Conservation Biology

Contribution of warm habitat to cold-water fisheries

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Article impact statement: Warm downstream habitats may be critical for cold-water fisheries but are overlooked by climate adaptation planning.

Abstract

A central tenet of landscape ecology is that mobile species depend on complementary habitats, which are insufficient in isolation, but combine to support animals through the full annual cycle. However, incorporating the dynamic needs of mobile species into conservation strategies remains a challenge, particularly in the context of climate adaptation planning. For cold-water fishes, it is widely assumed that maximum temperatures are limiting and that summer data alone can predict refugia and population persistence. We tested these assumptions in populations of redband rainbow trout (*Oncorhynchus mykiss newberrii*) in an arid basin, where the dominance of hot, hyperproductive water in summer emulates threats of climate change predicted for cold-water fish in other basins. We used telemetry to reveal seasonal patterns of movement and habitat use. Then, we compared contributions of hot and cool water to growth with empirical indicators of diet and condition (gut contents, weight–length ratios, electric phase angle, and stable isotope signatures) and a bioenergetics model. During summer, trout occurred only in cool tributaries or springs (<20 °C) and avoided Upper Klamath Lake (>25 °C). During spring and fall, ≥65% of trout migrated to the lake (5–50 km) to forage. Spring and fall growth (mean [SD] 0.58% per day [0.80%] and 0.34 per day [0.55%], respectively) compensated for a net loss of energy in cool summer refuges (–0.56% per day [0.55%]). In winter, ≥90% of trout returned to tributaries (25–150 km) to spawn. Thus, although perennially cool tributaries supported thermal refuge and spawning, foraging opportunities in the seasonally hot lake ultimately fueled these behaviors. Current approaches to climate adaptation would prioritize the tributaries for conservation but would devalue critical foraging habitat because the lake is unsuitable and unoccupied during summer. Our results empirically demonstrate that warm water can fuel cold-water fisheries and challenge the common practice of identifying refugia based only on summer conditions.

KEYWORDS
climate adaptation, climate change, fisheries, freshwater, landscape complementation, *Oncorhynchus*, salmonid, temperature

Resumen: Un principio central de la ecología de paisaje es que las especies ambulantes dependen de hábitats complementarios, los cuales son insuficientes en aislamiento, pero al combinarse mantienen a los animales durante el ciclo anual completo. Sin embargo, la incorporación de las necesidades dinámicas de las especies ambulantes dentro de las estrategias de conservación todavía es un reto, particularmente en el contexto de la planeación de la adaptación climática. Para los peces de agua fría, generalmente se asume que las temperaturas máximas son limitantes y que los datos estivales son suficientes para predecir refugios y la persistencia poblacional. Pusimos a prueba estas suposiciones en poblaciones de trucha arcoíris (*Oncorhynchus mykiss newberrii*) de una cuenca árida, en donde el dominio de aguas cálidas e hiperproductivas durante el verano emula las

amenazas del cambio climático pronosticadas para los peces de agua fría en otras cuencas. Usamos telemetría para descubrir los patrones estacionales de movimiento y uso de hábitat. Después, comparamos las contribuciones que tienen las aguas cálidas y frías al crecimiento con indicadores empíricos de dieta y condición (contenidos intestinales, proporciones peso-longitud, ángulo de fase eléctrica y huellas de isotopos estables) y un modelo bioenergético. Durante el verano, las truchas sólo estuvieron presentes en manantiales o afluentes fríos (<20°C) y evitaron el Lago Klamath Superior (>25°C). Durante la primavera y el otoño, ≥65% de las truchas migraron al lago (5-50 km) para procurar alimento. El crecimiento durante la primavera y el otoño (media [SD] 0.58% día^{-1} [0.80%] y 0.34 día^{-1} [0.55%], respectivamente) compensaron la pérdida neta de energía en los refugios fríos durante el verano (-0.56% día^{-1} [0.55%]). En el invierno, ≥90% de las truchas regresaron a los afluentes (25-150 km) para desovar. Entonces, mientras que los afluentes perennemente fríos fomentaron los refugios termales y el desove, fueron las oportunidades de alimentación en el lago cálido estacional las que finalmente alentaron estos comportamientos. Las estrategias actuales de adaptación climática pondrían como prioridad de conservación a los afluentes, pero devaluarían el hábitat crítico de alimentación porque el lago está desocupado y no es apto durante el verano. Nuestros resultados demuestran empíricamente que las aguas cálidas pueden promover las pesquerías de aguas frías y desafiar la práctica común de identificar refugios basándose solamente en las condiciones estivales.

