixing models that use C and N isotope ratios from homogenized bulk consumer tissues are influenced by assumptions made about trophic enrichment (Bond and Diamond 2011). We assumed a common trophic position of the Rainbow Trout in our study lakes, although it is possible that trout trophic position differs among and within the Rainbow Trout populations (Vander Zanden et al. 2000, Klobucar and Budy 2020). We also assumed enrichment was consistent between primary producers and consumers. However, there is evidence that trophic enrichment associated with food quality (recalcitrant detritus vs labile algae) could create a bias where little trophic enrichment occurs between consumers reliant on resources with low N availability (Adams and Sterner 2000). If we overestimated the isotopic distance between fish and terrestrially derived food pathways, then our mixing model results could have inflated terrestrial resource use. In our study, although trophic enrichment values influenced individual consumer proportional use of basal resources, the factors driving consumer use of basal resources, in particular the interaction between relative population abundance and littoral extent, were consistent across the assumptions we tested.

Moving forward, a promising alternative to running stable isotope mixing models on homogenized bulk consumer tissues may be completing compound-specific isotope analysis of amino acids for use in mixing models. The C-stable isotope composition of essential (non-synthesized) amino acids and the N-stable isotope composition of source amino acids both have near-zero trophic enrichment when assimilated into tissue (Whiteman et al. 2019). Using C and N isotope ratios from compound-specific isotope analysis of amino acids in mixing models could eliminate the need for model parameters related to trophic enrichment. Alternatively, the comparison of N isotopes in trophic vs source amino acids would enable individual consumer trophic level to be estimated (Chikaraishi et al. 2009, Ohkouchi et al. 2017), although some of the same issues of variability with bulk tissue trophic enrichment exist with this approach (McMahon and McCarthy 2016). Using amino acid C and N isotopes in mixing models has the potential to reduce bias caused by assumptions made regarding trophic enrichment.

Food webs as networks of consumer resource interactions have received increasing attention in ecology (Layman et al. 2015). By examining a suite of lakes with broad similarities related to climate and land cover, but with differences with regard to resource availability and relative trout population abundance, we have shown how littoral extent and population abundance interact to influence consumer resource use. Additional study is needed to further untangle myriad factors that determine the availability and consumer use of resources originating from multiple habitats. Insights into the drivers, magnitude, and mechanisms of consumer reliance on resources from multiple habitats will increase our understanding of how resource pathway variability affects community structure, secondary productivity, and ecosystem function in lakes.

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1.7 Literature cited

Adams, T. S., and R. W. Sterner. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. Limnology and Oceanography 45:601–607.

Alexander, T. J., P. Vonlanthen, G. Periat, F. Degiorgi, J.-C. Raymond, and O. Seehausen. 2015. Evaluating gillnetting protocols to characterize lacustrine fish communities. Fisheries Research 161:320–329.

Althouse, B., S. Higgins, and M. J. Vander Zanden. 2014. Benthic and planktonic primary production along a nutrient gradient in Green Bay, Lake Michigan, USA. Freshwater Science 33:487–498.

Bartels, P., P. E. Hirsch, R. Svanbäck, and P. Eklöv. 2016. Dissolved organic carbon reduces habitat coupling by top predators in lake ecosystems. Ecosystems 19:955–967.

Bartoń, K. 2020. *MuMIn*: Multi-model inference. (Available from: https://cran.r-project.org/web/packages/MuMIn/index.html)

Benjamin, J. R., K. D. Fausch, and C. V. Baxter. 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. Oecologia 167:503–512.

Berggren, M., L. Ström, H. Laudon, J. Karlsson, A. Jonsson, R. Giesler, A.-K. Bergström, and M. Jansson. 2010. Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers: Terrestrial LMWC and lake secondary production. Ecology Letters 13:870–880.

Berggren, M., S. E. Ziegler, N. F. St-Gelais, B. E. Beisner, and P. A. del Giorgio. 2014. Contrasting patterns of allochthony among three major groups of crustacean zooplankton in boreal and temperate lakes. Ecology 95:1947–1959.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Brett, M. T., S. E. Bunn, S. Chandra, A. W. E. Galloway, F. Guo, M. J. Kainz, P. Kankaala, D. C. P. Lau, T. P. Moulton, M. E. Power, J. B. Rasmussen, S. J. Taipale, J. H. Thorp, and J. D. Wehr. 2017. How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? Freshwater Biology 62:833–853.

Bunn, S. E., C. Leigh, and T. D. Jardine. 2013. Diet-tissue fractionation of $\delta^{15}N$ by consumers from streams and rivers. Limnology and Oceanography 58:765–773.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer, New York, New York.

Carpenter, S. R. 1983. Lake geometry: Implications for production and sediment accretion rates. Journal of Theoretical Biology 105:273–286.

Chikaraishi, Y., N. O. Ogawa, Y. Kashiyama, Y. Takano, H. Suga, A. Tomitani, H. Miyashita, H. Kitazato, and N. Ohkouchi. 2009. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids: Trophic level estimation by amino acid δ^{15}N. Limnology and Oceanography: Methods 7:740–750.

Craig, N., S. E. Jones, B. C. Weidel, and C. T. Solomon. 2015. Habitat, not resource availability, limits consumer production in lake ecosystems: Habitat drives zoobenthos production. Limnology and Oceanography 60:2079–2089.

Cremona, F., A. Laas, P. C. Hanson, M. Sepp, P. Nõges, and T. Nõges. 2019. Drainage ratio as a strong predictor of allochthonous carbon budget in hemiboreal lakes. Ecosystems 22:805–817.

Detmer, T., and W. M. Lewis. 2019. Influences of fish on food web structure and function in mountain lakes. Freshwater Biology 64:1572–1583.

Devlin, S. P., M. J. Vander Zanden, and Y. Vadeboncoeur. 2016. Littoral-benthic primary production estimates: Sensitivity to simplifications with respect to periphyton productivity and basin morphometry. Limnology and Oceanography: Methods 14:138–149.

Dolson, R., K. McCann, N. Rooney, and M. Ridgway. 2009. Lake morphometry predicts the degree of habitat coupling by a mobile predator. Oikos 118:1230–1238.

Doornik, J. A., and H. Hansen. 2008. An omnibus test for univariate and multivariate normality. Oxford Bulletin of Economics and Statistics 70:927–939.

Eloranta, A. P., K. K. Kahilainen, P.-A. Amundsen, R. Knudsen, C. Harrod, and R. I. Jones. 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecology and Evolution 5:1664–1675.

Epanchin, P. N., R. A. Knapp, and S. P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology 91:2406–2415.

Faraway, J. 2016. *faraway*: Functions and datasets for books by Julian Faraway. (Available from: https://cran.r-project.org/web/packages/faraway/index.html)

Fee, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments: Productivity of ELA lakes. Limnology and Oceanography 24:401–416.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression. 3rd edition. Sage, Thousand Oaks, California.

Francis, T. B., D. E. Schindler, G. W. Holtgrieve, E. R. Larson, M. D. Scheuerell, B. X. Semmens, and E. J. Ward. 2011. Habitat structure determines resource use by zooplankton in temperate lakes: Habitat and energetic support of lake zooplankton. Ecology Letters 14:364–372.

Gaeta, J. W., G. G. Sass, and S. R. Carpenter. 2014. Drought-driven lake level decline: Effects on coarse woody habitat and fishes. Canadian Journal of Fisheries and Aquatic Sciences 71:315–325.

Glassic, H. C., and J. W. Gaeta. 2019. Littoral habitat loss caused by multiyear drought and the response of an endemic fish species in a deep desert lake. Freshwater Biology 64:421–432.

Gratton, C., J. Donaldson, and M. J. Vander Zanden. 2008. Ecosystem linkages between lakes and the surrounding terrestrial landscape in northeast Iceland. Ecosystems 11:764–774.

Grosbois, G., P. A. del Giorgio, and M. Rautio. 2017. Zooplankton allochthony is spatially heterogeneous in a boreal lake. Freshwater Biology 62:474–490.

Guzzo, M. M., P. J. Blanchfield, and M. D. Rennie. 2017. Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. Proceedings of the National Academy of Sciences 114:201702584.

Hamilton, N. E., and M. Ferry. 2018. *ggtern*: Ternary diagrams using *ggplot2*. Journal of Statistical Software, Code Snippet 3 87:1–17.

Hayden, B., C. Harrod, S. M. Thomas, A. P. Eloranta, J.-P. Myllykangas, A. Siwertsson, K. Præbel, R. Knudsen, P.-A. Amundsen, and K. K. Kahilainen. 2019. From clear lakes to murky waters—Tracing the functional response of high-latitude lake communities to concurrent 'greening' and 'browning.' Ecology Letters 22:807–816.

Hubert, W. A., and M. C. Fabrizio. 2007. Relative abundance and catch per unit effort. Chapter 7 *in* C. S. Guy and M. L. Brown (editors). Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities—The roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.

Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature 460:506–509.

Kelly, P. T., N. Craig, C. T. Solomon, B. C. Weidel, J. A. Zwart, and S. E. Jones. 2016. Experimental whole-lake increase of dissolved organic carbon concentration produces unexpected increase in crustacean zooplankton density. Global Change Biology 22:2766–2775.

Kissman, C. E. H., C. E. Williamson, K. C. Rose, and J. E. Saros. 2017. Nutrients associated with terrestrial dissolved organic matter drive changes in zooplankton:phytoplankton biomass ratios in an alpine lake. Freshwater Biology 62:40–51.

Klobucar, S. L., and P. Budy. 2020. Trophic structure of apex fish communities in closed versus leaky lakes of arctic Alaska. Oecologia 194:491–504.

Knapp, R. A. 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, USA. Biological Conservation 121:265–279.

Knapp, R. A., K. R. Matthews, and O. Sarnelle. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecological Monographs 71:401–421.

Korkmaz, S., D. Goksuluk, and G. Zararsiz. 2014. *MVN*: An R package for assessing multivariate normality. The R Journal 6:151–162.

Lake, P. S. 2011. Drought and fish of standing and flowing waters. Pages 209–242 *in* Drought and aquatic ecosystems: Effects and responses. John Wiley & Sons, Hoboken, New Jersey.

Lattuca, M. E., M. A. Battini, and P. J. Macchi. 2008. Trophic interactions among native and introduced fishes in a northern Patagonian oligotrophic lake. Journal of Fish Biology 72:1306–1320.

Layman, C. A., S. T. Giery, S. Buhler, R. Rossi, T. Penland, M. N. Henson, A. K. Bogdanoff, M. V. Cove, A. D. Irizarry, C. M. Schalk, and S. K. Archer. 2015. A primer on the history of food web ecology: Fundamental contributions of fourteen researchers. Food Webs 4:14–24.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

Liss, W. J., G. L. Larson, E. A. Deimling, L. M. Ganio, R. L. Hoffman, and G. A. Lomnicky. 1998. Factors influencing the distribution and abundance of diaptomid copepods in high-elevation lakes in the Pacific Northwest. Hydrobiologia 379:63–75.

Marklund, M. H. K., R. Svanbäck, L. Faulks, M. F. Breed, K. Scharnweber, Y. Zha, and P. Eklöv. 2019. Asymmetrical habitat coupling of an aquatic predator—The importance of individual specialization. Ecology and Evolution 9:3405–3415.

Matthews, K. R., R. A. Knapp, and K. L. Pope. 2002. Garter Snake distributions in high-elevation aquatic ecosystems: Is there a link with declining amphibian populations and nonnative trout introductions? Journal of Herpetology 36:16–22.

McCutchan, J. H., W. M. Lewis, C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390.

McMahon, K. W., and M. D. McCarthy. 2016. Embracing variability in amino acid $\delta^{15}N$ fractionation: Mechanisms, implications, and applications for trophic ecology. Ecosphere 7:e01511.

Mehner, T., K. Attermeyer, M. Brauns, S. Brothers, J. Diekmann, U. Gaedke, H.-P. Grossart, J. Köhler, B. Lischke, N. Meyer, K. Scharnweber, J. Syväranta, M. J. Vanni, and S. Hilt. 2016. Weak response of animal allochthony and production to enhanced supply of terrestrial leaf litter in nutrient-rich lakes. Ecosystems 19:311–325.

Moser, K. A., J. S. Baron, J. Brahney, I. A. Oleksy, J. E. Saros, E. J. Hundey, S. Sadro, J. Kopáček, R. Sommaruga, M. J. Kainz, A. L. Strecker, S. Chandra, D. M. Walters, D. L. Preston, N. Michelutti, F. Lepori, S. A. Spaulding, K. R. Christianson, J. M. Melack, and J. P. Smol. 2019. Mountain lakes: Eyes on global environmental change. Global and Planetary Change 178:77–95.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences 98:166–170.

Ohkouchi, N., Y. Chikaraishi, H. G. Close, B. Fry, T. Larsen, D. J. Madigan, M. D. McCarthy, K. W. McMahon, T. Nagata, Y. I. Naito, N. O. Ogawa, B. N. Popp, S. Steffan, Y. Takano, I. Tayasu, A. S. J. Wyatt, Y. T. Yamaguchi, and Y. Yokoyama. 2017. Advances in the application of amino acid nitrogen isotopic analysis in ecological and biogeochemical studies. Organic Geochemistry 113:150–174.

Ooms, J. 2021. *magick*: Advanced graphics and image-processing in R. (Available from: https://cran.r-project.org/web/packages/magick/index.html)

Pace, M. L., J. J. Cole, S. R. Carpenter, J. F. Kitchell, J. R. Hodgson, M. C. Van De Bogert, D. L. Bade, E. S. Kritzberg, and D. Bastviken. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427:240–243.

Pedersen, T. L. 2020. *patchwork*: The composer of plots. (Available from: https://cran.r-project.org/web/packages/patchwork/index.html)

Pfeifer, B., M. Swayne, and B. Curtis. 2001. Washington Department of Fish and Wildlife's high lakes fishery management program. Management and Conservation Final Report, Washington Department of Fish and Wildlife, Olympia, Washington. (Available from: https://wdfw.wa.gov/publications/01131)

Phillips, D. L., and J. W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179.

Planas, D., J. Gibson, D. Vitt, T. Prowse, E. Prepas, W. Dinsmore, L. Halsey, P. McEachern, S. Paquet, G. Scrimgeour, W. Tonn, C. Paszkowski, and K. Wolfstein. 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: A comparison of wetland- and upland-dominated catchments. Canadian Journal of Fisheries and Aquatic Sciences 58:1286–1299.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Pope, K. L., S. E. Lochmann, and M. K. Young. 2010. Methods for assessing fish populations. Pages 325–351 *in* W. A. Hubert and M. C. Quist (editors). Inland fisheries management in North America. 3rd edition. American Fisheries Society, Bethesda, Maryland.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology 83:703–718.

Raymond, C. L., D. L. Peterson, and R. M. Rochefort. 2014. Climate change vulnerability and adaptation in the North Cascades region, Washington. General Technical Report PNW-GTR-892. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon. (Available from: https://www.fs.usda.gov/treesearch/pubs/47131)

Rivera Vasconcelos, F., S. Diehl, P. Rodríguez, J. Karlsson, and P. Byström. 2018. Effects of terrestrial organic matter on aquatic primary production as mediated by pelagic–benthic resource fluxes. Ecosystems 21:1255–1268.

Robillard, M. M., R. L. McLaughlin, and R. W. Mackereth. 2011. Diversity in habitat use and trophic ecology of Brook Trout in Lake Superior and tributary streams revealed through stable isotopes. Transactions of the American Fisheries Society 140:943–953.

Robinson, D., A. Hayes, S. Couch, I. Patil, D. Chiu, M. Gomez, B. Demeshev, D. Menne, B. Nutter, L. Johnston, B. Bolker, F. Briatte, J. Arnold, J. Gabry, L. Selzer, G. Simpson, J. Preussner, J. Hesselberth, H. Wickham, M. Lincoln, A. Gasparini, L. Komsta, F. Novometsky, W. Freitas, M. Evans , J. C. Brunson, S. Jackson, B. Whalley, K. Whiting, Y. Rosseel, M. Kuehn, J. Cimentada, E. Holgersen, K. Dunkle Werner, E. Christensen, S. Pav, P. PJ, B. Schneider, P. Kennedy, L. Medina, B. Fannin, J. Muhlenkamp, M. Lehman, B. Denney, N. Crane, A. Bates, V. Arel-Bundock, H. Hayashi, L. Tobalina, A. Wang, W. Y. Tham, C. Wang, A. Smith, J. Cooper, E. A. Krauska, A. Wang, M. Barrett, C. Gray, J. Wilber,V. Gegzna, E. Szoecs, F. Aust, A. Moore, N. Williams, M. Barth, B. Wundervald, J. Cahoon, G. McDermott, K. Zarca, S. Kuriwaki, L. Wallrich, J. Martherus, C. Xiao, J. Larmarange, M. Kuhn, M. Bojanowski, H. Malmedal, C. Wang, S. Oller, L. Sonnet, J. Hester, C. Brunson, B. Schneider, B. Gray, M. Averick, A. Jacobs, A. Bender, S. Templer, P.-C. Buerkner, M. Kay, E. Le Pennec, J. Junkka, H. Zhu, B. Soltoff, Z. Wilkinson Saldana, T. Littlefield, C. T. Gray, S. E. Banks, S. Robinson, R. Bivand, R. Ots, N. Williams, N. Jakobsen, M. Weylandt, L. Lendway, K. Hailperin, J. Rodriguez, J. Bryan, C. Jarvis, G. Macfarlane, B. Mannakee, D. Tyre, S. Singh, L. Geffert, H. Ooi, H. Bengtsson, E. Szocs, D. Hugh-Jones, M. Stigler, H. Tavares, R. W. Vervoort, B. M. Wiernik, and J. Yamamoto. 2021. *broom*: Convert statistical objects into tidy tibbles. (Available from: https://cran.r-project.org/web/packages/broom/broom.pdf)

Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442:265–269.

Sass, G. G., C. M. Gille, J. T. Hinke, and J. F. Kitchell. 2006. Whole-lake influences of littoral structural complexity and prey body morphology on fish predator–prey interactions. Ecology of Freshwater Fish 15:301–308.

Schindler, D. E., and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. Oikos 98:177–189.

Seekell, D. A., J.-F. Lapierre, M. L. Pace, C. Gudasz, S. Sobek, and L. J. Tranvik. 2014. Regional-scale variation of dissolved organic carbon concentrations in Swedish lakes. Limnology and Oceanography 59:1612–1620.

Sierszen, M. E., M. E. McDonald, and D. A. Jensen. 2003. Benthos as the basis for arctic lake food webs. Aquatic Ecology 37:437–445.

Sobek, S., L. J. Tranvik, Y. T. Prairie, P. Kortelainen, and J. J. Cole. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnology and Oceanography 52:1208–1219.

Solomon, C. T., S. R. Carpenter, M. K. Clayton, J. J. Cole, J. J. Coloso, M. L. Pace, M. J. V. Zanden, and B. C. Weidel. 2011. Terrestrial, benthic, and pelagic resource use in lakes: Results from a three-isotope Bayesian mixing model. Ecology 92:1115–1125.

Stewart, S. D., D. P. Hamilton, W. T. Baisden, M. Dedual, P. Verburg, I. C. Duggan, B. J. Hicks, and B. S. Graham. 2017. Variable littoral-pelagic coupling as a food-web response to seasonal changes in pelagic primary production. Freshwater Biology 62:2008–2025.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B: Biological Sciences 274:839–844.

Svanbäck, R., and L. Persson. 2004. Individual diet specialization, niche width and population dynamics: Implications for trophic polymorphisms: Density-dependent individual specialization. Journal of Animal Ecology 73:973–982.

Toporowska, M., B. Ferencz, and J. Dawidek. 2018. Impact of lake-catchment processes on phytoplankton community structure in temperate shallow lakes: Impact of lake-catchment processes on phytoplankton. Ecohydrology 11:e2017.

Tunney, T. D., K. S. McCann, L. Jarvis, N. P. Lester, and B. J. Shuter. 2018. Blinded by the light? Nearshore energy pathway coupling and relative predator biomass increase with reduced water transparency across lakes. Oecologia 186:1031–1041.

Turschak, B. A., D. Bunnell, S. Czesny, T. O. Höök, J. Janssen, D. Warner, and H. A. Bootsma. 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology 95:1243–1252.

