Received: 15 December 2023 | Revised: 30 May 2024 | Accepted: 9 July 2024

DOI: 10.1002/wat2.1752

ADVANCED REVIEW

WIREs WATER WILEY

Food for fish: Challenges and opportunities for quantifying foodscapes in river networks

Valerie Ouellet[1,2] | **Aimee H. Fullerton**[3] | **Matt Kaylor**[4] | **Sean Naman**[5] | **Ryan Bellmore**[6] | **Jordan Rosenfeld**[7] | **Gabriel Rossi**[8] | **Seth White**[9] | **Suzanne Rhoades**[10] | **David A. Beauchamp**[11] | **Martin Liermann**[3] | **Peter Kiffney**[3] | **Beth Sanderson**[3]

[1]Integrated Statistics Contractor for National Oceanic and Atmospheric Administration, Northeast Fisheries Science Center, Orono, Maine, USA

[2]Atlantic Salmon Federation, Chamcook, New-Brunswick, Canada

[3]Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, USA

[4]Columbia River Inter-Tribal Fish Commission, Portland, Oregon, USA

[5]Fisheries and Oceans Canada, Freshwater Ecosystems Section, Cultus Lake, British Columbia, Canada

[6]US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Juneau, Alaska, USA

[7]BC Ministry of Water, Land, and, Resource Stewardship, Aquatic Science Section, and University of British Columbia Institute for the Oceans and Fisheries, Vancouver, British Columbia, Canada

[8]Department of Environmental Science, Policy, and Management, University of California at Berkeley, Berkeley, California, USA

[9]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[10]McBain Associates—Applied River Sciences, Arcata, California, USA

[11]U.S. Geological Survey, Western Fisheries Research Center, Seattle, Washington, USA

Correspondence
Valerie Ouellet, Integrated Statistics Contractor for National Oceanic and Atmospheric Administration, Northeast Fisheries Science Center, 17 Godfrey Drive, Orono, ME 04473, USA.
Email: vouellet@asf.ca

Aimee H. Fullerton, Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.
Email: aimee.fullerton@noaa.gov

Edited by: Wendy Jepson, Editor-in-Chief

Abstract

Riverine fishes face many challenges including habitat degradation and climate change, which alter the productivity of the riverscapes in which fish live, reproduce, and feed. Understanding the watershed portfolio of foraging and growth opportunities that sustain productive and resilient fish populations is important for prioritizing conservation and restoration. However, the spatiotemporal distribution and availability of fish food are poorly understood relative to other factors such as abiotic habitat quantity and quality (e.g., water temperature). In this paper, we build on the concept of "foodscapes," and describe three components of food for fish, including abundance, accessibility, and quality. We then discuss methodological advances to help address three key questions: (1) Why is food availability hard to estimate? (2) What are the consequences of uncertainty in food availability estimates? and (3) What approaches are available or emerging for quantifying food available to fish? To address the first question, we characterize data acquisition and

analytical challenges; for the second, we demonstrate the importance of evaluating and communicating potential consequences of uncertainty; and for the third, we posit opportunities for future work. Collectively, we highlight the need for greater appreciation of the role food plays in stream fish conservation, especially given its critical influence on responses to warming temperatures.

This article is categorized under:

Water and Life > Nature of Freshwater Ecosystems

Water and Life > Conservation, Management, and Awareness

Water and Life > Methods

KEYWORDS

food availability, growth, method, prey, production, salmon, synthesis

1 | INTRODUCTION

Individual growth is a critical life process influencing survival (Clark et al., 2016; Zabel & Achord, 2004), collectively shaping population dynamics, productivity, and resilience (Ahti et al., 2020; Korman et al., 2021; Peters, 1986). For riverine fishes and other aquatic organisms, growth is regulated by a complex suite of abiotic and biological attributes. Water temperature, in particular, has received significant attention and is commonly used to characterize habitat suitability and to predict climate change impacts; temperature effects on growth rates are well understood, and predictive temperature models are increasingly well developed (Barbarossa et al., 2021; Isaak et al., 2018; Isaak & Rieman, 2013). However, food availability and the energetic costs of acquiring food may be as important as temperature in governing growth rates (Beauchamp, 2009; Brett et al., 1969; Huey & Kingsolver, 2019; Railsback, 2022). In contrast to temperature and other abiotic attributes, understanding of the processes driving food availability across river networks and through time is not well-developed, and predictive models and heuristics are generally lacking. Consequently, food availability often receives less attention in management contexts (Naiman et al., 2012; Whitney et al., 2020; Wipfli & Baxter, 2010).

Relative to physical habitat and abiotic conditions in rivers, information about food availability is more difficult to collect, interpret, and predict (Rosenfeld et al., 2014; Weber et al., 2017). As a result, our understanding of spatial and temporal patterns of food resources in streams and rivers lags behind progress made in lake and marine ecosystems (Albouy et al., 2019; Peake et al., 2022; Simonis & Merz, 2019). It is unclear, even at a coarse scale, how food availability varies across river networks and through time (Rossi et al., 2024). Most studies have evaluated food variability only at discrete locations (but see Bellmore et al., 2013; Cross et al., 2013) and relatively small spatial scales (Heino et al., 2004). Furthermore, most studies only examine a short snapshot of food availability, generally during summer when stream flows are low and temperatures warm, overlooking seasonal variation that can be consequential to fish growth (Armstrong et al., 2021; Bacon et al., 2004). These limitations are often a consequence of the time and cost of collecting and processing samples at higher spatial and temporal resolution and scale, lack of standardized and comparable methodological approaches for collecting data, and a paucity of techniques for modeling the diverse ways that lotic consumers access prey across space and time.

The "foodscape" (Rossi et al., 2024) is a dynamic mosaic of linked habitats with different growth potential phenologies as seen through the eyes of mobile consumers that move among habitats and experience a shifting mosaic of food abundance, food accessibility, and physiological growth potential that together provide diverse foraging and growth opportunities across the landscape. Adopting a foodscape perspective when monitoring riverine ecosystems could promote better understanding of spatiotemporal patterns of food production for fish in rivers, what drives these patterns, and how they may change in the future. Embracing foodscape concepts can facilitate robust management and targeted conservation for threatened freshwater fishes (Strayer & Dudgeon, 2010).

Salmonids are an excellent model for understanding the complex effects of foodscapes on mobile stream consumers across different geographic regions (Muhlfeld et al., 2019). They are also widely distributed and occupy diverse habitats from headwaters to estuaries, tracking variable foraging opportunities and integrating across biophysical conditions to maximize growth. Understanding of how salmonids respond to their environments is relatively informed compared to other riverine fishes (Beauchamp, 2009; Brett et al., 1982; Rosenfeld et al., 2024; Zabel & Achord, 2004). However, the spatiotemporal availability of food has remained a critical but elusive element for evaluating salmonid growth potential

(Jensen et al., 2023; Thompson & Beauchamp, 2016), which is often estimated solely from water temperature and fish size (Bellmore, Fellman, et al., 2022; Rossi et al., 2024).

In our attempt to better understand the magnitude and variation of food availability for stream fishes, we elucidate three important components of food availability: food abundance (e.g., what is on display in the store window), food accessibility (e.g., the means for acquiring merchandize despite potential closures in the store, competition with other shoppers, concern about personal safety, and taxation), and food quality (e.g., the caloric and nutritional value of the purchase). The first two elements are key components described by Rossi et al. (2024), who also describe resource tracking (e.g., acquiring some goods from a local grocery store and others from the farmers market or big box chain to maximize food value at minimum cost) and physiological assimilation processes required for growth (e.g., health and genetic makeup of an individual that define its potential and realized growth). Here, we focus on abundance, accessibility, and additionally assert that food quality can play an important role (Figure 1).

Using this framework, we pose three key questions to ignite discussion about how best to collect, analyze, and use food availability information to improve conservation and management of lotic fishes: (1) Why is fish food availability hard to estimate? (2) What are the consequences of uncertainty in food availability estimates? And (3) What approaches are available for quantifying food availability? The first two questions characterize the challenges we face, and the third question identifies opportunities for addressing these challenges. Although we primarily draw examples from salmonids in North America, we suggest the take-home messages apply more broadly to other fish species and regions across the globe. We end with a synthesis of relevant future research directions.

2 | CONCEPTUAL FOUNDATION

Food availability can be defined as the proportion of food that foragers could potentially consume in a given habitat at a given time, as influenced by intrinsic and extrinsic biotic factors and abiotic factors that affect a fish's ability to detect,

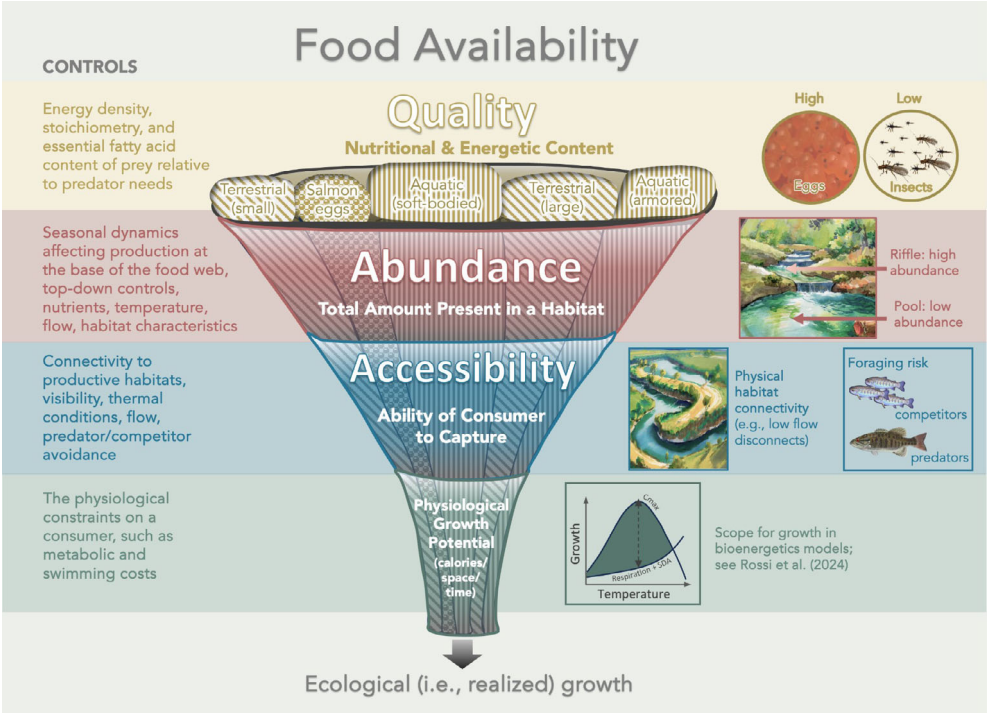


FIGURE 1 Food quality, abundance, and accessibility determine what food is available for fish to consume. For each element in the hierarchy of food availability, controlling factors are described along the left, and examples are illustrated along the right. The width of the hierarchy "funnel" illustrates the relative biomass available to fish as it passes through each filter. At the broadest level, abundance is set by food production, but what is ultimately assimilated by fish is filtered by how accessible food is to fish (reflecting foraging costs), and physiological constraints on the ecological growth, which is defined in foodscape models as the maximum growth rate a given consumer could achieve in a foraging patch as a function of food abundance, food accessibility, and physiological growth potential in space and time. Food quality broadly depends on its source and provenance, as illustrated with what is fed into the top of the funnel). *Source*: Adapted and expanded from elements in Rossi et al. (2024, fig. B1).

encounter, capture and assimilate said food (Rossi et al., 2024). Here, we focus on three important elements: (1) food abundance—the total amount of food present in a given habitat at a given time; (2) food accessibility—the ability of the consumer to encounter, capture, and consume food to gain energy despite foraging costs; and (3) food quality—the digestibility, energetic, and nutritional quality of food. Each of these elements varies through space and time across river networks (Box 1; Rossi et al., 2024; Wipfli & Baxter, 2010).

Some variability is broadly predictable over space and time (e.g., seasonality); however, variation in food availability at finer scales can be highly stochastic. Additionally, energy flow to fish in river networks arises from multiple pathways both within and outside streams, which vary in importance temporally and spatially (Wipfli & Baxter, 2010). Considering these different scales and sources of variability is paramount for quantifying food availability. Here, we briefly summarize factors that influence these three components of food availability, highlighting variability across scales. We focus on invertebrates as prey, but the discussion is also applicable to other food sources such as eggs or small fish. While the nature of some of these processes is well understood, others remain speculative, and few examples from empirical studies exist. It is our hope that highlighting this knowledge gap and its consequences spurs the additional work needed to comprehensively synthesize how these processes are influenced by anthropogenic impacts, including pollution, contaminants, and climate change.

2.1 | Food abundance

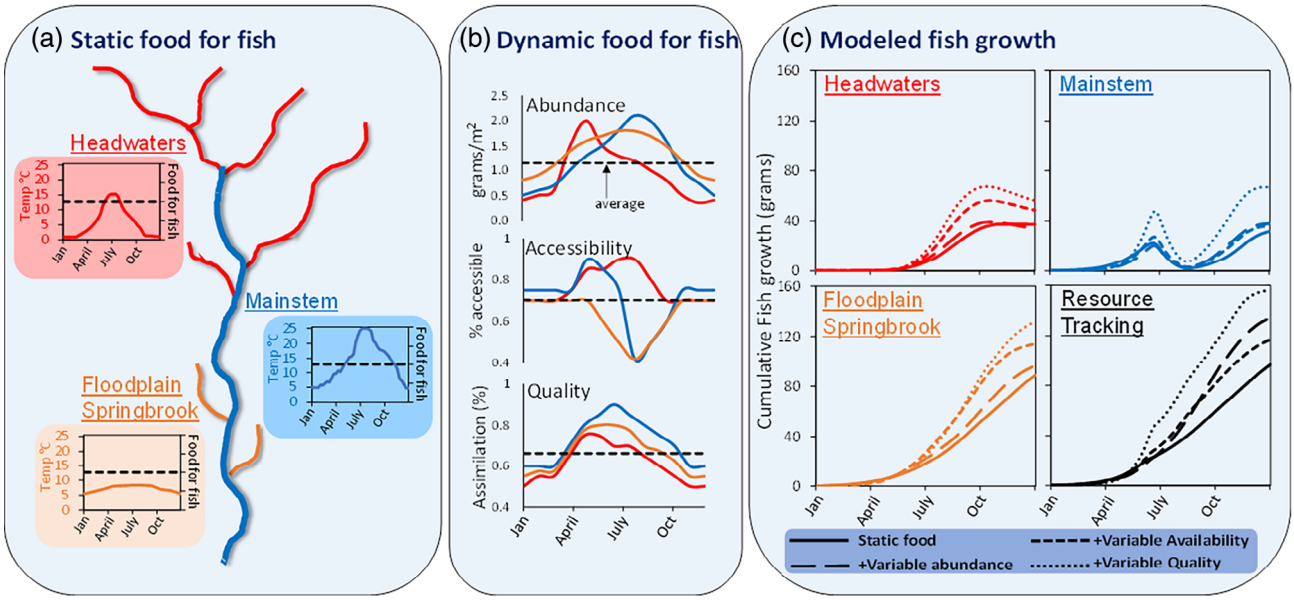
The abundance of food for fish is driven by in situ production rates as well as the timing, magnitude, and duration of resource subsidies, that is, food that is supplied from terrestrial, upstream, and marine sources (Wipfli & Baxter, 2010). At the broadest spatial scale, food abundance is expected to vary throughout river networks in somewhat predictable ways, tracking both in situ primary production and subsidies (Power et al., 2008). Seasonal and diel fluctuations in temperature and light drive variability in invertebrate production and behavior (Bishop, 1969; Nakano et al., 1999), and the river continuum concept (Vannote & Sweeney, 1980) predicts a general downstream increase in in situ production in more sunlit mainstem and floodplain habitats relative to narrow, shaded upstream headwaters where terrestrially-derived food can dominate (Nakano & Murakami, 2001). Spatial and temporal trends in prey abundance are driven by nutrient availability (N, P) (LaPerriere et al., 1983), which often limits primary production at the base of food webs (algae, macrophytes, and heterotrophic microbes), and is influenced by anthropogenic inputs (e.g., fertilizer), underlying geology, biotic contributions (e.g., nitrogen fixers such as alder) and in-stream cycling (Newbold et al., 1981). Primary production then facilitates productive riverine invertebrate communities, depending on its edibility, nutrient content, and assemblage structure (Lusardi et al., 2018; Power et al., 2008).

At smaller channel units or microhabitat scales, food abundance can vary considerably with substrate, velocity, depth, and structural complexity (Scholl et al., 2022). For example, Huryn (1996) reported five times greater benthic invertebrate production in areas with complex structural elements like wood relative to simplified and more easily mobilized sand substrate. Similarly, numerous studies demonstrate higher abundance of macroinvertebrates in riffles relative to pools (Herbst et al., 2018; Naman et al., 2017), and in off-channel wetlands relative to river mainstems (Bellmore et al., 2012). These observations suggest food abundance is frequently greater in some locations than in others (Fausch, 1984). Prey abundance also tends to be elevated in stream reaches with coarser unembedded substrate that provides moderately stable and abundant interstitial habitat (Scholl et al., 2022).