PALABRAS CLAVE:
adaptación climática, agua dulce, cambio climático, complementación de paisajes, pesquerías, salmónido, temperatura, *Oncorhynchus*

INTRODUCTION

One of the key goals of planning for climate adaptation is to identify and conserve habitats that could serve as refugia from climate warming (Ashcroft, 2010; Dobrowski, 2011; Morelli et al., 2016). Although refuges harbor individuals from acute threats to survival, refugia additionally provide all resources needed for populations to persist. Yet efforts to identify future refugia often focus mainly on where the temperature will remain suitable rather than where multiple resources will remain available (Ashcroft, 2010; Briscoe et al., 2016; Morelli et al., 2016). This perspective overlooks the fact that mobile populations can depend on complementary resources, of which temperature is just one, spread over multiple habitats across the landscape (Dunning et al., 1992; Small-Lorenz et al., 2013; Troia et al., 2019). The search for climate refugia should be broadened to consider the suite of complementary habitats that mobile animals can link in space and time.

For animals with low thermal tolerances, such as cold-water fishes, climate adaptation planning often focuses on the threat of summer heat stress, defining habitat quality or refugia based on whether areas exceed threshold temperatures (Eaton & Scheller, 1996; Isaak et al., 2016). In riverine landscapes, this summer-focused adaptation planning identifies perennially cold headwater networks as refugia and worthy investments for conservation (Isaak et al., 2015), whereas downstream regions that become hot during summer are considered lost (Almodóvar et al., 2012; Merriam et al., 2017; Ruesch et al., 2012) or even a liability (Rahel, 2013). Data on the spatial distributions of cold-water fishes appear to support these conclusions, often showing that summer temperature is strongly associated with fish occupancy. However, fieldwork is biased toward summer months and rarely spans the annual cycle, particularly for studies of riverscape fish distribution (Brady et al., 2020 [preprint]). Thus, frameworks for climate adaptation are effective at identifying refuges from summer heat stress, but may overlook how additional habitats function at other times of year to contribute to refugia (Fausch et al., 2002; McMeans et al., 2020).

Recent work shows that headwaters and main-stem habitat may exhibit complementary "growth regimes" and express physiologically optimal conditions during different seasons (Armstrong et al., 2021). In an individual-based simulation, fish achieved the majority of annual growth in warm main-stem habitats that were avoided in summer but provided rapid growth during cooler periods of spring and fall. However, it remains largely unknown whether fish in nature can track large-scale shifts in growth potential and whether warm habitats actually support foraging during spring and fall. We empirically tested these model predictions in a relevant ecological context—a cold-water fish stock complex currently facing extreme temperatures and eutrophication that resemble climate change projections for many temperate aquatic systems. Specifically, we quantified seasonal patterns of habitat use in relation to water temperature across the landscape; inferred the function of habitat use in each season; and measured energetic condition and growth outcomes during each season.

METHODS

Study system

We evaluated the predictions of the growth regime conceptual framework (Armstrong et al., 2021) in redband trout (*Oncorhynchus mykiss newberrii*), a subspecies of one of the most widely occurring cold-water fishes in the world, rainbow trout (*Oncorhynchus mykiss*). In the predominantly warm, but thermally heterogeneous upper Klamath Basin (UKB) of southern Oregon, native redband trout occur throughout the watershed and are among the largest of any freshwater resident rainbow trout (Behnke, 2002). These large-bodied trout provide the last remaining subsistence fishery for the Klamath Tribes (Thomson, 2012) and an iconic recreational fishery.

Upper Klamath Lake (~270 km²) dominates the waters of the UKB by surface area and has an extreme temperature regime, similar to projections for downstream portions of cooler watersheds under climate change (Isaak et al., 2015). The lake typically freezes over for several months in winter and reaches at least 25 °C in summer, 5 °C warmer than the current water quality standard for redband trout (ODEQ, 2021). Although the lake was historically eutrophic, nutrient overloading and wetland conversion have caused the lake to become hypereutrophic. Concurrently, the dominant algae-like species has shifted to *Aphanizomenon flos-aquae* cyanobacteria (Bradbury et al., 2004; Eilers et al., 2004). Every summer, *A. flos-aquae* blooms push alkalinity and dissolved oxygen to levels that prove stressful or lethal for fishes, including taxa that are more tolerant than salmonids (Burdick et al., 2020; Perkins et al., 2000). Thus, the lake emulates 2 commonly predicted outcomes of climate change, high maximum temperatures (Isaak et al., 2015) and eutrophic conditions (Lu et al., 2019; Sinha et al., 2017).

The porous geology of the basin's mountains gives rise to several groundwater-dominated tributaries and seeps (Gannett et al., 2007). Compared with the lake, these areas are small (streams up to fourth-order and 50-m wide) and characterized by less extreme temperature regimes that generally remain below 20 °C (Appendix S2), similar to headwater regions that are predicted to become climate refugia (Isaak et al., 2016).