Vadeboncoeur, Y., S. P. Devlin, P. B. McIntyre, and M. J. Vander Zanden. 2014. Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshwater Science 33:524–536.

Vadeboncoeur, Y., G. Peterson, M. J. Vander Zanden, and J. Kalff. 2008. Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. Ecology 89:2542–2552.

Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: Reintegrating benthic pathways into lake food web models. BioScience 52:44.

van den Boogaart, K. G., and R. Tolosana-Delgado. 2013. Analyzing compositional data with R. Springer-Verlag, Berlin, Heidelberg, Germany.

van den Boogaart, K. G., R. Tolosana-Delgado, and M. Bren. 2021. *compositions*: Compositional data analysis. (Available from: https://mirror.las.iastate.edu/CRAN/web/packages/compositions/compositions.pdf)

Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464–467.

Vander Zanden, M. J., B. J. Shuter, N. P. Lester, and J. B. Rasmussen. 2000. Within- and among-population variation in the trophic position of a pelagic predator, lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 57:725–731.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2020. Putting the lake back together 20 years later: What in the benthos have we learned about habitat linkages in lakes? Inland Waters 10:305–321.

Vander Zanden, M. J., Y. Vadeboncoeur, and S. Chandra. 2011. Fish reliance on littoral–benthic resources and the distribution of primary production in lakes. Ecosystems 14:894–903.

Vasconcelos, F. R., S. Diehl, P. Rodríguez, P. Hedström, J. Karlsson, and P. Byström. 2016. Asymmetrical competition between aquatic primary producers in a warmer and browner world. Ecology 97:2580–2592.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. 4th edition. Springer-Verlag, New York, New York.

Vlah, M. J., G. W. Holtgrieve, and S. Sadro. 2018. Low levels of allochthony in consumers across three high-elevation lake types. Ecosystems 21:1101–1117.

Wei, T., V. Simko, M. Levy, Y. Xie, Y. Jin, J. Zemla, M. Freidank, J. Cai, and T. Protivinsky. 2017. *corrplot*: Visualization of a correlation matrix. (Available from: https://cran.r-project.org/web/packages/corrplot/corrplot.pdf)

Whiteman, J. P., E. A. E. Smith, A. C. Besser, and S. D. Newsome. 2019. A guide to using compound-specific stable isotope analysis to study the fates of molecules in organisms and ecosystems. Diversity 11:8.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. Pedersen, E. Miller, S. Bache, K. Müller, J. Ooms, D. Robinson, D. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. Welcome to the Tidyverse. Journal of Open Source Software 4:1686.

1.8 Tables

Table 1.1. Study lakes represented a range of bathymetries and had differing recommended stocking numbers and frequencies of Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) as decided by Washington State Department of Fish and Wildlife (retrieved from https://wdfw.wa.gov/fishing/locations/high-lakes on 3 January 2021). Our estimates of population abundance, littoral extent, and terrestrial loading are presented alongside the total captured Rainbow Trout from each study lake.

Lake	Elevation (m)	Surface area (km^2)	Maximum depth (m)	Stocking status (count, frequency)	Last stocked (date, count)	Population abundance (# fish/h)	Littoral extent (%)	Terrestrial loading (m)	Capture (count)
Annette	1103	0.082	26	Self-sustaining	8/4/10, 1050	2.21	100.0	1.6	43
Blazer	1237	0.026	18	600, 5 y	7/4/17, 659	0.40	62.5	1.7	9
Denny	1335	0.058	70	200, 5 y	9/16/17, 720	0.94	40.6	0.4	19
Island	1298	0.072	31	1025, 3 y	9/29/13, 1340	0.05	65.9	1.6	3
Kulla Kulla	1148	0.241	64	5400, 5 y	8/19/17, 2500	0.47	41.3	0.2	12
Lodge	953	0.038	5	300, 1 y	8/20/17, 300	0.24	100.0	8.9	3
Mason	1274	0.132	28	780, 3 y	6/29/17, 800	0.59	62.4	0.4	13

Mason, Little	1298	0.022	7	400, 4 y	7/15/16, 420	0.29	100.0	1.9	6
Melakwa, Lower	1369	0.091	14	580, 4 y	9/20/14, 200	0.52	100.0	4.7	17
Melakwa, Upper	1372	0.009	5	65, 4 y	8/10/16, 250	0.67	100.0	45.4	11
Olallie	1152	0.054	12	Self-sustaining	None listed	0.83	62.5	3.5	17
Scout	1173	0.024	5	200, 3 y	8/7/16, 230	0.39	100.0	10.7	2
Tusco Out-In Pot, Large	1113	0.024	5	Self-sustaining	None listed	4.62	100.0	0.4	17
Tusco Out-In Pot, Small	1109	0.005	4	Self-sustaining	None listed	1.94	100.0	3.6	7
Tuscohatchie, Lower	1042	0.129	40	Self-sustaining	None listed	0.83	39.5	0.5	10
Tuscohatchie, Upper	1225	0.241	66	Self-sustaining	None listed	0.71	38.9	0.3	14

Table 1.2. Top 5 candidate models, listed in order of Akaike Information Criterion (AIC) values, relating the isometric log-transformed composition of Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) use of terrestrial, littoral, and pelagic derived resources to fish length (LEN, cm), lake population abundance (PA, no. fish/h), littoral extent (LE, %), terrestrial loading (TL, m), and interactions. Shown is the Pillai's trace statistic value from a Type II multivariate analysis of variance indicating predictor contribution to the model, with the corresponding p-value listed below each Pillai statistic. Bold values indicate $p < 0.05$. Model adjusted R^2 values are provided for an additional aspect of model comparison.

	Parameters								**Model performance**		
Model	LEN	PA	LE	TL	PA × LE	PA × TL	LE × TL	PA × LE × TL	AIC	ΔAIC	Adjusted R^2
Nitrogen: Δ^{15}N = 4.3 ± 1.5‰, Carbon: Δ^{13}C = 0.0 ± 0.0‰											
1	0.09	0.05	0.12	0.04	0.30	0.07	0.18	0.06	–228.4	0.0	0.36
	0.001	**0.026**	**<0.001**	0.066	**<0.001**	**0.006**	**<0.001**	**0.016**			
2	0.11	0.05	0.11	0.04	0.30	0.07	0.18		–222.8	5.6	0.35
	<0.001	**0.028**	**<0.001**	0.075	**<0.001**	**0.007**	**<0.001**				
3	0.09	0.05	0.16	0.03	0.29		0.17		–218.2	10.2	0.34
	0.001	**0.027**	**<0.001**	0.082	**<0.001**		**<0.001**				

4	0.02	0.35	0.03	0.29	0.05	0.14	0.07	–211.4	17.0	0.32
	0.164	**<0.001**	0.110	**<0.001**	**0.020**	**<0.001**	**0.004**			
5	0.02	0.34	0.03	0.29	0.05	0.14		–202.0	26.4	0.30
	0.162	**<0.001**	0.128	**<0.001**	**0.021**	**<0.001**				

1.9 Figures

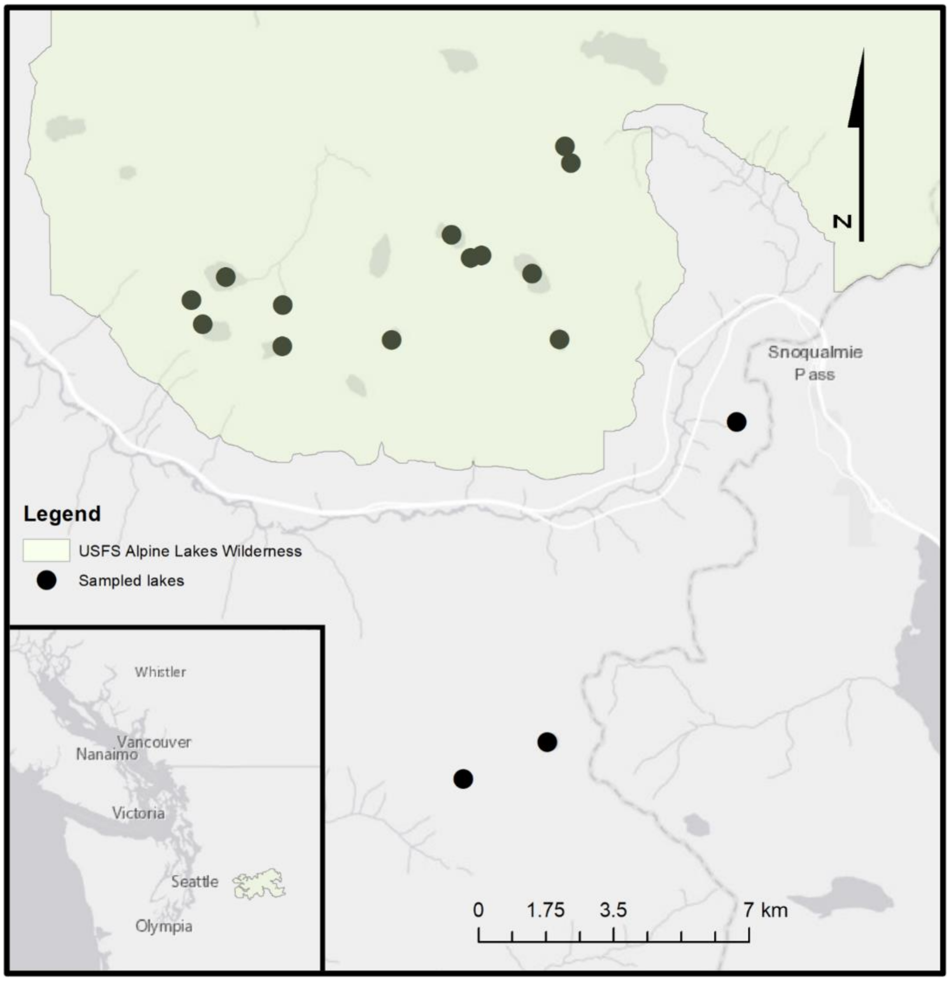


Figure 1.1 Study lakes (black points) are all located on the western slope of the Cascade Range in Washington, USA. The star in the inset indicates the approximate location of the study lakes relative to major cities. Rainbow Trout (Oncorhynchus mykiss Walbaum, 1792), primary producers, and data for bathymetry were collected from each lake. USFS = United States Forest Service.

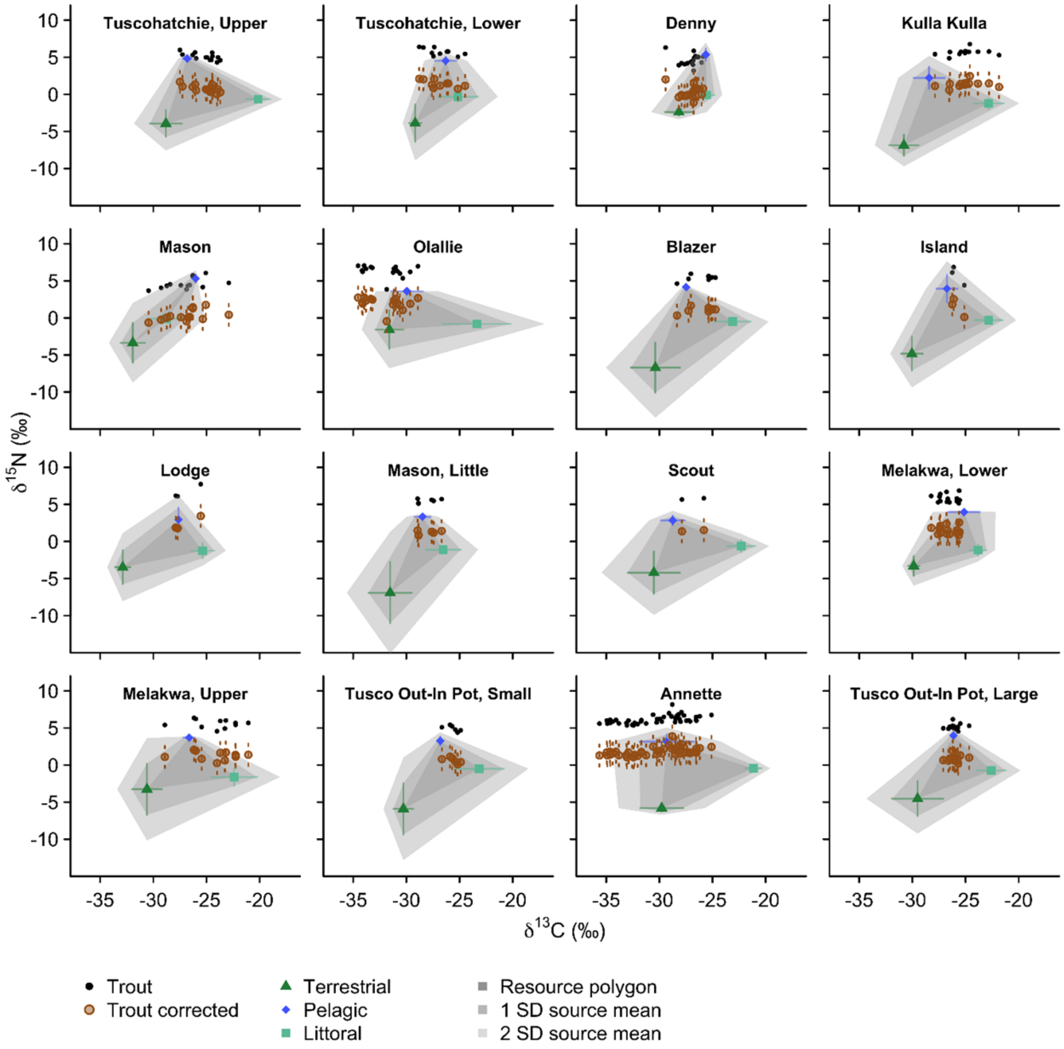
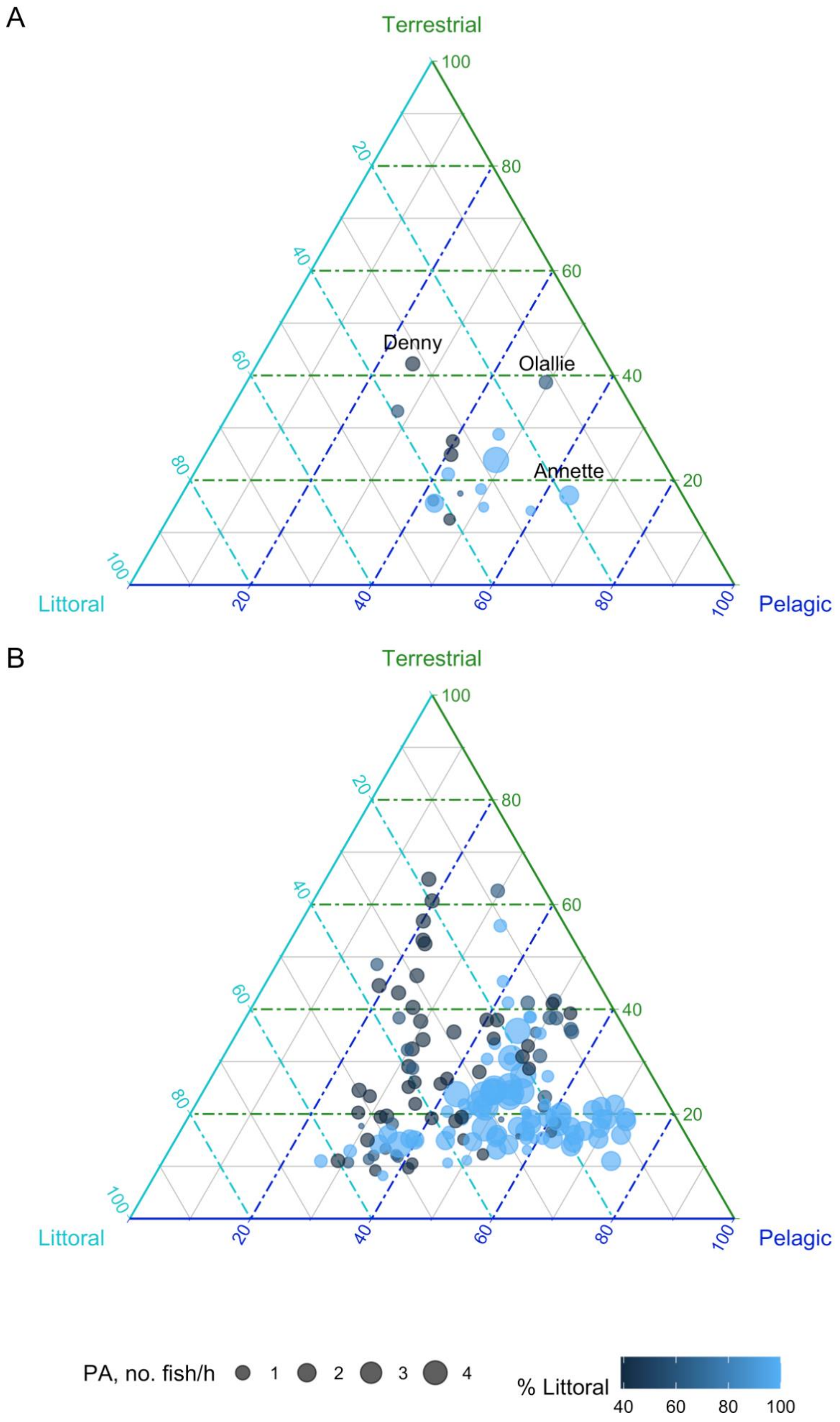


Figure 1.2 Isotope biplots for Rainbow Trout (Oncorhynchus mykiss Walbaum, 1792) and primary producers collected in 16 lakes in Washington, USA. Mean values are shown for source pools of terrestrial (▲), pelagic (◆), and littoral (■) basal resources for each lake; error bars are 1 SD of the pooled mean of samples from each habitat. The darkest shaded area designates the outer area of the resource polygon drawn from source means, the medium shade encompasses 1 SD of mean source isotope ratios, and the lightest shade delineates 2 SD from source means. Units are

per mil relative to international standards. Raw data from individual fish are shown as solid black points, whereas the same data corrected for N enrichment (4.3‰) are shown as hollow (brown in digital pdf) points (Trout corrected), which includes uncertainty (± 1.5‰).


A
Terrestrial
Littoral
Pelagic
100
80
60
40
20
20
40
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100
20
40
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80
100
Denny
Olallie
Annette
B
Terrestrial
Littoral
Pelagic
100
80
60
40
20
20
40
60
80
100
20
40
60
80
100
PA, no. fish/h
1
2
3
4
% Littoral
40
60
80
100

Figure 1.3 Ternary diagrams displaying use of basal resources by Rainbow Trout (Oncorhynchus mykiss Walbaum, 1792) in 16 Washington, USA, lakes estimated from stable isotope mixing models (assumed N enrichment of 4.3 ± 1.5‰). Points are shaded by the littoral extent (LE, %) of the lake that fish were captured in, sized according to population abundance (PA, no. fish/h), and plotted according to proportional reliance on basal resources (colored axes). A.—Mean use of basal resources by trout in each lake. Highlighted are the lakes with the greatest mean use of terrestrial derived (Denny) and pelagic derived (Annette) resources as well as the lake with lowest mean use of littoral derived resources (Olallie). B.—Individual fish compositional use of basal resources.