Investigations into discontinuities in river networks and abrupt changes in river network conditions and geomorphic processes (Benda et al., 2004; Montgomery, 1999) lead to the general prediction that productivity "hotspots" arise in areas of higher physical and biogeochemical complexity, such as tributary junctions and floodplains (Bellmore et al., 2012; Benda et al., 2004; Brewitt et al., 2017; Kiffney et al., 2006). Production hot spots in rivers (e.g., riffles), may differ from places where accessibility and settling of food are highest (e.g., pools) due to riverine hydraulics, and can occur from meso to microhabitat scales (Brewitt et al., 2017). The hydraulic-driven processes of deposition, concentration, and storage of organic matter can be primary drivers of spatial variation in food abundance (Bakun & Csirke, 1998; Humphries et al., 2020). Transitions in velocity (heads of pools, stream margins) may concentrate prey at low flows (Anderson et al., 2013) or the head of pool units (Hayes, Goodwin, et al., 2019).

Variation in food abundance from subsidies is also somewhat predictable over broad temporal scales. For example, seasonal cycles of temperature and sunlight in temperate regions drive relatively predictable fluctuations in terrestrial invertebrate subsidies from adjacent riparian vegetation (Marcarelli et al., 2020; Nakano & Murakami, 2001). Other resource subsidies like anadromous salmon spawning events have distinct seasonal components that provide key

BOX 1 The foodscape concept: riverscape heterogeneity promotes spatial and temporal variation in food availability



A main tenant of the foodscape concept is that riverscape heterogeneity promotes spatial and temporal variation in food availability, which in turn, promotes the growth of mobile fish consumers that can track foraging and growth opportunities as they shift across space and through time (Rossi et al., 2024). Many fish growth studies, however, implicitly assume that food availability is static across space, through time, or both (Panel A) and that difference in fish growth between habitats (e.g., headwaters, mainstems, floodplains) is solely a function of variation in water temperature (Panel A; Falke et al., 2019)—a variable that is relatively easy to monitor and is becoming widely available (Armstrong et al., 2021). Although water temperature directly influences growth and sets the maximum growth rates of fishes, the extent to which this maximum potential is realized is controlled by the quantity and quality of food consumed—which changes through time (Panel B). A growing number of studies suggest that food abundance, accessibility, and quality exhibit distinct seasonal cycles across heterogeneous river networks and collectively shape food availability. Not accounting for this spatiotemporal resource variation could result in inaccurate annual fish growth predictions for fish residing in different habitats, and especially for fish that move among habitats to maximize growth (Panel C).

We modeled juvenile salmonids growth in three different watershed locations (headwaters, mainstem, and floodplain) over a 1-year period. We first simulated growth assuming that food quantity and quality were static through time; that is, where simulated growth differences between habitats were solely affected by variation in thermal regimes (Panel A). For the static scenario, values of food abundance, accessibility, and quality were set at the global average of the dynamic food values presented in Panel B (the average is represented by dotted black lines). We then explored how seasonal variation in food abundance, food accessibility (proportion of food available to fish), and food quality (food assimilation efficiency) affected fish growth (see Figure 1), with each of these three components being iteratively added to the model analysis. Food variation substantially impacted simulated fish growth relative to static food assumptions, with cumulative effects observed as each component of food variation was added to the simulation (Panel C). Growth after 1 year was up to 100% greater in simulations that accounted for food resource variation. We also modeled how food variation impacts the growth of mobile fishes that track favorable foraging conditions as they shift through time across the landscape ("resource tracking" graph in Panel C). Seasonal variation in food resources had similar impacts on the annual growth of these mobile consumers.

Food abundance (α_t), food accessibility (δ_t), and food quality (ε_t) were used to model total energy assimilation on a daily timestep (t), as follows:

$$assimilation(t) = C\max_t \times \left(\frac{a_t\delta_t}{a_t\delta_t + k}\right) \times \varepsilon_t$$

where $C\max_t$ is the theoretical maximum rate of food consumption, and is a density-dependent food-availability half-saturation value (value at which consumption is half the theoretical maximum value). $C\max_t$ was calculated using the Wisconsin Bioenergetic model (Deslauriers et al., 2017; Hanson et al., 1997) parameterized for rainbow trout (*Oncorhynchus mykiss*). Fish growth was calculated at each time step by subtracting energy costs (respiration and specific dynamic action) from food assimilation. Values of food abundance, availability, and quality (Panel B) were synthesized to illustrate how spatiotemporal variation in food resources can affect fish growth. Although it would have been ideal to use empirical estimates, studies have yet to quantify the temporal dynamics of these different facets of food quantity and quality (Rossi et al., 2024). Thus, we made informed guesses about when and where food availability would be high or low. Both the static and variable food scenarios assumed an equal total amount of food.

energy inputs into streams that can comprise most of the annual energy budget for resident consumers in systems with sufficient run sizes (Schindler et al., 2008).

Finer scale temporal variability (e.g., diel fluctuations) in food abundance is also common. For example, invertebrate drift can be orders of magnitude higher at night and during crepuscular periods (Bishop, 1969). Decreasing flow along a receding hydrograph or increasing flow following spates can affect temporal concentrations of suspended invertebrates (Kennedy et al., 2016). Increasing flows may effectively dilute (Hayes, Moreira, et al., 2019; Naman et al., 2016) or conversely increase invertebrate drift (Naman et al., 2016), depending on invertebrate responses to changing hydraulics. Despite this complexity, most observations suggest seasonal declines in drift concentration with flow (Rashidabadi et al., 2022), reducing food availability during summer (Rosenfeld & Ptolemy, 2012; Rossi et al., 2021). Conversely, high flows may expand the resource-shed (Power & Rainey, 2000), the geographic extent over which invertebrates contribute to fish diets, by reconnecting habitats and transporting resources farther. Downstream fluxes may support drift feeding fishes by incorporating prey from a greater diversity of habitats (FitzGerald et al., 2023; Power & Rainey, 2000).

Disturbance and stochasticity are defining features of river ecosystems (Lake, 2000) and drive large and often unpredictable fluctuations in food abundance (FitzGerald et al., 2023). For example, short-term events in terrestrial riparian ecosystems, such as windstorms and high overland flows, can deliver pulses of terrestrial invertebrates to streams (Epele et al., 2021; Šabacká et al., 2012). Similarly, substrate disturbance from small storm events, landslides, or animal activity can temporarily elevate invertebrate drift and/or dislodge eggs from the substrate (Dewson et al., 2007; Moore et al., 2008).

2.2 | Food accessibility

Only a limited proportion of total prey energy is available to fish because numerous abiotic and biotic factors limit the ability of consumers to exploit food. Temperature, stream flow, velocity, visibility, and habitat structure are the primary abiotic determinants of prey accessibility in riverine networks, imposing key limitations on the ability of fish to encounter, capture, and consume food. Temperature imposes key physiological constraints on the amount of food fish can consume and assimilate, with consumption rates increasing alongside temperature to a threshold where sublethal and lethal effects occur (Brett et al., 1969). Variation in temperature across river networks is therefore a filter on the amount of food that can be consumed, and it can also influence access to productive foraging habitats via effects on swimming performance and aerobic capacity.

Flow also influences prey accessibility. First, hydraulic forces like velocity and turbulence impose constraints on the energy fish spend to encounter and capture prey (Hughes & Dill, 1990), rendering food inaccessible when water velocities exceed swimming abilities (Rosenfeld et al., 2007; Rosenfeld et al., 2024). Second, fluctuations in flow can alter foraging behaviors as fish respond to flow-induced changes in prey abundance (Caldwell et al., 2018; Rossi et al., 2021). Finally, flow fluctuations mediate access to seasonally disconnected off-channel habitats, floodplains, and ephemeral streams, where high prey abundance, lower velocities, and more optimal thermal conditions can fuel rapid growth (Jeffres et al., 2020).

Other abiotic determinants of prey accessibility also warrant consideration. Light and turbidity influence prey detectability (Fiksen et al., 2002; Young et al., 1997). Oxygen and other water quality attributes can act in a similar

manner as high temperatures and render foraging habitats inhospitable. Structural habitat complexity can both facilitate and constrain food accessibility; for example, flow obstructions can create favorable hydraulics for drift-foraging in otherwise harsh conditions (Shearer et al., 2015), but also create prey refuges that limit capture efficiency (Crowder & Cooper, 1982).

Food accessibility is also determined by an array of biological processes. Adaptive behaviors protect prey from fish predators (e.g., reduced diurnal activity to avoid visual hunters; Douglas et al., 1994; Peckarsky & McIntosh, 1998), but fish can adapt to accommodate shifts in prey composition (e.g., during adult insect emergence events; Wesner, 2016). Some invertebrate taxa such as case-making caddisflies have structural defenses that reduce their vulnerability to predation (Wootton et al., 1996). Even without structural defenses, some taxa may provide poor quality food as they remain mostly undigested (e.g., mud snails; Bruce et al., 2009; Vinson & Baker, 2008). As well, fish must be on the lookout for their own aquatic and terrestrial predators, balancing the benefits of foraging (net gain of energy to allocate toward growth and reproduction) with the risk of mortality from predators and environmental factors like flow (Railsback et al., 2005; Rossi et al., 2024; Werner & Gilliam, 2008). This effectively limits fish from accessing food in riskier areas and during riskier times (Metcalfe et al., 1999; Walters & Juanes, 1993). Finally, competitive interactions between conspecifics and other fish consumers can limit food accessibility (Giannico & Healey, 1999). As a result, food availability exerts control on consumer production, but competitive interactions shape how this production is distributed among consumers. For example, a given level of prey availability could support a corresponding amount of production represented by a few larger individuals (e.g., older age class) or a greater number of smaller individuals (e.g., cohorts).

Food accessibility may be broadly driven by water temperature and hydraulic geometry across river networks. For example, constraints on food accessibility from high temperatures likely occur more often in downstream habitats and from ice in small streams at high elevations. Hydraulic constraints on food accessibility may generally track longitudinal patterns in hydraulic geometry (Laliberte et al., 2016; Leopold & Maddock, 1953). Accessibility patterns are sensitive to habitat complexity, riverscape discontinuities (Benda et al., 2004), and altered geomorphology and flow regimes arising from anthropogenic river management. Temperature and hydraulics also show predictable seasonal variation, with consequences for prey accessibility. By contrast, generalizable temporal predictions are more difficult because biotic influences on food accessibility vary temporally through river networks. Diel fluctuations in light may be the clearest indicator of risk (for both fish and their food), but how that risk is balanced against foraging benefits can vary with temperature, food abundance, energetic state, and body size (Metcalfe et al., 1999; Reinhardt & Healey, 1999). Among well-connected habitats and over seasonal timescales, the concentration of invertebrate drift may track temporal patterns of benthic invertebrate density, but with high variation among taxa nested within this broader pattern (Kennedy et al., 2016). Stochastic influences on food accessibility may also be driven by episodic events such as rapid changes in flow that connect or disconnect foraging habitats (Heim et al., 2019; Huntsman & Falke, 2019; Limm & Marchetti, 2009), or rapid changes in conditions that influence predation risk (e.g., water clarity, predator density; Pinto et al., 2013).

Food assimilation, or consumption of accessible prey, is a natural extension of food accessibility. Realized prey consumption relies on the detectable encounter and successful ingestion of prey. For drifting invertebrates with limited mobility, capture success by fishes and other larger drift-foraging predators upon encounter can approach 100% at low velocities, whereas capture success could be considerably lower at higher velocities (Hill & Grossman, 2010) and turbidity levels (e.g., Zamor & Grossman, 2007). We refer readers to Rossi et al. (2024) for a fuller discussion of the physiological consequences of prey assimilation on individual fish growth, and how resource tracking by mobile consumers can lead to population-level consequences.

2.3 | Food quality

The food that fish encounter in rivers varies considerably in energy and nutrient content. The biomass, digestibility, and energy density of individuals vary widely among taxa (Cummins & Wycheck, 1971). For example, salmon eggs are energy-rich with 2–4 times greater energy content per unit mass than common aquatic invertebrates. There is growing appreciation for the importance of attributes of food beyond digestibility and energy content, including elemental composition (i.e., stoichiometry) and biochemical constituents such as fatty acids (Twining et al., 2016). For example, certain long-chain polyunsaturated fatty acids (PUFAs) are essential for physiological functions but are not found in similar concentrations across prey types (Guo et al., 2017). Arguably, food quality may be equally important to quantity as a dimension of food availability, and it is therefore important to understand how it varies in river networks.

Although assimilable energy varies among prey taxa, size distributions of prey relate to their taxonomic composition and seasonal phenology, which may be broadly predictable (Metcalfe et al., 2002; Myrvold & Kennedy, 2020). Prey communities and size distributions differ across ecosystems; for example, invertebrates consumed by salmonids in streams are generally larger than those in lakes and floodplains (Dodrill et al., 2021; Jeffres et al., 2020; Keeley & Grant, 2001). However, at finer scales prey size distributions are often highly skewed toward smaller taxa (Neuswanger et al., 2022). This may partially reflect bias stemming from processing invertebrate samples (Dodrill et al., 2016), but also suggests that encounters with larger prey are less common and more stochastic (Dodrill et al., 2016; Hayes et al., 2000). Yet, body mass scales non-linearly with length (Sabo et al., 2002), such that the contributions of larger prey items to fish energy intake can be disproportionately high relative to their abundance. Consequently, the energetics of foraging should favor selection of larger prey items since consuming an equivalent biomass of smaller individuals requires increased time and energy spent. For example, by modeling shifts in the distribution of prey size toward larger individuals without changing biomass, Dodrill et al. (2016) demonstrated the potential for prey size to limit rainbow trout growth and maximum size. Alternately, small prey such as midges and mayflies can turn over rapidly (Huryn & Wallace, 2000), sometimes supporting most fish production (Bellmore et al., 2013), especially for juvenile or smaller bodied, gape-limited fishes (FitzGerald et al., 2023).

The origin of prey can yield vastly different nutritional quality as food resources. The energetic quality of food (i.e., caloric value) generally declines with water content, and increases with the digestible fraction of tissues (e.g., excluding shell or exoskeleton), life stage, and mass of prey taxa. Adult aquatic and all terrestrial insects contain much less water than immature aquatic insects, resulting in manyfold higher energy density (Cummins & Wycheck, 1971). Thus, there is an underlying value of aquatic insect hatches and terrestrial insect subsidies, as these preys can provide more energy than larval aquatic insects of similar mass (Back & King, 2013; Parmar et al., 2022).

More subtle but nonetheless consequential attributes of food quality may be strongly linked to resource subsidy pathways. Food from aquatic-derived carbon contains essential PUFAs that are not available from terrestrial sources, and may limit riverine consumers (Brett et al., 2017; Závorka et al., 2021). Variation in the availability of these PUFAs may track spatial and seasonal trends in in situ productivity. Other pulsed subsidies, such as marine-derived salmon carcasses and eggs that result in increased growth of juvenile salmonids (FitzGerald et al., 2023; Kaylor et al., 2019) may contribute similar nutritional benefits and are broadly predictable in time and space (Gende et al., 2004).

Taken together, this suggests that it may be possible to coarsely approximate food quality based on knowledge of prey taxa composition and resource subsidy dynamics across a river network. Accounting for food quality (e.g., energy or lipid content) as well as the energetic costs of acquiring prey (i.e., Net Energy Intake) is one way to generate a more accurate estimate of energy availability than total prey abundance. However, true availability should also account for predation risk in food acquisition; this remains a challenge, and while risk is incorporated into some bioenergetic drift-foraging models (e.g., InSTREAM; Railsback et al., 2021), it is complex to parameterize and not universally implemented. Moreover, our understanding of how food quality varies at finer spatial and temporal scales and alongside environmental attributes such as temperature, nutrients, and flow remains rudimentary at best.

2.4 | Toward an integrated perspective on food availability

The constituent factors of food availability, together with the metabolic costs of acquiring and assimilating food are primary drivers of growth potential for fish (Fausch, 1984; Rossi et al., 2024; Warren & Davis, 1967). Dynamic changes in food abundance, accessibility (including foraging costs), and quality collectively create a foodscape that describes the variation in the growth of mobile consumers across riverscapes (Rossi et al., 2024). The foodscape concept encourages ecologists and resource managers to measure and model factors that drive food availability, and ultimately consumer growth potential, at spatiotemporal scales that match the life history of mobile consumers in river networks (Rossi et al., 2024).

Food *availability* is an emergent property of food abundance, accessibility, and quality, all of which are subject to stochasticity and interact in complex ways; for example, the heterogeneity of aquatic habitats may simultaneously increase opportunities for foraging and growth but reduce accessibility by providing predation refuges for different prey items (Bellmore et al., 2015; Williams et al., 1993). The dominant role of stochastic variation also implies that quantifying variance is as important as characterizing the mean (e.g., Jensen's inequality; Bernhardt, Sunday, et al., 2018). For example, some fish adaptively move throughout river networks to exploit variability in abundance, accessibility, and quality (Armstrong et al., 2010; Gowan & Fausch, 2002). In addition, clarifying the role of prey quantity vs. quality also

remains a critical uncertainty. Consequently, the role of prey quality for wild fish remains poorly understood. There may also be nuanced ways that nutritional diet composition influences fish performance; for example, research on other consumers (including humans) has suggested that eating a diversity of foods, including some that are perceived as low quality, could be beneficial for individual fitness and population stability (Provenza et al., 2021). This is poorly understood in wild fish and warrants future attention.

