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

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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.

Key words: basal resources, cross-habitat linkages, biotic–abiotic interaction, habitat coupling, aquatic food web, consumer carbon, rainbow trout, mountain lakes, compositional data, stable isotopes

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 foodweb 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 foodweb 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 et al. 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 pop-

ulation 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 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.

METHODS
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). 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
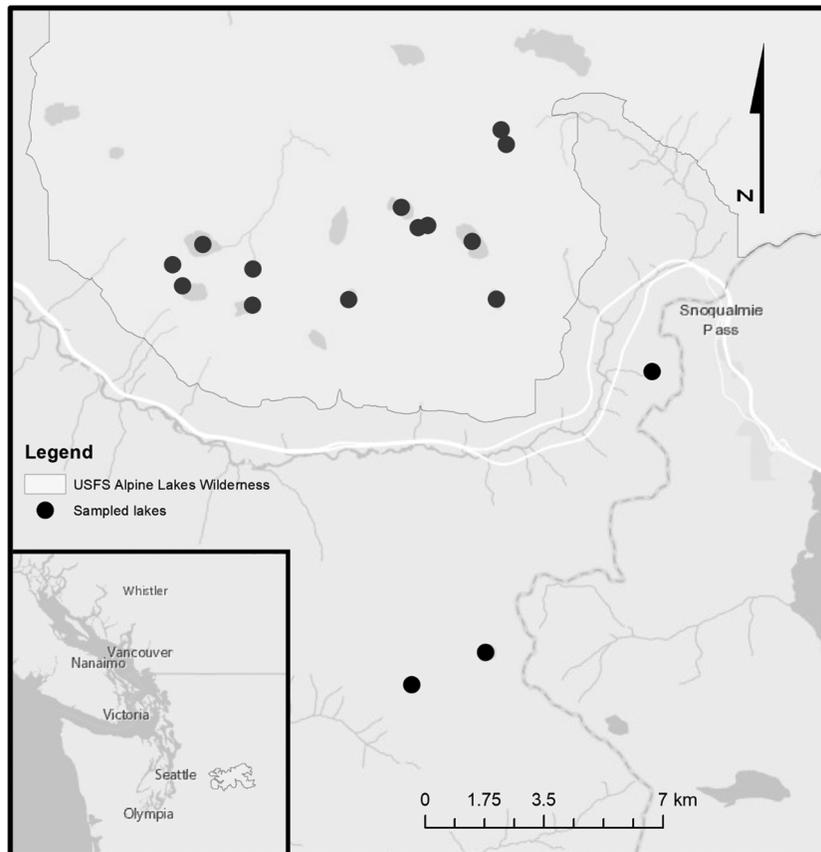
Figure 1. Study lakes (black points) are all located on the western slope of the Cascade Range in Washington, USA. The star in the inset indicates the approximate location of the study lakes relative to major cities. Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792), primary producers, and data for bathymetry were collected from each lake. USFS = United States Forest Service.

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). 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.

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

Table 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 (km²)	Maximum depth (m)	Stocking status (count, frequency)	Last stocked (date, count)	Population abundance (# fish/h)	Littoral extent (%)	Terrestrial loading (m⁻¹)	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

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 cm² 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 $\delta^{13}C$.

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.

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

$$\begin{aligned} \varphi T_{ijk}(\delta^{13}C_{\text{leaves}_{ik}}) + \varphi P_{ijk}(\delta^{13}C_{\text{seston}_{ik}}) \\ + \varphi L_{ijk}(\delta^{13}C_{\text{periphyton}_{ik}}) = \delta^{13}C_{\text{fish}_{ik}} \end{aligned} \qquad \text{(Eq. 2)}$$

$$\begin{aligned} \varphi T_{ijk}(\delta^{13}N_{\text{leaves}_{ik}}) + \varphi P_{ijk}(\delta^{13}N_{\text{seston}_{ik}}) \\ + \varphi L_{ijk}(\delta^{13}N_{\text{periphyton}_{ik}}) = \delta^{13}N_{\text{fish}_{ik}} - \Delta^{15}N_k \end{aligned} \qquad \text{(Eq. 3)}$$

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; Ta-

ble 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 nonnegative 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 $comp_{ij} = [\overline{\phi T_{ij}}, \overline{\phi P_{ij}}, \overline{\phi L_{ij}}]$.