Water temperatures

We mapped annual water temperature variation across the basin based on multiple data sources. We used spatially continuous temperatures from the NorWeST model, a prominent tool for climate adaptation (Isaak et al., 2015), but these data were only available for August and in the tributaries. To capture variation beyond the spatial and temporal extent of NorWeST at a coarser scale, we divided the basin into thermal habitat units consisting of stream segments, groundwater upwelling areas, and the lake (Figure 1). For each unit, we either retrieved data from U.S. Geological Survey monitoring stations (waterdata.usgs.gov/nwis) or deployed loggers (HOBO, Onset, Bourne, Massachusetts) to characterize temperature when and where NorWeST data were not available. We deployed a single logger per habitat
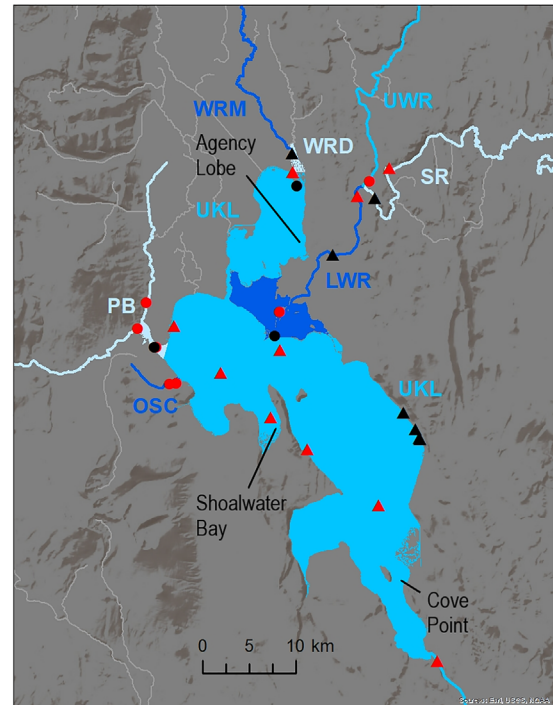

FIGURE 1 Map of the upper Klamath Basin showing the different habitat units (blue shading): Upper Klamath Lake (UKL), Sprague River (SR), upper and lower Williamson River (UWR and LWR), Wood River main stem (WRM), Wood River delta (WRD), Pelican Bay and its tributaries (PB), and Odessa Creek complex (OSC) (includes adjacent Short Creek) (red geometric shapes, temperature monitoring locations; circles, locations where loggers were deployed; triangles, stations operated by U.S. Geological Survey [USGS]; black shapes, passive tracking locations, including radiotelemetry stations [circles] and passive integrated transponder arrays maintained by USGS and 3 areas where tagged fish were released)

unit, except in Pelican Bay, where we deployed 3 loggers to characterize temperatures of the bay itself and each of its tributaries. Although only 1 monitoring station in the lake was operated year-round, comparison with 8 seasonal monitoring stations suggested that spatial variation in temperature is minimal throughout the lake at least from mid-spring to early fall (Appendix S1). We also verified, using temperature-sensing radio tags (below), that if there was substantial spatial variation in lake temperature from fall to spring, such variation was not taken advantage of by redband trout. We therefore considered the lake a single thermal habitat, represented by the year-round Link River Dam station.

Habitat use

To elucidate seasonal habitat use and individual movements, we implanted radio tags (model MCFT2-3A, Lotek, Newmarket, Ontario) in adult redband trout captured from Upper Klamath Lake (444–760 mm FL, 0.9–3.9 kg) in early to mid-spring in 2016 (*n* = 40) and 2017 (*n* = 51). Fish were released in Shoalwater Bay in both years, and in 2017 some fish were released near the southern and northern ends of the lake (Cove Point and Agency Lobe). Tags transmitted an individual

identification code, temperature, and motion-sensor information (active or inactive) to identify shed tags or dead individuals. Each trout also received a passive integrated transponder (PIT) tag with a unique identifier. We then tracked these trout through October 2018 at the scale of the habitats labeled in Figure 1 (total tracking duration = 31 months).

We employed mobile and stationary radio tracking methods to characterize seasonal movement patterns. To maximize the number of fish detected, mobile surveys were conducted opportunistically in space and time on foot, by boat, and by automobile. We also conducted at least 1 basin-wide tracking flight in all 4 seasons over the course of the study. To ensure our inferences of habitat use were not confounded by high-frequency (i.e., hourly to weekly) movements, we installed 24-h fixed telemetry stations at boundaries between the lake and the 3 largest tributary or groundwater habitats. We supplemented these data with PIT-tag detections on existing arrays in the basin that are used by U.S. Geological Survey to monitor other species.

We defined habitat use during a given time of year (e.g., April) as the percentage of fish found in a particular habitat, out of all live fish detected within that time of year throughout the study. Individuals surviving the same period in multiple years (e.g., April 2016 and 2017) were counted separately. We aggregated data by month across years (including 2018 when mobile tracking effort was lower) because months showed a similar seasonal pattern each year, and we detected the majority of fish in all aggregated months (Appendix S8). The median monthly detection rate for mobile tracking was 71% (n = 31 months, range = 28–100%; Appendix S7). Contingency analysis of mobile versus stationary methods estimated that we failed to detect only 3% of movements between lake and tributary habitats overall (bootstrap 95% CI, 2–5) (Appendix S9).