To operationalize this integrated perspective on food availability will require methods to estimate watershed-scale food availability. Collectively, the unknowns surrounding prey variability and quality challenge efforts to quantify and predict food for fish. In Sections 3 and 4, we summarize the key challenges in understanding what drives uncertainty around food available to fish and practical consequences of this uncertainty. In Section 5, we identify opportunities for better empirical assessment of food availability, the use of proxies to generate predictive models of potential food availability, and more effectively communicating potential effects of uncertainty in food availability. But first, we briefly consider how food availability may influence populations.

2.5 | Population level consequences of food availability

Although this review focuses on characterizing the nature and drivers of variation in prey availability in streams, predicting consequences for fish populations is an obvious applied extension. Scaling up individual-level mechanisms to population-level consequences is a formidable challenge for any environmental driver (e.g., temperature; Chevalier et al., 2022; Ficke et al., 2007; Savage et al., 2004), and linking food availability to population outcomes involves multiple assumptions that are often difficult to validate. These include assumptions that increased food translates to individual growth, that increased growth translates into increased survival and/or reproductive success (i.e., larger fish are better able to avoid predation), and that other factors are not more limiting than food availability. Nevertheless, because growth and consumption are commonly below satiation for many riverine fishes in the wild (Armstrong & Schindler, 2011; McCarthy et al., 2009), it is reasonable to infer that increased food should generally increase growth and survival in many ecological contexts.

However, population dynamics often exhibit emergent complexity associated with stage-specific habitat bottlenecks, compensatory density-dependence, and metapopulation dynamics that can dampen or amplify realized population outcomes relative to simplistic assumptions based on individual responses (Rose et al., 2001; Sirot et al., 2015; Wilson et al., 2023). Thus, not all food availability scenarios will have equal population-level consequences. Co-limitation by multiple factors (e.g., habitat and food) is common, and in scenarios where habitat for an early life stage is severely limiting (e.g., minimal spawning habitat) the population-level consequences of increased prey may be limited. However, food limitation is arguably unique because increases in individual growth often translate into elevated survival even under habitat limitation, which propagates to later life stages and can result in increased population size or stability (Rosenfeld & Hatfield, 2006); this will be true for increased growth and survival of individuals before or after any habitat bottleneck. While the relationship between food and population performance likely follows a saturating function, food effects will ultimately be mediated by other limiting factors, such as suitable spawning habitat or marine survival for anadromous fishes.

We can envision different scenarios where food availability is likely or unlikely to benefit populations. Conditions when food is likely to matter for populations include: (1) when habitat is sufficient but food resources are limiting due to low production (e.g., oligotrophic systems); and (2) when fish are abundant and per-capita food resources are limited due to high density-dependence. Food is less likely to matter for populations when factors such as low habitat availability, high temperatures, or stressful biological interactions are more limiting than food resources. High food levels may even be associated with negative population-level impacts when generated by drivers like eutrophication that create hypoxic conditions. In addition, food availability may have different population level consequences in different life stages. For instance, food supplementation may accrue minor benefits for a 2-year-old fish that is already large enough to avoid predation, whereas increased food may allow age-0 fish to grow large enough to avoid mortality by gape-limited predators. In this case, food supplementation for age-0 fish should convey larger population benefits than food supplementation for older fish would.

Despite this complexity, population effects of changes in prey can be measured or modeled. For instance, measures of prey abundance (e.g., invertebrate drift or secondary production) can be multiplied by stream discharge or habitat area to describe population-level prey availability (i.e., Bellmore et al., 2013; Naman et al., 2018). Empirical correlations between prey flux and fish density or biomass could then reflect the influence of food at the population level

(Jowett, 1992). Ecosystem ecologists have also long used estimates of prey production combined with eco-trophic efficiencies to estimate production of higher trophic levels (Lindeman, 1942), with many examples for stream fish populations (e.g., Bellmore et al., 2013; Poff & Huryn, 1998). For instance, drift-foraging models that estimate net energy intake (e.g., Naman et al., 2020) and in some cases growth can also be applied to predict fish densities based on the total area of energetically suitable microhabitats, which can be used to infer carrying capacity (e.g., Hayes et al., 2007; Wall et al., 2016) linked to dynamic population-scale life cycle models (e.g., McHugh et al., 2017). Individual-based models that account for prey effects on fish growth across life stages (e.g., InSTREAM; Ayllón et al., 2019; Railsback et al., 2021) provide a more formal framework for integrating changes in prey abundance into population-level effects. To fully address population consequences of food availability, practitioners should consider how density-dependence, habitat capacity and mortality risk change temporally across the foodscape. A comprehensive exploration of food-population linkages is beyond the scope of this review, but are fertile ground for future investigations.

3 | WHY IS FOOD AVAILABILITY HARD TO ESTIMATE?

To improve our ability to accurately characterize food available for stream salmonids, we need to better understand what controls prey variability and how these controls are nested across spatial and temporal scales (Neuswanger et al., 2022; Table 1). Although space and time are fundamentally linked, we explore these elements separately below.

Estimating variability in food availability at multiple spatial and temporal scales is logistically challenging (Heino et al., 2004). This has been exacerbated, in part, by studies more commonly targeting the assessment of invertebrate community structure and stream productivity rather than an explicit focus on food for fish. Consequently, fish ecologists have adopted sampling approaches that may be less suited for estimating resource availability for fish, and face uncertainty in translating these metrics (i.e., indices of biological integrity, IBI) into consumption, growth, or proxy indices of prey quality. Approaches for estimating aquatic invertebrate abundance and production typically use methods that only sample a small fraction (generally <1%) of habitat, such as with benthic samplers (e.g., Surber sampler) and drift nets. These sampling devices can be inefficient in river sections that are very slow (<0.1 m/s), very fast (>1–2 m/s), deep (>1 m), or structurally complex (Baxter et al., 2017; Rosenfeld & Naman, 2019). Although these approaches have been successful in estimating food availability at small spatial and short temporal scales, they are not as appropriate for empirically evaluating resource availability over longer time scales for mobile consumers that forage widely throughout river networks. In this case, errors associated with samples collected over very small spatiotemporal scales may become large when extrapolated over the much larger foraging areas used by fish across different months and seasons (Table 1). Due to the intensive nature of collecting and processing traditional drift and benthic samples, in

TABLE 1 Hypothesized types of uncertainty contributing to the relative variation in prey abundance among ecosystems, including stochastic variation, sampling (observation) error, and translation of sampled prey to prey availability.

		(1) Stochastic variation			(2) Sampling error		(3) Prey availability	
	Habitat heterogeneity (complexity)	Flow	Wind	Waves	Temporal sampling error variation	Spatial sampling error variation	Remote sensing potential for prey	Confidence in estimates of prey availability
Freshwater								
Streams	High	High	Low	Low	High	High	Low	Medium
Lakes	Low/medium	Medium	High	High	Medium	High	Medium	High
Estuaries	High	High	Medium	Medium	High	High	Medium	Low/Medium
Marine								
Nearshore	Medium	Medium	High	High	Medium	Medium	Low	Medium
Pelagic	Low	Low	High	Medium	Low	Medium	High	Medium

Note: Each cell indicates the relative level of variation from low to high.

most cases, it would be prohibitively expensive and time-consuming to collect and process the samples required to adequately resolve these issues of scale for entire watersheds.

Response metrics (e.g., biomass, counts, IBI scores) vary across studies; thus, the transferability of results is unclear, and few generalizable proxies for food availability have been developed. Cross-system comparisons are further challenged by differences in the dominant factors limiting food production and availability (e.g., aspect, geology, vegetation), even among adjacent watersheds sharing many abiotic and biotic features. In lentic and marine environments, remote-sensing approaches exist for estimating primary production, and by extension, zooplankton production over broad spatial extents (Platt & Sathyendranath, 1988), but such broad-scale approaches are both rare and complex in lotic systems due to the unidirectional movement of water, channel complexity, and the difficulty of remote sensing in small streams covered by riparian forests.

Quantifying annual, seasonal, or daily estimates of food availability may obscure important episodic pulses in food subsidies (Armstrong et al., 2013; Bellmore, Fellman, et al., 2022; Rossi et al., 2024) that play a key role in the growth and survival of individuals, particularly sub-dominant fish whose survival may be highly dependent on resource pulses (Bailey & Moore, 2020). Ephemeral spikes in food abundance that are crucial for getting fish through lean periods may be hard to detect with traditional sampling approaches, but may become increasingly important to population dynamics in a changing climate as warmer temperatures drive higher energetic demand for food (Neubauer & Andersen, 2019; Wood & McDonald, 1997). Fish spawning windows provide pulsed subsidies of eggs, which are nutritionally rich but only present for a short duration. Traditional low-frequency sampling approaches are likely to miss these important events. Moreover, because salmonids are mobile and use a variety of habitats that shift through ontogeny, understanding resource availability requires understanding the portfolio of resource cycles that support fish in different habitats, including headwaters, tributaries, mainstems, and floodplains (Figure 2; Rossi et al., 2024). The ability to accurately sample prey differs across these habitats; it is easier to frequently sample wadeable streams compared to larger mainstems. Furthermore, many habitats are in remote locations that make repeat sampling intractable.

4 | WHAT ARE POTENTIAL CONSEQUENCES OF UNCERTAINTY IN FOOD AVAILABILITY ESTIMATES?

Practitioners need information about how environmental change and management interventions affect food available to fish to make robust management decisions. This is underscored by strategies such as the Glen Canyon Dam Adaptive Management Program on the Colorado River that explicitly supported incorporation of food production and availability into management decisions, which was supported by large-scale experiments to probe uncertainty with respect to the foodscape responses and fish population linkages (including salmonids) (Cross et al., 2011; Deemer et al., 2022). Although the role of physical habitat in driving salmonid abundance is sufficiently well understood to meaningfully influence habitat management (Jorgensen et al., 2021), the equally important role of prey availability is not at the same level of empirical maturity to support informed management interventions. Below, we discuss challenges that assessments naive to food availability create for scientific understanding and effective management.

Recent advances in energetic and individual-based modeling have opened new frontiers for characterizing watershed-scale growth potential and climate impacts (Fullerton et al., 2022; Kaylor et al., 2021; Rosenberger et al., 2015). Yet these approaches have been primarily driven by advances in water temperature modeling, with limited characterization of food. For example, bioenergetics models have been used extensively to characterize growth and consumption rates (Falke et al., 2019; Sethi et al., 2022; Thompson & Beauchamp, 2016). Food availability and quality (energy density) are key parameters in these models, in addition to water temperature and fish size (Beauchamp, 2009; Railsback et al., 2021; Railsback & Harvey, 2011). Yet, for many bioenergetic model applications, food availability data are unavailable, and models resort to simple assumptions, for example, that food is of constant quantity and quality (Bellmore, Sergeant, et al., 2022; Fullerton et al., 2022; Railsback et al., 2021). Assessments such as climate-envelope or habitat reintroduction scenarios cannot predict future growth performance or fish distributions (Jensen et al., 2023) without considering how these may be mediated by food availability (Ayllón et al., 2019). Growth and its drivers can offer considerable insight into population dynamics of salmonids because size-selective mortality can play a significant role in regulating populations at multiple life stages, and growth performance at an earlier life stage can strongly influence survival in subsequent freshwater and marine life stages (Duffy & Beauchamp, 2011; Korman et al., 2021; Thompson & Beauchamp, 2014).

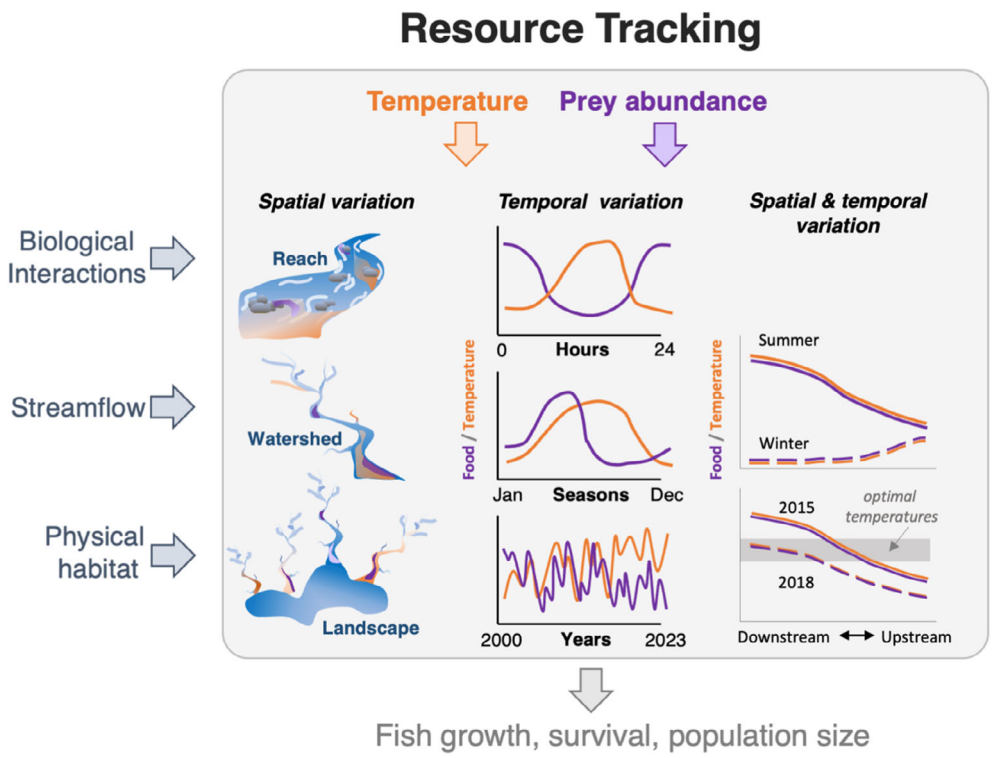


FIGURE 2 Fish are adapted to optimize fitness by tracking thermal and food resources that will maximize their growth and survival (Armstrong et al., 2021; Rossi et al., 2024; Schlosser, 1991). Both thermal and prey resources vary across a range of spatial scales including reach, watershed, and landscape (left column), and temporal scales including hourly, seasonal, and decadal (middle column). Variation in prey resources available to stream fish is affected by biological interactions, flow, and habitat in ways that remain poorly understood. For instance, downstream interactions between food and temperature may create upstream–downstream gradients (upper right panel) in the ratio of food to temperature that could maximize growth downstream in the summer, but minimize winter weight loss in upstream reaches. Similarly, interannual variation in food and temperature (lower right panel) may cause upstream or downstream shifts in the longitudinal distribution of optimal growth conditions.

Certain models have accounted for prey variation over time and space (Benjamin et al., 2020; Dodrill et al., 2016; Hayes et al., 2000). For instance, Hayes et al. (2007) presented a coupled hydrology and drift-transport model that aimed to predict spatial and temporal variation in food availability. Importantly, however, food is not directly addressed in life cycle models (LCMs), which are becoming an increasingly important tool for assessing factors limiting salmonid populations (e.g., Jorgensen et al., 2021). These models commonly incorporate density-dependent spawner-offspring relationships in which incremental increases in reproductive output correspond to decreasing additional juvenile production as competition for limited resources intensifies. Restoration efforts and modeled scenarios in LCMs often focus on reducing density dependence and increasing a system's carrying capacity by increasing suitable habitat area; however, increasing food availability can also reduce density dependence and support greater fish production. As an extreme example, hatcheries raise extremely high densities of juvenile salmonids within very small areas because they feed them and largely eliminate food limitations. Incorporating plausible management scenarios affecting the foodscape into LCMs may be an effective approach to evaluating population-level effects and food limitation. Prey abundance is typically simplified and assumed constant through time, which is not realistic. This can result in dramatically over- or underestimating potential fish growth (Box 1) and can bias management decisions. Recent modeling demonstrates that the net effect of climate change on ectotherms is highly dependent on how prey resources change with increasing temperatures (Ayllón et al., 2019; Huey & Kingsolver, 2019), and our current inability to predict climate-driven changes in food abundance with any confidence highlights the consequences of our current state of ignorance.

Uncertainty about food available to fish can undermine management plans. Overconfidence in predictions of population production without accounting for food availability could lead to over- or under-estimates of habitat value, which could influence population and habitat management decisions. Even if food is considered, unwarranted extrapolation could be inappropriate. Few restoration plans aim to restore food availability directly (Bilby et al., 2023; Naiman

et al., 2012). In most cases, there are longstanding and mostly unverified assumptions that fish are limited by physical habitat conditions, and restoring physical habitat will also benefit the food base (Whitney et al., 2020). Thus, restoration prioritization and effectiveness evaluation could benefit from considering how food availability affects growth potential rather than considering physical habitat attributes alone.