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 (versions 3.6.2 and 4.0.3; R Project for Statistical Computing, Vienna, Austria) with use of the *tidyverse* (version 1.3.0; Wickham et al. 2019), *MASS*

(version 7.3-53.1; Venables and Riley 2002), *MVN* (version 5.8; Korkmaz et al. 2014), *car* (version 3.0-10; Fox and Weisberg 2019), *faraway* (version 1.0.7; Faraway 2016), *MuMIn* (version 1.43.17; Bartoń 2020), *compositions* (version 2.0-1; van den Boogaart et al. 2021), *broom* (version 0.7.6; Robinson et al. 2021), *patchwork* (version 1.1.1; Pedersen 2020), *ggtern* (version 3.3.0; Hamilton and Ferry 2018), *corrplot* (version 0.84; Wei et al. 2017), and *magick* (version 2.6.0; Ooms 2021) packages.

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.

RESULTS
Lake foodweb 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. 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. 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. 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. 3A). Compared to other lakes, trout in Olallie Lake relied the least on littoral–benthic derived resources (Fig. 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. 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%.

Determinants of Rainbow Trout resource use

Fish use of littoral, pelagic, and terrestrial resources varied as a function of littoral extent, fish length, relative
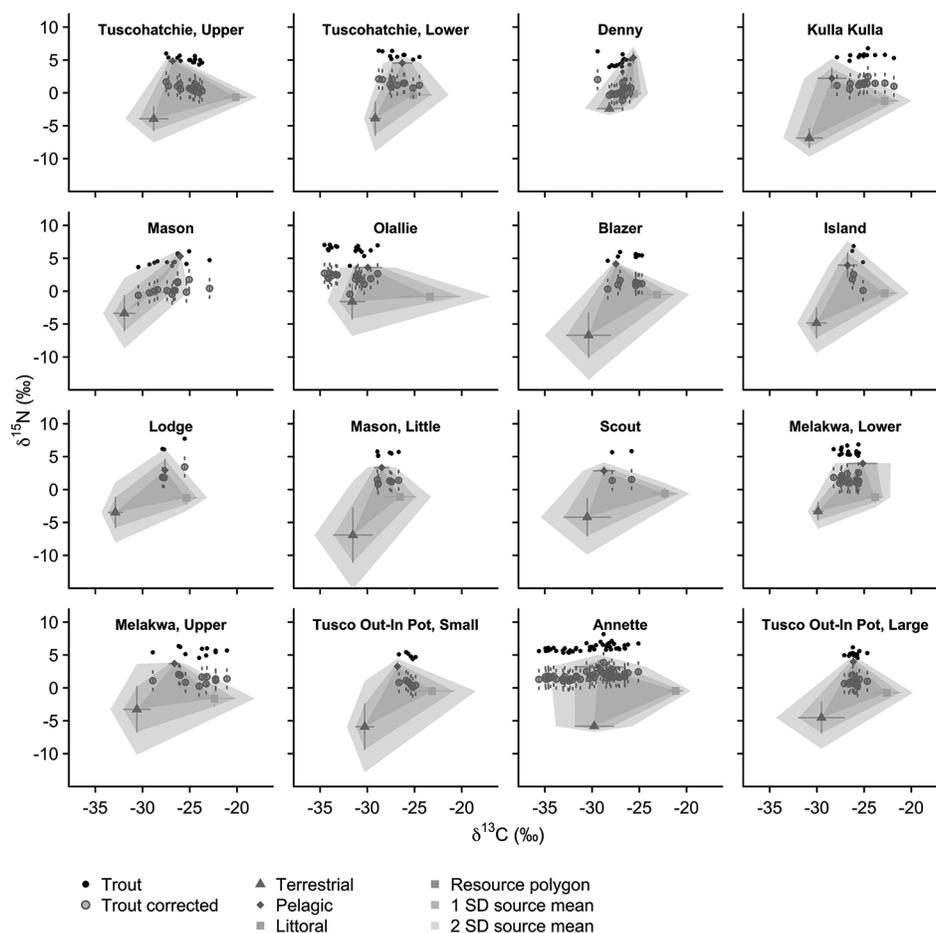
Figure 2. Isotope biplots for Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) and primary producers collected in 16 lakes in Washington, USA. Mean values are shown for source pools of terrestrial (▲), pelagic (◆), and littoral (■) basal resources for each lake; error bars are 1 SD of the pooled mean 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‰).