Function of habitat use

To infer thermal habitat use, we recorded temperatures transmitted from radio tags during mobile telemetry surveys, including flights. We compared these tag temperatures with the corresponding daily mean lake temperature to determine whether temperatures experienced by fish differed from ambient conditions or the vast majority of available temperatures in the basin.

To infer spawning-driven habitat use, we interpreted our telemetry results in the context of independent spawn timing data from ongoing monitoring conducted by the Oregon Department of Fish and Wildlife (ODFW) (Tinniswood & Harrington, 2015). The ODFW conducts surveys of all known redband trout spawning sites by visually enumerating live fish and their spawning nests (i.e., redds). Their spawning survey events occur every 2 weeks throughout the spawning run for each site, and sites have been surveyed for between 5 and 48 years. We averaged all years of fish and redd counts (n = 7 and 9 sites, respectively) for each 2-week period to characterize spawn timing at each site. We then summed these averages across sites to characterize basin-wide spawn timing. Radio detections overlapping in time and space with peak spawning suggested by ODFW visual monitoring were considered indicative of spawning behavior.

To infer foraging-driven habitat use, we collected fish diet samples in 2017 and 2018 along the dominant migration pattern we observed during spring, summer, and fall (i.e., during lake, tributary, and lake residence, respectively) (see RESULTS). Sample sizes and biological characteristics are summarized in Table 1. Adult redband trout were captured by hook and line between sunrise and sunset and anesthetized. We did not sample any radio tagged fish. We measured weight (nearest 5 g) and fork length, then conducted gastric lavage to obtain gut contents. Prey items from the gut were classified (to order at a minimum; to family or genus when possible) and measured to the nearest mm. Weight of prey by taxon was estimated using length regressions from the literature (Appendix S10). To estimate total daily consumption from these instantaneous rations, we multiplied prey weights by a temperature-dependent gut evacuation rate (Scheuerell et al., 2007) based on logger temperatures from the habitat and day of year corresponding to each fish sampled. This method assumes that prey mass in the gut represents the steady-state outcome of constant feeding and digestion rates. Energy rations were then calculated using literature values for prey energy density at the lowest taxonomic level available (Appendix S10).

Energetic condition and growth

During our 2017–2018 diet sampling, we also assessed energetic condition and growth. Sometimes, only a subset of diet, condition, and growth data were collected from an individual fish to reduce handling time, resulting in variable sample sizes for each metric (Table 1). Data from 2017 and 2018 were pooled because accounting for interannual variation did not change our conclusions (Appendix S3).

To characterize condition, we calculated Fulton's condition factor K, a traditional metric based on the ratio of weight to cubed length (Ricker, 1975), and phase angle, a novel metric based on electrical properties of tissue (Cox & Heintz, 2009). Because both metrics correlate positively and imperfectly with condition at different timescales (Appendix S1), we analyzed phase angle throughout each season and K at the end of each season, and considered congruency between the 2 to indicate a true pattern in condition. To calculate phase angle, resistance and reactance (nearest 0.1 ohm) were measured externally along the lateral line just behind the operculum using a commercial hand-held unit (Seafood Analytics, Juneau, Alaska).

To determine which habitats supported fish growth, we analyzed stable isotope signatures in trout fin tissue. Under laboratory conditions with unlimited feeding, half of fin tissue turns over every 9 days and isotopically resembles the recent diet (Heady & Moore, 2013). However, when food level is too low to support growth, signatures from the prior growth period can persist in somatic tissue for nearly a year after a dietary switch (Armstrong & Bond, 2013). We analyzed carbon-13 content (δ^{13}C) of 5 essential amino acids (Val, Leu, Ileu, Thr, and Phe), which are not typically altered during assimilation by consumers

TABLE 1 Lengths and weights for all redband trout sampled and sample sizes for each metric

Metric	Spring 2017	Summer 2017	Spring 2018	Summer 2018	Fall 2018
Fork length (mm)[a]	561 (62)	518 (68)	583 (49)	485 (116)	599 (41)
Wet weight (g)[a]	2146 (714)	1629 (616)	2305 (570)	1523 (937)	2491 (426)
Fulton's K (n)	15	4	39	61	14
Phase angle (n)	97	5	40	196	16
Dietary ration (n)	21	7	15	146	16
Modeled growth (n)	21	7	15	146	16
Amino acid δ^{13}C (n)[b]	8	6	2	4	0

Note: Data from 2017 to 2018 were pooled for all analyses (Appendix S3).
[a]Expressed as mean (SD).
[b]Does not include Wood and Williamson samples, which were removed after preliminary analysis.

(McMahon et al., 2016) and can thus match tissue to the food web that supported its growth. We extracted and separated each amino acid with acid hydrolysis and gas chromatography and measured δ^{13}C with mass spectrometry according to McMahon et al. (2016). Further details are in Appendix S1.