Productivity and food availability have already been considered in restoration approaches to some extent. For instance, increasing instream nutrients, for example, via carcass additions or nutrient fertilization (Samways et al., 2018) typically translates into an increased periphyton, macroinvertebrates, and growth of juvenile salmonids (Guyette et al., 2013; Kaylor et al., 2019; Kiffney et al., 2014; Samways & Cunjak, 2015). However, as pointed out by Benjamin et al. (2020), the persistence of increased fish productivity is dependent on sustained nutrient supplementation, recovery of the spawning population to a self-sustaining level, or the implementation of actions addressing other factors limiting production. Manipulation of riparian plant composition and structure is another way to improve food available to fish. It has been demonstrated that terrestrial invertebrate productivity in riparian areas adjacent to streams may be partly dependent on riparian plant species composition, with higher terrestrial invertebrate inputs to streams in reaches with higher diversity (Deal, 2007) and density of deciduous species compared to reaches dominated by evergreen species (Duncan et al., 1989). Reaches dominated by deciduous species may be associated with higher in situ invertebrate production because of higher light levels, especially before and after leaf-out (Hill et al., 2001).

Given that the intrinsic potential for producing prey differs across the landscape, food availability is critical for understanding the potential effectiveness of restoration strategies before investments are made. This knowledge can potentially lead to restoration practices that not only address physical habitat limitation but also food limitation.

5 | WHAT APPROACHES ARE AVAILABLE FOR QUANTIFYING FOOD AVAILABILITY?

Many of the challenges outlined in the previous sections are not insurmountable, and below we propose a variety of ways that researchers can better characterize *food for fish*. This involves rethinking how we collect information, repurposing and re-analyzing existing information, and more intentional assessment of the consequences of uncertainty about food and its management implications.

Although we focus on providing solution to quantify food availability, it is important to acknowledge that this knowledge needs to be integrated with the numerous facets of habitat diversity that influence spatiotemporal patterns of food availability, such as flow and temperature regimes, organism dispersal, resource subsidies, species invasion, antecedent conditions, and numerous other factors (nutrients, turbidity, etc.) (Naman et al., 2016; Wipfli & Baxter, 2010; Whitney et al., 2020). We also need to account for bidirectional relations on how physical habitat restoration also influences food availability (Coe et al., 2009). Finally, drivers of food availability including habitat characteristics are evolving rapidly under climate change, which not only modifies the drivers but also how they interact with each other. Accounting for these evolving dynamics remains a challenge that can be partially addressed by reducing uncertainties in foodscape knowledge.

5.1 | Acquiring data that can reduce uncertainty about food availability

Characterizing both stochastic and deterministic drivers of prey variation is a key step in generating more realistic predictions of growth and survival (Ayllón et al., 2019.). Thus, we present a hierarchy of options from simple to complex and from individual fish to watersheds to help identify sampling approaches at the appropriate scales (Table 2 and Figure 3). The hierarchy ranges from coarse and inexpensive methods to precise and expensive methods, which should ideally be cross-calibrated as part of an overall validation process. As always, the best approach for data collection should be tied to specific research or management questions. Functionally, the approach will also depend on available resources for sampling, processing, and evaluating the data.

At the coarse end of the spectrum, food data can be broadly characterized using techniques that focus on analyzing bulk samples (i.e., total mass or abundance across all taxa) collected from the environment. For instance, plankton counters are routinely used to assess aggregate food abundance in lakes and oceans (Fulton, 1972; Kydd et al., 2018). Bulk samples could be useful for questions in streams, such as assessing total biomass or energy content available to fish. Bomb calorimetry (Ciancio et al., 2007) and whole sample mass are relatively fast (after sorting prey from detritus),

TABLE 2 Hierarchy of methods for assessing food availability for fish, that is, from simple (top) to complex (bottom).

Method complexity	What is collected	What it tells you	Cost	Accuracy	Scale	Limitations	Question addressed
Simple	eDNA—water or fish stomach, benthos/drift	Presence/absence	Low	Accurate, but need to account for environmental factors affecting eDNA turnover	Easily repeatable at different spatiotemporal scales. However, the scale over which the sample integrates, can be hard to determine and may change among species in the sample	Currently does not provide information on abundance, biomass or life stage	What prey are present and potentially available for fish to consume?
	Diet sampling (fish stomach content)	Prey consumed	Low	Accurate, but represents only recently-consumed items	Easily repeatable at different spatiotemporal scales. Could be repeated seasonally and combined with bioenergetics modeling to provide an integrative view of consumption and seasonal prey importance to annual consumer energy budgets	Can provide biased estimates for easily digestible prey and important feeding relationships can be missed	What prey are fish actually consuming regardless of what may be available in the habitat?
	Prey sampling (drift, benthic, etc.)	Prey abundance and flux at a specific time and place	High	Represents a snapshot of availability at a specific time and place, not necessarily what the fish consume	Difficult to repeat at different spatiotemporal scales due to time, cost and sample processing time	Each technique is biased toward certain types of prey (e.g., can exclude terrestrial subsidies) and may not align with prey consumed	What are estimated prey biomass and taxa proportions that are potentially available for fish to consume?
Complex	Stable isotopes/ Fatty acids	Energy transfer from prey to predator, integrating what was assimilated over time (rather than merely ingested)	Medium to high Can be decreased by targeting representative inverts	Potentially more accurate than other methods. Used to identify primary energy channels fueling fish production, with uncertainty		Elucidates types of energy ingested, but not specific taxa. Can be sensitive to isotope fractionation rates across trophic levels	How is energy transferred over weeks, seasons, or years?

Note: For each approach, we provide information about result type, costs, accuracy, appropriate spatiotemporal scale, limitations, and the questions it is best suited to answer.

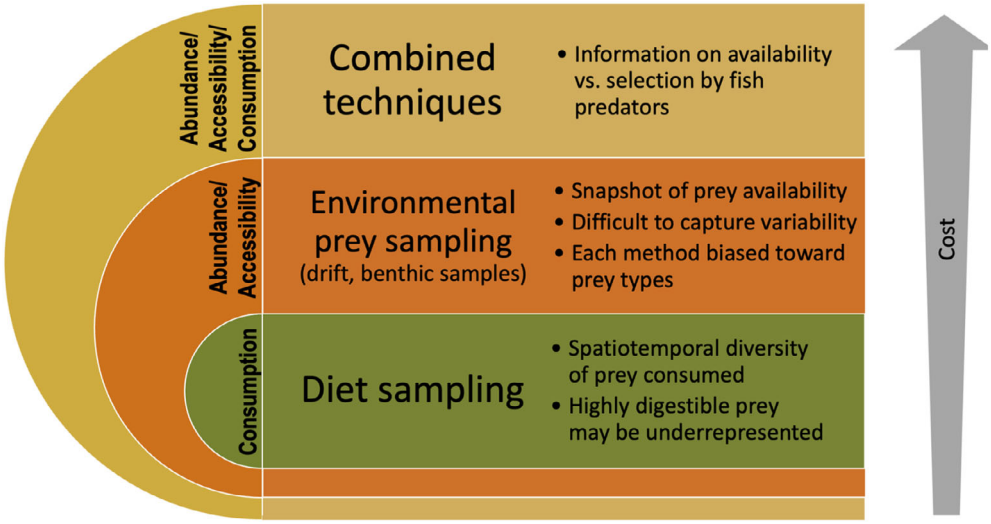


FIGURE 3 Sampling approaches for assessing food availability, accessibility, and consumption for stream fishes. Combined techniques provide more information about the availability of prey and what is selected by fish, but the cost (time and money) of combined sampling could make it difficult to replicate at spatiotemporal scales needed to characterize riverine foodscapes.

inexpensive, and feasible ways to address such questions. Environmental DNA (eDNA) sampling of taxa presence represents an avenue for broad-brush characterization of prey presence and diversity that has rapidly expanded in recent decades (Brantschen et al., 2021), but it is not yet a reliable approach for estimating prey quantity. This method could be particularly useful in cross-ecosystem comparisons, but if the goal is to generate improved empirical estimates of abundance, eDNA is unlikely to contribute to this in the short term. The tradeoff for the ease of data collection associated with these methods is that they involve many assumptions that need to be clearly articulated and evaluated.

At the next level down the resolution hierarchy are efficient methods that balance cost with information gained. Torgersen et al. (2021) provided a useful construct for efficient stratified sampling of a riverscape; they suggest that sampling more space at lower detail (i.e., seeing a sketch of the riverscape instead of detailed bits of the picture through holes in fabric) can provide a clearer picture of ecosystem function than traditional site-based approaches. A riverscape approach typically employs a large team of people to collect data synoptically. New community science methods based on rapid streamside identification of invertebrate prey taxa to family resolution (verified by experienced taxonomists) have proven useful for water quality monitoring (Armanini et al., 2011; Edwards et al., 2018) and could be an effective way to implement a riverscape approach for understanding food availability for fish. Streamside identification is only accurate to higher taxonomic levels, yet it still provides estimates of food groups (soft-bodied vs. armored insects or eggs), prey size and life stage, and provenance (terrestrial vs. aquatic taxa) that can generate empirical metrics of relative prey abundance. Traits of invertebrates, such as propensity to drift based on body morphology and habitat use can be translated into coarse estimates of availability (Esteban & Marchetti, 2004; Rader, 1997). Other active and promising areas of research include automation of traditional invertebrate drift collection (Neuswanger et al., 2022) and sample processing, and identification of invertebrates using artificial intelligence to process videos and images (Gurí et al., 2023).

At the base of the resolution hierarchy are traditional site-based approaches that are detailed and precise but expensive, especially as sample size increases. Samples need to be identified to the lowest appropriate taxonomic level or functional group (McCarthy et al., 2009), and established regressions are then used to associate taxa with energy content for fish (Ciancio et al., 2007; Morley et al., 2020). Regressions to estimate energy content for new taxa may need to be developed by oven-drying samples in the lab, which can add time and expense. These sampling approaches risk missing important food pulses that are patchy or episodic. A potential benefit of this traditional detailed approach is that samples could be processed using chemical analyses to identify not just energy but also prey quality, including fatty acid content (e.g., Naman et al., 2022).

Instead of inferring what fish could potentially eat from environmental samples, a more direct approach is to evaluate fish stomach contents to see what fish are actually eating. Sampling fish diets may reduce costs because diets integrate food items from benthic, drift, and terrestrial sources, each of which would otherwise require separate

environmental sampling. When collected at high frequency, diet samples can detect ephemeral resource pulses that are typically not captured in drift and benthic samples, including large and/or highly nutritious prey such as salmon eggs (Armstrong et al., 2010; FitzGerald et al., 2023). The sample resolution hierarchy (Table 2 and Figure 2) is also relevant for characterizing fish diets. For instance, eDNA metabarcoding of fish diets can tell us what taxa fish are consuming (i.e., taxa presence), but at a coarser resolution than diet samples (i.e., taxa presence and biomass). As the number of fish diets sampled increases, so does investment, and there are clearly tradeoffs at different levels in the resolution hierarchy (Table 2 and Figure 2). The optimal tradeoff between investment and information depends on the study and the question(s) it is designed to resolve.

Although diet sampling may be a more direct representation of what food was actually consumed. It can be difficult to relate sampled prey abundance to what is functionally available for fish consumption. Prey sampling could represent what the predator could in theory consume (given accessibility constraints), or it could represent unconsumed surplus, that is, the leftovers; dynamics that depend on the respective densities of preys and predators (Yard et al., 2023). Fish feeding selectively on one taxon may suggest that it is the sole or primary source of energy available in the environment and may not reflect that there are abundant but less preferred options available. Additionally, fish can only eat what is served, and the lack of items in a diet sample may under-represent the importance of food items that are infrequently available (e.g., eggs). As well, soft-bodied invertebrates that are easily digested may be less well detected or identified in diet samples than in environmental samples (Chipps & Garvey, 2006), but this uncertainty can be minimized by sampling consumers during routine feeding periods. Diets can also be strongly influenced by density, so to interpret diets in the context of food availability, we need to know about the population, that is, are stomachs empty because of low food production or high densities of fish depleting resources. Existing sampling protocols generally measure indicators of prey abundance and use these to infer food availability for fish without considering that fish may not be able to consume all available food due to processes like encounter and attack rates, capture success, and prey selection, even if these parameters are estimated from foraging models (Naman et al., 2020; Railsback et al., 2021). Therefore, fish diet sampling methods are in need of widespread adoption of standardized methods (Amundsen & Sánchez-Hernández, 2019) so that data are comparable across river reaches, riverscapes, and regions.

Tracers such as fatty acids and natural levels of stable isotopes offer a valuable, time-integrated complement to diet analysis. Fatty acids have potentially higher resolution among functional taxa than stable isotopes in lotic systems where invertebrates are the predominant energy source (Brett et al., 2017). Compound-specific stable isotope methods are becoming easier and cheaper to implement and estimate carbon sources used for somatic growth over several months (Thorp & Bowes, 2017). Stable isotopes are most valuable when isotopic signatures of all primary prey categories are represented and distinguishable. When both diet and ambient samples of invertebrate drift and benthos are available, deviation between what is present in the diet and in the environment provides a basis for empirically converting ambient abundance to available food (Rader, 1997). Using bioenergetics models in combination with diet, fish growth, and thermal regime can provide additional insights about prey taxa importance to seasonal growth and overall annual energy budgets (Jensen et al., 2023; Thompson & Beauchamp, 2016). Explicitly fish-focused approaches for quantifying prey availability can facilitate integration across multiple studies.

In addition to evaluating diet information, field estimates of fish growth can potentially inform *food for fish* through consumption estimates (Weber et al., 2014). Growth patterns, when coupled with bioenergetic modeling that accounts for variation in temperature and other factors, can estimate prey consumption, which can be used to provide an indication of food abundance, availability, and quality. Such information can be particularly informative when scaled or coupled with population level demographic information (Korman et al., 2021; Yard et al., 2023). This approach (starting with observed growth) turns the inference problem around (i.e., what food resources must have been available to support this growth?). Fish can be viewed as effective samplers of food resources, indexing food abundance, availability, and quality through their growth, and ultimately address questions at the population level.

5.2 | Using heuristics as indices of food availability

While the suggestions above could improve our understanding of the food available to fish, management decisions often cannot wait years or decades for new data collection. In the near term, heuristics based on existing information could be used as proxies. Heuristics could explain when and where we would expect ecosystems to be more productive, and these hypotheses could be used to inform decision-making.

Some predictions of spatiotemporal patterns of food availability from environmental characteristics exist. For instance, Bellmore et al. (2017) presented a model linking river food web dynamics to in-stream habitat and riparian conditions. This model was later parameterized with empirical physicochemical data (Bellmore, Fellman, et al., 2022) to predict seasonal biomass dynamics of aquatic primary producers and consumers and the growth of juvenile salmon in a simplified river network. This demonstrates that environmental proxies can be used to represent food available to fish. Proxies could include water chemistry (LaPerriere et al., 1983), conductivity, temperature, nutrients, light penetration, geomorphology, hydrology (groundwater, snowmelt, rainfall), stream metabolism, or biological factors. Some have postulated that benthic invertebrates collected commonly in biomonitoring programs could be used as a proxy for rapidly assessing the food available in drift (Sullivan & White, 2017). A meta-analysis comparing (or cross-calibrating) invertebrate drift or benthic abundance with a suite of proxies could inform whether proxies are strongly related or too variable or context-specific to be transferable across streams (Shearer et al., 2003) and extrapolated across geographic space.

Bernhardt, Heffernan, et al. (2018) pleaded for linking stream metabolism and gross primary production (GPP) to organism productivity and phenology. Despite logistical challenges to quantify GPP across broad spatiotemporal scales in streams (which are more difficult than in marine and lentic systems), it has become easier to model due to inexpensive dissolved oxygen loggers and widely available software (Appling et al., 2018). Invertebrate productivity is linked in principle to GPP, and pathways linking GPP to fish can be modeled, representing an inexpensive approach complementary to empirical invertebrate and fish monitoring (Rüegg et al., 2021). However, a high proportion of GPP may be inedible or poor quality as food for aquatic invertebrates (e.g., thick algae mats, macrophytes) and thus not tightly linked. Moreover, there may be temporal mismatches attributed to invertebrate life cycles such as loss of biomass and production from invertebrate emergence coinciding with high GPP. More research is needed to improve the linkage of GPP to fish food.

5.3 | Assessing the consequences of uncertainty

Few studies have examined the consequences of using inaccurate predictions about food (but see Ayllón et al., 2019; Dodrill et al., 2016; Huey & Kingsolver, 2019). It would be invaluable to decision-makers to have estimates of food uncertainty magnitude and how uncertainty might propagate to decisions about managing fish populations. It is worth considering how far off a decision target would be if assumptions about food are wrong. Here, we posit some opportunities for better clarifying potential consequences of uncertainties.