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). 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 dem-

onstrate that when littoral extent is high (orange points, Fig. 4A, B), resource use is relatively similar among fish regardless of relative population abundance (line thickness within Fig. 4A, B) or terrestrial loading (location of orange points in Fig. 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. 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. 4A, B). Likewise, at low relative population abundance (thin lines in Fig. 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,
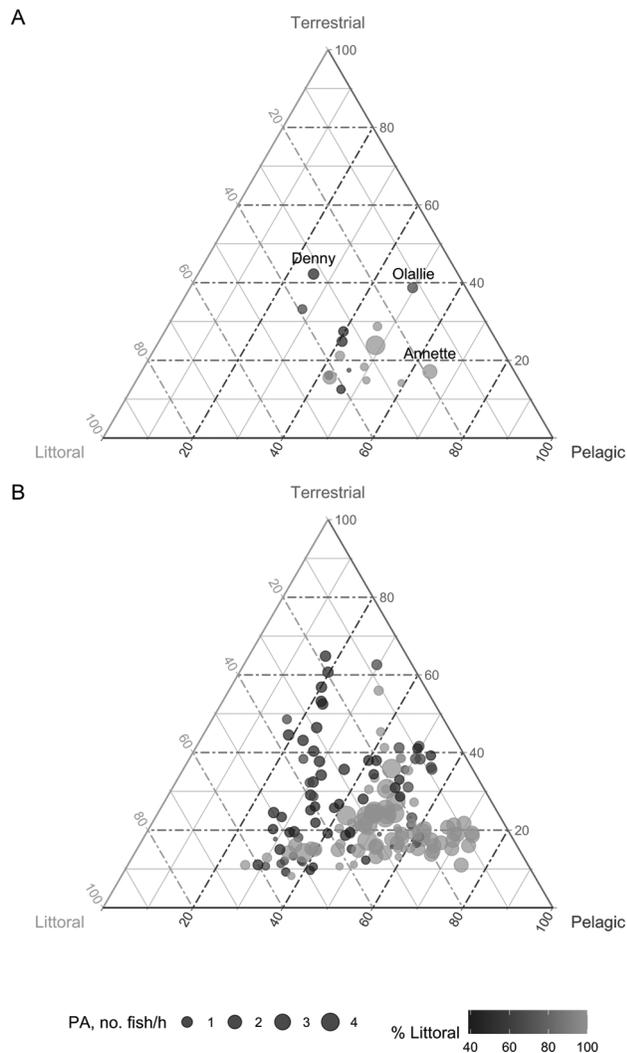
Figure 3. Ternary diagrams displaying use of basal resources by Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) in 16 Washington, USA, lakes estimated from stable isotope mixing models (assumed N enrichment of 4.3 ± 1.5‰). Points are shaded by the littoral extent (LE, %) of the lake that fish were 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.

the models suggest that littoral extent becomes more influential on determining resource use (thick lines in Fig. 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 (deter-

mined by comparison of prediction plots with fish lengths of 100, 200, and 300 mm; Fig. S1).

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. 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 $1.9 \pm 0.51‰$) 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. 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).

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.

Table 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^{-1}), 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: $\Delta^{15}N = 4.3 \pm 1.5‰$, Carbon: $\Delta^{13}C = 0.0 \pm 0.0‰$											
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**				