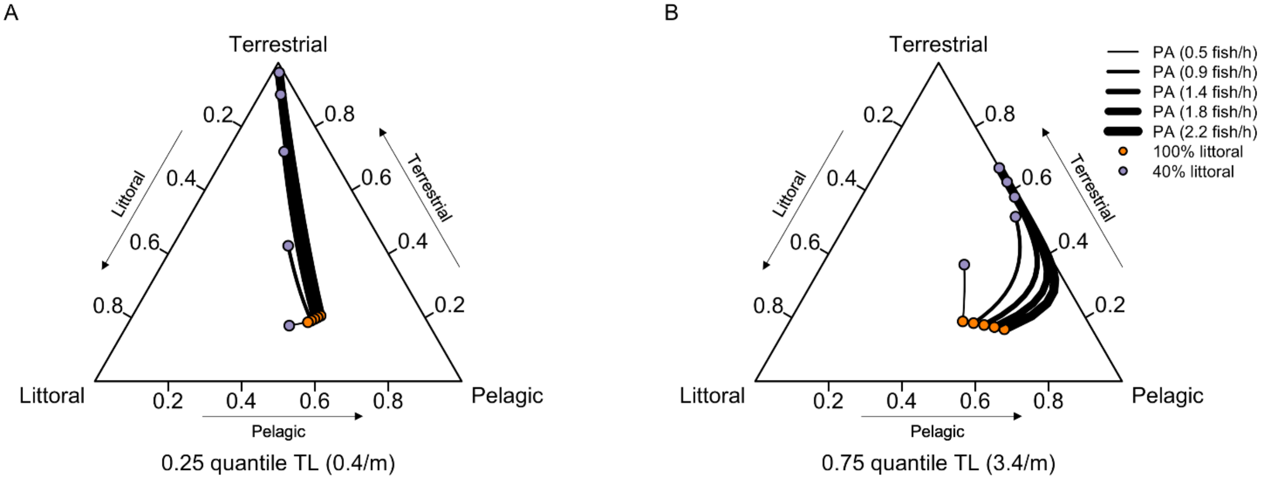


Figure 1.4 Ternary diagrams displaying predicted use of terrestrial, littoral–benthic, and pelagic derived resources by 200 mm Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) in the study lakes when littoral extent and population abundance vary. Orange points represent compositions expected within 100% littoral habitats; purple points represent compositions predicted with 40% littoral resource availability. Lines linking pairs of orange and purple points trace the range of compositions expected as littoral availability changes. Increasing line widths represent greater population abundance (PA). A.—Predicted compositions in low terrestrial loading (TL) circumstances (0.4/m). B.—Predicted range of compositions resulting from high TL conditions (3.4/m). Plotting predicted compositions of incrementally changing variables allows for visualizing the direction of compositional change owing to interaction terms in the model.

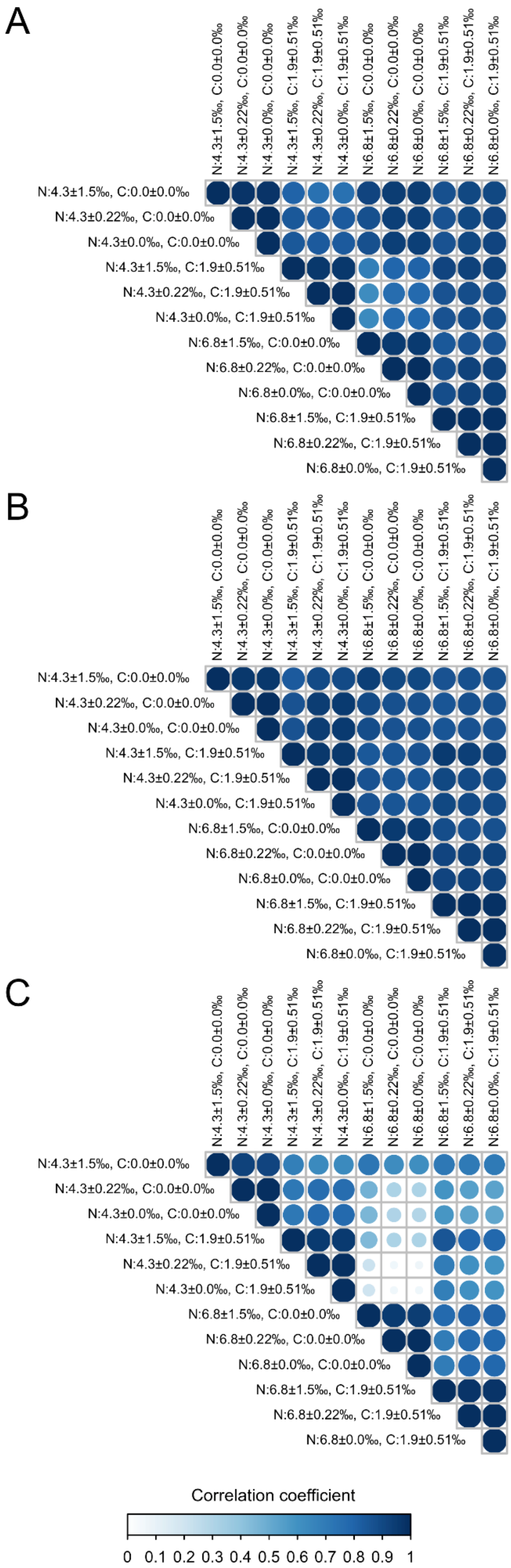

A
N:4.3±1.5‰, C:0.0±0.0‰
N:4.3±0.22‰, C:0.0±0.0‰
N:4.3±0.0‰, C:0.0±0.0‰
N:4.3±1.5‰, C:1.9±0.51‰
N:4.3±0.22‰, C:1.9±0.51‰
N:4.3±0.0‰, C:1.9±0.51‰
N:6.8±1.5‰, C:0.0±0.0‰
N:6.8±0.22‰, C:0.0±0.0‰
N:6.8±0.0‰, C:0.0±0.0‰
N:6.8±1.5‰, C:1.9±0.51‰
N:6.8±0.22‰, C:1.9±0.51‰
N:6.8±0.0‰, C:1.9±0.51‰
B
N:4.3±1.5‰, C:0.0±0.0‰
N:4.3±0.22‰, C:0.0±0.0‰
N:4.3±0.0‰, C:0.0±0.0‰
N:4.3±1.5‰, C:1.9±0.51‰
N:4.3±0.22‰, C:1.9±0.51‰
N:4.3±0.0‰, C:1.9±0.51‰
N:6.8±1.5‰, C:0.0±0.0‰
N:6.8±0.22‰, C:0.0±0.0‰
N:6.8±0.0‰, C:0.0±0.0‰
N:6.8±1.5‰, C:1.9±0.51‰
N:6.8±0.22‰, C:1.9±0.51‰
N:6.8±0.0‰, C:1.9±0.51‰
C
N:4.3±1.5‰, C:0.0±0.0‰
N:4.3±0.22‰, C:0.0±0.0‰
N:4.3±0.0‰, C:0.0±0.0‰
N:4.3±1.5‰, C:1.9±0.51‰
N:4.3±0.22‰, C:1.9±0.51‰
N:4.3±0.0‰, C:1.9±0.51‰
N:6.8±1.5‰, C:0.0±0.0‰
N:6.8±0.22‰, C:0.0±0.0‰
N:6.8±0.0‰, C:0.0±0.0‰
N:6.8±1.5‰, C:1.9±0.51‰
N:6.8±0.22‰, C:1.9±0.51‰
N:6.8±0.0‰, C:1.9±0.51‰
Correlation coefficient
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

Figure 1.5 Pairwise Pearson correlations according to lake-wide estimates of relative use of (A) terrestrial, (B) pelagic, and (C) littoral–benthic derived resources based on alternative assumptions related to N and C enrichment due to trophic enrichment. The assumed mean and standard deviation of trophic enrichment is indicated for N and C for each alternative tested.

1.10 Chapter 1 Appendix 1.

Table S1. The mean number of iterations out of 10,000 that were inside the mixing space in each lake per TEF alternative.

Lake	$\Delta^{15}N = 4.3 \pm 1.5$‰, $\Delta^{13}C = 0.0 \pm 0.0$‰	$\Delta^{15}N = 4.3 \pm 0.22$‰, $\Delta^{13}C = 0.0 \pm 0.0$‰	$\Delta^{15}N = 4.3 \pm 0.0$‰, $\Delta^{13}C = 0.0 \pm 0.0$‰	$\Delta^{15}N = 4.3 \pm 1.5$‰, $\Delta^{13}C = 1.9 \pm 0.51$‰	$\Delta^{15}N = 4.3 \pm 0.22$‰, $\Delta^{13}C = 1.9 \pm 0.51$‰	$\Delta^{15}N = 4.3 \pm 0.0$‰, $\Delta^{13}C = 1.9 \pm 0.51$‰	$\Delta^{15}N = 6.8 \pm 1.5$‰, $\Delta^{13}C = 0.0 \pm 0.0$‰	$\Delta^{15}N = 6.8 \pm 0.22$‰, $\Delta^{13}C = 0.0 \pm 0.0$‰	$\Delta^{15}N = 6.8 \pm 0.0$‰, $\Delta^{13}C = 0.0 \pm 0.0$‰	$\Delta^{15}N = 6.8 \pm 1.5$‰, $\Delta^{13}C = 1.9 \pm 0.51$‰	$\Delta^{15}N = 6.8 \pm 0.22$‰, $\Delta^{13}C = 1.9 \pm 0.51$‰	$\Delta^{15}N = 6.8 \pm 0.0$‰, $\Delta^{13}C = 1.9 \pm 0.51$‰
Annette	3321	3384	3385	2700	2917	2917	5915	6456	6462	4314	4587	4569
Blazer	5891	7105	7172	7997	8875	8874	6175	6917	6913	5958	6450	6493
Denny	4168	5668	5720	1773	2469	2436	2026	987	925	1042	1214	1223
Island	6251	7234	7259	4298	4525	4461	6244	6954	6969	5302	5848	5834
Kulla Kulla	3798	3290	3292	3867	3580	3547	5097	6834	6924	6556	7897	7913
Lodge	6128	6848	6852	2458	1853	1835	4997	6041	6092	5406	6820	6867
Mason	2809	3641	3687	2570	3299	3358	1242	993	952	1362	1164	1131
Mason, Little	4209	4799	4806	3847	4372	4343	5113	6038	6048	3532	4019	3988
Melakwa, Lower	5176	5660	5643	3397	3062	3033	5946	7794	7866	3962	5440	5483
Melakwa, Upper	4509	5653	5714	4743	5552	5576	3465	4200	4254	4455	5197	5202
Olallie	3143	3887	3905	2082	2524	2533	3470	3929	3926	1755	2018	2012
Scout	4973	5766	5807	4075	5020	5020	6452	7623	7616	5132	5766	5795
Tusco Out-In Pot, Large	7874	8849	8861	3303	3668	3683	5963	6511	6546	3921	4661	4669

Tusco Out-In Pot, Small	6018	7719	7792	6143	7098	7069	4820	4968	4996	5723	6262	6268
Tuscohatchie, Lower	4242	5004	5031	3918	4472	4495	3385	3759	3751	3390	3799	3812
Tuscohatchie, Upper	8311	9394	9415	7360	7835	7831	6148	6702	6672	5551	6220	6251

Table S2. Top five candidate models, listed in order of Akaike's information criterion (AIC) values, relating the isometric log transformed composition of Rainbow Trout use of terrestrial, littoral, and pelagic derived resources to fish length (LEN, cm), population abundance (PA, no. fish/h^{-}), littoral extent (LE, %), terrestrial loading (TL, per m), and interactions for all trophic enrichment alternatives. Shown is the Pillai's trace statistic value from a Type II multivariate analysis of variance (MANOVA) indicating predictor contribution to the model, with the corresponding p-value listed below each Pillai statistic. Bold values indicate p <0.05. Model adjusted R-squared provided for an additional aspect of model comparison.

	Parameters								**Model performance**		
	LEN	PA	LE	TL	PA×LE	PA×TL	LE×TL	PA×LE×TL	AIC	ΔAIC	Adjusted R^2
Model											
Nitrogen: Δ^{15}N = 4.3 ± 1.5‰, Carbon: Δ^{13}C = 0.0 ± 0.0‰ (also presented in main manuscript)											
1	0.09	0.05	0.12	0.04	0.30	0.07	0.18	0.06	-228.4	0.0	0.36
	0.001	**0.026**	**<0.001**	0.066	**<0.001**	**0.006**	**<0.001**	**0.016**			
2	0.11	0.05	0.11	0.04	0.30	0.07	0.18		-222.8	5.6	0.35
	<0.001	**0.028**	**<0.001**	0.075	**<0.001**	**0.007**	**<0.001**				
3	0.09	0.05	0.16	0.03	0.29		0.17		-218.2	10.2	0.34

	0.001	**0.027**	**<0.001**	0.082	**<0.001**		**<0.001**				
4		0.02	0.35	0.03	0.29	0.05	0.14	0.07	-211.4	17.0	0.32
		0.164	**<0.001**	0.110	**<0.001**	**0.020**	**<0.001**	**0.004**			
5		0.02	0.34	0.03	0.29	0.05	0.14		-202.0	26.4	0.30
		0.162	**<0.001**	0.128	**<0.001**	**0.021**	**<0.001**				
Nitrogen: $\Delta^{15}N = 4.3 \pm 0.22‰$, Carbon: $\Delta^{13}C = 0.0 \pm 0.0‰$											
1	0.10	0.05	0.14	0.04	0.28	0.06	0.18	0.08	-126.5	0.0	0.39
	0.001	**0.022**	**<0.001**	0.062	**<0.001**	**0.009**	**<0.001**	**0.003**			
2	0.12	0.05	0.14	0.04	0.27	0.06	0.17		-117.2	9.3	0.38
	<0.001	**0.021**	**<0.001**	0.076	**<0.001**	**0.010**	**<0.001**				
3		0.07	0.39	0.03	0.26	0.07	0.14	0.10	-112.0	14.5	0.37
	LEN	PA	LE	TL	PA×LE	PA×TL	LE×TL	PA×LE×TL	AIC	ΔAIC	Adjusted R^2
Nitrogen: $\Delta^{15}N = 4.3 \pm 0.22‰$, Carbon: $\Delta^{13}C = 0.0 \pm 0.0‰$ (continued)											
		0.007	**<0.001**	0.105	**<0.001**	**0.007**	**<0.001**	**<0.001**			
4	0.12	0.05	0.19	0.03	0.27		0.17		-110	16.5	0.36
	<0.001	**0.022**	**<0.001**	0.08	**<0.001**		**<0.001**				
5		0.06	0.37	0.03	0.26	0.07	0.13		-98.9	27.5	0.34
		0.009	**<0.001**	0.129	**<0.001**	**0.007**	**<0.001**				
Nitrogen: $\Delta^{15}N = 4.3 \pm 0.0‰$, Carbon: $\Delta^{13}C = 0.0 \pm 0.0‰$											
1	0.09	0.05	0.14	0.04	0.28	0.06	0.18	0.08	-119.9	0.0	0.39
	0.001	**0.021**	**<0.001**	0.072	**<0.001**	**0.011**	**<0.001**	**0.003**			
2	0.11	0.05	0.14	0.03	0.27	0.06	0.17		-110.6	9.3	0.37
	<0.001	**0.021**	**<0.001**	0.086	**<0.001**	**0.013**	**<0.001**				
3		0.07	0.39	0.03	0.26	0.07	0.14	0.1	-106	13.9	0.36
		0.007	**<0.001**	0.117	**<0.001**	**0.008**	**<0.001**	**0.001**			
4	0.12	0.05	0.19	0.03	0.27		0.17		-103.8	16.1	0.36
	<0.001	**0.022**	**<0.001**	0.09	**<0.001**		**<0.001**				
5		0.06	0.37	0.03	0.26	0.06	0.13		-93.1	26.8	0.34

		0.008	**<0.001**	0.142	**<0.001**	**0.008**	**<0.001**				
Nitrogen: Δ^{15}N = 6.8 ± 1.5‰, Carbon: Δ^{13}C = 0.0 ± 0.0‰											
1	0.09	0.04	0.10	0.13	0.31	0.11	0.16	0.05	-197.3	0	0.38
	0.001	0.068	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.023**			
2	0.10	0.04	0.10	0.13	0.31	0.11	0.16		-196.3	1.1	0.38
	<0.001	0.068	**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**				
3	0.05	0.03	0.14	0.13	0.31		0.15		-180.6	16.8	0.35
	0.028	0.068	**<0.001**	**<0.001**	**<0.001**		**<0.001**				
4		0.07	0.30	0.13	0.32	0.06	0.13	0.06	-180.1	17.2	0.35
		0.005	**<0.001**	**<0.001**	**<0.001**	**0.006**	**<0.001**	**0.01**			
5		0.06	0.29	0.13	0.31	0.06	0.13		-178.2	19.1	0.34
		0.006	**<0.001**	**<0.001**	**<0.001**	**0.008**	**<0.001**				

	LEN	PA	LE	TL	PA×LE	PA×TL	LE×TL	PA×LE×TL	AIC	ΔAIC	Adjusted R^2
Nitrogen: Δ^{15}N = 6.8 ± 0.22‰, Carbon: Δ^{13}C = 0.0 ± 0.0‰											
1	0.09	0.02	0.06	0.12	0.42	0.14	0.13	0.14	-97.9	0.0	0.43
	0.001	0.167	**0.011**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**			
2	0.11	0.02	0.05	0.12	0.39	0.13	0.13		-83.6	14.3	0.40
	<0.001	0.172	**0.019**	**<0.001**	**<0.001**	**<0.001**	**<0.001**				
3		0.09	0.29	0.12	0.44	0.07	0.11	0.15	-81.6	16.3	0.40
		0.001	**<0.001**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**			
4		0.08	0.26	0.12	0.41	0.07	0.11		-65.5	32.4	0.37
		0.003	**<0.001**	**<0.001**	**<0.001**	**0.005**	**<0.001**				
5	0.05	0.02	0.09	0.12	0.39		0.13		-62.1	35.7	0.36
	0.024	0.177	**0.001**	**<0.001**	**<0.001**		**<0.001**				
Nitrogen: Δ^{15}N = 6.8 ± 0.0‰, Carbon: Δ^{13}C = 0.0 ± 0.0‰											
1	0.09	0.02	0.06	0.12	0.43	0.14	0.13	0.15	-91.6	0.0	0.43
	0.001	0.181	**0.013**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**			

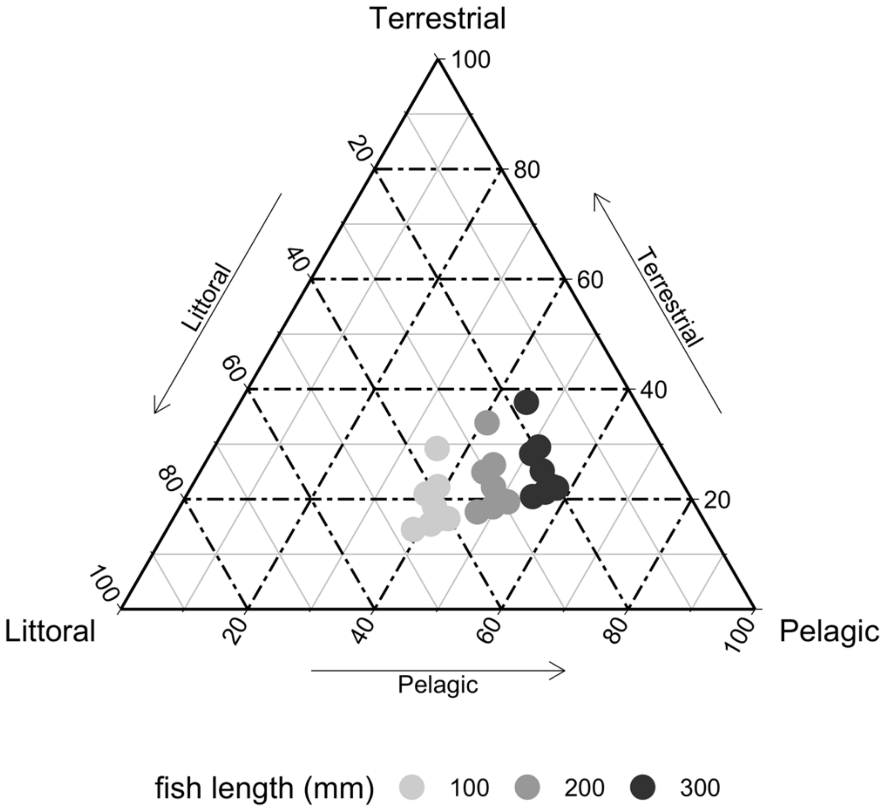
2	0.11	0.02	0.05	0.12	0.40	0.13	0.13		-75.9	15.7	0.40
	<0.001	0.185	**0.022**	**<0.001**	**<0.001**	**<0.001**	**<0.001**				
3		0.09	0.29	0.12	0.45	0.07	0.11	0.16	-75.5	16.1	0.40
		0.001	**<0.001**	**<0.001**	**<0.001**	**0.003**	**<0.001**	**<0.001**			
4		0.07	0.25	0.12	0.41	0.07	0.11		-58.1	33.5	0.37
		0.003	**<0.001**	**<0.001**	**<0.001**	**0.005**	**<0.001**				
5	0.05	0.02	0.09	0.11	0.40		0.12		-54.7	36.9	0.36
	0.024	0.192	**0.001**	**<0.001**	**<0.001**		**<0.001**				
Nitrogen: $\Delta^{15}N = 4.3 \pm 1.5‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$											
1	0.06	0.15	0.12	0.08	0.24	0.07	0.05	0.06	-178.4	0.0	0.27
	0.032	**<0.001**	**0.001**	**0.013**	**<0.001**	**0.026**	0.058	**0.031**			
2	0.05	0.14	0.11	0.08	0.23	0.06	0.05		-173.3	5.1	0.25
	0.058	**<0.001**	**0.002**	**0.013**	**<0.001**	**0.031**	0.059				
3		0.11	0.13	0.08	0.20	0.12	0.04	0.05	-173.0	5.4	0.25
		0.003	**0.001**	**0.013**	**<0.001**	**0.001**	0.104	0.057			