At the broadest level, we can ask—and attempt to answer—where and when understanding food availability for fish is important enough to warrant additional scientific inquiry (Beauchamp, 2009; Huey & Kingsolver, 2019; Railsback et al., 2021). There may be general conditions under which information about food is critical (e.g., when water temperatures or fish densities are high) and when it can be given lower priority or held constant because effects of non-food drivers of fish production predominate (e.g., water temperatures or fish densities are within tolerable ranges) (Dill & Fraser, 1984; Martel, 1996; Metcalfe et al., 1986). Take, for example, a decision about whether to introduce anadromous salmonids above a dam. If growth potential above the dam is likely to be insufficient to support smolt production at levels consistent with population productivity goals, that should be a signal that more research is needed to evaluate options before investing in introductions and fish passage efforts (Jensen et al., 2023). During critical periods when growth disproportionately influences survival or production, understanding food availability in either quantifiable or categorical terms can provide valuable insights regarding vulnerabilities or consequences for individual and population-level outcomes (Duffy & Beauchamp, 2011; Thompson & Beauchamp, 2016).

Uncertainties may be most important to quantify along the steep cline of bioenergetic response curves where rates (metabolism, consumption, growth) change rapidly, whereas relatively flat portions of response curves may be less consequential (Lusardi et al., 2019). Generalities in understanding will help us address contextual questions such as when fish can withstand increased water temperatures due to climate or anthropogenic change by simply consuming more (Huey & Kingsolver, 2019); what habitats and life stages allow fish to grow rapidly, thereby escaping gape-limited predators; and what refuge habitats will be needed for fish to maintain stasis during stressful conditions.

One element of food availability that may contribute substantially to uncertainty is food quality. Food quality remains of unknown importance in fish production estimates and is an emerging research frontier. Until we better grasp the dynamics of this process, we can acknowledge its potential importance in a simplified way. One way is to categorize baseline ecosystem productivity as key trophic pathways along axes such as oligotrophic-eutrophic or

allochthonous-autochthonous. Ecological community description (Cohen et al., 2003) could link prey size, abundance, and trophic status to predation susceptibility of prey assemblages. By separating trophic pathways, uncertainty associated with food quality could be somewhat isolated, as well as its relative effect on fish growth compared to other elements of food availability (abundance, accessibility).

Sensitivity analysis is a powerful tool that can highlight useful generalities, establishing which elements we most need to understand, and the consequences of varying prey abundance for population outcomes (Ayllón et al., 2019). Sensitivity analysis is a standard feature in modeling (Fullerton et al., 2010; Pianosi et al., 2016; Steel et al., 2009) and can help us understand where assumptions of food invariance are most likely to lead us astray. Outcomes can identify the most sensitive variables (Power et al., 1998) which will help users optimize investment in monitoring and restoration. For instance, Armstrong et al. (2013) found that averaging conditions within a larger reach (1–2 km) or modeling smaller reaches (e.g., 200 m) without considering daily fish movement would not capture the potential of the larger site in aggregate. In Box 1, our simple heuristic bioenergetic simulation illustrates that inadequate knowledge about food quantity and quality can dramatically affect predicted growth of juvenile salmonids. We illustrate that seasonal patterns in food abundance, accessibility, and quality are important determinants of fish growth. Similar analyses could be performed using existing empirical data and used to examine potential impacts of uncertainty in food availability in real riverine ecosystems.

6 | CONCLUSIONS AND FUTURE DIRECTIONS

Arriving at a better empirical (and above all predictive) understanding of the drivers of fish food in streams is a logical and necessary progression in fisheries management. Practical necessity favors accelerating this process relative to the decades of studies that were necessary to arrive at our current empirical understanding of physical habitat or temperature constraints on salmonid production. While conceptual insights into the processes driving food availability are essential, credible conservation and management decisions require a parallel focus on developing empirical (Rashidabadi et al., 2022) or mechanistic (Ayllón et al., 2019) models of variation in food availability. To this end, we identify a short list of key research priorities:

1. Develop new and innovative sampling methods for more accurately characterizing food abundance in streams that can be optimized for different study designs and for making comparisons across scales (Neuswanger et al., 2022). Sampling protocols should describe how to position samplers relative to depth, channel width, and velocity (Weber et al., 2017). Protocols should include guidance on sample timing that accounts for periodicity (e.g., diel cycles) in when invertebrates drift and drop, and when stream fishes feed. Community science data collection and automated sampling can especially benefit from standardized protocols. For instance, emergent aquatic invertebrates can be collected by river rafters, enabling more synthetic analysis over an unusually broad spatial extent (Kennedy et al., 2016; Metcalfe et al., 2023).
2. Advance methods to convert abundance of prey to metrics of available prey. New methods should integrate biological and abiotic factors holistically into credible, quantitative, and generalizable methods that translate ambient prey abundance to metrics of what is accessible to fish. Such methods should reflect process (Green et al., 2019), habitat, and biotic-driven context-dependence (Rosenfeld et al., 2022). This includes expanding and validating the use of easily-measured proxies of food abundance (benthos, drift, terrestrial drop; LaPerriere et al., 1983) that can be cross-calibrated to more direct measures of available food (i.e., based on diet analysis or bioenergetic estimates of consumption).
3. Perform research to better understand how flow, temperature and physical habitat affect prey availability. More work is needed to quantitatively understand how these factors affect the production and availability of prey for stream fishes. Flow regimes influence nutrient and sediment retention and accumulation and set the stage for what types of prey colonize and live in different habitats. Flow influences prey distribution and concentration, that is, through transport (Hayes et al., 2007) and deposition at high flows (Humphries et al., 2020). Flow also affects intrinsic substrate associations (Scholl et al., 2022) and the potential for baseline hydraulics to concentrate drift (Shanks et al., 2018). As well, many empirical studies have established relationships between temperature and biological production. Meta-analysis synthesizing temperature effects on aquatic invertebrate production in streams is needed as a first step toward developing predictive models of temperature effects on fish food production. Given that empirical

approaches are often expensive and slow to implement, testing different predictions from metabolic theory could help clarify uncertainties and improve modeling predictive power.

4. Produce predictive models of food availability that can be used in conservation and management. More general development of quantitative, transferrable, predictive models of how food availability responds to multiple drivers are needed (Bellmore et al., 2017). This may involve complex relationships among many factors beyond temperature, flow, and physical habitat. Predicted food availability can be mapped across a watershed or plotted over time to provide information to managers tasked with deciding when and where to implement nutrient supplementation or other restoration actions.
5. Conduct integrative or bioenergetic modeling simulations to understand more explicitly the importance of variance in prey availability (including stochasticity) to individual fish growth, survival, and population persistence. These models can clarify the impacts of changing environmental conditions and can help parse effects of water temperature, flow, and food availability, among other stressors. Such models can help answer, for example, when and where sufficient food enables fish to withstand unfavorable temperatures and, conversely, when optimal temperatures are insufficient due to a lack of food. Sensitivity analyses can help bracket and inform the myriad sources of uncertainty. Individual-based and bioenergetics models can be coupled with population level demographics information to provide broader insights into population and community viability.
6. Align monitoring and research with ongoing habitat manipulations associated with large-scale restoration projects to understand the direct effects of management interventions on prey availability and food webs (i.e., adaptive management; Naman et al., 2022). For instance, food supplementation and system fertilization experiments have had both positive effects on salmonids (Johnston et al., 1990) and neutral effects (Compton et al., 2006; Janetski et al., 2009). These results likely depend on the spatial and temporal scales over which results were assessed.
7. Finally, integrative research is needed that explicitly connects individual and population-level processes to help assess the circumstances under which foodscapes are limiting to fish and when populations are more limited by other factors, as described in Section 2.5.

A coherent and effective research program focused on variation in *fish for food* is essential because we know that the outcome of environmental change scenarios (e.g., climate change effects on temperature and flow) will likely be highly sensitive to concomitant changes in prey availability (Huey & Kingsolver, 2019). Increased food abundance or quality under climate warming may partially mitigate negative impacts, while decreased food could make impacts much more severe than anticipated. Similarly, fish habitat management can be enhanced by a better empirical understanding of drivers of food availability and better techniques to monitor those drivers. Food availability remains a surprisingly untapped frontier for fish ecology, whose timely and efficient synthesis is long overdue.

AUTHOR CONTRIBUTIONS

Valerie Ouellet: Conceptualization (lead); project administration (lead); supervision (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Aimee H. Fullerton:** Conceptualization (lead); project administration (lead); supervision (lead); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Matt Kaylor:** Conceptualization (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Sean Naman:** Conceptualization (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Ryan Bellmore:** Conceptualization (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Jordan Rosenfeld:** Conceptualization (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Gabriel Rossi:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Seth White:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Suzanne Rhoades:** Conceptualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **David A. Beauchamp:** Conceptualization (equal); writing – original draft (supporting); writing – review and editing (supporting). **Peter Kiffney:** Conceptualization (equal); writing – original draft (supporting); writing – review and editing (supporting). **Martin Liermann:** Writing – review and editing (supporting). **Beth Sanderson:** Writing – review and editing (equal).

ACKNOWLEDGMENTS

We thank J. Chamberlain, M. Dodrill, and two anonymous reviewers, and editors for critical evaluation of manuscript drafts. We thank G. Rossi and coauthors for working with us to coordinate material to highlight in our paper that would be complementary to content in Rossi et al. (2024).

FUNDING INFORMATION

We did not receive any specific funding for this project.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. [Correction added on 28 October 2024, after first online publication: The disclaimer statement has been added.]

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

RELATED WIREs ARTICLES

Status and trends of dam removal research in the United States

ORCID

Valerie Ouellet https://orcid.org/0000-0001-7410-1857
Aimee H. Fullerton https://orcid.org/0000-0002-5581-3434
Matt Kaylor https://orcid.org/0000-0001-5331-9830
Sean Naman https://orcid.org/0000-0002-2113-8311
Ryan Bellmore https://orcid.org/0000-0002-5140-6460
Jordan Rosenfeld https://orcid.org/0000-0002-5827-9740
Gabriel Rossi https://orcid.org/0000-0003-3010-9480
Seth White https://orcid.org/0000-0003-4918-6865
Suzanne Rhoades https://orcid.org/0000-0002-4632-6263
David A. Beauchamp https://orcid.org/0000-0002-3592-8381
Martin Liermann https://orcid.org/0009-0004-5019-1471
Peter Kiffney https://orcid.org/0000-0003-0863-0085
Beth Sanderson https://orcid.org/0000-0003-2982-4815

FURTHER READING

Lino, Y., Kitagawa, T., Abe, T. K., Nagasaka, T., Shimizu, Y., Ota, K., Kawashima, T., & Kawamura, T. (2022). Effect of food amount and temperature on growth rate and aerobic scope of juvenile chum salmon. *Fisheries Science*, *88*, 397–409. https://doi.org/10.1007/s12562-022-01599-w

REFERENCES

Ahti, P. A., Kuparinen, A., & Uusi-Heikkilä, S. (2020). Size doses matter—The eco-evolutionary effects of changing body size in fish. *Environmental Reviews*, *28*(3), 311–324.

Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R., Fortin, M. J., Galiana, N., Leroux, S. J., Pellisier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D. (2019). The marine fish food web is globally connected. *Nature Ecology and Evolution*, *3*(8), 1153–1161. https://doi.org/10.1038/s41559-019-0950-y

Amundsen, P. A., & Sánchez-Hernández, J. (2019). Feeding studies take guts—Critical review and recommendations of methods for stomach contents analysis in fish. *Journal of Fish Biology*, *95*(6), 1364–1373. https://doi.org/10.1111/jfb.14151

Anderson, K. E., Harrison, L. R., Nisbet, R. M., & Kolpas, A. (2013). Modeling the influence of flow on invertebrate drift across spatial scales using a 2D hydraulic model and a 1D population model. *Ecological Modeling*, *265*(10), 207–220. https://doi.org/10.1016/j.ecolmodel.2013.06.011

Appling, A. P., Hall, R. O., Jr., Yackulic, C. B., & Arroita, M. (2018). Overcoming equifinality: Leveraging long time series for stream metabolism estimation. *Journal of Geophysical Research: Biogeosciences*, *123*(2), 624–645. https://doi.org/10.1002/2017JG004140

Armanini, D. G., Horrigan, N., Monk, W. A., Peters, D. L., & Baird, D. J. (2011). Development of a benthic macroinvertebrate flow sensitivity index for Canadian rivers. *River Research and Applications*, *27*(6), 723–737. https://doi.org/10.1002/rra.1389

Armstrong, J. B., Fullerton, A. H., Jordan, C. E., Ebersole, J. L., Bellmore, J. R., Arismendi, I., Brooke, E. P., & Reeves, G. H. (2021). The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, *11*(4), 354–361. https://doi.org/10.1038/s41558-021-00994-y

Armstrong, J. B., & Schindler, D. E. (2011). Excess digestive capacity in predators reflects a life of feast and famine. *Nature*, *476*(7358), 84–87. https://doi.org/10.1038/nature10240

Armstrong, J. B., Schindler, D. E., Omori, K. L., Ruff, C. P., & Quinn, T. P. (2010). Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. *Ecology*, *91*(5), 1445–1454. https://doi.org/10.1890/09-0790.1

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E., & Torgersen, C. E. (2013). Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, *94*(9), 2066–2075. https://doi.org/10.1890/12-1200.1

Ayllón, D., Railsback, S. F., Harvey, B. C., García Quirós, I., Nicola, G. G., Elvira, B., & Almodóvar, A. (2019). Mechanistic simulations predict that thermal and hydrological effects of climate change on Mediterranean trout cannot be offset by adaptive behaviour, evolution, and increased food production. *Science of the Total Environment*, *693*, 133648. https://doi.org/10.1016/j.scitotenv.2019.133648

Back, J. A., & King, R. S. (2013). Sex and size matter: Ontogenetic patterns of nutrient content of aquatic insects. *Freshwater Science*, *32*, 837–848. https://doi.org/10.1899/12-181.1

Bacon, P. J., Gurney, W. S. C., Jones, W., McLaren, I. S., & Youngson, A. F. (2004). Seasonal growth patterns of wild juvenile fish: Partitioning variation among explanatory variables, based on individual growth trajectories of Atlantic salmon (*Salmo salar*) parr. *Journal of Animal Ecology*, *74*(1), 1–11. https://doi.org/10.1111/j.1365-2656.2004.00875.x

Bailey, C. J., & Moore, J. W. (2020). Resource pulses increase the diversity of successful competitors in a multi-species stream fish assemblage. *Ecosphere*, *11*(9), e03211. https://doi.org/10.1002/ecs2.3211

Bakun, A., & Csirke, J. (1998). Chapter 6. Environmental processes and recruitment variability. In P. G. Rodhouse, E. G. Dawe, & R. K. O'Dor (Eds.), *Squid recruitment dynamics: The genus Illex as a model, the commercial Illex species and influences of variability* (Fish. Tech. Pap., 376) (pp. 105–124). FAO. https://www.fao.org/3/w9000e/w9000e06.pdf

Barbarossa, V., Bosmans, J., Wanders, N., King, H., Bierkens, M. F. P., Huijbregts, M. A. J., & Schipper, A. M. (2021). Threats of global warming to the world's freshwater fishes. *Nature Communications*, *12*(1), 1–10. https://doi.org/10.1038/s41467-021-21655-w

Baxter, C. V., Kennedy, T. A., Miller, S. W., Muehlbauer, J. D., & Smock, L. A. (2017). Macroinvertebrate drift, adult insect emergence and oviposition. *Methods in Stream Ecology: Third Edition*, *1*, 435–456. https://doi.org/10.1016/B978-0-12-416558-8.00021-4

Beauchamp, D. A. (2009). Bioenergetic ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *American Fisheries Society Symposium*, *70*, 1–19. http://www.fisheriessociety.org/proofs/ayk/beauchamp.pdf

Bellmore, J., Duda, J. J., Craig, L. S., Greene, S. L., Torgersen, C. E., Collins, M. J., & Vittum, K. (2017). Status and trends of dam removal research in the United States. *WIREs Water*, *4*, 1–13. https://doi.org/10.1002/wat2.1164

Bellmore, J. R., Baxter, C. V., & Connolly, P. J. (2015). Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology*, *96*(1), 274–283. https://doi.org/10.1890/14-0733.1

Bellmore, J. R., Baxter, C. V., Martens, K., & Connolly, P. J. (2013). The floodplain food web mosaic: A study of its importance to salmon and steelhead with implications for their recovery. *Ecological Applications*, *23*(1), 189–207. https://doi.org/10.1890/12-0806.1

Bellmore, J. R., Baxter, C. V., Ray, A. M., Denny, L., Tardy, K., & Galloway, E. (2012). Assessing the potential for salmon recovery via floodplain restoration: A multitrophic level comparison of dredge-mined to reference segments. *Environmental Management*, *49*(3), 734–750. https://doi.org/10.1007/s00267-012-9813-x

Bellmore, J. R., Fellman, J. B., Hood, E., Dunkle, M. R., & Edwards, R. T. (2022). A melting cryosphere constrains fish growth by synchronizing the seasonal phenology of river food webs. *Global Change Biology*, *28*(16), 4807–4818. https://doi.org/10.1111/gcb.16273

Bellmore, J. R., Sergeant, C. J., Bellmore, R. A., Falke, J. A., & Fellman, J. B. (2022). Modeling coho salmon (*Oncorhynchus kisutch*) population response to streamflow and water temperature extremes. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(2), 243–260. https://doi.org/10.1139/cjfas-2022-0129

Benda, L., Poff, N. L., Miller, D., Dunne, T., Reeves, G., Pess, G., & Pollock, M. (2004). The network dynamics hypothesis: How channel networks structure riverine habitats. *Bioscience*, *54*(5), 413–427. https://doi.org/10.1641/0006-3568(2004)054[0413:TNDHHC]2.0.CO;2

Benjamin, J. R., Bellmore, J. R., Whitney, E., & Dunham, J. B. (2020). Can nutrient additions facilitate recovery of pacific salmon? *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(10), 1601. https://doi.org/10.1139/cjfas-2019-0438

Bernhardt, E. S., Heffernan, J. B., Grimm, N. B., Stanley, E. H., Harvey, J. W., Arroita, M., Appling, A. P., Cphen, M. J., McDowell, W. H., Hall Jr., R. O., Read, J. S., Roberts, B. J., Stets, E. G., & Yackulic, C. B. (2018). The metabolic regimes of flowing waters. *Limnology and Oceanography*, *63*, S99–S118. https://doi.org/10.1002/lno.10726

Bernhardt, J. R., Sunday, J. M., Thompson, P. L., & O'Connor, M. L. (2018). Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment. *Proceeding of the Royal Society*, 2018;285(1886):2018107. https://doi.org/10.3389/fevo.2019.00236

Bilby, R. E., Currens, K. P., Fresh, K. L., Booth, D. B., Fuerstenberg, R. R., & Lucchetti, G. L. (2023). Why aren't salmon responding to habitat restoration in the Pacific northwest? *Fisheries*, *49*, 16–27. https://doi.org/10.1002/fsh.10991

Bishop, J. E. (1969). Light control of aquatic insect activity and drift. *Ecology*, *50*(3), 371–380. https://doi.org/10.2307/1933885

Brantschen, J., Blackman, R. C., Walser, J. C., & Altermatt, F. (2021). Environmental DNA gives comparable results to morphology-based indices of macroinvertebrates in a large-scale ecological assessment. *PLoS One*, *16*(9), e0257510. https://doi.org/10.1371/journal.pone.0257510

Brett, J. R., Clarke, W. C., & Shelbourn, J. E. (1982). Experiments on thermal requirements for growth and food conversion efficiency of juvenile chinook salmon *Oncorhynchus tshawytscha*. *Canadian Technical Report of Fisheries and Aquatic Sciences*, *1127*, 1–29.