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
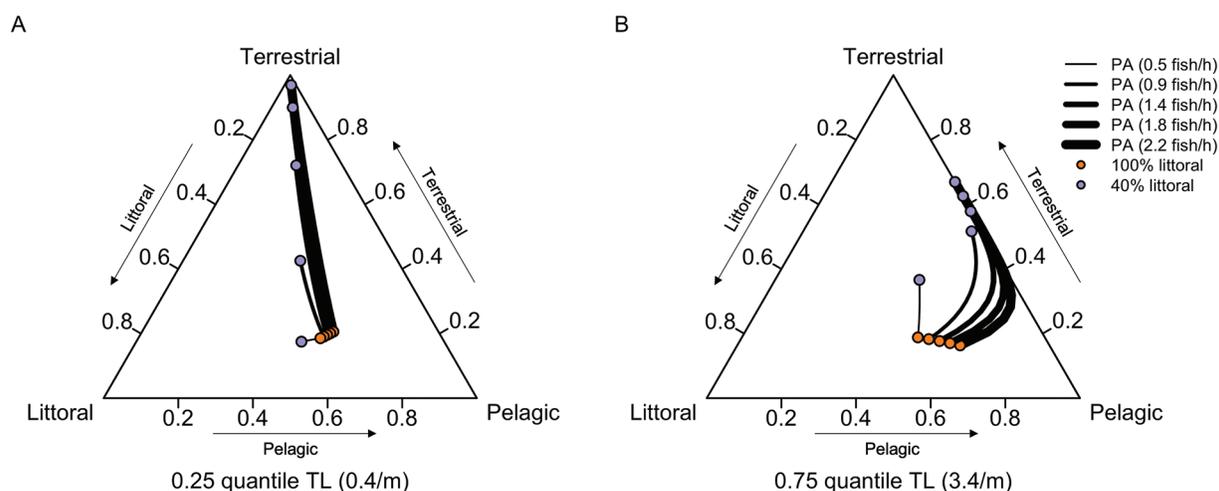

Figure 4. Ternary diagrams displaying predicted use of terrestrial, littoral–benthic, and pelagic derived resources by 200 mm Rainbow Trout (*Oncorhynchus mykiss* Walbaum, 1792) in the study lakes when littoral extent and population abundance vary. Orange points represent compositions expected within 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.
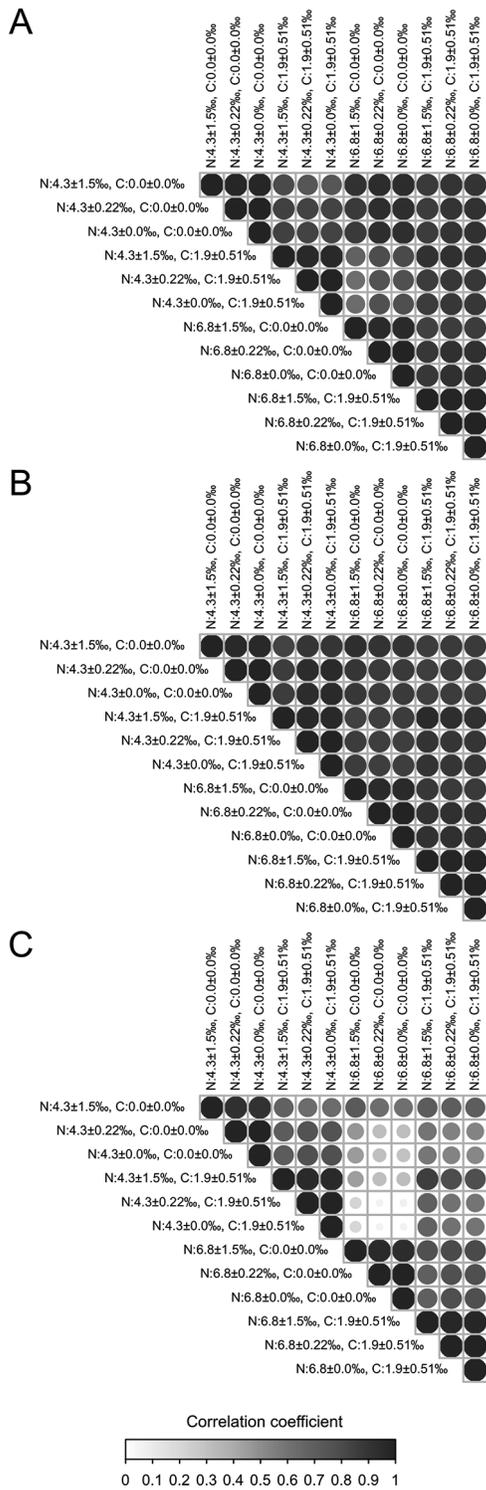
Figure 5. Pairwise Pearson correlations according to lake-wide estimates of relative use of (A) terrestrial, (B) pelagic, and (C) littoral–benthic derived resources based on alternative assumptions related to N and C enrichment due to trophic enrichment. The assumed mean and standard deviation of trophic enrichment is indicated for N and C for each alternative tested.

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 in-

fluence 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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