	LEN	PA	LE	TL	PA×LE	PA×TL	LE×TL	PA×LE×TL	AIC	ΔAIC	Adjusted R^2
Nitrogen: $\Delta^{15}N = 4.3 \pm 1.5‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$ (continued)											
4		0.10	0.13	0.08	0.19	0.11	0.04		-169.1	9.4	0.24
		0.003	**0.001**	**0.013**	**<0.001**	**0.002**	0.103				
5	0.04	0.13	0.11	0.08	0.21	0.07			-168.7	9.7	0.24
	0.101	**<0.001**	**0.002**	**0.015**	**<0.001**	**0.025**					
Nitrogen: $\Delta^{15}N = 4.3 \pm 0.22‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$											
1	0.07	0.16	0.14	0.04	0.21	0.07	0.05	0.10	-89.7	0.0	0.28
	0.030	**<0.001**	**<0.001**	0.114	**<0.001**	**0.025**	0.070	0.004			
2		0.11	0.17	0.04	0.17	0.12	0.04	0.09	-84.1	5.6	0.26
		0.002	**<0.001**	0.113	**<0.001**	**0.001**	0.132	**0.008**			
3	0.05	0.15	0.13	0.04	0.19	0.06	0.05		-78.6	11.0	0.25
	0.065	**<0.001**	**0.001**	0.112	**<0.001**	**0.033**	0.073				

4	0.04	0.14	0.13	0.04	0.18	0.07			-75.5	14.1	0.24
	0.118	**<0.001**	**0.001**	0.120	**<0.001**	**0.024**					
5		0.10	0.16	0.04	0.16	0.12	0.04		-74.7	15	0.23
		0.003	**<0.001**	0.111	**<0.001**	**0.001**	0.133				
Nitrogen: $\Delta^{15}N = 4.3 \pm 0.0‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$											
1	0.07	0.16	0.15	0.04	0.21	0.07	0.05	0.10	-86.4	0.0	0.28
	0.03	**<0.001**	**<0.001**	0.118	**<0.001**	**0.024**	0.072	**0.004**			
2		0.11	0.17	0.04	0.17	0.12	0.04	0.09	-80.9	5.5	0.26
		0.003	**<0.001**	0.116	**<0.001**	**0.001**	0.134	**0.008**			
3	0.05	0.15	0.14	0.04	0.19	0.06	0.05		-75.5	10.9	0.25
	0.067	**<0.001**	**<0.001**	0.115	**<0.001**	**0.032**	0.075				
4	0.04	0.14	0.13	0.04	0.18	0.07			-72.4	13.9	0.24
	0.12	**<0.001**	**<0.001**	0.123	**<0.001**	**0.023**					
5		0.10	0.16	0.04	0.16	0.12	0.04		-71.6	14.8	0.23
		0.004	**<0.001**	0.114	**<0.001**	**0.001**	0.135				
Nitrogen: $\Delta^{15}N = 6.8 \pm 1.5‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$											
1	0.03	0.01	0.08	0.17	0.32	0.12	0.1	0.06	-220.7	0.0	0.34
	0.125	0.579	**0.005**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**0.021**			
	LEN	PA	LE	TL	PA×LE	PA×TL	LE×TL	PA×LE×TL	AIC	ΔAIC	Adjusted R^2
Nitrogen: $\Delta^{15}N = 6.8 \pm 1.5‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$ (continued)											
2		0.02	0.19	0.17	0.33	0.11	0.08	0.06	-217.2	3.4	0.33
		0.312	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**	**0.021**			
3	0.03	0.01	0.08	0.17	0.31	0.11	0.10		-215.3	5.4	0.33
	0.131	0.588	0.006	**<0.001**	**<0.001**	**<0.001**	**0.001**				
4		0.02	0.19	0.17	0.32	0.11	0.08		-212.4	8.2	0.32
		0.329	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.004**				
5	0.02	0.01	0.12	0.17	0.31		0.09		-203.6	17.0	0.30
	0.201	0.587	**<0.001**	**<0.001**	**<0.001**		**0.002**				
Nitrogen: $\Delta^{15}N = 6.8 \pm 0.22‰$, Carbon: $\Delta^{13}C = 1.9 \pm 0.51‰$											

1	0.04	0.01	0.09	0.19	0.42	0.11	0.09	0.11	-167.7	0.0	0.42
	0.074	0.7	**0.002**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**			
2		0.04	0.27	0.18	0.44	0.1	0.08	0.11	-163.7	4.0	0.41
		0.073	**<0.001**	**<0.001**	**<0.001**	0.001	**0.005**	**<0.001**			
3	0.04	0.00	0.09	0.19	0.39	0.11	0.09		-153.6	14.1	0.39
	0.06	0.72	**0.003**	**<0.001**	**<0.001**	**0.001**	**0.002**				
4		0.03	0.25	0.18	0.41	0.09	0.08		-149.7	18.0	0.38
		0.096	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.005**				
5	0.02	0.00	0.08	0.17	0.38	0.1			-141.2	26.4	0.36
	0.192	0.784	**0.003**	**<0.001**	**<0.001**	**0.001**					
Nitrogen: Δ^{15}N = 6.8 ± 0.0‰, Carbon: Δ^{13}C = 1.9 ± 0.51‰											
1	0.04	0.01	0.09	0.19	0.43	0.12	0.09	0.12	-165.5	0.0	0.42
	0.069	0.698	**0.002**	**<0.001**	**<0.001**	**<0.001**	**0.002**	**<0.001**			
2		0.04	0.27	0.19	0.44	0.10	0.08	0.12	-161.4	4.1	0.42
		0.059	**<0.001**	**<0.001**	**<0.001**	**0.001**	**0.005**	**<0.001**			
3	0.04	0.00	0.09	0.19	0.40	0.11	0.09		-150.6	14.9	0.39
	0.056	0.721	**0.003**	**<0.001**	**<0.001**	**<0.001**	**0.002**				
4		0.04	0.25	0.19	0.42	0.09	0.07		-146.5	19.0	0.39
		0.08	**<0.001**	**<0.001**	**<0.001**	**0.002**	**0.006**				
	LEN	PA	LE	TL	PA×LE	PA×TL	LE×TL	PA×LE×TL	AIC	ΔAIC	Adjusted R^2
Nitrogen: Δ^{15}N = 6.8 ± 0.0‰, Carbon: Δ^{13}C = 1.9 ± 0.51‰ (continued)											
5	0.03	0.00	0.08	0.17	0.38	0.11			-138.5	27.1	0.37
	0.176	0.765	**0.003**	**<0.001**	**<0.001**	**0.001**					

Figure S1. A ternary diagram displaying predicted use of terrestrial, littoral–benthic, and pelagic derived resources by 100 (light gray), 200 (medium gray), and 300 (dark gray) mm Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) in the study lakes at combinations of 40, 70, and 100% littoral extent, low-high terrestrial loading (range 0.4 – 3.4/m), and low population abundance (0.5 fish/h) for each size class.



2 Chapter 2

Estimating the effects of environmental context and morphological traits on habitat coupling

2.1 Abstract

Mobile consumers frequently acquire and use resources from two or more differing habitats. This habitat coupling can influence ecosystem function, stability, and structure. Species-specific studies have shown that some species and individuals are strong couplers, while others remain relative resource specialists. Studies also show the extent an organism couples habitats may vary according to environmental context or consumer traits. In this study, we consider the influence of environmental factors (mean annual temp, elevation, area, average depth, shoreline irregularity), relative ^{15}N:^{14}N increase, and fish community species richness on habitat coupling by fishes worldwide. We also consider how morphological traits related to feeding, locomotion, and metabolism influences habitat coupling. Using a global dataset consisting of fish muscle ^{13}C:^{12}C and ^{15}N:^{14}N, we developed an index of habitat coupling for fish populations in lake communities around the world. We then used Bayesian hierarchical and non-hierarchical beta regressions to estimate the effects of environmental context and morphological traits on habitat coupling by fishes. Our results show high rates of habitat coupling among fishes globally with differences in mean habitat coupling among freshwater fish families and species. Increases in relative habitat coupling was slightly associated with decreases in mean annual temp and elevation, while other environmental context factors had little or no relationship to habitat coupling. Relative habitat coupling was associated with morphological traits, in particular traits related to locomotion. Overall, we highlight the prevalence of multiple resources supporting fish populations and the importance of studying, conserving, and protecting littoral habitat.

2.2 Introduction

Mobile consumers can connect or “couple” distinct habitats across both space and time via the mechanisms of predation and grazing (Schindler and Scheuerell 2002; Rooney et al. 2008). Wide ranging examples of habitat coupling include Arctic polar bears *Ursus maritimus* linking pelagic and sympagic energy pathways through predation on seals (Horton et al. 2009), Red-necked grebes *Podiceps grisegena* using nutrients acquired in marine and freshwater habitats for egg formation (Kloskowski et al. 2019), *Anolis* lizards integrating understory and canopy food webs (Giery et al. 2013), and adult siscowet trout *Salvelinus namaycush siscowet* forging benthic and pelagic food chains in lakes (Gorman et al. 2012). The extent an organism or species 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 factors (Tunney et al. 2018; Stiling et al. 2021).

Habitat coupling by mobile consumers has several important implications for ecosystem structure, function and stability (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 (Takada et al. 2002; Tunney et al. 2012). Additionally, ecosystem productivity may be enhanced when consumers integrate resources acquired in differing habitats through the mobilization and transport of nutrients (Schindler and Scheuerell 2002; Holdo et al. 2007; McIntyre et al. 2007). Coupling also impacts ecosystem stability, such as the persistence of community composition or the maintenance of consumer population biomass through time, potentially resulting from consumers merging differing energy channels (Rooney et al. 2006;

McCann and Rooney 2009; Blanchard et al. 2011; Wolkovich et al. 2014; Marklund et al. 2019). Despite the well-established implications of habitat coupling for ecosystems, our understanding of the abiotic factors and biotic attributes driving habitat coupling by consumers remains much less clear.

The degree of habitat coupling is a result of consumer behavior, which can be influenced by environmental and climate conditions. Temperature and precipitation are two climactic variables that affects foraging behavior and resource availability (Burles et al. 2009; Dell et al. 2014; Gilbert et al. 2014; Payne et al. 2015; Papastamatiou et al. 2015; Irons et al. 2017). For example, movement between marine and freshwater habitats by American alligators (*Alligator mississippiensis*) is influenced by climactic factors such as temperature and humidity, which can influence osmoregulation (Nifong and Silliman 2017). In addition to climate factors, habitat size and shape can influence consumer foraging behavior and resource use (Francis et al. 2011; Hayden et al. 2019).

Species traits of consumers, 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 component of food webs, with larger consumers hypothesized to occupy higher trophic positions, however this structure varies among ecosystem types (Peters 1983; Romero-Romero et al. 2016; Kopf et al. 2021). Closely linked with body size, organisms with greater mobility tend to be exposed to more macrohabitats and prey types, thereby potentially more able to coupling habitats (Pyke et al. 1977; 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 acquired in multiple habitats (Edmonds 2016). Last, traits associated with visual predation have been shown to predict foraging behavior and resource use (Tunney et al. 2018).

The occurrence of distinct littoral-benthic and pelagic habitats, along with consumer assemblages consisting of multiple fish habitat couplers, make freshwater lakes a valuable context to explore drivers of habitat coupling (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002, 2020). Here we provide a global assessment of habitat coupling by fish populations including the identification of geomorphic, climactic, and contextual factors that influence the extent freshwater fish use resources derived from multiple habitats. Our study leverages the vast diversity of freshwater fish fauna by first using ^{13}C:^{12}C ratios to quantify habitat coupling for fish populations around the globe, and then we 1) assess differences in habitat coupling estimates among fish species and variability within species, 2) relate environmental (climactic and geomorphic) and community context factors to habitat coupling, 3) identify fish morphology and food acquisition traits associated with shifts in habitat coupling, and 4) examine the use of a species-specific approach for determining relationships between environmental factors and habitat coupling.

2.3 Materials and methods

2.3.1 Data collected from literature

We compiled stable isotope data of tissues from 59 published and unpublished (university theses and reports) lake studies as a result of a comprehensive literature review. We augmented a previously compiled dataset that reviewed the literature published through early 2014 (Sagouis et al. 2015; Pool et al. 2016; Comte et al. 2016, 2017) with a literature search in Web of Science with the search term, "TS = (isotope* AND fish* AND carbon AND nitrogen) AND TS = (lake* OR reservoir*), Indexes=SCI-EXPANDED, SSCI, A&HCI, ESCI Timespan=2014-2020," and Google Scholar with "all the words: isotope, fish, C, N; at least one word: lake, reservoir; and dates: 2014 – now." If more than one set of isotope values were recorded for a single lake (e.g., differing seasons, years, or studies) we kept only one set of records. For studies that sampled both wet and dry season, we included the wet season values in our analysis; when multiple sampling events occurred, we included the most comprehensive (greatest number of fish species) or recent sampling event. We extracted the ^{13}C:^{12}C and ^{15}N:^{14}N ratios (typically reported in delta notation as $\delta^{13}C$ vs VPDB and $\delta^{15}N$ vs air respectively) from tables, appendices, supplements, or figures for freshwater fish populations (fish population as the average among individuals of the same species within a single lake) (Appendix S1). Most reported values came from fish muscle tissue. 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. Local fish communities were considered as the set of fish species for which stable isotope values were quantified at a given location as reported in the original publications A statement in the methods indicating the captured species were fairly representative of the community and a threshold of four species or more, were set as criterion to avoid studies targeted on specific species. 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 final dataset contained 972 populations, comprised of 237 fish species in 104 lakes located in 22 countries spanning North America, South America, Europe, Africa, Asia, and Oceana (Fig. 2.1).

2.3.2 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 (φ) for each fish species from each lake (i.e., 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:

Equation 1:

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

Where $\delta^{13}C_{pop}$ is the mean ^{13}C:^{12}C ratios of the population and $\delta^{13}C_{pel\_end}$ and $\delta^{13}C_{lit\_end}$ are lake specific pelagic and littoral end members.

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

Equation 2:

$$\varphi'_{pop} = \frac{\delta^{13}C_{pop} - \delta^{13}C_{pop\_min}}{\delta^{13}C_{pop\_max} - \delta^{13}C_{pop\_min}}$$

After comparing the estimates of littoral resource use between the two methods and finding that populations were consistently constrained within the $\delta^{13}C$ range (Appendix 1), we selected a simple adjustment to capture as many lakes as possible including those that did not report end member values. Based on our observations 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:

Equation 3:

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

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 (Chapter 2 Appendix 1).

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*) 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 (Eq. 4, *sensu* Tunney et al. 2018).

Equation 4:

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

2.3.3 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 (Dep), shoreline development index (a measure of shoreline irregularity relative to a perfect circle, hereafter Shoreline Irregularity [SI]), lake elevation (Elev) (HydroLAKES: Messager et al. 2016), and total water area (TotA) (Global Lake area, Climate, and Population dataset [GLCP]: Meyer et al. 2020). We used total water area from the GLCP to ensure lake area estimates included seasonal high waters, when applicable, mirroring our use of wet season fish community data. Mean depth, lake surface area, elevation, and shoreline irregularity were included as factors thought to influence relative availability of littoral vs pelagic derived resources (Vadeboncoeur et al. 2008). Shallower and smaller lakes potentially have proportionally more illuminated lake bottom than larger deeper lakes (Vadeboncoeur et al. 2008). Oligotrophic lakes, commonly found at higher elevations, can have lower dissolved nutrients in the water column, limiting pelagic primary production (Sierszen et al. 2003). Greater shoreline irregularity (higher lake perimeter: lake area ratio) is associated with increased terrestrial connection, which can result in either increased terrestrial carbon or increased groundwater inputs (Gasith and Hosier 1976; Hanson et al. 2007), possibly decreasing littoral primary production due reduced light penetration. The climactic variables, mean annual temperature (Temp) and total annual accumulated precipitation (Prec), as estimated for each lake's watershed in 2015, were also acquired from the GLCP (Meyer et al. 2020). Temperature can have a significant impact on fish behavior, either effecting metabolic demands or threatening thermal tolerances (Jeppesen et al. 2010). We included all lakes smaller than 500 km^2 (Alin and Johnson 2007) and were limited to lakes greater than 0.1 km^2 (cutoff for inclusion for HydroLAKES and GLCP).

We obtained fish species morphometry and food acquisition traits according to species (Manjarrés-Hernández et al. 2021; Brosse et al. 2021). Body morphometry traits associated with locomotion comprised of body elongation, body lateral shape, pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling (Brosse et al. 2021). Body elongation and body lateral shape are associated with hydrodynamism, where higher values are related to increased capacity for sustained cruising and sprint swimming (Webb 1984; Brosse et al. 2021). Pectoral fins are generally associated with precise maneuvering and efficient low speed swimming (Webb 1984). Increased pectoral fin vertical position may relate to increased ability to control body rotation, including during breaking and turning (Drucker 2002). Pectoral fin size, or fin aspect-ratio is related to swimming where higher aspect ratio fins may be associated with fast swimming and planktivory (Wainwright et al. 2002). Traits associated with feeding included vertical eye position, relative eye size, and oral gape position, and relative maxillary length (Brosse et al. 2021). Vertical eye position is thought to be associated with diet where increased relative eye vertical position is related with benthic feeding while lower eye vertical position is associated with feeding in the water column (Hugueny and Pouilly 1999). Larger relative eye size might be associated with predation in benthic and low abyssopelagic zones belonging to specialists (Podder et al. 2021). Oral gape position is expected to be associated with the location of feeding in the water column (Su et al. 2019) and increased relative maxillary length is thought to be associated with omnivory (Podder et al. 2021). Maximum body length, frequently associated with metabolism, consisted of maximum body length (Brosse et al. 2021). Trophic guild encompassed five categories, primary consumer, secondary consumer, top-predator, omnivorous and detritivorous; feeding was divided into three habitats, pelagic, benthopelagic and benthic (Manjarrés-Hernández et al. 2021).

We determined local characteristics according to each lake community and population within the lake. Species richness (Rich) for each lake community was calculated as the sum of unique species recorded in the dataset per lake. Relative change in ^{15}N:^{14}N ratios (ΔN), measured 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 the total change in isotope value, ΔN, rather than estimate a relative trophic position by dividing the difference by a traditional 3.4‰ (Post 2002) because we did not want blur relative trophic position within the fish community with overall trophic position relative to the base of the food web. Dividing by 3.4‰ followed by scaling and centering predictor terms for a regression (as methods will state below) would lead to the same result.