Brett, J. R., Shelbourn, J. E., & Shoop, C. T. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada*, *26*(9), 2363–2394. https://doi.org/10.1139/f69-230

Brett, M. T., Bunn, S. E., Chandra, S., Galloway, A. W. E., Guo, F., Kainz, M. J., Kankaala, P., Lau, D. C. P., Moulton, T. P., Power, M. E., Rasmussen, J. B., Taipale, S. J., Thorp, J. H., & Wehr, J. D. (2017). How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? *Freshwater Biology*, *62*(5), 833–853. https://doi.org/10.1111/fwb.12909

Brewitt, K. S., Danner, E. M., & Moore, J. W. (2017). Hot eats and cool creeks: Juvenile Pacific salmonids use mainstem prey while in thermal refuges. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(10), 1588–1602. https://doi.org/10.1139/cjfas-2016-0395

Bruce, R. L., Moffitt, C. M., & Dennis, B. (2009). Survival and passage of ingested New Zealand mudsnails through the intestinal tract of rainbow trout. *North American Journal of Aquaculture*, *71*, 287–301. https://doi.org/10.1577/a08-033.1

Caldwell, T. J., Rossi, G. J., Henery, R. E., & Chandra, S. (2018). Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance. *River Research and Applications*, *34*(8), 965–976. https://doi.org/10.1002/rra.3340

Chevalier, M., Tedesco, P., & Grenouillet, G. (2022). Spatial patterns in the contribution of biotic and abiotic factors to the population dynamics of three freshwater fish species. *PeerJ*, *10*, 1–28. https://doi.org/10.7717/peerj.12857

Chipps, S. R., & Garvey, J. E. (2006). Chapter 11. Assessment of food habits and feeding patterns. In D. C. Dauwalter (Ed.), *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society.

Ciancio, J. E., Pascual, M. A., & Beauchamp, D. A. (2007). Energy density of Patagonian aquatic organisms and empirical predictions based on water content. *Transactions of the American Fisheries Society*, *136*(5), 1415–1422. https://doi.org/10.1577/T06-173.1

Clark, T. D., Furey, N. B., Rechisky, E. L., Gale, M. K., Jeffries, K. M., Porter, A. D., Casselman, M. T., Lotto, A. G., Patterson, D. A., Cooke, S. J., Farrell, A. P., Welch, D. W., & Hinch, S. G. (2016). Tracking wild sockeye salmon smolts to the ocean reveals distinct regions of nocturnal movement and high mortality. *Ecological Applications*, *26*(4), 959–978. https://doi.org/10.1890/15-0632

Coe, H. J., Kiffney, P. M., Pess, G. R., Kloehn, K. K., & McHenry, M. L. (2009). Periphyton and invertebrate response to wood placement in large pacific coastal rivers. *River Research and Applications*, *25*(8), 1025–1035. https://doi.org/10.1002/rra.1201

Cohen, J. E., Jonsson, T., & Carpenter, S. R. (2003). Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences*, *100*(4), 1781–1786. https://doi.org/10.1073/pnas.232715699

Compton, J. E., Andersen, C. P., Phillips, D. L., Brooks, J. R., Johnson, M. G., Robbins Church, M., Hogsett, W. E., Cairns, M. A., Rygiewicz, P. T., McComb, B. C., & Shaff, C. D. (2006). Ecological and water quality consequences of nutrient addition for salmon restoration in the Pacific Northwest. *Frontiers in Ecology and the Environment*, *4*(1), 18–26. https://doi.org/10.1890/1540-9295(2006)004[0018:EAWQCO]2.0.CO;2

Cross, W. F., Baxter, C. V., Donner, K. C., Rosi-Marshall, E. J., Kennedy, T. A., Hall, R. O., Jr., Kelly, H. A. W., & Rogers, R. S. (2011). Ecosystem ecology meets adaptive management: Food web response to a controlled flood on the Colorado River, Glen Canyon. *Ecological Applications*, *21*(6), 2016–2033. https://doi.org/10.1890/10-1719.1

Cross, W. F., Baxter, C. V., Rosi-Marshall, E. J., Hall, R. O., Kennedy, T. A., Donner, K. C., Wellard, H. A., Seegert, S. E. Z., Behn, K. E., & Yard, M. D. (2013). Food-web dynamics in a large river discontinuum. *Ecological Monographs*, *83*(3), 311–337. https://doi.org/10.1890/12-1727.1

Crowder, L. B., & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, *63*(6), 1802–1813. https://doi.org/10.2307/1940122

Cummins, K. W., & Wycheck, J. C. (1971). Caloric equivalents for investigations in ecological energetics. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen*, *18*(1), 1–158. https://doi.org/10.1080/05384680.1971.11903918

Deal, R. L. (2007). Management strategies to increase stand structural diversity and enhance biodiversity in coastal rainforests of Alaska. *Biological Conservation*, *137*, 520–532. https://doi.org/10.1016/j.biocon.2007.03.014

Deemer, B. R., Yackulic, C. B., Hall, R. O., Jr., Dodrill, M. J., Kennedy, T. A., Muehlbauer, J. D., Topping, D. J., Voichick, N., & Yard, M. D. (2022). Experimental reductions in subdaily flow fluctuations increased gross primary productivity for 425 river kilometers downstream. *PNAS Nexus*, *1*(3), pgac094. https://doi.org/10.1093/pnasnexus/pgac094

Deslauriers, D., Chipps, S. R., Breck, J. E., Rice, J. A., & Madenjian, C. P. (2017). Fish bioenergetics 4.0: An R-based modeling application. *Fisheries*, *42*(11), 586–596. https://doi.org/10.1080/03632415.2017.1377558

Dewson, Z. S., James, A. B. W., & Death, R. G. (2007). Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology*, *52*(2), 357–369. https://doi.org/10.1111/j.1365-2427.2006.01682.x

Dill, L. M., & Fraser, A. H. G. (1984). Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology*, *16*(1), 65–71. https://doi.org/10.1007/BF00293105

Dodrill, M. J., Yackulic, C. B., Kennedy, T. A., & Hayes, J. W. (2016). Prey size and availability limits maximum size of rainbow trout in a large tailwater: Insights from a drift-foraging bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(5), 759–772. https://doi.org/10.1139/cjfas-2015-0268

Dodrill, M. J., Yackulic, C. B., Kennedy, T. A., Yard, M. D., & Korman, J. (2021). As the prey thickens: Rainbow trout select prey based upon width not length. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(7), 809–819. https://doi.org/10.1139/cjfas-2020-0113

Douglas, P. L., Forrester, G. E., & Cooper, S. D. (1994). Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia*, *98*(1), 48–56. https://doi.org/10.1007/BF00326089

Duffy, E. J., & Beauchamp, D. A. (2011). Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(2), 232–240. https://doi.org/10.1139/F10-144

Duncan, W. F. A., Brusven, M. A., & Bjornn, T. C. (1989). Energy-flow response models for evaluation of altered riparian vegetation in three southeast Alaskan streams. *Water Research*, *23*(8), 965–974. https://doi.org/10.1016/0043-1354(89)90169-3

Edwards, P. M., Shaloum, G., & Bedell, D. (2018). A unique role for citizen science in ecological restoration: A case study in streams. *Restoration Ecology*, *26*(1), 29–35. https://doi.org/10.1111/rec.12622

Epele, L. B., Dos Santos, D. A., Sarremejane, R., Grech, M. G., Macchi, P. A., Manzo, L. M., Miserendino, M. L., Bonada, N., & Cañedo-Argüelles, M. (2021). Blowin' in the wind: Wind directionality affects wetland invertebrate metacommunities in Patagonia. *Global Ecology and Biogeography*, *30*(6), 1191–1203. https://doi.org/10.1111/geb.13294

Esteban, E. M., & Marchetti, M. P. (2004). What's on the menu? Evaluating a food availability model with young-of-the-year Chinook salmon in the Feather River, California. *Transactions of the American Fisheries Society*, *133*(3), 777–788. https://doi.org/10.1577/t03-115.1

Falke, J. A., Huntsman, B. M., & Schoen, E. R. (2019). Climatic variation drives growth potential of juvenile Chinook Salmon along a subarctic boreal riverscape. *Advances in Understanding Landscape Influences on Freshwater Habitats and Biological Assemblages, American Fisheries Society Symposium*, *90*, 57–82.

Fausch, K. D. (1984). Profitable stream positions for salmonids: Relating specific growth rate to net energy gain. *Canadian Journal of Zoology*, *62*(3), 441–451. https://doi.org/10.1139/z84-067

Ficke, A. D., Myrick, C. A., & Hansen, L. J. (2007). Potential impacts of global climate change on freshwater fisheries. *Review in Fish Biology and Fisheries*, *17*, 581–613. https://doi.org/10.1007/s11160-007-9059-5

Fiksen, Ø., Aksnes, D. L., Flyum, M. H., & Giske, J. (2002). The influence of turbidity on growth and survival of fish larvae: A numerical analysis. In O. Vadstein & Y. Olsen (Eds.), *Sustainable increase of marine harvesting: Fundamental mechanisms and new concepts. Developments in hydrobiology* (Vol. 167). Springer. https://doi.org/10.1007/978-94-017-3190-4_5

FitzGerald, K. A., Bellmore, J. R., Fellman, J. B., Cheng, M. L. H., Delbecq, C. E., & Falke, J. A. (2023). Stream hydrology and a pulse subsidy shape patterns of fish foraging. *Journal of Animal Ecology*, *92*(12), 2386–2398. https://doi.org/10.1111/1365-2656.14018

Fullerton, A. H., Jensen, D., Steel, E. A., Miller, D., & McElhany, P. (2010). How certain are salmon recovery forecasts? A watershed-scale sensitivity analysis. *Environmental Modeling & Assessment*, *15*, 13–26. https://doi.org/10.1007/s10666-008-9185-z

Fullerton, A. H., Sun, N., Baerwalde, M. J., Hawkins, B. L., & Yan, H. (2022). Mechanistic simulations suggest riparian restoration can partly counteract climate impacts to juvenile salmon. *Journal of the American Water Resources Association*, *58*(4), 525–546. https://doi.org/10.1111/1752-1688.13011

Fulton, J. (1972). Trials with an automated plankton counter. *Journal of the Fisheries Research Board of Canada*, *29*(7), 1075–1078. https://doi.org/10.1139/f72-154

Gende, S. M., Quinn, T. P., Willson, M. F., Heintz, R., & Scott, T. M. (2004). Magnitude and fate of salmon-derived nutrients and energy in a coastal stream ecosystem. *Journal of Freshwater Ecology*, *19*(1), 149–160. https://doi.org/10.1080/02705060.2004.9664522

Giannico, G. R., & Healey, M. C. (1999). Ideal free distribution theory as a tool to examine juvenile coho salmon (*Oncorhynchus kisutch*) habitat choice under different conditions of food abundance and cover. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(12), 2362–2373. https://doi.org/10.1139/f99-173

Gowan, C., & Fausch, K. D. (2002). Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes*, *64*(1), 139–153. https://doi.org/10.1023/A:1016010723609

Green, S. J., Dilley, E. R., Benkwitt, C. E., Davis, A. C. D., Ingeman, K. E., Kindinger, T. L., Tuttle, L. J., & Hixon, M. A. (2019). Trait-mediated foraging drives patterns of selective predation by native and invasive coral-reef fishes. *Ecosphere*, *10*(6):e02752. https://doi.org/10.1002/ecs2.2752

Guo, F., Bunn, S. E., Brett, M. T., & Kainz, M. J. (2017). Polyunsaturated fatty acids in stream food webs—High dissimilarity among producers and consumers. *Freshwater Biology*, *62*(8), 1325–1334. https://doi.org/10.1111/fwb.12956

Gurí, R., Arranz, I., Ordeix, M., & García-Comas, C. (2023). Automatic image processing to determine the community size structure of riverine macroinvertebrates. *Journal of Visualized Experiments*, *191*, e64320. https://doi.org/10.3791/64320

Guyette, M. Q., Loftin, C. S., & Zydlewski, J. (2013). Carcass analog addition enhances juvenile Atlantic salmon (*Salmo salar*) growth and condition. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(6), 860–870. https://doi.org/10.1139/cjfas-2012-0496

Hanson, P. C., Johnson, T. B., Schindler, D. E., & Kitchell, J. F. (1997). *Fish bioenergetics 3.0* (Technical report WISCU-T-97-001). University of Wisconsin Sea Grant Institute.