We measured δ^{13}C in trout caudal fin samples collected from Upper Klamath Lake in spring and from the 3 most heavily used cool habitats in summer (Wood River Delta, lower Williamson River, and Pelican Bay). To characterize the potentially different isotopic signatures of these 4 food webs, we measured δ^{13}C in an assortment of prey items from each habitat (Appendix S11). We used linear discriminant analysis of prey δ^{13}C to create a classifier capable of distinguishing between the signatures of each food web and identifying which is most similar to the signature of each fin sample. Preliminary analysis indicated that the classifier struggled to distinguish the Wood and Williamson food webs from the lake, but effectively distinguished the Pelican Bay food web from the lake (Appendix S4). Because this outcome left us unable to confidently determine whether Wood and Williamson fin samples derived growth from warm or cool food webs, we dropped those locations from the analysis. We recreated the classifier with only prey from Pelican Bay ($n = 16$) and the lake ($n = 12$) and analyzed fin samples from only these 2 locations.

We also estimated daily growth with the Wisconsin bioenergetics model. We used the equations and parameters developed by Rand et al. (1993) for another migratory lake-dwelling population of *O. mykiss*. Generally, the model for growth (G) takes the form

$$G = C\,(w,\ T,\ P_\mathrm{F}) - R_\mathrm{r}\,(w,\ T) - R_\mathrm{sda}\,(w,\ T,\ P_\mathrm{F})$$

$$- F\,(w,\ T,\ P_\mathrm{F}) - U\,(w,\ T,\ P_\mathrm{F}),$$

where C is consumption, R_r is routine metabolic costs (including activity), R_sda is specific dynamic action, F is egestion, and U is excretion. These terms represent quantities of energy gained or lost and are defined by equations with up to 3 variables: fish weight (w), temperature (T), and feeding level (P_F), which is a proportion between 0 and 1. We solved for P_F based on our field estimates of C (see Appendix S1) and then used w, T, and P_F to calculate G for each fish. The complete set of model equations and parameters is in Rand et al. (1993).

We did not collect fish weights or diet samples in winter to protect spawning fish, so we could not model winter growth. However, many studies show that salmonids lose substantial energy throughout the spawning season (Hendry & Berg, 1999), though the amount varies across taxa (12–70%) (Hendry & Berg, 1999). Because the lack of energy gain rather than the amount of loss was more relevant to our hypothesis, we roughly characterized winter growth in Klamath redband trout based on estimates of mean spawning cost from other lake-dwelling *O. mykiss* (Rand et al., 1993). We divided that estimate (22.1% total loss of body weight) by the mean duration of winter tributary residence (87 days, $n = 13$ estimates with daily precision) to obtain average daily growth in winter. We assumed all fish that resided in tributary habitats in winter incurred this net spawning cost. Although we cannot be certain that spawning costs apply to every fish, all tagged fish that entered tributaries in winter were found at known spawning locations, suggesting that this assumption is reasonable for the dominant life history.

RESULTS

Habitat use and functionality

During summer, redband trout were generally restricted to perennially cool tributaries and springs of Upper Klamath Lake (Figure 2b). Mean body temperatures transmitted by radio tags during July through August were 14.6 °C (SD 3.5) or 7.6 °C (SD 3.6) cooler than the lake daily mean, suggesting that the tributaries provided critical thermal habitat in summer. However, in spring and fall, when temperatures in the lake and tributaries were similar, 90% and 70% of fish (i.e., 68 of 75 and 45 of 64), respectively, were detected in the lake (Figures 2b & 4a). Average differences between body and lake temperatures from March through May and October through November were within 1 °C of 0, indicating that
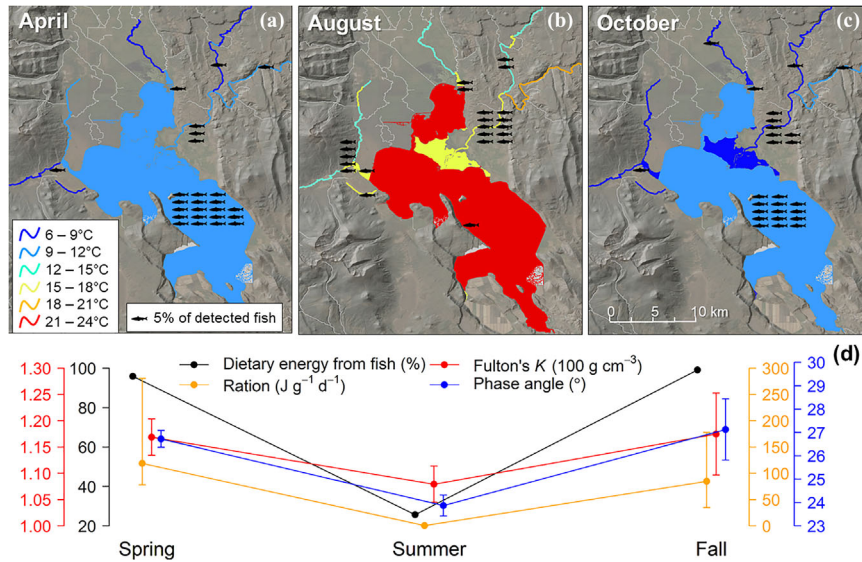
FIGURE 2   Map of the upper Klamath Basin with monthly mean water temperatures and redband trout habitat use during (a) April, (b) August, and (c) October, specified by the legend in panel (a). Representation of habitat units and resolution of habitat use corresponds to Figure 1. Location of fish icons in each habitat unit is arbitrary. Habitat use sums to >100% because some fish used multiple habitats in a month. (d) Patterns in foraging and energetic condition of redband trout in spring (in the lake), summer (in tributaries), and fall (in the lake). Each metric and its axis are coordinated by color as specified in the legend. For energetic condition metrics (K and phase angle), values expressed are mean (points) and normal 95% confidence intervals (bars). For right-skewed daily ration, a gamma distribution was used to estimate median and 95% confidence intervals (Armstrong & Schindler, 2011) after conversion of 0s to a trivial positive value. Dietary energy from fish represents the percentage of total dietary energy (summed across individuals) derived from forage fish. Sample sizes are in Table 1