Equation 5:

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

2.3.4 Statistical analysis

We used a Bayesian hierarchical beta regression to estimate how environmental characteristics influence habitat coupling by freshwater fish (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 (ΔN, Rich), lake geomorphic features (Dep, Elev, SI, TotA) and climactic elements (Temp and Prec) (i.e., fixed effects). Predictor variables were not correlated. We accounted for observations that occur in populations of the same species by allowing intercepts to differ among species (i.e., random effects)(McElreath 2020). For this analysis, owing to a high number of species occurring infrequently in the dataset, we only included species found in ≥5% of the communities, resulting in an examination of 496 populations, comprised of 45 species in 100 lakes. We created all Bayesian models with a Stan computational framework (http://mc-stan.org/) accessed with the brms package (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 on account of not having applicable information about these parameters. For the same reason, for the Beta-regression specific precision parameter theta (θ) we used the default Gamma prior (shape term of 0.01 and a scaling term of 0.01) and uninformative flat priors for each β. Models were sampled using a Hamiltonian Monte-Carlo algorithm, the No-U-Turn Sampler. We ran all models with 4 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 (α), species specific intercepts (α_j) and the sum all 8 (k) environmental predictor parameters (β) times the $i * k$ matrix (X) of environmental values associated with each population and 2) θ, the Beta distribution precision parameter.

$$Y_{ij} \sim Beta(p_{ij}, \theta)$$

$$logit(p_{ij}) = \alpha + \alpha_j + \sum_{k=1}^{8} \beta_k * X_{ik}$$

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

$$\alpha_j \sim Normal(0, \sigma_\alpha)$$

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

$$\sigma_\alpha \sim Student.{t_3}^+(0, 2.5)$$

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

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

To estimate the extent that fish traits influence habitat coupling, we used Bayesian (non-hierarchical) beta regression. 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 (body elongation, vertical body lateral shape, pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling), four traits related to feeding (eye position, relative eye size, oral gape position, relative maxillary length), and one trait related to metabolism (maximum 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 (α) and the sum all 10 (k) trait predictor parameters (β) times the $i * k$ matrix (X) of trait values associated with each population and 2) θ, 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 (≥10% of the lakes), we visually inspected species-specific relationship between environmental factors and habitat coupling by completing linear regression and plotting relationships between factors and responses according to species.

2.4 Results

Fish populations consistently use resources derived from both the littoral and pelagic habitats despite displaying widely ranging habitat coupling scores. The average coupling score of fishes, considering all populations together, was 0.68 ± 0.22 on a scale 0–1 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. 2.2). 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. For species that occur 3 or more times in the dataset, mean species habitat coupling values ranged from 0.33 to 0.92. Mean species habitat coupling values are distributed across the range of scaled coupling values, demonstrating a continuum slightly skewed towards 1. Most species (84%) had mean coupling scores greater than 0.5.

Within species, inter-population habitat coupling was highly variable. For example, coupling scores among populations of walleye (*Sander vitreus*; Mitchill, 1818) ranged narrowly from 0.77 to 0.93, whereas cisco (*Coregonus artedi*; Lesueur, 1818) displayed much greater differences among population habitat coupling values which ranged from 0.21 to 0.97. Species with coupling scores that spanned wide ranges 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, along with walleye, include highfin catfish (*Neoarius berneyi*; Whitley, 1941), North African catfish (*Clarias gariepinus*; Burchell, 1822), and sockeye salmon (*Oncorhynchus nerka*; Walbaum, 1792).

Of the environmental context factors we considered for the Bayesian hierarchical beta regression, the primary variables related to habitat coupling of fishes include geomorphic and climactic elements. While the 95% credible interval of all predictors tested included zero (Fig 2.2.), Temp and Elev had the strongest association with decreases in habitat coupling. The Bayesian hierarchical beta regression suggested posterior probability median estimates for Temp and Elev were -.10 (95% highest posterior density credible interval, -0.22–0.01) and -0.09 (95% highest posterior density credible interval, -0.18–0.01) respectively. Increases in shoreline index had a slight association with increased species coupling (posterior probability estimate of 0.04 [-0.07–0.16]). Increases in ΔN, Prec, Dep, TotA, and Rich exhibited low association with habitat coupling (ΔN: 0.02 [-0.08–0.14], Prec: 0.01 [-0.09–0.11], Dep: -0.00 [-0.10–0.10], TotA: -0.02 [-0.13–0.10], and Rich: -0.04 [-0.15–0.08]).

Grouping fish populations according to food acquisition categorical traits revealed little differences in habitat coupling. Although habitat coupling between at least two trophic guilds differed (Welch's corrected ANOVA F(4, 37.7) = [161.6], p = <0.001), it was only fish associated with the trophic guild detritivorous that differed from all other trophic guilds (post hoc Games-Howell $p < 0.05$) (Fig 2.4A). Other than detritivorous populations, populations of all trophic guilds had wide ranging coupling scores with top-predators having the highest mean. There was little difference in habitat coupling between omnivorous species, primary consumers, and secondary consumers (Figure 2.4A). We found no difference in habitat coupling after grouping populations according to feeding habitats (ANOVA F(2, 115) = [2.2], p = 0.11) (Fig 2.3B). All feeding habitat groups exhibited widely distributed habitat coupling values. Species that feed primarily in the pelagic environment coupled slightly less than either benthivorous and benthopelagic populations, which had similar habitat coupling scores (Figure 2.4B).

Species-level habitat coupling showed strong associations with morphological traits describing feeding habit and locomotion. Three of the five locomotion traits had strong effect with habitat coupling: pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling (Fig 2.5). Of the four feeding traits, only oral gape position had a significant association with habitat coupling (Fig 2.5). Maximum body size was not associated with coupling (Fig 2.5).

Habitat coupling varied as a function environmental factors and individual species (Fig. 2.6). Diverging responses related to environmental factors included species specific slopes and intercepts. Slope relationships between scaled coupling against average lake depth or total lake area ranged from neutral to strongly positive and strongly negative (Fig. 2.6A, B). We observe as similar divergence with richness, with some species decreasing coupling and others increasing coupling as the lakes that they inhabit include more fish species (Fig 2.6C). By contrast, the majority of the species spanning habitats with differing mean annual temperatures exhibit decreased coupling as mean annual temperature increases (Fig 2.6D).

2.5 Discussion

Across 104 freshwater fish communities in lakes, our results show that fish populations around the globe use resources that originate in multiple habitats, that habitat coupling varies taxonomically but can be influenced by environmental context or mediated by locomotive traits. We found some species consistently coupling littoral and pelagic derived resource pathways while other species tend towards more single pathway use. Moreover, several species exhibited high variability in habitat coupling, in particular species within the family Salmonidae. Drivers of habitat coupling include elevation and mean annual temperature as well as traits related to feeding and swimming.

The vast majority of fish populations in our study had relatively high (>0.50) habitat coupling scores, reflecting the interconnected nature of lake food webs (Thompson et al. 2007). Had we seen the opposite, where the bulk of habitat coupling values were constrained to <0.50, we would infer that fish communities were generally divided into isolated food chains, each reliant on separate basal resources. In this study of lake ecosystems, we approximated the use of littoral and pelagic derived resources which are known to play an important role in lake foods webs (Vadeboncoeur et al. 2002; Vander Zanden and Vadeboncoeur 2020) and found littoral and pelagic habitats to be strongly coupled by fishes globally. Given all of the lakes we sampled were less than 500 km^2 and the littoral zones of lakes are extensive (littoral zones are 78% of earths total lake area) (Seekell et al. 2021), coupling may be common as a result of primary production occurring in habitats within close proximity (Schindler and Scheuerell 2002).

Fish families exhibit broad differences in habitat coupling. Both Salmonidae and Cyprinidaes families exhibit variability and contain species that are strong and weak couplers, whereas Catostomidae and Centrarchidae are limited to moderate couplers (median scores between 0.5 and 0.75, Fig. 2.2). Percidae contains primarily strong couplers with median values greater than 0.75 (Fig. 2.2). The one species from the Chiclidae family, the Nile talapia (*Oreochromis niloticus;* Linnaeus, 1758) has a relatively low coupling score. While our metric doesn’t differentiate between increased littoral or pelagic derived resource use for low coupling scores, Nile tilapia is thought to prefer periphyton and is known to also consume phytoplankton (Dempster et al. 1993).

Within families some species were strong couplers and others were generally more reliant on one resource pool. Walleye are strong couplers, and have been previously shown to couple both pelagic and littoral habitats, with maximum coupling occurring in lakes with low visibility (Tunney et al. 2018). Like walleye, Berney’s catfish (*Neoarius berneyi*; Whitley, 1941) and northern pikeminnow (*Ptychocheilus oregonensis*; Richardson, 1836) demonstrated high habitat coupling reflecting evidence that both species exhibit flexible diets and consume foods derived from multiple habitats (McIntyre et al. 2006; Pusey et al. 2020). By contrast, of the species that we tested (those that occurred in 5% or more of the lakes), European whitefish (*Coregonus lavaretus*; Linnaeus, 1758), sockeye, and cisco had low median coupling values compared to all other species. Since our coupling score does not indicate what resources are used when coupling values are low, from our metric alone we don't know whether these species are somewhat specialized in either pelagic or littoral pathways, or if they are flexible tending to use either littoral or littoral pathways. We can guess that cisco was likely reliant on pelagic resources. We also saw the populations classified detritivorous, demonstrated relatively low habitat coupling (Fig 2.4A). These species were all from the genus Potamorhina (*Potamorhina altamazonica*, *Potamorhina latior*, *Potamorhina pristigas*ter and are known to use on detrital pathways.

In addition to wide ranging mean coupling scores for salmonid, several salmonids exhibited high variances in habitat coupling, in particular Arctic char. The wide variance displayed in our data is also reflected in studies that reveal the highly flexible diet of Arctic char (Rikardsen et al. 2000; 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 (Andersson et al. 2005; Woods et al. 2013). In contrast to the wide variance of Arctic char, another salmonid, sockeye salmon had one of the lowest variances relative to the other species in the dataset. Considered a considered plankivorous species, in lakes diet studies on both juvenile sockeye and land-locked kokanee (lacustrine *Oncorhynchus nerka*) revealing primary consumption of pelagic resources (Beauchamp et al. 2004; Schoen et al. 2015). These broad differences in mean species average habitat coupling as well as differences in variance around coupling reflect the high diversity of in the salmonid family.

Environmental conditions effecting habitat coupling by fishes include geomorphic and climactic factors. The strong relationship between increased mean annual temp and decreased habitat coupling may be a result of some species that are found in a range of temperatures sticking to deep cold water habitats for refuge in warmer climates, thereby shifting towards increased pelagic resource use (Guzzo et al. 2017). Vice-versa, mean annual temp 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, high elevation lakes can be fueled primarily by attached algae and littoral primary production with very little pelagic primary production (Loria et al. 2020). The slight positive relationship between shoreline index and increased habitat coupling may reflect increased use of both edge and open water habitat by fish in lakes with more meandrous shorelines. However, littoral extent in smaller lakes is not as tightly related to shoreline index as previously considered (Seekell et al. 2021). Relative littoral extent in lakes is primarily a function of water chemistry (e.g., clarity and light penetration) and the maximum lake depth relative to the average depth (Seekell et al. 2021). In the absence of data on light attenuation or mean lake depth (we only have max depth), we are not able to estimate littoral extent for the lakes. Although the 95% credible interval of the coefficient posterior distribution is included with the negative relationship between lake area and increased coupling, this trend tracks with observations that in large systems, 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 had the overall highest influence on habitat coupling. Pectoral fin vertical position, pectoral fin size, and caudal peduncle throttling were strongly associated with increases or decreases habitat coupling and have been shown to relate to swimming and propulsion efficiency (Villéger et al. 2017; Brosse et al. 2021). Increased pectoral fin vertical position, which may be associated with increased maneuverability, was found to be associated with increased habitat coupling. A low value for pectoral fin vertical position is associated with a more ventral body position generally found on more basal taxa and lower teleosts (Drucker 2002). A higher value for pectoral fin vertical position corresponds with a more dorsolateral pectoral fin position which is associated with greater maneuverability and thrust during low-speed turning relative to ventrally located pectoral fins (Drucker et al. 2005). Increased maneuverability may translate to foraging in a range of habitats thereby coupling both littoral and derived resource pathways. Unlike pectoral fin vertical position, caudal peduncle throttling and pectoral fin size are associated with decreased habitat coupling which implies increased use of either pelagic or littoral derived resources (single source pathway is unspecified by our metric). It is possible that increased caudal peduncle throttling may be associated with increased pelagic derived resource use owing to the increased ability to sprint and cruise which could allow for the capture of evasive or widely dispersed pelagic derived resources (Blake 2004). By contrast, the decrease in habitat coupling predicted with increased pectoral fin size may be associated with increased littoral derived resource use. The increased ability to hover for extended periods of time is associated with larger pectoral fin size and supports foraging in littoral habitats (Ehlinger and Wilson 1988). Pectoral fin morphology has been linked to swimming speed and habitat use in *Labridae*, specifically facilitation the use of reef habitats exposed to high wave action (Bellwood and Wainwright 2001; Wainwright et al. 2002).

Along with locomotive traits, oral gape position is associated with habitat coupling. We observed a negative relationship with coupling where maximum coupling occurred with a more ventral position, meaning as oral gape position increased, coupling decreased. On one extreme of oral gape position is the ventral position or subterminal position, which is generally associated with bottom feeding (Villéger et al. 2017) and the other extreme is the upturned mouth, or dorso-terminal displayed by surface feeders (Keast and Webb 1966; Langerhans et al. 2003). A terminal mouth, a middle value for oral gape position, is typical of a midwater forager that would generally categorized by swimming with an open mouth (sometimes called "townet" filter feeding) (Sibbing and Nagelkerke 2000). The direction of our results suggest that the subterminal mouth is more associated with coupling and upturned mouth is less associated coupling. We infer that the upturned mouth and terminal mouth positions are associated with pelagic derived feeding (Keast and Webb 1966) and that the subterminal mouth, although known to be related to benthic foraging also allows for selective feeding on foods derived from both littoral and pelagic habitats.

We did not find support for relative eye size (visual acuity), vertical eye position (position of fish relative to prey), nor relative maxillary length as being linked to habitat coupling. Although eyes and mouth are useful mechanisms when foraging, locomotion and maneuverability may be more associated with prey capture by fishes than gape (Higham 2007). Our finding, which considered freshwater species globally, is in contrast to a study focused on a single species that found intraspecific variation in pectoral fin location and size was less associated with flow habitat use and that eye vertical position and relative eye size was related to habitat use (Abecia et al. 2018).

In contrast to terrestrial ecosystems, we found little evidence for a strong relationship between body size and habitat coupling. Our findings contrast theory and recent literature demonstrating larger body size can be associated with increased habitat coupling (Rooney et al. 2008; Keppeler et al. 2021). These differences in findings may, in part, be explained by our examination focused on freshwater lakes rather than marine-terrestrial linkage as has been the focus of other studies (Keppeler et al. 2021). Body size, habitat coupling, and trophic position are all closely involved in theory surrounding food webs with the suggestion that large bodied higher trophic position organisms are also strong couplers (Rooney et al. 2008). Alongside our lack of support for habitat coupling increasing with body size, we also did not find support that strong couplers are associated with top trophic positions within aquatic communities. Although some evidence points to a relationship between body size and trophic position in marine ecosystems (Potapov et al. 2019), recent work specifically focused on freshwater fishes demonstrates that body size is not associated with trophic position (Keppeler et al. 2020). Instead of body size, trophic position may be associated with other traits, for example maxillary jaw length, a feeding related feature of fishes (Kopf et al. 2021).

The categorical functional trait trophic guild is moderately associated with habitat coupling. We found that fishes classified as top predator, omnivore, and secondary consumers are generally couplers whereas detritivores were rarely found to be littoral-pelagic habitat couplers. We also found that primary consumers coupled slightly less than fish in higher trophic levels, which aligns with food web theory (Rooney et al. 2008). We found that categorizations according to trophic guilds did not reflect that freshwater fish within the same guild may specialize on differing resources derived from different energy sources (Lopes et al. 2015). We also did not find statistically significant differences in overall habitat coupling between fish grouped according to preferred feeding habitat, benthivous, benthopelagic, or pelagic. We did find the median coupling score for pelagic species was lower than benthivous or benthopelagic, which tracks with the idea of pelagic species using only pelagic resources in larger systems. Not only did we not find statistical differences in coupling among most classifications, the wide variances 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).

The importance of coupled pelagic and littoral resources to consumers varies along some environmental gradients for some species, but not all species. Species-specific responses illustrate that the near-zero relationship between habitat coupling and most tested environmental factors such as depth (Fig 2.3) may not a result of a uniform neutral response, but rather species-specific responses to environmental context summing to zero. Some trends we observed reflect what has been demonstrated by other studies. For example, lake trout *Salvelinus namaycush* has been shown to decrease coupling as lake area increases, owing to increased excusive pelagic foraging (Tunney et al. 2012). Similarly, Cisco *Coregonus aretedi* increased coupling in deeper and larger lakes. We also observed the habitat coupling of both suckers (*Catosomidae*) shift in similar ways according to context factor, specifically increased richness and depth lead to increased coupling, and increased lake area had a slightly negative response. Perch (*Perca fluvaitilis*), who have been shown to partition niche space within the same community (Quevedo et al. 2009), show an overall decreased in coupling associated with increased lake depth, but increased coupling associated with increased lake area and species richness. Common carp

(*Cyprinus carpio*) appears to couple habitats consistently, relatively unaffected by environmental context.

Habitat coupling is a result of individual organism behaviors related to movement and foraging. Given the aggregated nature of our data set we were unable to explore the role of individual organism behavior, and potential variability within populations. However, there is 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; Quevedo et al. 2009; Lopes et al. 2015; Elliott Smith et al. 2021). There is ample opportunity explore environmental drivers or individual trait characteristics that may determine drivers of species coupling and the role organism foraging behavior might play in the function of an ecosystem, including stability.

Given the heavy reliance on both pelagic and littoral derived resources by freshwater fishes, near shore habitat losses may put habitat coupling at risk (Hampton et al. 2011). Global change and human manipulation leading to water level fluctuations may destabilize linkages between littoral and pelagic regions (Evtimova and Donohue 2016; Hansen et al. 2018). Increased nutrients, non-native species, and climate may lead to changes in the structure and composition of the littoral attached algae community, including shifts towards filamentous algae blooms (Vadeboncoeur et al. 2021). Changes to near shore habitat threaten to sever the structuring and stabilizing outcomes provided by the coupling of littoral and pelagic habitats in freshwater lakes by fish and warrants increased littoral zone research and lake shoreline conservation and protection efforts.