Hayes, D. S., Moreira, M., Boavida, I., & Haslauer, M. (2019). Life stage-specific hydropeaking flow rules. *Sustainability*, *11*(6), 1547. https://doi.org/10.3390/su11061547

Hayes, J. W., Goodwin, E. O., Shearer, K. A., & Hicks, D. M. (2019). Relationship between background invertebrate drift concentration and flow over natural flow recession and prediction with a drift transport model. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(6), 871–885. https://doi.org/10.1139/cjfas-2017-0340

Hayes, J. W., Hughes, N. F., & Kelly, L. H. (2007). Process-based modeling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. *Ecological Modeling*, *207*(2–4), 171–188. https://doi.org/10.1016/j.ecolmodel.2007.04.032

Hayes, J. W., Stark, J. D., & Shearer, K. A. (2000). Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. *Transactions of the American Fisheries Society*, *129*, 315–332. https://doi.org/10.1577/1548-8659(2000)129<0315:datoaw>2.0.co;2

Heim, K. C., McMahon, T. E., Calle, L., Wipfli, M. S., & Falke, J. A. (2019). A general model of temporary aquatic habitat use: Water phenology as a life history filter. *Fish and Fisheries*, *20*(4), 802–816. https://doi.org/10.1111/faf.12386

Heino, J., Louhi, P., & Muotka, T. (2004). Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. *Freshwater Biology*, *49*(9), 1230–1239. https://doi.org/10.1111/j.1365-2427.2004.01259.x

Herbst, D. B., Cooper, S. D., Medhurst, R. B., Wiseman, S. W., & Hunsaker, C. T. (2018). A comparison of the taxonomic and trait structure of macroinvertebrate communities between the riffles and pools of montane headwater streams. *Hydrobiologia*, *820*(1), 115–133. https://doi.org/10.1007/s10750-018-3646-4

Hill, J., & Grossman, G. D. (2010). An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology*, *74*(3), 685–698. https://doi.org/10.2307/1940796

Hill, W. R., Mulholland, P. J., & Marzolf, E. R. (2001). Stream ecosystem responses to forest leaf emergence in spring. *Ecology*, *82*(8), 2306–2319. https://doi.org/10.1890/0012-9658(2001)082[2306:SERTFL]2.0.CO;2

Huey, R. B., & Kingsolver, J. G. (2019). Climate warming, resource availability, and the metabolic meltdown of ectotherms. *American Naturalist*, *194*(6), E140–E150. https://doi.org/10.1086/705679

Hughes, N. F., & Dill, L. M. (1990). Position choice by drift-feeding salmonids: Model and test for Arctic Grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(10), 2039–2048. https://doi.org/10.1139/f90-228

Humphries, P., King, A., McCasker, N., Kopf, R. K., Stoffels, R., Zampatti, B., & Price, A. (2020). Riverscape recruitment: A conceptual synthesis of drivers of fish recruitment in rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(2), 213–225. https://doi.org/10.1139/cjfas-2018-0138

Huntsman, B. M., & Falke, J. A. (2019). Main stem and off-channel habitat use by juvenile Chinook salmon in a sub-Arctic riverscape. *Freshwater Biology*, *64*(3), 433–446. https://doi.org/10.1111/fwb.13232

Huryn, A. D. (1996). An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography*, *41*(2), 243–252. https://doi.org/10.4319/lo.1996.41.2.0243

Huryn, A. D., & Wallace, J. B. (2000). Life history and production of stream insects. *Annual Review of Entomology*, *45*(1), 83–110. https://doi.org/10.1146/annurev.ento.45.1.83

Isaak, D. J., Luce, C. H., Horan, D. L., Chandler, G. L., Wollrab, S. P., & Nagel, D. E. (2018). Global warming of salmon and trout rivers in the northwestern U.S.: Road to ruin or path through purgatory? *Transactions of the American Fisheries Society*, *147*(3), 566–587. https://doi.org/10.1002/tafs.10059

Isaak, D. J., & Rieman, B. E. (2013). Stream isotherm shifts from climate change and implications for distributions of ectothermic organisms. *Global Change Biology*, *19*(3), 742–751. https://doi.org/10.1111/gcb.12073

Janetski, D. J., Chaloner, D. T., Tiegs, S. D., & Lamberti, G. A. (2009). Pacific salmon effects on stream ecosystems: A quantitative synthesis. *Oecologia*, *159*, 583–595. https://doi.org/10.1007/s00442-008-1249-x

Jeffres, C. A., Holmes, E. J., Sommer, T. R., & Katz, J. V. E. (2020). Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. *PLoS One*, *15*(9), e0216019. https://doi.org/10.1371/journal.pone.0216019

Jensen, B. L., Johnson, R. C., Duda, J. J., Ostberg, C. O., Code, T. J., Mclean, J. H., Stenberg, K. D., Larsen, K. A., Hoy, M. S., & Beauchamp, D. A. (2023). Growth performance of rainbow trout in reservoir tributaries and implications for steelhead growth potential above Skagit River dams. *North American Journal of Fisheries Management*, *43*(5), 1427–1446. https://doi.org/10.1002/nafm.10944

Johnston, N. T., Perrin, C. J., Slaney, P. A., & Ward, B. R. (1990). Increased juvenile salmonid growth by whole-river fertilization. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(5), 862–872. https://doi.org/10.1139/f90-099

Jorgensen, J. C., Nicol, C., Fogel, C., & Beechie, T. J. (2021). Identifying the potential of anadromous salmonid habitat restoration with life cycle models. *PLoS One*, *16*(9), 1–22. https://doi.org/10.1371/journal.pone.0256792

Jowett, I. G. (1992). Models of the abundance of large brown trout in New Zealand rivers. *North American Journal of Fisheries Management*, *12*, 417–432. https://doi.org/10.1577/1548-8675(1992)012<0417:MOTAOL>2.3.CO;2

Kaylor, M. J., Justice, C., Armstrong, J. B., Staton, B. A., Burns, L. A., Sedell, E., & White, S. M. (2021). Temperature, emergence phenology and consumption drive seasonal shifts in fish growth and production across riverscapes. *Journal of Animal Ecology*, *90*(7), 1727–1741. https://doi.org/10.1111/1365-2656.13491

Kaylor, M. J., White, S. M., Sedell, E. R., & Warren, D. R. (2019). Carcass additions increase juvenile salmonid growth, condition, and size in an interior Columbia River basin tributary. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(4), 703–715. https://doi.org/10.1139/cjfas-2019-0215

Keeley, E. R., & Grant, J. W. (2001). Prey size of salmonid fishes in streams, lakes, and oceans. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(6), 1122–1132. https://doi.org/10.1139/f01-060

Kennedy, T. A., Muehlbauer, J. D., Yackulic, C. B., Lytle, D. A., Miller, S. W., Dibble, K. L., Kortenhoeven, E. W., Metcalfe, A. N., & Baxter, C. V. (2016). Flow management for hydropower extirpates aquatic insects, undermining river food webs. *Bioscience*, *66*(7), 561–575. https://doi.org/10.1093/biosci/biw059

Kiffney, P. M., Buhle, E. R., Naman, S. M., Pess, G. R., & Klett, R. S. (2014). Linking resource availability and habitat structure to stream organisms: An experimental and observational assessment. *Ecosphere*, *5*(4), 1–27. https://doi.org/10.1890/ES13-00269.1

Kiffney, P. M., Greene, C., Hall, J., & Davies, J. (2006). Tributary streams create spatial discontinuities in habitat, biological productivity, and diversity in mainstem rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(11), 2518–2530. https://doi.org/10.1139/f06-138

Korman, J., Yard, M. D., Dzul, M. C., Yackulic, C. B., Dodrill, M. J., Deemer, B. R., & Kennedy, T. A. (2021). Changes in prey, turbidity, and competition reduce somatic growth and cause the collapse of a fish population. *Ecological Monographs*, *91*(1), e01427. https://doi.org/10.1002/ecm.1427

Kydd, J., Rajakaruna, H., Briski, E., & Bailey, S. (2018). Examination of a high resolution laser optical plankton counter and FlowCAM for measuring plankton concentration and size. *Journal of Sea Research*, *133*, 2–10. https://doi.org/10.1016/j.seares.2017.01.003

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, *19*(4), 573–592. https://doi.org/10.2307/1468118

Laliberte, J. J., Post, J. R., Rosenfeld, J. S., & Mee, J. A. (2016). Modelling temperature, body size, prey density, and stream gradient impacts on longitudinal patterns of potential production of drift-feeding trout. *River Research and Applications*, *32*(10), 2045–2055. https://doi.org/10.1002/rra.3048

LaPerriere, J. D., Bjerklie, D. M., Simmons, R. C., Van Nieuwenhuyse, E., Wagener, S. M., & Reynolds, J. B. (1983). *Effect of gold placer mining on interior Alaska stream ecosystems. Managing water resources for Alaska's development* (Institute of Water Resources Report IWR-105). University of Alaska, Fairbanks.

Leopold, L. B., & Maddock, T., Jr. (1953). The hydraulic geometry of stream channels and some physiographic implications. *Professional Paper*. Series number 252, vi, 57 p. https://doi.org/10.3133/pp252

Limm, M. P., & Marchetti, M. P. (2009). Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) growth in off-channel and main-channel habitats on the Sacramento River, CA using otolith increment widths. *Environmental Biology of Fishes*, *85*(2), 141–151. https://doi.org/10.1007/s10641-009-9473-8

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*(4), 399–417. https://doi.org/10.2307/1930126

Lusardi, R. A., Hammock, B. G., Jeffres, C. A., Dahlgren, R. A., & Kiernan, J. D. (2019). Oversummer growth and survival of juvenile coho salmon (*Oncorhynchus kisutch*) across a natural gradient of stream water temperature and prey availability: An in situ enclosure experiment. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(2), 413–424. https://doi.org/10.1139/cjfas-2018-0484

Lusardi, R. A., Jeffres, C. A., & Moyle, P. B. (2018). Stream macrophytes increase invertebrate production and fish habitat utilization in a California stream. *River Research and Applications*, *34*(8), 1003–1012. https://doi.org/10.1002/rra.3331

Marcarelli, A. M., Baxter, C. V., Benjamin, J. R., Miyake, Y., Murakami, M., Fausch, K. D., & Nakano, S. (2020). Magnitude and direction of stream–forest community interactions change with timescale. *Ecology*, *101*(8), 1–10. https://doi.org/10.1002/ecy.3064

Martel, G. (1996). Growth rate and influence of predation risk on territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(3), 660–669. https://doi.org/10.1139/f95-225

McCarthy, S. G., Duda, J. J., Emlen, J. M., Hodgson, G. R., & Beauchamp, D. A. (2009). Linking habitat quality with trophic performance of steelhead along forest gradients in the South Fork Trinity River watershed, California. *Transactions of the American Fisheries Society*, *138*(3), 506–521. https://doi.org/10.1577/t08-053.1

McHugh, P. A., Saunders, W. C., Bouwes, N., Wall, C. E., Bangen, S., Wheaton, J. M., Nahorniak, M., Ruzycki, J. R., Tattam, I. A., & Jordan, C. E. (2017). Linking models across scales to assess the viability and restoration potential of a threatened population of steelhead (*Oncorhynchus mykiss*) in the Middle Fork John Day River, Oregon, USA. *Ecological Modelling*, *355*(C), 24–38.

Metcalfe, A. N., Fritzinger, C. A., Weller, T. J., Dodrill, M. J., Muehlbauer, J. D., Yackulic, C. B., Holton, P. B., Szydlo, C. M., Durning, L. E., Sankey, J. B., & Kennedy, T. A. (2023). Insectivorous bat foraging tracks the availability of aquatic flies (Diptera). *The Journal of Wildlife Management*, *87*, e22414. https://doi.org/10.1002/jwmg.22414

Metcalfe, N. B., Bull, C. D., & Mangel, M. (2002). Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. *Evolutionary Ecology Research*, *4*(6), 871–881.

Metcalfe, N. B., Fraser, N. H. C., & Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, *68*(2), 371–381. https://doi.org/10.1046/j.1365-2656.1999.00289.x

Metcalfe, N. B., Huntingford, F. A., & Thorpe, J. E. (1986). Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology*, *64*(11), 2439–2446. https://doi.org/10.1139/z86-364

Montgomery, D. R. (1999). Process domains and river continuum. *Journal of the American Water Resources Association*, *35*(2), 397–410. https://doi.org/10.1111/j.1752-1688.1999.tb03598.x

Moore, J. W., Schindler, D. E., & Ruff, C. P. (2008). Habitat saturation drives thresholds in stream subsidies. *Ecology*, *89*(2), 306–312. https://doi.org/10.1890/07-1269.1

Morley, S. A., Foley, M. M., Duda, J. J., Beirne, M. M., Paradis, R. L., Johnson, R. C., McHenry, M. L., Elofson, M., Sampson, E. M., McCoy, R. E., Stapleton, J., & Pess, G. R. (2020). Shifting food web structure during dam removal—Disturbance and recovery during a major restoration action. *PLoS One*, *16*(1), e0246517. https://doi.org/10.1371/journal.pone.0239198

Muhlfeld, C. C., Dauwalter, D. C., D'angelo, V. S., Ferguson, A., Giersch, J. J., Impson, D., Koizumi, D. I., Kovack, R., McGinnity, P., Shoeffmann, J., Epifano, J. & Vøllestad, L. A., J. (2019). Chapter 21: Global status of trout and char: Conservation challenges in the twenty-first century. In J. L. Kershner, J. E. Williams, R. E. Gresswell, & J. Lobón-Cerviá (Eds.), *Trout and char of the world* (pp. 717–760). American Fisheries Society.

Myrvold, K. M., & Kennedy, B. P. (2020). Seasonal variation in growth, consumption and growth efficiency in overwintering juvenile steelhead. *Ecology of Freshwater Fish*, *29*(3), 450–464. https://doi.org/10.1111/eff.12526

Naiman, R. J., Alldredge, J. R., Beauchamp, D. A., Bisson, P. A., Congleton, J., Henny, C. J., Huntly, N., Lamberson, R., Levings, C., Merrill, E. N., Pearcy, W. G., Rieman, B. E., Ruggerone, G. T., Scarnecchia, D., Smouse, P.E., & Wood, C. C. (2012). Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(52), 21201–21207. https://doi.org/10.1073/pnas.1213408109

Nakano, S., Miyasaka, H., & Kuhara, N. (1999). Terrestrial–aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, *80*(7), 2435–2441. https://doi.org/10.1890/0012-9658(1999)080[2435:TALRAI]2.0.CO;2

Nakano, S., & Murakami, M. (2001). Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(1), 166–170. https://doi.org/10.1073/pnas.98.1.166

Naman, S. M., Rosenfeld, J. S., Kiffney, P. M., & Richardson, J. S. (2018). The energetic consequences of habitat structure for forest stream salmonids. *Journal of Animal Ecology*, *87*, 1383–1394. https://doi.org/10.1111/1365-2656.12845

Naman, S. M., Rosenfeld, J. S., Neuswanger, J. R., Enders, E. C., Hayes, J. W., Goodwin, E. O., Jowett, I. G., & Eaton, B. C. (2020). Bioenergetic habitat suitability curves for instream flow modeling: Introducing user-friendly software and its potential applications. *Fisheries*, *45*(11), 605–613. https://doi.org/10.1002/fsh.10489

Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2016). Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(8), 1292–1305. https://doi.org/10.1139/cjfas-2015-0363

Naman, S. M., Rosenfeld, J. S., Third, L. C., & Richardson, J. S. (2017). Habitat-specific production of aquatic and terrestrial invertebrate drift in small forest streams: Implications for drift-feeding fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(8), 1208–1217. https://doi.org/10.1139/cjfas-2016-0406

Naman, S. M., White, S. M., Bellmore, J. R., McHugh, P. A., Kaylor, M. J., Baxter, C. V., Danehy, R. J., Naiman, R. J., & Puls, A. L. (2022). Food web perspectives and methods for riverine fish conservation. *Wiley Interdisciplinary Reviews: Water*, *9*, 1–21. https://doi.org/10.1002/wat2.1590

Neubauer, P., & Andersen, K. H. (2019). Thermal performance of fish is explained by an interplay between physiology, behaviour and ecology. *Conservation Physiology*, *7*(1), 1–14. https://doi.org/10.1093/conphys/coz025

Neuswanger, J. R., Schoen, E. R., Wipfli, M. S., Volk, C. J., & Savereide, J. W. (2022). A suction pump sampler for invertebrate drift detects exceptionally high concentrations of small invertebrates that drift nets miss. *Hydrobiologia*, *849*(9), 2077–2089. https://doi.org/10.1007/s10750-022-04849-1

Newbold, J. D., Elwood, J. W., O'Neill, R. V., & van Winkle, W. (1981). Measuring nutrient spiralling in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(7), 860–863. https://doi.org/10.1139/f81-114

Parmar, T. P., Kindinger, A. L., Mathieu-Resuge, M., Twining, C. W., Shipley, J. R., Kainz, M. J., & Martin-Creuzburg, D. (2022). Fatty acid composition differs between emergent aquatic and terrestrial insects—A detailed single system approach. *Frontiers in Ecology and Evolution*, *10*, 1–13. https://doi.org/10.3389/fevo.2022.952292

Peake, J. A., MacDonald, T. C., Thompson, K. A., & Stallings, C. D. (2022). Community dynamics of estuarine forage fishes are associated with a latitudinal basal resource regime. *Ecosphere*, *13*(5), e4038. https://doi.org/10.1002/ecs2.4038

Peckarsky, B. L., & McIntosh, A. R. (1998). Fitness and community consequences of avoiding multiple predators. *Oecologia*, *113*(4), 565–576. https://doi.org/10.1007/s004420050410

Peters, R. H. (1986). *The ecological implications of body size*. Cambridge University Press.

Pianosi, F., Beven, K., Freer, J., Hall, J. W., Rougier, J., Stephenson, D. B., & Wagener, T. (2016). Sensitivity analysis of environmental models: A systematic review with practical workflow. *Environmental Modelling & Software*, *79*, 214–232. https://doi.org/10.1016/j.envsoft.2016.02.008

Pinto, M. C., Post, J. R., Paul, A. J., Johnston, F. D., Mushens, C. J., & Stelfox, J. D. (2013). Lateral and longitudinal displacement of stream-rearing juvenile bull trout in response to upstream migration of spawning adults. *Transactions of the American Fishy Society*, *142*, 1590–1601. https://doi.org/10.1080/00028487.2013.822419

Platt, T., & Sathyendranath, S. (1988). Oceanic primary production: Estimation by remote sensing at local and regional scales. *Science*, *241*(4873), 1613–1620. https://doi.org/10.1126/science.241.4873.1613

Poff, N. L., & Huryn, A. D. (1998). Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 201–217. https://doi.org/10.1139/cjfas-55-s1-201

Power, M. E., Dietrich, W. E., & Sullivan, K. (1998). Experimentation, observation, and inference in river and watershed investigations—Chapter 6. In *Experimental ecology* (pp. 113–132). Oxford University Press.

Power, M. E., & Rainey, W. E. (2000). Food webs and resource sheds: Towards spatially delimiting trophic interactions. In M. J. Hutchings, E. A. John, & A. J. A. Stewart (Eds.), *Ecological consequences of habitat heterogeneity* (pp. 291–314). Blackwell Scientific.