temperature was not a primary driver of habitat use in spring and fall. Instead, gut contents indicated that redband trout used the lake as foraging grounds in these seasons, consuming primarily fish at rates typically exceeding 100 J•g⁻¹•day⁻¹ (Figure 2d). In contrast, most summer rations in tributary habitats were near or equal to 0 and contained primarily insects (Appendix S5). The differences in diet composition between the 2 habitat types amounted to a 35% discrepancy in energy density (lake: 5.1 kJ•g⁻¹ [SD 1.0]; tributaries: 3.3 kJ•g⁻¹ [SD 1.0]). Telemetry and diet data together suggested that in general, habitats served as either thermal refuges or foraging grounds but not both.

A second period of tributary use occurred during late fall through early spring, corresponding closely to basin-wide patterns of spawn timing (Appendix S6). Together, the primary seasonal patterns of habitat use we observed portrayed a biannual adfluvial (i.e., between lake and stream) migration (Figure 4a). At least 65% of tagged individuals exhibited this life history, migrating to the lake twice annually between periods of tributary residence for thermal refuge and spawning ($n = 46$ fish found alive in both periods of tributary use). Estimated migration distances to foraging habitats spanned up to 50 km from thermal refuges and 150 km from spawning grounds. Our telemetry methods were not intended to characterize movement rates, but our results provide some insights into what our focal populations are capable of. For example, 1 fish migrated over 125 km downstream from spawning grounds in the upper Sprague River in just 1 day. Five others navigated at least 10 km across the lake to locate thermal refuges or foraging grounds within a day. Fast, directed movement even permitted 6 fish to migrate among multiple thermal refuges, presumably enduring summer conditions in the lake for several kilometers. Additionally, we observed 96% fidelity to specific thermal refuges among fish observed for multiple summers ($n = 26$). Thus, it appears movement was driven by knowledge of the landscape rather than random search.
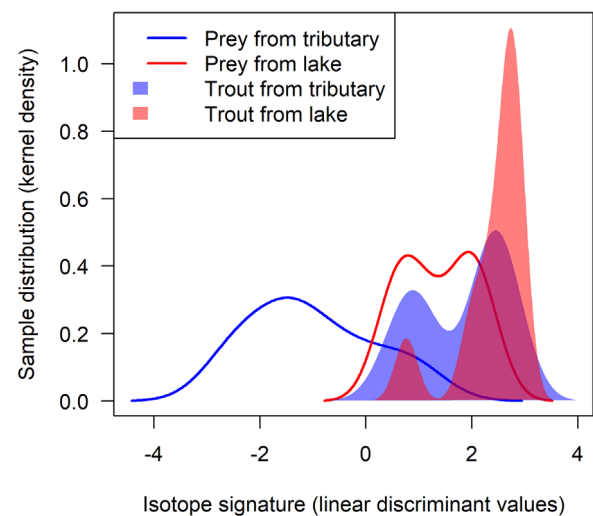

FIGURE 3   Comparison of distributions of isotopic signatures in tissue in redband trout (shading) and their prey (line) sampled in different habitats (red, warm Upper Klamath Lake; blue, cool Pelican Bay). The overall isotope signature of each sample (linear discriminant values, *x*-axis) is the sum of 5 isotope signatures (δ^{13}C values) for individual amino acids, each multiplied by a coefficient determined by linear discriminant analysis (valine 0.426, isoleucine −0.100, leucine 0.019, threonine −0.045, phenylalanine −0.033)

Energetic condition and growth

Empirical measures and modeling indicated that energy balance of redband trout fluctuated substantially between seasonal migration stages. Energy storage, indicated by K and phase angle, was higher in lake habitats during spring and fall and lower in thermal refuges during summer (Figure 2d). Isotopic signatures of the lake food web closely matched the signatures of all redband trout from both Upper Klamath Lake and Pelican Bay (Figure 3) (median posterior probability of lake