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2.7 Literature cited

Abecia JED, Luiz OJ, King AJ (2018) Intraspecific morphological and reproductive trait variation in mouth almighty GLOSSAMIA APRION (Apogonidae) across different flow environments. J Fish Biol 93:961–971. https://doi.org/10.1111/jfb.13821

Alin SR, Johnson TC (2007) Carbon cycling in large lakes of the world: A synthesis of production, burial, and lake-atmosphere exchange estimates: CARBON CYCLING IN LARGE LAKES. Global Biogeochem Cycles 21:n/a-n/a. https://doi.org/10.1029/2006GB002881

Andersson J, Byström P, Persson L, De Roos AM (2005) Plastic resource polymorphism: effects of resource availability on Arctic char (Salvelinus alpinus) morphology: PLASTIC RESOURCE POLYMORPHISM. Biological Journal of the Linnean Society 85:341–351. https://doi.org/10.1111/j.1095-8312.2005.00501.x

Beauchamp DA, Sergeant CJ, Mazur MM, et al (2004) Spatial–Temporal Dynamics of Early Feeding Demand and Food Supply for Sockeye Salmon Fry in Lake Washington. Transactions of the American Fisheries Society 133:1014–1032. https://doi.org/10.1577/T03-093.1

Bellwood D, Wainwright P (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs 20:139–150. https://doi.org/10.1007/s003380100156

Blake RW (2004) Fish functional design and swimming performance. Journal of Fish Biology 65:1193–1222. https://doi.org/10.1111/j.0022-1112.2004.00568.x

Blanchard JL, Law R, Castle MD, Jennings S (2011) Coupled energy pathways and the resilience of size-structured food webs. Theor Ecol 4:289–300. https://doi.org/10.1007/s12080-010-0078-9

Bolnick DI, Svanbäck R, Fordyce JA, et al (2003) The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist 161:1–28. https://doi.org/10.1086/343878

Brosse S, Charpin N, Su G, et al (2021) FISHMORPH: A global database on morphological traits of freshwater fishes. Global Ecol Biogeogr geb.13395. https://doi.org/10.1111/geb.13395

Bürkner P-C (2017) brms: An R Package for Bayesian Multilevel Models Using Stan. J Stat Soft 80:. https://doi.org/10.18637/jss.v080.i01

Burles DW, Brigham RM, Ring RA, Reimchen TE (2009) Influence of weather on two insectivorous bats in a temperate Pacific Northwest rainforest. Can J Zool 87:132–138. https://doi.org/10.1139/Z08-146

Chamberlain SA, Szöcs E (2013) taxize: taxonomic search and retrieval in R. F1000Res 2:191. https://doi.org/10.12688/f1000research.2-191.v2

Comte L, Cucherousset J, Boulêtreau S, Olden JD (2016) Resource partitioning and functional diversity of worldwide freshwater fish communities. Ecosphere 7:. https://doi.org/10.1002/ecs2.1356

Comte L, Cucherousset J, Olden JD (2017) Global test of Eltonian niche conservatism of nonnative freshwater fish species between their native and introduced ranges. Ecography 40:384–392. https://doi.org/10.1111/ecog.02007

Dell AI, Pawar S, Savage VM (2014) Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. J Anim Ecol 83:70–84. https://doi.org/10.1111/1365-2656.12081

Dempster PW, Beveridge MCM, Baird DJ (1993) Herbivory in the tilapia *Oreochromis niloticus:* a comparison of feeding rates on phytoplankton and periphyton. Journal of Fish Biology 43:385–392. https://doi.org/10.1111/j.1095-8649.1993.tb00573.x

Dolson R, McCann K, Rooney N, Ridgway M (2009) Lake Morphometry Predicts the Degree of Habitat Coupling by a Mobile Predator. Oikos 118:1230–1238

Drucker EG (2002) Wake Dynamics and Locomotor Function in Fishes: Interpreting Evolutionary Patterns in Pectoral Fin Design. Integrative and Comparative Biology 42:997–1008. https://doi.org/10.1093/icb/42.5.997

Drucker EG, Walker JA, Westneat MW (2005) Mechanics of Pectoral Fin Swimming in Fishes. In: Fish Physiology. Elsevier, pp 369–423

Edmunds NB, Laberge F, McCann KS (2016) A role for brain size and cognition in food webs. Ecol Lett 19:948–955. https://doi.org/10.1111/ele.12633

Ehlinger TJ, Wilson DS (1988) Complex foraging polymorphism in bluegill sunfish. Proceedings of the National Academy of Sciences 85:1878–1882. https://doi.org/10.1073/pnas.85.6.1878

Elliott Smith EA, Harrod C, Docmac F, Newsome SD (2021) Intraspecific variation and energy channel coupling within a Chilean kelp forest. Ecology 102:. https://doi.org/10.1002/ecy.3198

Eloranta AP, Kahilainen KK, Amundsen P-A, et al (2015) Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecol Evol 5:1664–1675. https://doi.org/10.1002/ece3.1464

Evtimova VV, Donohue I (2016) Water-level fluctuations regulate the structure and functioning of natural lakes. Freshw Biol 61:251–264. https://doi.org/10.1111/fwb.12699

Ferrari S, Cribari-Neto F (2004) Beta Regression for Modelling Rates and Proportions. Journal of Applied Statistics 31:799–815. https://doi.org/10.1080/0266476042000214501

Francis TB, Schindler DE, Holtgrieve GW, et al (2011) Habitat structure determines resource use by zooplankton in temperate lakes: Habitat and energetic support of lake zooplankton. Ecology Letters 14:364–372. https://doi.org/10.1111/j.1461-0248.2011.01597.x

Gasith A, Hosier AD (1976) Airborne litterfall as a source of organic matter in lakes1: Airborne litterfall in lakes. Limnol Oceanogr 21:253–258. https://doi.org/10.4319/lo.1976.21.2.0253

Giery ST, Lemoine NP, Hammerschlag-Peyer CM, et al (2013) Bidirectional trophic linkages couple canopy and understorey food webs. Funct Ecol 27:1436–1441. https://doi.org/10.1111/1365-2435.12139

Gilbert B, Tunney TD, McCann KS, et al (2014) A bioenergetic framework for the temperature dependence of trophic interactions. Ecol Lett 17:902–914. https://doi.org/10.1111/ele.12307

Gorman OT, Yule DL, Stockwell JD (2012) Habitat use by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Islands region. Aquatic Ecosystem Health & Management 15:333–354. https://doi.org/10.1080/14634988.2012.715972

Gregersen F, Aass P, Vollestad LA, L'Abee-Lund JH (2006) Long-term variation in diet of Arctic char, Salvelinus alpinus, and brown trout, Salmo trutta: effects of changes in fish density and food availability. Fisheries Manage 13:243–250. https://doi.org/10.1111/j.1365-2400.2006.00500.x

Guzzo MM, Blanchfield PJ, Rennie MD (2017) Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. Proc Natl Acad Sci USA 114:9912–9917. https://doi.org/10.1073/pnas.1702584114

Hampton SE, Fradkin SC, Leavitt PR, Rosenberger EE (2011) Disproportionate importance of nearshore habitat for the food web of a deep oligotrophic lake. Mar Freshwater Res 62:350. https://doi.org/10.1071/MF10229

Hansen AG, Gardner JR, Connelly KA, et al (2018) Trophic compression of lake food webs under hydrologic disturbance. Ecosphere 9:. https://doi.org/10.1002/ecs2.2304

Hanson PC, Carpenter SR, Cardille JA, et al (2007) Small lakes dominate a random sample of regional lake characteristics. Freshwater Biol 52:814–822. https://doi.org/10.1111/j.1365-2427.2007.01730.x

Hayden B, Harrod C, Thomas SM, et al (2019) From clear lakes to murky waters – tracing the functional response of high-latitude lake communities to concurrent 'greening' and 'browning.' Ecol Lett 22:807–816. https://doi.org/10.1111/ele.13238

Hecky RE, Hesslein RH (1995) Contributions of Benthic Algae to Lake Food Webs as Revealed by Stable Isotope Analysis. Journal of the North American Benthological Society 14:631–653. https://doi.org/10.2307/1467546

Higham TE (2007) The integration of locomotion and prey capture in vertebrates: Morphology, behavior, and performance. Integrative and Comparative Biology 47:82–95. https://doi.org/10.1093/icb/icm021

Horton TW, Blum JD, Xie Z, et al (2009) Stable isotope food-web analysis and mercury biomagnification in polar bears (Ursus maritimus). Polar Research 28:443–454. https://doi.org/10.1111/j.1751-8369.2009.00114.x

Hugueny B, Pouilly M (1999) Morphological correlates of diet in an assemblage of West African freshwater fishes. Journal of Fish Biology 54:1310–1325. https://doi.org/10.1111/j.1095-8649.1999.tb02057.x

Irons RD, Harding Scurr A, Rose AP, et al (2017) Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore. Proc R Soc B 284:20170412. https://doi.org/10.1098/rspb.2017.0412

Jeppesen E, Meerhoff M, Holmgren K, et al (2010) Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia 646:73–90. https://doi.org/10.1007/s10750-010-0171-5

Keast A, Webb D (1966) Mouth and Body Form Relative to Feeding Ecology in the Fish Fauna of a Small Lake, Lake Opinicon, Ontario. J Fish Res Bd Can 23:1845–1874. https://doi.org/10.1139/f66-175

Keppeler FW, Montaña CG, Winemiller KO (2020) The relationship between trophic level and body size in fishes depends on functional traits. Ecol Monogr 90:. https://doi.org/10.1002/ecm.1415

Keppeler FW, Olin JA, López-Duarte PC, et al (2021) Body size, trophic position, and the coupling of different energy pathways across a saltmarsh landscape. Limnol Oceanogr 6:360–368. https://doi.org/10.1002/lol2.10212

Kloskowski J, Trembaczowski A, Filipiuk M (2019) Stable isotope tracing of links between marine wintering and freshwater breeding habitats of Red-necked Grebes. J Ornithol 160:593–605. https://doi.org/10.1007/s10336-019-01642-1

Kopf RK, Yen JDL, Nimmo DG, et al (2021) Global patterns and predictors of trophic position, body size and jaw size in fishes. Global Ecol Biogeogr 30:414–428. https://doi.org/10.1111/geb.13227

Langerhans RB, Layman CA, Langerhans AK, Dewitt TJ (2003) Habitat-associated morphological divergence in two Neotropical fish species. Biological Journal of the Linnean Society 80:689–698. https://doi.org/10.1111/j.1095-8312.2003.00266.x

Lopes CA, Manetta GI, Figueiredo BRS, et al (2015) Carbon from littoral producers is the major source of energy for bottom-feeding fish in a tropical floodplain. Environ Biol Fish 98:1081–1088. https://doi.org/10.1007/s10641-014-0343-7

Loria KA, McKnight D, Ragar DM, Johnson PTJ (2020) The life aquatic in high relief: shifts in the physical and biological characteristics of alpine lakes along an elevation gradient in the Rocky Mountains, USA. Aquat Sci 82:11. https://doi.org/10.1007/s00027-019-0684-6

Manjarrés-Hernández A, Guisande C, García-Roselló E, et al (2021) Predicting the effects of climate change on future freshwater fish diversity at global scale. NC 43:1–24. https://doi.org/10.3897/natureconservation.43.58997

Marklund MHK, Svanbäck R, Eklöv P (2019) Habitat coupling mediates trophic cascades in an aquatic community. Ecosphere 10:. https://doi.org/10.1002/ecs2.2863

McCann KS, Rooney N (2009) The more food webs change, the more they stay the same. Phil Trans R Soc B 364:1789–1801. https://doi.org/10.1098/rstb.2008.0273

McElreath R (2020) Statistical rethinking: a Bayesian course with examples in R and Stan, 2nd edn. Taylor and Francis, CRC Press, Boca Raton

McIntyre JK, Beauchamp DA, Mazur MM, Overman NC (2006) Ontogenetic Trophic Interactions and Benthopelagic Coupling in Lake Washington: Evidence from Stable Isotopes and Diet Analysis. Transactions of the American Fisheries Society 135:1312–1328. https://doi.org/10.1577/T05-099.1

Messager ML, Lehner B, Grill G, et al (2016) Estimating the volume and age of water stored in global lakes using a geo-statistical approach. Nat Commun 7:13603. https://doi.org/10.1038/ncomms13603

Meyer MF, Labou SG, Cramer AN, et al (2020) The global lake area, climate, and population dataset. Sci Data 7:174. https://doi.org/10.1038/s41597-020-0517-4

Nifong JC, Silliman B (2017) Abiotic factors influence the dynamics of marine habitat use by a highly mobile “freshwater” top predator. Hydrobiologia 802:155–174. https://doi.org/10.1007/s10750-017-3255-7

Papastamatiou YP, Watanabe YY, Bradley D, et al (2015) Drivers of Daily Routines in an Ectothermic Marine Predator: Hunt Warm, Rest Warmer? PLoS ONE 10:e0127807. https://doi.org/10.1371/journal.pone.0127807

Payne N, van der Meulen D, Suthers I, et al (2015) Rain-driven changes in fish dynamics: a switch from spatial to temporal segregation. Mar Ecol Prog Ser 528:267–275. https://doi.org/10.3354/meps11285

Peters RH (1983) The Ecological Implications of Body Size, 1st edn. Cambridge University Press

Podder A, Panja S, Chaudhuri A, et al (2021) Patterns of morphological traits shaping the feeding guilds in the intertidal mudflat fishes of the Indian Sundarbans. J Fish Biol 99:1010–1031. https://doi.org/10.1111/jfb.14800

Pool TK, Cucherousset J, Boulêtreau S, et al (2016) Increased taxonomic and functional similarity does not increase the trophic similarity of communities: Functional versus trophic diversity similarity. Global Ecology and Biogeography 25:46–54. https://doi.org/10.1111/geb.12384

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Potapov AM, Brose U, Scheu S, Tiunov AV (2019) Trophic Position of Consumers and Size Structure of Food Webs across Aquatic and Terrestrial Ecosystems. The American Naturalist 194:823–839. https://doi.org/10.1086/705811

Pusey BJ, Jardine TD, Bunn SE, Douglas MM (2020) Sea catfishes (Ariidae) feeding on freshwater floodplains of northern Australia. Mar Freshwater Res 71:1628. https://doi.org/10.1071/MF20012

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal Foraging: A Selective Review of Theory and Tests. The Quarterly Review of Biology 52:137–154. https://doi.org/10.1086/409852

Quevedo M, Svanbäck R, Eklöv P (2009) Intrapopulation niche partitioning in a generalist predator limits food web connectivity. Ecology 90:2263–2274. https://doi.org/10.1890/07-1580.1

Rikardsen AH, Amundsen P-A, Bjorn PA, Johansen M (2000) Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. Journal of Fish Biology 57:1172–1188. https://doi.org/10.1111/j.1095-8649.2000.tb00479.x

Romero-Romero S, Molina-Ramírez A, Höfer J, Acuña JL (2016) Body size-based trophic structure of a deep marine ecosystem: A Size-Based Trophic Structure. Ecology 97:171–181. https://doi.org/10.1890/15-0234.1

Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. Nature 442:265–269. https://doi.org/10.1038/nature04887

Rooney N, McCann KS, Moore JC (2008) A landscape theory for food web architecture. Ecology Letters 11:867–881. https://doi.org/10.1111/j.1461-0248.2008.01193.x

Sagouis A, Cucherousset J, Villéger S, et al (2015) Non-native species modify the isotopic structure of freshwater fish communities across the globe. Ecography 38:979–985. https://doi.org/10.1111/ecog.01348

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients: *Interpretation of regression coefficients*. Methods in Ecology and Evolution 1:103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Schindler DE, Scheuerell MD (2002) Habitat coupling in lake ecosystems. Oikos 98:177–189. https://doi.org/10.1034/j.1600-0706.2002.980201.x

Schoen ER, Beauchamp DA, Buettner AR, Overman NC (2015) Temperature and depth mediate resource competition and apparent competition between *Mysis diluviana* and kokanee. Ecological Applications 25:1962–1975. https://doi.org/10.1890/14-1822.1

Seekell D, Cael B, Norman S, Byström P (2021) Patterns and Variation of Littoral Habitat Size Among Lakes. Geophys Res Lett 48:. https://doi.org/10.1029/2021GL095046

Sibbing FA, Nagelkerke LAJ (2000) Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. Reviews in Fish Biology and Fisheries 10:393–437. https://doi.org/10.1023/A:1012270422092

Sierszen ME, McDonald ME, Jensen DA (2003) Benthos as the basis for arctic lake food webs. Aquatic Ecology 37:437–445. https://doi.org/10.1023/B:AECO.0000007042.09767.dd

Stiling RR, Holtgrieve GW, Olden JD (2021) Population structure and habitat availability determine resource use by Rainbow Trout in high elevation lakes. Freshwater Science 40:508–523. https://doi.org/10.1086/716184

Su G, Villéger S, Brosse S (2019) Morphological diversity of freshwater fishes differs between realms, but morphologically extreme species are widespread. Global Ecol Biogeogr 28:211–221. https://doi.org/10.1111/geb.12843

Takada M, Asada M, Miyashita T (2002) Cross-habitat foraging by sika deer influences plant community structure in a forest-grassland landscape. Oecologia 133:389–394. https://doi.org/10.1007/s00442-002-1037-y

Thompson RM, Hemberg M, Starzomski BM, Shurin JB (2007) TROPHIC LEVELS AND TROPHIC TANGLES: THE PREVALENCE OF OMNIVORY IN REAL FOOD WEBS. Ecology 88:612–617. https://doi.org/10.1890/05-1454

Tunney TD, McCann KS, Jarvis L, et al (2018) Blinded by the light? Nearshore energy pathway coupling and relative predator biomass increase with reduced water transparency across lakes. Oecologia 186:1031–1041. https://doi.org/10.1007/s00442-017-4049-3

Tunney TD, McCann KS, Lester NP, Shuter BJ (2012) Food web expansion and contraction in response to changing environmental conditions. Nat Commun 3:1105. https://doi.org/10.1038/ncomms2098

Vadeboncoeur Y, Moore MV, Stewart SD, et al (2021) Blue Waters, Green Bottoms: Benthic Filamentous Algal Blooms Are an Emerging Threat to Clear Lakes Worldwide. BioScience 71:1011–1027. https://doi.org/10.1093/biosci/biab049

Vadeboncoeur Y, Peterson G, Vander Zanden MJ, Kalff J (2008) Benthic Algal Production across lake size gradients: Interactions among morphometry, nutrients, and light. Ecology 89:2542–2552. https://doi.org/10.1890/07-1058.1

Vadeboncoeur Y, Vander Zanden MJ, Lodge DM (2002) Putting the Lake Back Together: Reintegrating Benthic Pathways into Lake Food Web Models. BioScience 52:44. https://doi.org/10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2

Vander Zanden MJ, Vadeboncoeur Y (2002) Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152–2161. https://doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2

Vander Zanden MJ, Vadeboncoeur Y (2020) Putting the lake back together 20 years later: what in the benthos have we learned about habitat linkages in lakes? Inland Waters 1–17. https://doi.org/10.1080/20442041.2020.1712953

Villéger S, Brosse S, Mouchet M, et al (2017) Functional ecology of fish: current approaches and future challenges. Aquat Sci 79:783–801. https://doi.org/10.1007/s00027-017-0546-z

Wainwright PC, Bellwood DR, Westneat MW (2002) Ecomorphology of Locomotion in Labrid Fishes. Environmental Biology of Fishes 65:47–62. https://doi.org/10.1023/A:1019671131001

Webb PW (1984) Body Form, Locomotion and Foraging in Aquatic Vertebrates. Am Zool 24:107–120. https://doi.org/10.1093/icb/24.1.107

Wolkovich EM, Allesina S, Cottingham KL, et al (2014) Linking the green and brown worlds: the prevalence and effect of multichannel feeding in food webs. Ecology 95:3376–3386. https://doi.org/10.1890/13-1721.1

Woods PJ, Young D, Skúlason S, et al (2013) Resource polymorphism and diversity of Arctic charr *Salvelinus alpinus* in a series of isolated lakes. Journal of Fish Biology 82:569–587. https://doi.org/10.1111/jfb.12011

2.8 Figures

Figure 2.1. Each ● represents a study lake. Gray shading indicates one or more lake communities from that country are included in the dataset.

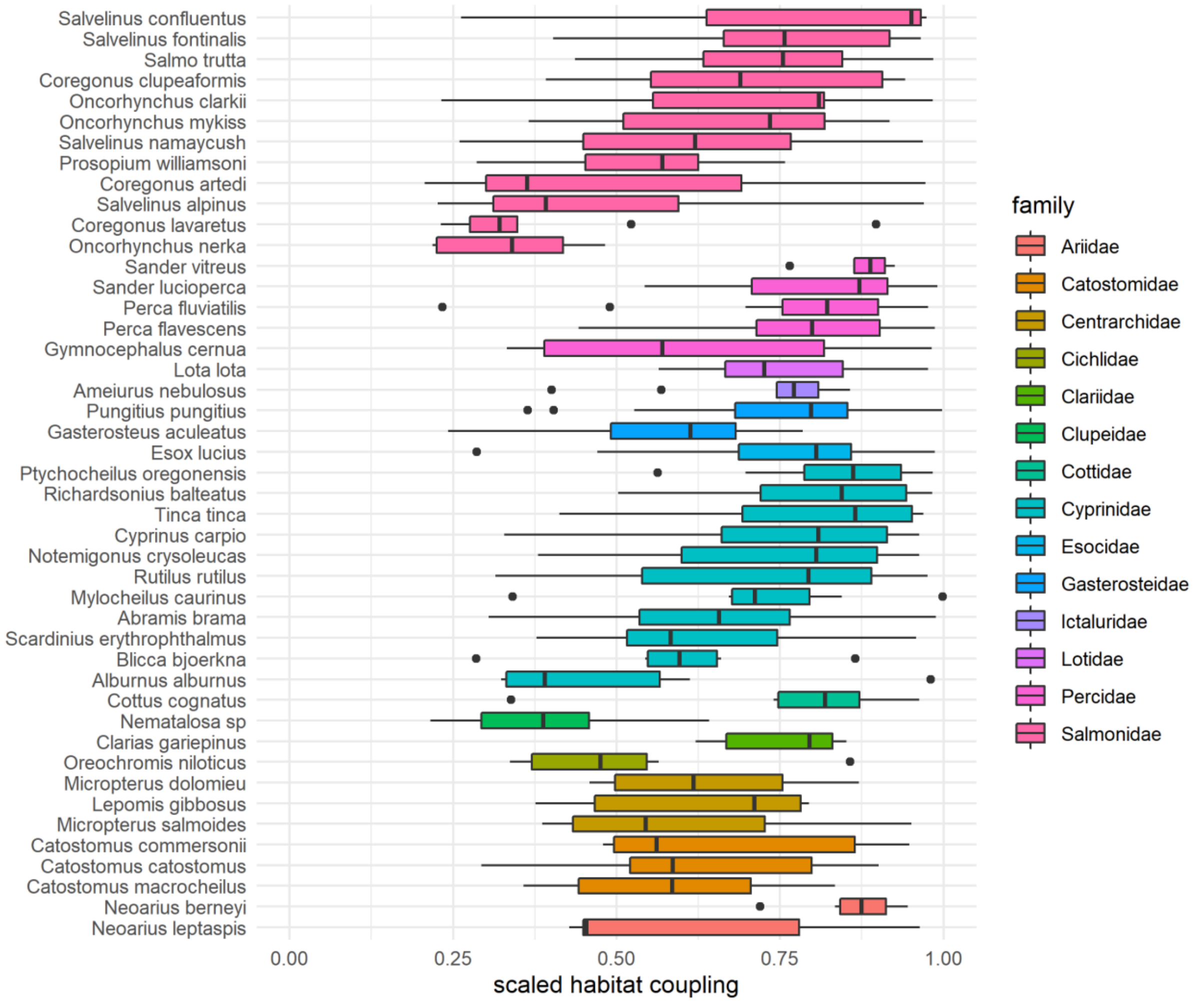

Figure 2.2. Boxplots represent the median and 1st and 3rd quantile. Sorted by mean habitat coupling values within colored groupings according to family. Species presented represents of a subset of 45 species that occur in 5% or more of the lakes within the dataset.