Power, M. E., Parker, M. S., & Dietrich, W. E. (2008). Seasonal reassembly of a river food web: Floods, droughts, and impacts of fish. *Ecological Monographs*, *78*(2), 263–282. https://doi.org/10.1890/06-0902.1

Provenza, F. D., Anderson, C., & Gregorini, P. (2021). We are the earth and the earth is us: How palates link foodscapes, landscapes, heartscapes, and thougtscapes. *Frontiers in Sustainable Food Systems*, *5*, 1–16. https://doi.org/10.3389/fsufs.2021.547822

Rader, R. B. (1997). A functional classification of the drift: Traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 1211–1234. https://doi.org/10.1139/f97-025

Railsback, S. F., & Harvey, B. C. (2011). Importance of fish behaviour in modelling conservation problems: Food limitation as an example. *Journal of Fish Biology*, *79*(6), 1648–1662. https://doi.org/10.1111/j.1095-8649.2011.03050.x

Railsback, S. F. (2022). What we don't know about the effects of temperature on salmonid growth. *Transactions of the American Fisheries Society*, *151*(1), 3–12. https://doi.org/10.1002/tafs.10338

Railsback, S. F., Ayllón, D., & Harvey, B. C. (2021). InSTREAM 7: Instream flow assessment and management model for stream trout. *River Research and Applications*, *37*(9), 1294–1302. https://doi.org/10.1002/rra.3845

Railsback, S. F., Harvey, B. C., Hayse, J. W., & LaGory, K. E. (2005). Tests of theory for diel variation in salmonid feeding activity and habitat use. *Ecology*, *86*(4), 947–959. https://doi.org/10.1890/04-1178

Rashidabadi, F., Rosenfeld, J. S., Abdoli, A., Naman, S. M., & Nicolas, A. (2022). Seasonal changes in invertebrate drift: Effects of declining summer flows on prey abundance for drift-feeding fishes. *Hydrobiologia*, *849*(8), 1855–1869. https://doi.org/10.1007/s10750-022-04831-x

Reinhardt, U. G., & Healey, M. C. (1999). Season- and size-dependent risk taking in juvenile coho salmon: Experimental evaluation of asset protection. *Animal Behaviour*, *57*(4), 923–933. https://doi.org/10.1006/anbe.1998.1051

Rose, K. A., Cowan, J. H., Jr., Winemiller, K. O., Myers, R. A., & Hilborn, R. (2001). Compensatory density dependence in fish populations: Importance, controversy, understanding and prognosis. *Fish and Fisheries*, *2*, 293–327. https://doi.org/10.1046/j.1467-2960.2001.00056.x

Rosenberger, A. E., Dunham, J. B., Neuswanger, J. R., & Railsback, S. F. (2015). Legacy effects of wildfire on stream thermal regimes and rainbow trout ecology: An integrated analysis of observation and individual-based models. *Freshwater Science*, *34*(4), 1571–1584. https://doi.org/10.1086/683338

Rosenfeld, J., Gonzalez-Espinosa, P., Jarvis, L., Enders, E., Bayly, M., Paul, A., MacPherson, L., Moor, J., sullivan, M., Ulaski, M., & Wilson, K. (2022). Stressor–response functions as a generalizable model for context dependence. *Trends in Ecology and Evolution*, *37*(12), 1032–1035. https://doi.org/10.1016/j.tree.2022.09.010

Rosenfeld, J. S., Ayllón, D., Grant, J. W. A., Naman, S. M., Post, J. R., Matte, J.-M., & Monnet, G. (2024). Determinants of productive capacity for stream salmonids. In J. Lobon-Cervia, P. Budy, & R. Gresswell (Eds.), *Advances in the ecology of stream-dwelling salmonids* (pp 491–549). Springer.

Rosenfeld, J. S., Bouwes, N., Wall, C. E., & Naman, S. M. (2014). Successes, failures, and opportunities in the practical application of drift-foraging models. *Environmental Biology of Fishes*, *97*(5), 551–574. https://doi.org/10.1007/s10641-013-0195-6

Rosenfeld, J. S., & Hatfield, T. (2006). Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*, 683–698. https://doi.org/10.1139/F05-242

Rosenfeld, J. S., & Naman, S. M. (2019). A simple method for sampling invertebrate drift in large rivers and boulder—Bed streams. *River Research and Applications*, *35*(4), 442–447. https://doi.org/10.1002/rra.3424

Rosenfeld, J. S., Post, J., Robins, G., & Hatfield, T. (2007). Hydraulic geometry as a physical template for the river continuum: Application to optimal flows and longitudinal trends in salmonid habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(5), 755–767. https://doi.org/10.1139/F07-020

Rosenfeld, J. S., & Ptolemy, R. (2012). Modelling available habitat versus available energy flux: Do PHABSIM applications that neglect prey abundance underestimate optimal flows for juvenile salmonids? *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(12), 1920–1934. https://doi.org/10.1139/f2012-115

Rossi, G. J., Bellmore, J. R., Armstrong, J. B., Jeffres, C., Naman, S. M., Carlson, S. M., Grantham, T. E., Kaylor, M. J., White, S., Katz, J., & Power, M. E. (2024). Foodscapes for salmon and other mobile consumers in river networks. *Biosciences*. https://doi.org/10.1101/2023.08.30.555604

Rossi, G. J., Power, M. E., Pneh, S., Neuswanger, J. R., & Caldwell, T. J. (2021). Foraging modes and movements of *Oncorhynchus mykiss* as flow and invertebrate drift recede in a California stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(8), 1045–1056. https://doi.org/10.1139/cjfas-2020-0398

Rüegg, J., Conn, C. C., Anderson, E. P., Battin, T. J., Bernhardt, E. S., Boix Canadell, M., Bonjour, S. M., Hosen, J. D., Marzolf, N., & Yackulic, C. B. (2021). Thinking like a consumer: Linking aquatic basal metabolism and consumer dynamics. *Limnology and Oceanography Letters*, *6*(1), 1–17. https://doi.org/10.1002/lol2.10172

Šabacká, M., Priscu, J. C., Basagic, H. J., Fountain, A. G., Wall, D. H., Virginia, R. A., & Greenwood, M. C. (2012). Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. *Geomorphology*, *155–156*, 102–111. https://doi.org/10.1016/j.geomorph.2011.12.009

Sabo, J. L., Bastow, J. L., & Power, M. E. (2002). Length–mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society*, *21*(2), 336–343. https://doi.org/10.2307/1468420

Samways, K. M., Soto, D. X., & Cunjak, R. A. (2018). Aquatic food-web dynamics following incorporation of nutrients derived from Atlantic anadromous fishes. *Journal of Fish Biology*, *92*(2), 399–419. https://doi.org/10.1111/jfb.13519

Samways, K. M., & Cunjak, R. A. (2015). Increases in benthic community production and metabolism in response to marine-derived nutrients from spawning Atlantic salmon (*Salmo salar*). *Freshwater Biology*, *60*(8), 1647–1658. https://doi.org/10.1111/fwb.12597

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, *163*(3), 429–441.

Schindler, D. E., Augerot, X., Fleishman, E., Mantua, N. J., Riddell, B., Ruckelshaus, M., Seeb, J., & Webster, M. (2008). Climate change, ecosystem impacts, and management for Pacific salmon. *Fisheries*, *33*(10), 502–506. https://doi.org/10.1577/1548-8446-33.10.502

Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *Bioscience*, *41*(10), 704–712. https://doi.org/10.2307/1311765

Scholl, E. A., Cross, W. F., & Guy, C. S. (2022). Geomorphology shapes relationships between animal communities and ecosystem function in large rivers. *Oikos*, *2023*(2), e09431. https://doi.org/10.1111/oik.09431

Sethi, S. A., Carey, M. P., Gerken, J., Harris, B. P., Wolf, N., Cunningham, C., Restrepo, F., & Ashline, J. (2022). Juvenile Salmon habitat use drives variation in growth and highlights vulnerability to river fragmentation. *Ecosphere*, *13*(8), e4192. https://doi.org/10.1002/ecs2.4192

Shanks, A. L., Morgan, S. G., MacMahan, J., Reniers, A. J. H. M., Jarvis, M., Brown, J., Fujimura, A., Ziccarelli, L., & Griesemer, C. (2018). Persistent differences in horizontal gradients in phytoplankton concentration maintained by surf zone hydrodynamics. *Estuaries and Coasts*, *41*(1), 158–176. https://doi.org/10.1007/s12237-017-0278-2

Shearer, K. A., Hayes, J. W., Jowett, I. G., & Olsen, D. A. (2015). Habitat suitability curves for benthic macroinvertebrates from a small New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, *49*(2), 178–191. https://doi.org/10.1080/00288330.2014.988632

Shearer, K. A., Stark, J. D., Hayes, J. W., & Young, R. G. (2003). Relationships between drifting and benthic invertebrates in three New Zealand rivers: Implications for drift-feeding fish. *New Zealand Journal of Marine and Freshwater Research*, *37*(4), 809–820. https://doi.org/10.1080/00288330.2003.9517210

Simonis, J. L., & Merz, J. E. (2019). Prey availability, environmental constraints, and aggregation dictate population distribution of an imperiled fish. *Ecosphere*, *10*(3), e02634. https://doi.org/10.1002/ecs2.2634

Sirot, C., Villéger, S., Mouillot, D., Darnaude, A. M., Ramos-Miranda, J., Flores-Hernandez, D., & Panfili, J. (2015). Combinations of biological attributes predict temporal dynamics of fish species in response to environmental changes. *Ecological Indicators*, *48*, 147–156. https://doi.org/10.1016/j.ecolind.2014.07.038

Steel, E. A., Beechie, T. J., Ruckelshaus, M. H., Fullerton, A. H., McElhany, P., & Roni, P. (2009). Mind the gap: Uncertainty and model communication between managers and scientists. In E. E. Knudsen & J. H. Michael, Jr. (Eds.), *Pacific Salmon environmental and life history models. 71* (pp. 357–372). American Fisheries Society Symposium.

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, *29*(1), 344–358. https://doi.org/10.1899/08-171.1

Sullivan, S. P., & White, S. M. (2017). *Methods supporting the development of food web metrics from benthic macroinvertebrate data* (Technical Report 17-05). Columbia River Inter-Tribal Fish Commission. https://critfc.org/wp-content/uploads/2021/08/17_05.pdf

Thompson, J. N., & Beauchamp, D. A. (2014). Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. *Transactions of the American Fisheries Society*, *143*(4), 910–925. https://doi.org/10.1080/00028487.2014.901253

Thompson, J. N., & Beauchamp, D. A. (2016). Growth of juvenile steelhead *Oncorhynchus mykiss* under size-selective pressure limited by seasonal bioenergetic and environmental constraints. *Journal of Fish Biology*, *89*(3), 1720–1739. https://doi.org/10.1111/jfb.13078

Thorp, J. H., & Bowes, R. E. (2017). Carbon sources in riverine food webs: New evidence from amino acid isotope techniques. *Ecosystems*, *20*(5), 1029–1041. https://doi.org/10.1007/s10021-016-0091-y

Torgersen, C. E., Le Pichon, C., Fullerton, A. H., Dugdale, S. J., Duda, J. J., Giovannini, F., Tales, E., Belliard, J., Branco, P. Bergeron, N. E., Roy, M. L., Tonolla, D., Lamouroux, N., Capra, H., & Baxter, C. V. (2021). Riverscape approaches in practice: Perspectives and applications. *Biological Reviews*, *97*(2), 481–504. https://doi.org/10.1111/brv.12810

Twining, C. W., Brenna, J. T., Lawrence, P., Shipley, J. R., Tollefson, T. N., & Winkler, D. W. (2016). Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *Proceedings of the National Academy of Sciences*, *113*(39), 10920–10925. https://doi.org/10.1073/pnas.1603998113

Vannote, R. L., & Sweeney, B. W. (1980). Geographic analysis of thermal equilibria: A conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist*, *115*(5), 667–695. https://doi.org/10.1086/283591

Vinson, M. R., & Baker, M. A. (2008). Poor growth of rainbow trout fed New Zealand mud snails *Potamopyrgus antipodarum*. *Northerican American Journal of Fisheries Management*, *28*, 701–709. https://doi.org/10.1577/m06-039.1

Wall, C. E., Bouwes, N., Wheaton, J. M., Saunders, W. C., & Bennett, S. N. (2016). Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse basins from a large monitoring program. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(7), 1081–1091. https://doi.org/10.1139/cjfas-2015-0290

Walters, C. J., & Juanes, F. (1993). Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*(10), 2058–2070. https://doi.org/10.1139/f93-229

Warren, C. E., & Davis, G. E. (1967). *Laboratory studies on the feeding, bioenergetics, and growth of fish*. https://api.semanticscholar.org/CorpusID:54756867

Weber, N., Bouwes, N., & Jordan, C. (2017). Accounting for spatial and temporal variation in macroinvertebrate community abundances when measuring the food supply of stream salmonids. *Freshwater Science*, *36*(2), 364–376. https://doi.org/10.1086/692012

Weber, N., Bouwes, N., & Jordan, C. E. (2014). Estimation of salmonid habitat growth potential through measurements of invertebrate food abundance and temperature. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 1158–1170. https://doi.org/10.1139/cjfas-2013-0390

Werner, E. E., & Gilliam, J. F. (2008). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Wesner, J. S. (2016). Contrasting effects of fish predation on benthic versus emerging prey: A meta-analysis. *Oecologia*, *180*(4), 1205–1211. https://doi.org/10.1007/s00442-015-3539-4

Whitney, E. J., Bellmore, J. R., Benjamin, J. R., Jordan, C. E., Dunham, J. B., Newsom, M., & Nahorniak, M. (2020). Beyond sticks and stones: Integrating physical and ecological conditions into watershed restoration assessments using a food web modeling approach. *Food Webs*, *25*, e00160. https://doi.org/10.1016/j.fooweb.2020.e00160

Williams, D. D., Barnes, J.-A., & Beach, P. C. (1993). The effects of prey profitability and habitat complexity on the foraging success and growth of stonefly (Plecoptera) nymphs. *Freshwater Biology*, *29*(1), 107–117. https://doi.org/10.1111/j.1365-2427.1993.tb00749.x

Wilson, K. L., Sawyer, A. C., Potapova, A., Bailey, C. J., LoScerbo, D., Sweeney-Bergen, E. K., Hodgson, E. E., Pitman, K. J., Seitz, K. M., Law, L. K., & Warkentin, L. (2023). The role of spatial structure in at-risk metapopulation recoveries. *Ecological Applications*, *33*(6), e2898.

Wipfli, M. S., & Baxter, C. V. (2010). Linking ecosystems, food webs, and fish production: Subsidies in salmonids watersheds. *Fisheries*, *35*, 373–387. https://doi.org/10.1577/1548-8446-35.8.373

Wood, C. M., & McDonald, D. G. (1997). *Global warming: Implications for freshwater and marine fish* (p. 444). Cambridge University Press.

Wootton, J. T., Parker, M. S., Power, M. E., Wootton, J. T., Parker, M. S., & Power, M. E. (1996). Effects of disturbance on river food webs. *Science*, *273*(5281), 1558–1561. https://doi.org/10.1126/science.273.5281.1558

Yard, M. D., Yackulic, C. B., Korman, J., Dodrill, M. J., & Deemer, B. R. (2023). Declines in prey production during the collapse of a tailwater rainbow trout population are associated with changing reservoir conditions. *Transactions of the American Fisheries Society*, *152*, 35–50. https://doi.org/10.1002/tafs.10381

Young, M. K., Rader, R. B., & Belish, T. A. (1997). Influence of macroinvertebrate drift and light on the activity and movement of Colorado river cutthroat trout. *Transactions of the American Fisheries Society*, *126*(3), 428–437. https://doi.org/10.1577/1548-8659(1997)126<0428:IOMDAL>2.3.CO;2

Zabel, R. W., & Achord, S. (2004). Relating size of juveniles to survival within and among populations of Chinook salmon. *Ecology*, *85*(3), 795–806. https://doi.org/10.1890/02-0719

Zamor, R. M., & Grossman, G. D. (2007). Turbidity affects foraging success of drift-feeding Rosyside dace. *Transactions of the American Fisheries Society*, *136*, 167–176. https://doi.org/10.1577/T05-316.1

Závorka, L., Crespel, A., Dawson, N. J., Papatheodoulou, M., Killen, S. S., & Kainz, M. J. (2021). Climate change-induced deprivation of dietary essential fatty acids can reduce growth and mitochondrial efficiency of wild juvenile salmon. *Functional Ecology*, *35*(9), 1960–1971. https://doi.org/10.1111/1365-2435.13860

How to cite this article: Ouellet, V., Fullerton, A. H., Kaylor, M., Naman, S., Bellmore, R., Rosenfeld, J., Rossi, G., White, S., Rhoades, S., Beauchamp, D. A., Liermann, M., Kiffney, P., & Sanderson, B. (2025). Food for fish: Challenges and opportunities for quantifying foodscapes in river networks. *WIREs Water*, *12*(1), e1752. https://doi.org/10.1002/wat2.1752