FIGURE 4 Complementary warm and cool habitat support for a migratory cold-water fish (redband trout): (a) biannual migrations between lake (red) and tributary (blue) habitat (arrows on outer ring, migration stages based on congruence among telemetry, diet sampling, and spawning surveys; shading, monthly habitat use expressed as a fraction from 0–1; red line, daily scope for growth in the lake based on water temperature expressed as percent body weight per day with negative values in summer equivalent to 0; habitat use may sum to >1 because some fish used multiple habitats in some months) and (b) predicted daily growth during each migration stage (mean and 95% CI) based on bioenergetics modeling in spring, summer, and fall, and estimated cost of spawning in migratory *O. mykiss* from another lake (Rand et al., 1993) in winter (red, seasonally warm lake habitat; blue, cool tributary habitat; sample sizes in Table 1)
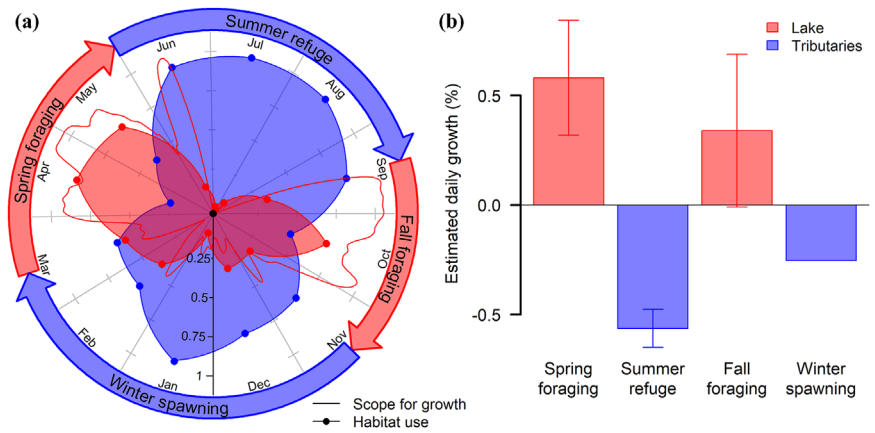
classification 0.99, both groups [minimum 0.75 and 0.71, respectively]). The retention of lake $\delta^{13}C$ signatures in trout sampled throughout the summer suggested that foraging in at least 1 primary thermal refuge was not enough to sustain somatic growth and tissue turnover. Estimates of model parameter P_F indicated that in terms of prey mass consumed, 35% of trout sampled in either spring or fall were feeding at or near their physiological limit (i.e., $P_F > 0.95$), compared with just 10% of trout sampled in summer. Similarly, 72% of trout sampled in summer were in or near a state of fasting (i.e., $P_F < 0.05$), compared with just 10% of trout sampled in spring or fall. Model estimates of growth confirmed that fish from all thermal refuges likely failed to meet basal energetic demands in summer. On average, fish gained weight during spring and fall residence in the lake and lost weight at similar rates in the tributaries during the following seasons (Figure 4b).

DISCUSSION

Based on patterns of water temperature and summer habitat use, existing climate adaptation frameworks would identify the cool tributaries of the UKB as climate refugia (Isaak et al., 2015), but would not place value on the seasonally warm habitat downstream. By incorporating additional complexities of seasonality, movement, and foraging, we found that these warm habitats—in addition to cool habitats—played an essential role in supporting thermoregulation of cold-water fish. Though unsuitable during summer, Upper Klamath Lake served as critical foraging habitat for redband trout populations during other seasons, particularly in spring and fall. Based on multiple empirical metrics (and the conservative assumption that spawning incurs a net energetic cost), we found that fish were in negative energy balance when residing in cool tributaries during summer and winter, but foraging in the lake allowed fish to offset these losses in the interceding seasons when conditions were favorable. Thus, foraging in seasonally warm habitat appears to fuel the migratory life history that in turn supports cold-water fisheries in this landscape of environmental extremes.

Our data empirically support the predicted importance of growth regimes because fish tracked peak physiological growth potential as they moved up and down the watershed over 3 seasons and derived even more growth from seasonally warm habitat than predicted by prior simulations (Armstrong et al., 2021). The latter observation is striking because in addition to reaching stressful temperatures, the warm habitat in our study system was distant from refuges and exhibited low oxygen and high alkalinity. Further, the warm habitat in our focal system offered a smaller physiological growth advantage in spring because the tributary habitats in our study were influenced by groundwater rather than snowmelt and did not become as suboptimally cool outside of summer. The fact that warm habitat provided an overwhelming majority of growth despite these additional constraints in the UKB suggests that reliance on warm productive habitat could be common in many other watersheds, particularly where seasonal foraging habitats are closer to refuges, less degraded, and more physiologically advantageous in cooler seasons. More work is needed to understand how realized growth regimes vary among basins and species, but there is accumulating evidence of seasonally warm habitats providing enough foraging opportunity for cold-water fishes to achieve their physiological growth potential (Katz et al., 2017; Kaylor et al., 2021; Lusardi et al., 2020).