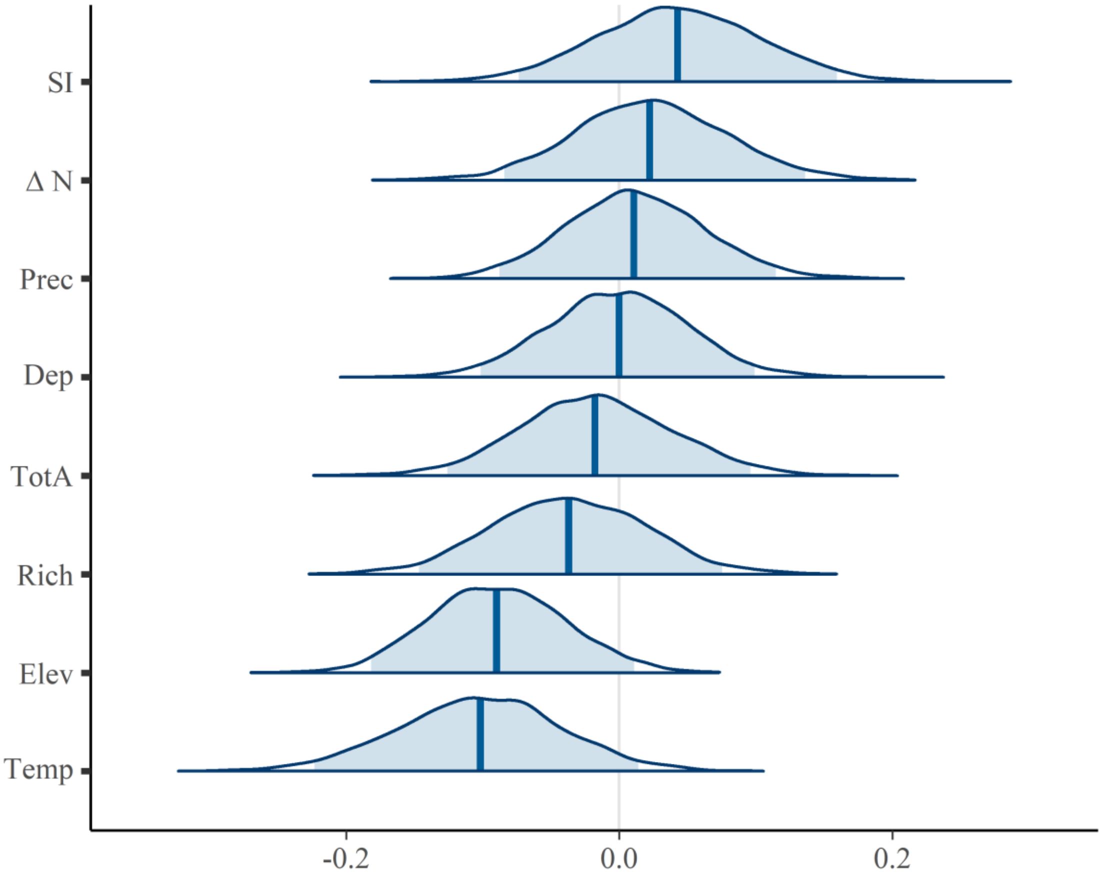

Figure 2.3. Posterior distributions of environmental condition as estimated by a Bayesian hierarchical beta regression ordered by posterior mean estimates. Shading indicates 95% credible interval. The x-axis indicates the effect of each scaled and centered parameter on habitat coupling. Samples included 496 populations in 100 lakes with varying intercepts according to species (45 species).

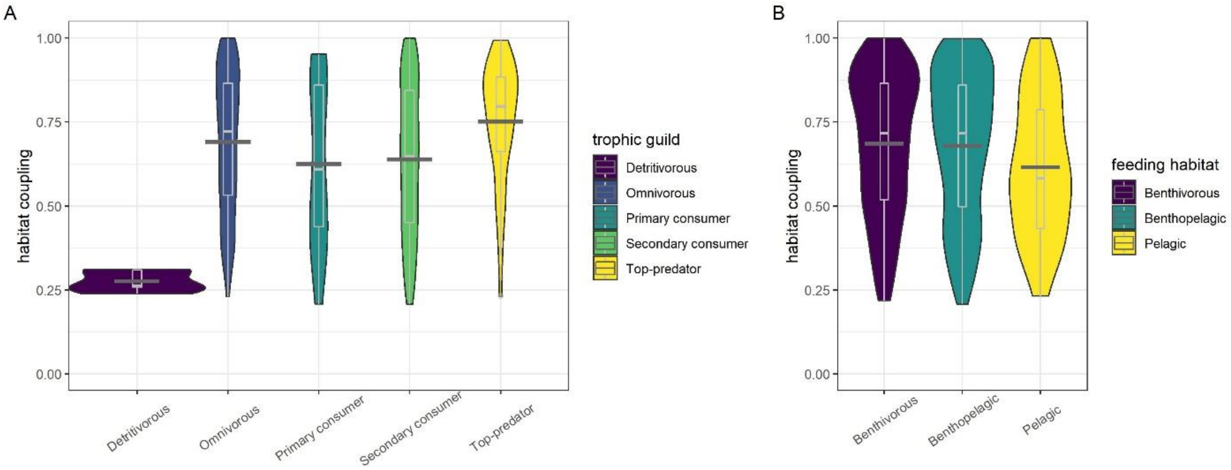

Figure 2.4. Distribution of habitat coupling according to categorical food acquisition traits. Grouped violin plots including light gray boxplots which represent the median and 1st and 3rd quantile values for habitat coupling according to group. Mean habitat coupling score overlaid as a dark bar.

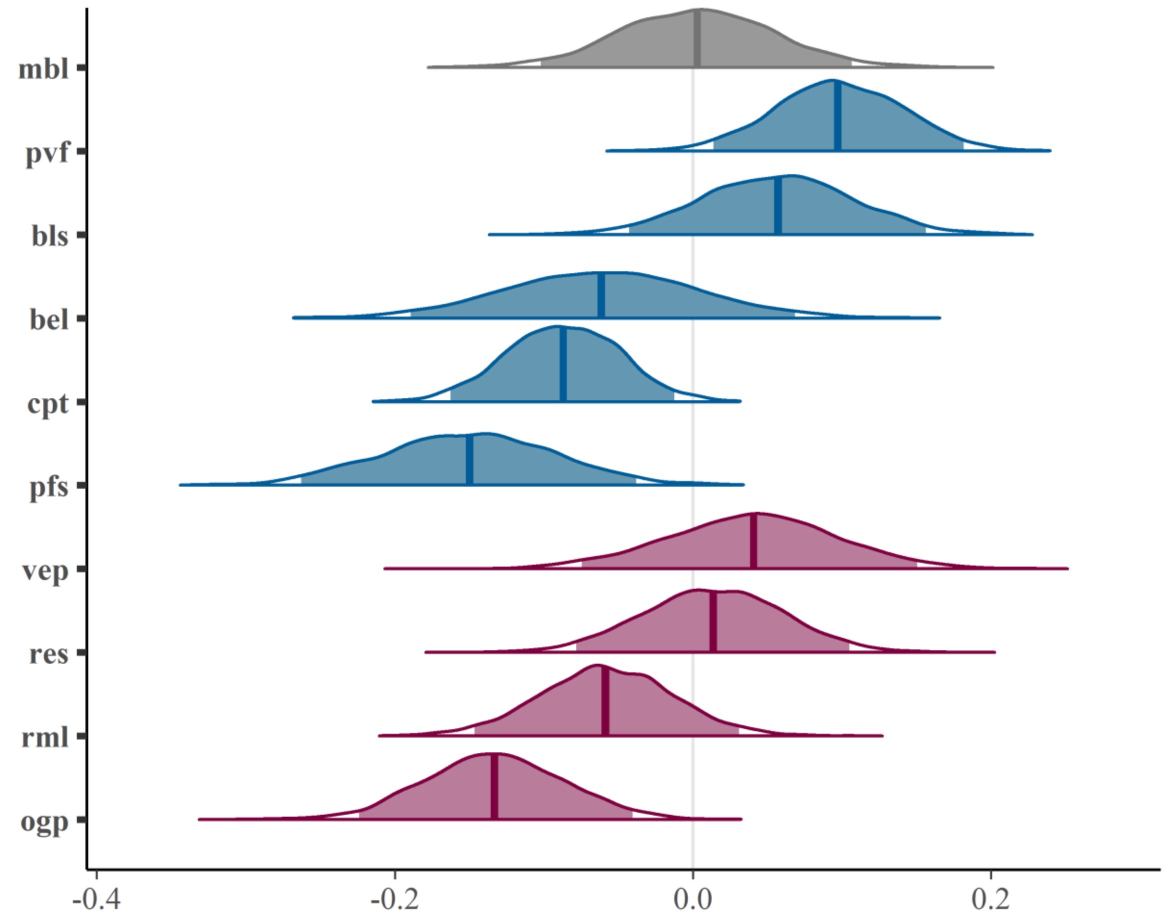

Figure 2.5. Posterior distributions by morphological traits as estimated by a Bayesian non-hierarchical model ordered by trait category and posterior mean with include a shaded 95% credible interval. The x-axis indicates the effect of each scaled and centered parameter on habitat coupling. Grey is metabolism, blue locomotive traits, pink feeding traits. Model completed on 733 populations across 104 lakes.

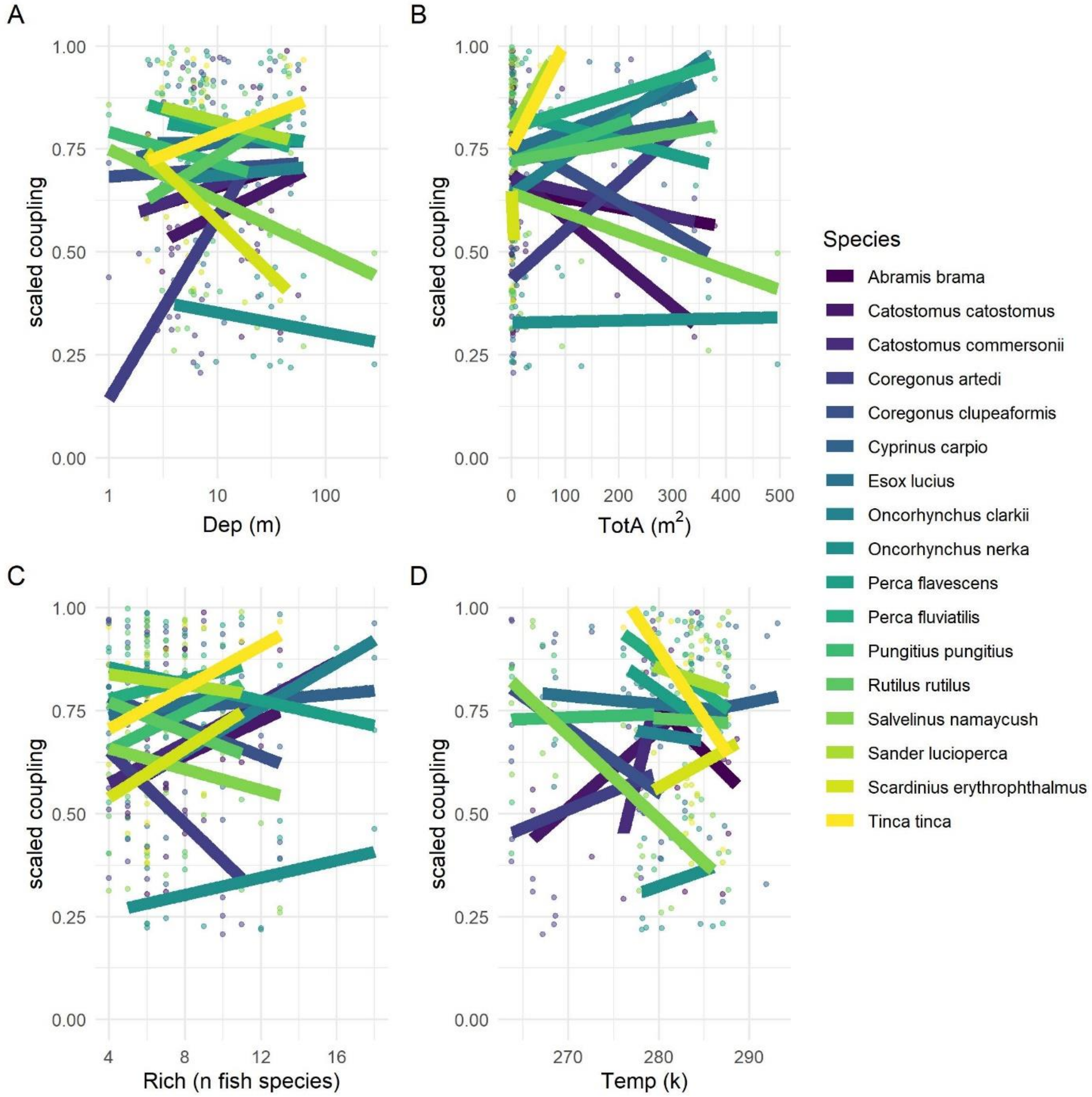

Figure 2.6. Differing relationships between habitat coupling and environmental factors (depth, total area, mean annual temp, and fish species richness) among species observed in 10% or more of the study lakes (17 species). Colors are according to species. Depth is presented on a log scale, accounting for the majority of lakes being less than 100 m deep.

2.9 Chapter 2 Appendix 1.

Methods

In 20 studies that reported 13C:12C for pelagic and littoral end member taxa as well as fishes, we estimated littoral resource use (φ) for each fish species from each lake (i.e., 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:

Equation 1:

$$\varphi_{\mathrm{pop}} = \frac{\delta^{13}\mathrm{C}_{\mathrm{pop}}\text{-}\delta^{13}\mathrm{C}_{\mathrm{pel\_end}}}{\delta^{13}\mathrm{C}_{\mathrm{lit\_end}}\text{-}\delta^{13}\mathrm{C}_{\mathrm{pel\_end}}}$$

Where δ13Cpop is the mean 13C:12C ratios of the population and δ13Cpel_end and δ13Clit_end are lake specific pelagic and littoral end members.

Second, we designated the greatest δ13C population value as a littoral end member value and the lowest δ13C population value as a pelagic end member, and then calculated littoral resource use for each fish population as:

Equation 2:

$$\varphi'_{\mathrm{pop}} = \frac{\delta^{13}\mathrm{C}_{\mathrm{pop}}\text{-}\delta^{13}\mathrm{C}_{\mathrm{pop\_min}}}{\delta^{13}\mathrm{C}_{\mathrm{pop\_max}}\text{-}\delta^{13}\mathrm{C}_{\mathrm{pop\_min}}}$$

We compared the estimates of littoral resource use between the two methods and finding that populations were consistently constrained within the δ13C range calculating the mean differences between the most enriched and depleted fish and end members. We also took the mean difference in ranges between the most enriched and depleted fish and the most enriched and depleted end members, then calculated the mean fraction of the fish range relative to the end member range as a proportion.

Then, with the information gathered after estimates comparing Equation 1 and 2, we tested to alternative methods for calculating littoral reliance as if there were no end member information. For the first alternative we adjusted the fish values according to the mean differences we observed between end members and fish as:

Equation 3:

$$\varphi''_{\mathrm{pop}} = \frac{\delta^{13}\mathrm{C}_{\mathrm{pop}}\text{-}(\delta^{13}\mathrm{C}_{\mathrm{pop\_min}}\text{-}\mathrm{adj}_{\mathrm{pel}})}{(\delta^{13}\mathrm{C}_{\mathrm{pop\_max}} + \mathrm{adj}_{\mathrm{lit}})\text{-}(\delta^{13}\mathrm{C}_{\mathrm{pop\_min}}\text{-}\mathrm{adj}_{\mathrm{pel}})}$$

For the second alternative we adjusted the fish values according to a relative amount (not a fixed amount) by first calculating a new range that was 1.25 % wider than the fish difference, then adjusting the most enriched and most depleted fish values according to the mean portion that goes to littoral adjustment and the mean portion towards the pelagic adjustment.

Equation 4:

$$(\delta^{13}\mathrm{C}_{\mathrm{pop\_max}}\text{-}\delta^{13}\mathrm{C}_{\mathrm{pop\_min}})^{*}1.25 = \mathrm{new.range}$$

$$\mathrm{new.range}^{*}0.621 = \mathrm{adj}_{\mathrm{rel\_lit}}$$

$$\mathrm{new.range}^{*}0.379 = \mathrm{adj}_{\mathrm{rel\_pel}}$$

$$\varphi'''_{\mathrm{pop}} = \frac{\delta^{13}\mathrm{C}_{\mathrm{pop}}\text{-}(\delta^{13}\mathrm{C}_{\mathrm{pop\_min}}\text{-}\mathrm{adj}_{\mathrm{rel\_pel}})}{(\delta^{13}\mathrm{C}_{\mathrm{pop\_max}} + \mathrm{adj}_{\mathrm{rel\_lit}})\text{-}(\delta^{13}\mathrm{C}_{\mathrm{pop\_min}}\text{-}\mathrm{adj}_{\mathrm{rel\_pel}})}$$

Results

We found that estimates of littoral reliance between the two approaches were moderately correlated (Pearson’s correlation coefficient, 0.60) (Fig S1). Differences between the pelagic and littoral endmembers for each of the lakes ranged from 4 per mil to about 19 per mil (Fig. S2A). The differences in fish community ranged from just over 2 to about 13 per mil (Fig. S2B). Fish population ranges (diff between fish max/min) was generally about 5 per mil less than the end member δ13C range in per mil (Fig. S2C). Taken as a proportion, the per community difference in range between end members and fish max/min as a function of total range difference (relative range) was median of 0.6 and mean of 0.8 (Fig. S2D). Differences between the most pelagic fish and the pelagic end members were smaller and less variable than difference between the most enriched fish and the littoral endmember (Fig. S3A, B). We also compared these differences to overall end member spread and fish spread, in case the difference was dictated by the end members and/or the fish community (Fig. S4A-D)

We tested a) overall difference, b) littoral difference, c) pelagic difference, or d) relative difference related to latitude and richness (Fig. S5A-D, Fig. S6A-D), to see if there was an adjustment to fish endmembers in related to an environmental or community variable that would allow us to capture as many lakes as possible including those that did not report end member values as a function of latitude. We determined that including them as a driver for the adjustment, given the large confidence intervals around these slopes, would not add additional clarity if we were to include this metric in the adjustment. Including either latitude or richness in the development of stand-in end members would have also required we drop them from the remaining analysis.

We found that on average, the pelagic end member was 1.55 ‰ lower than the most depleted fish and the littoral end member was 2.54 ‰ greater than the most enriched fish. We edited our mixed model equation to include this adjustment and re-ran the population estimates for the 20 lakes. We compared all approaches and determined the mean adjustment would provide a fair estimate of littoral vs pelagic reliance and eliminate zeros and ones from the dataset (Figure S6A-E).

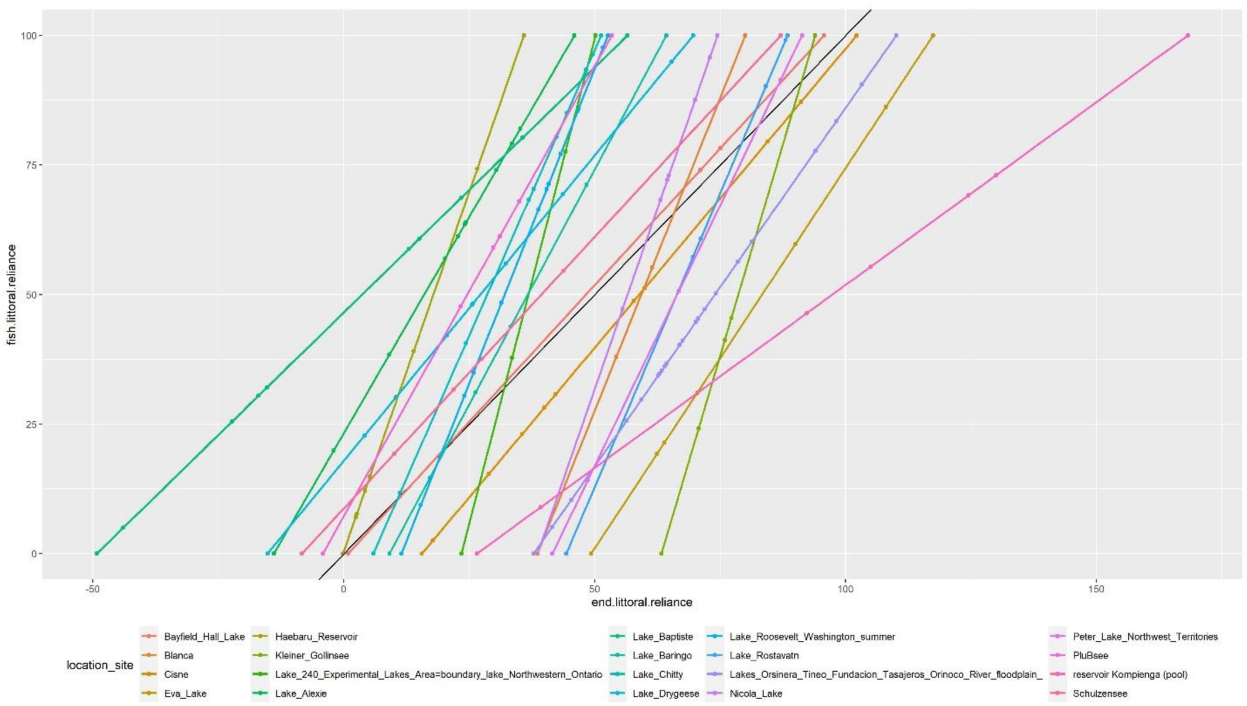

Figure S1. Fish population estimates using end members when compared to fish only littoral reliance estimates for 20 lakes. Each lake is a different color with the 1:1 line colored in black. Slopes that are steeper than 1:1 line reflect systems where the difference in fish min-max is narrower than the difference between end members. End points closer to the 0,0 or 100,100 mark indicate lakes where fish and end members stable isotope ratios were similar and greater distances resulted with fish and endmember values were different.

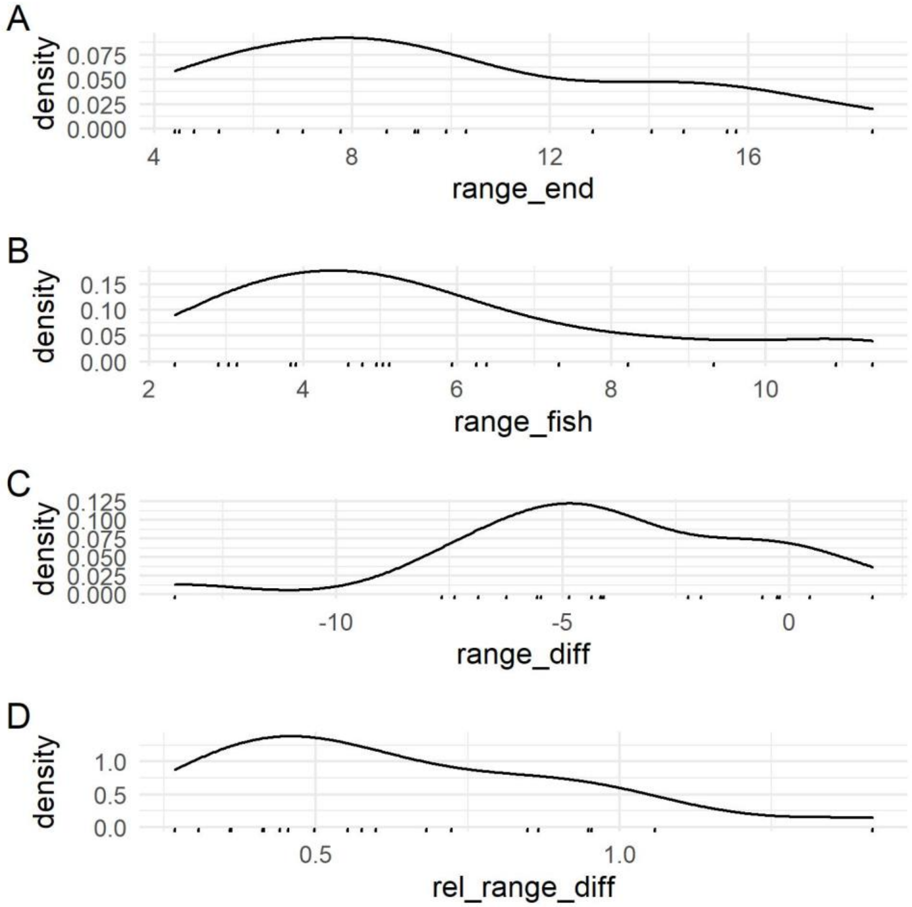

Figure S2. Panel A is the difference between littoral and pelagic end members for each of the 20 populations. Panel B, the differences in fish community minimum and maximum fish δ^{13}C values. Panel C. The per community difference in range between end members and fish max/min. Panel C. The per community difference in range between end members and fish max/min as a function of total range difference (relative range).

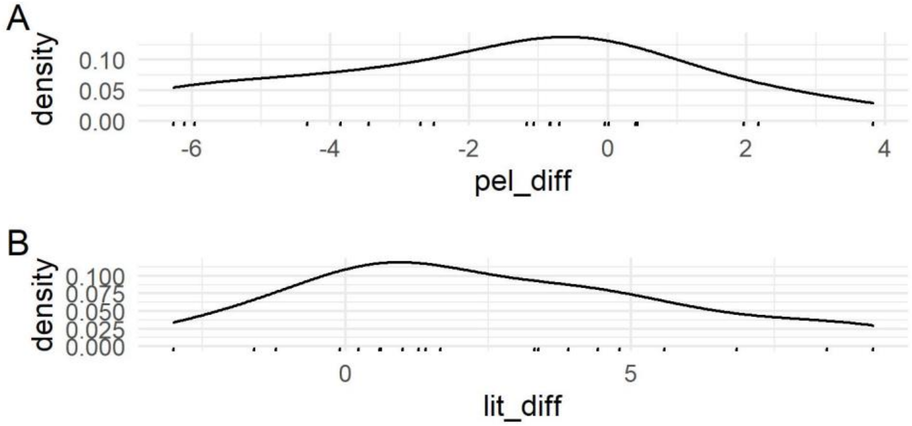

Figure S3. A. Difference between the pelagic end member and most pelagic fish (most depleted δ^{13}C ratios). Negative values indicate pelagic end member is more depleted than fish. B. Difference between the littoral end member and most littoral fish (most enriched δ^{13}C ratios). Positive values indicate pelagic end member is more enriched than fish.

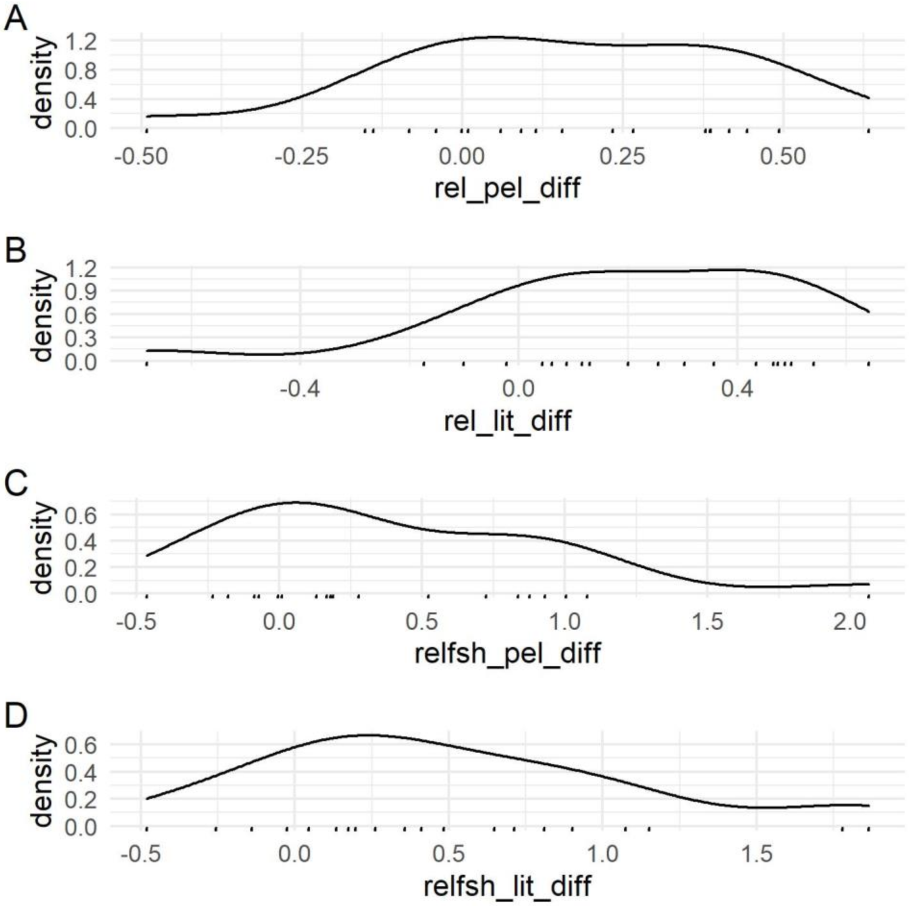

Figure S4. Differences in pelagic end member vs pelagic fish as a portion of the end member range (A). Differences in littoral end member vs littoral fish as a portion of the end member range (B). Differences in pelagic end member vs pelagic fish as a portion of the fish range (C). Differences in littoral end member vs littoral fish as a portion of the fish range (D).

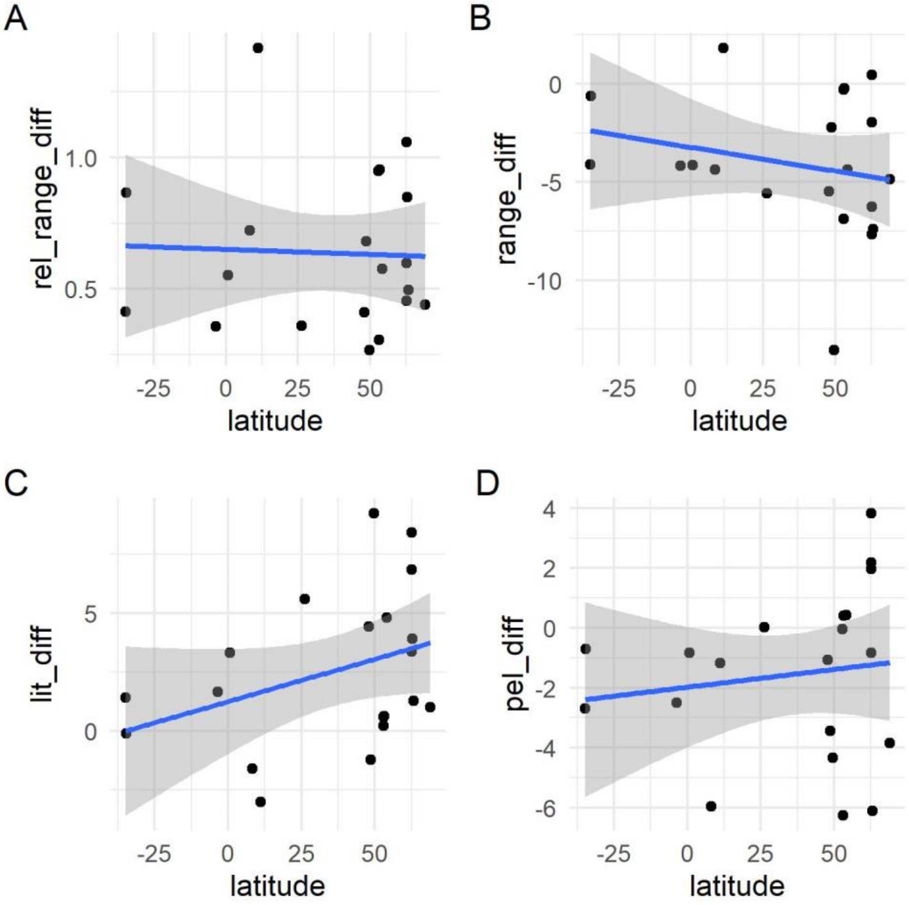

Figure S5. No tight trend in a) overall difference, b) littoral difference, c) pelagic difference, or d) relative difference related to latitude. Maybe a little bit, but outlier makes it difficult to assess.

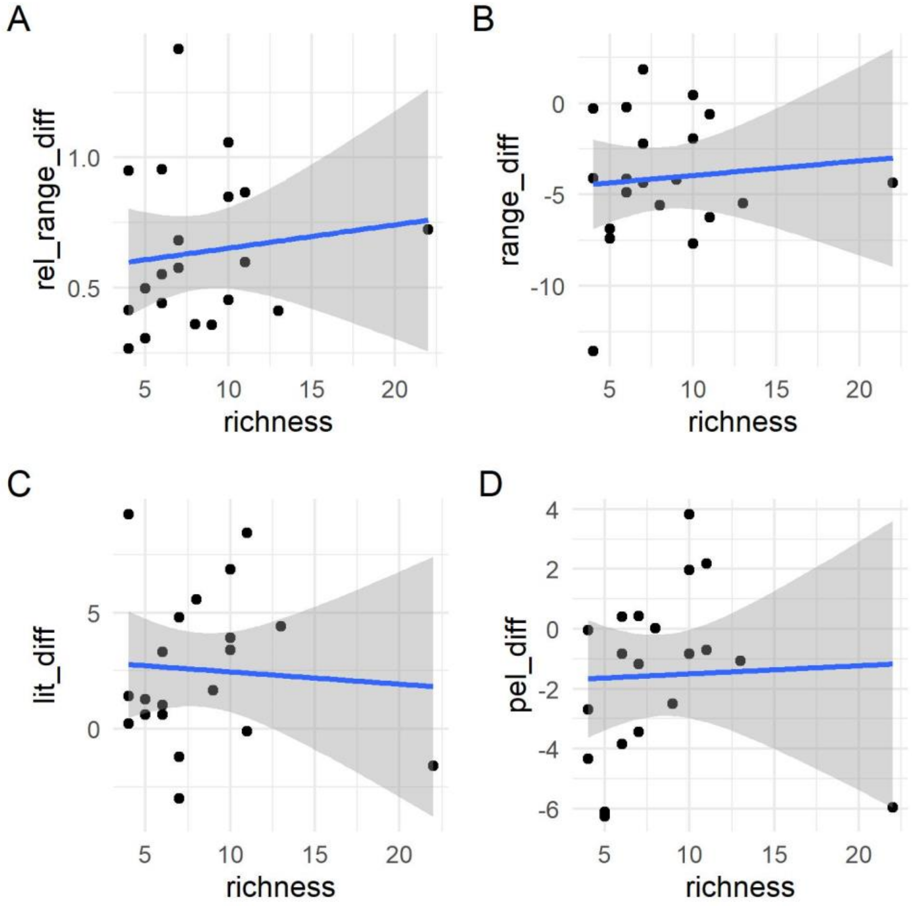

Figure S6. No tight trend in a) overall difference, b) littoral difference, c) pelagic difference, or d) relative difference related to richness.

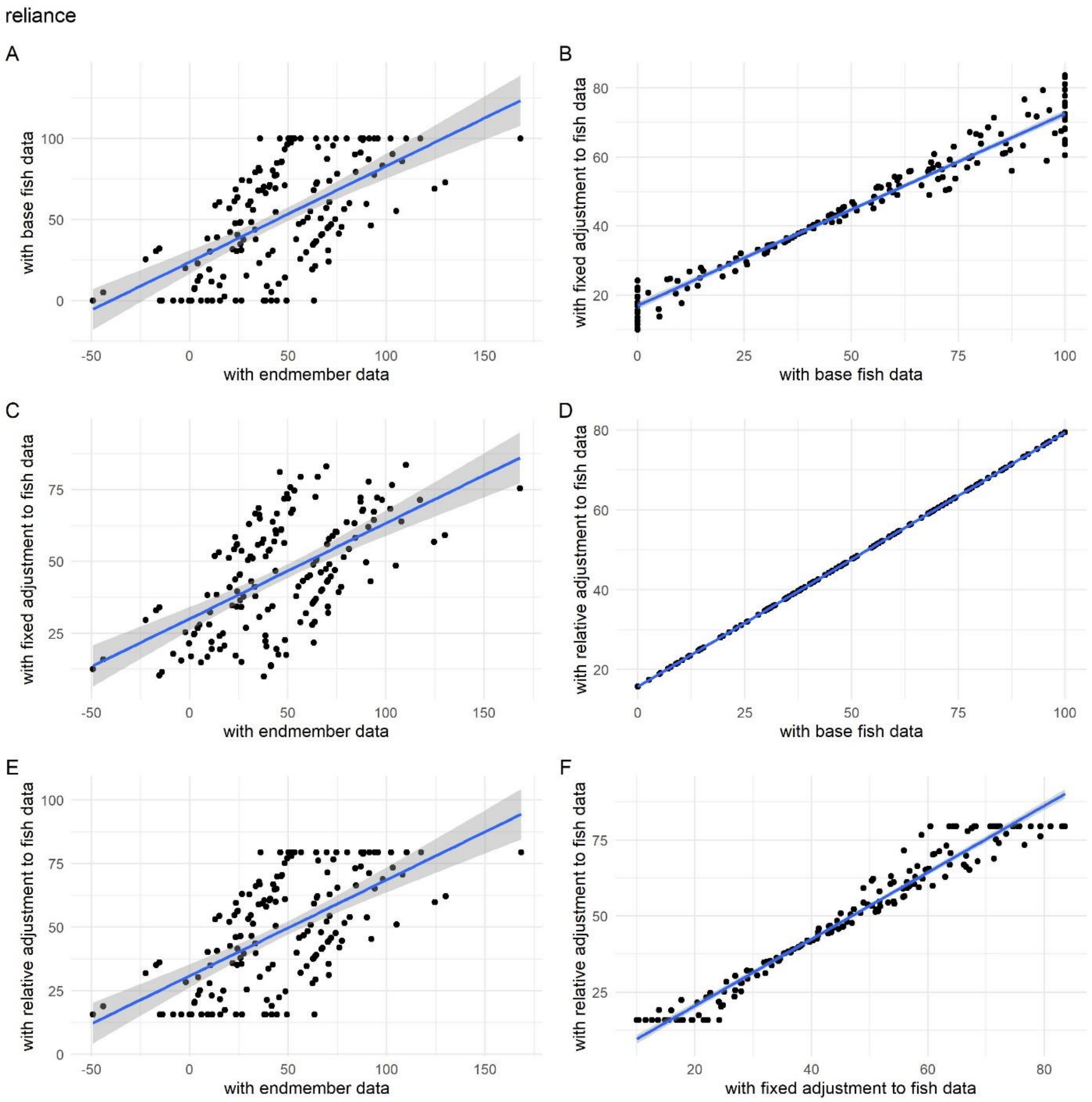

Figure S6. The comparison of population estimates of littoral reliance. The study moved forward with scenario C, fixed adjustment.