Though a small number of studies have empirically shown cold-water fishes linking thermal refuge and foraging habitats (Brewitt et al., 2017; Guzzo et al., 2017; Petty et al., 2014), our empirical demonstration of landscape complementation occurred at a novel spatial and temporal scale. Most refuge studies have shown fish moving small distances to exploit fine-scale temperature variation, demonstrating how coarse-scale climate and riverscape information can overlook locally important habitats (Ebersole et al., 2001; Fullerton et al., 2018; Petty et al., 2012). In contrast, we found that fish can also exploit coarse-scale thermal features of the riverscape through long-distance seasonal migration. This demonstrates that warm habitats can be valuable for cold-water fish even if they lack fine-scale temperature variation and are distant from cooler habitats. In addition, riverscape ecology theory predicts that fish should move

multiple times per year to link foraging, spawning, and refuge habitat (Fausch et al., 2002), yet formally described life histories typically include just 1 migration to each habitat type annually (Arostegui & Quinn, 2019; Dodson et al., 2013; Thurow, 2016) (but see Hayes et al., 2011; Osterback et al., 2018). Within stratified lakes, there is some evidence that fish seeking summer refuge in the cool, deep middle of the lake migrate in spring and fall to seasonally warm foraging habitats near shore (although the fall migration may be influenced more by spawning than foraging [Guzzo et al., 2017]). The biannual migration between lake and stream that we documented may be widespread, but we know of no published examples prior to this study, despite the myriad ways in which salmonids are known to use lakes (Arostegui & Quinn, 2019). As climate warming makes unstratified lakes seasonally stressful for cold-water fish, this life history should be increasingly favored in other basins.

Large-bodied fish generally require larger, more energy-dense prey (such as forage fish) to grow and store energy (Keeley & Grant, 2001). The scarcity of such prey can constrain growth potential in headwater environments (Huntsman et al., 2016; Leeseberg & Keeley, 2014). Mounting evidence suggests that the piscivorous and downstream migratory behaviors that enable larger body sizes can be limited to genetically distinct ecotypes (Arostegui et al., 2019; Taylor et al., 2019; Wollebaek et al., 2018), which may be lost if they are confined within headwaters, where smaller resident ecotypes are likely better adapted to compete (Keeley et al., 2007). Thus, a diverse suite of habitats, including seasonally warm productive habitats in the downstream portions of aquatic systems, may be broadly important for long-term persistence of diverse life histories, including the large-bodied, migratory fish that support cold-water fisheries (Moyle et al., 2017). Declining body size is a major concern in fisheries worldwide (Audzijonyte et al., 2019; Ohlberger et al., 2019). By focusing on cool habitats upstream, climate adaptation may tend to overlook productive habitats downstream that are capable of provisioning large cold-water fish.

Although some populations of our focal species, *O. mykiss*, cope with high temperatures through physiological adaptations (Chen et al., 2015), the fish in our study behaviorally avoided high temperatures. There is increasing interest in the potential for movement to "behaviorally rescue" thermally sensitive animals from climate warming (Fey et al., 2019; Sears et al., 2011), and a new framework argues that the energetic costs of thermoregulation will ultimately mediate species viability (Fey et al., 2019). We demonstrated the energetic costs of thermoregulation; thermal refuges provided poor foraging and a decline in fish condition. However, we reached a different conclusion—the ability of animals to thermoregulate at seasonal time scales depends on their foraging opportunities in the seasons adjacent to heat stress. Animals, particularly fish, maintain excess digestive capacity that allows them to rapidly store energy and survive subsequent periods of negative energy balance (Armstrong & Schindler, 2011; McWilliams & Karasov, 2014). This adaptation is often thought of as a response to temporal variation in food abundance, such as resource pulses. However, for mobile animals, spatiotemporal variation in temperature may also drive pulses of energy gain as productive foraging habitats

transition through physiologically advantageous temperature ranges.

Efforts to identify climate refugia are tackling increasing ecological complexity by considering a broader suite of environmental variables (Lusardi et al., 2021) and organismal traits (Ebersole et al., 2020; Morelli et al., 2020; Troia et al., 2019), yet they often overlook the role of seasonal foraging habitat in the persistence of thermally sensitive animals in landscapes with environmental extremes. Productive downstream habitats that support seasonal foraging, such as lakes (our study), floodplains (Katz et al., 2017), and estuaries (Hayes et al., 2011), are typically more degraded and less protected than headwater streams due to historical patterns of human development. Current strategies for climate adaptation that focus on the hazard of summer temperatures tend to conclude that protecting and restoring headwater streams is the optimal way to use limited conservation resources. Yet in many watersheds, the greater room for improvement downstream could offer more return on investment toward conservation goals (e.g., Battin et al., 2007). Restoring access to rich seasonal foraging in downstream environments could promote species persistence by providing energy stores that are used later to support the critical refuge and spawning functions of less productive upstream reaches. Our results underscore the need to incorporate landscape complementation (Dunning et al., 1992) and seasonal interactions (O'Connor et al., 2014) in planning for climate adaptation. These considerations will be fundamental to understanding how ecosystems services such as fisheries for cold-water fish can be maintained within changing thermal landscapes.

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