Foodscapes for salmon and other mobile consumers in river networks

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Abstract

Mobile consumers track fluctuating resources across heterogeneous landscapes to grow and survive. In river networks, the abundance and accessibility of food and the energetic consequences of foraging vary among habitats and through time, providing a shifting mosaic of growth opportunities for mobile consumers. However, a framework integrating the spatiotemporal dynamics of growth potential within riverscapes has been lacking. We present the concept of foodscapes to depict the dynamic changes in food abundance, food accessibility, and consumer physiology that contribute to spatial and temporal variation of fish growth in rivers. Drawing on case studies of salmonid fishes from Alaska to California, we illustrate how foodscapes can provide a plethora of foraging, growth, and life history opportunities that potentially contribute to population resilience. We identify knowledge gaps in understanding foodscapes and approaches for stewardship that focus on restoring diverse foraging and growth opportunities for fish and other mobile consumers in river networks.

Keywords: riverscapes, growth, food web phenology, bioenergetics, resource tracking

To grow and survive, mobile consumers must track fluctuating resources across heterogeneous environments, sometimes over vast distances (e.g., Sinclair and Beyers 2021). Although some species migrate from the north pole to the south pole and others move thousands of kilometers annually (Joly et al. 2019), few encounter such extreme variation in habitats as migratory salmonids. As juveniles, Pacific and Atlantic salmon and other migratory salmonids may use most types of aquatic habitats available in river networks, with many species emerging in headwaters to rear in small streams before moving into mainstem rivers, backwaters, or lakes. They may cross inundated floodplains and off-channel habitats or rear in estuaries and saltwater sloughs before finally moving to nearshore environments and the open ocean (Quinn 2007).

The importance of physical heterogeneity across watersheds for fish has long been recognized (e.g., Schlosser 1991). Fausch and colleagues (2002) and Wiens (2002), adapting concepts from landscape ecology, encouraged moving beyond studies of isolated stream reaches to consider the riverscape: the continuous, hierarchical, and heterogeneous nature of riverine ecosystems (table 1). The riverscape concept, along with similar frameworks (e.g., shifting habitat mosaics; Stanford et al. 2005), emphasizes the diversity and connectivity of habitats that fish use to complete their life cycles. Much of the subsequent research and application of these frameworks to habitat assessment and restoration has been focused on physical habitat conditions, such as channel form, stream hydraulics, and water temperature (as was discussed in Wipfli and Baxter 2010, and Bilby et al. 2024). But the persistence and success of fish in these dynamic environments also depends on their ability to grow, which is not only a function of physical conditions such as temperature and water velocity but also of biotic conditions, including the abundance, quality, and accessibility of prey (Elton 1927, Chapman 1966, Poff and Huryn 1998, Whitney et al. 2020).

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Table 1. Definition of terms that apply to foodscapes.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
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<tbody>
<tr>
<td>Food</td>
<td>A nutritious substance that consumers eat and assimilate.</td>
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<tr>
<td>Riverscape</td>
<td>The continuous, hierarchical, and heterogeneous mosaic of habitats along a drainage network.</td>
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<tr>
<td>Nutritional resources</td>
<td>Includes both food and the constituents fueling food production (e.g., inorganic nutrients, solar energy).</td>
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<tr>
<td>Resource shed</td>
<td>Source areas within a foodscape that contribute food and nutritional resources that support consumers.</td>
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<tr>
<td>Resource flux</td>
<td>The transport or movement of nutritional resources through the environment. We focus on fluxes to, and among, foraging patches within foodscapes.</td>
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<tr>
<td>Trophic pathways</td>
<td>The pathways through a food web along which nutritional resources flow—from primary producers to consumers. A trophic pathway is like a resource flux, but the focus is on energetics and food web links, rather than spatial fluxes.</td>
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<tr>
<td>Resource or food phenology</td>
<td>The temporal (often seasonal) sequence of biological events that produce food or make it accessible to consumers. We focus on the temporal patterns of food production, delivery, quality, and availability.</td>
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<tr>
<td>Prey (or food) accessibility</td>
<td>Proportion of food abundance within a foraging patch that a forager can consume. This proportion is determined by both prey and habitat features (biotic and abiotic) that affect the consumer’s ability to encounter, detect, and capture food items.</td>
</tr>
<tr>
<td>Prey (or food) assimilation</td>
<td>Ingested food that is absorbed (crossing the gut walls of animal consumers) and converted to energy or cytoplasm to support the consumer.</td>
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<tr>
<td>Gut passage time</td>
<td>The time it takes for food to move through an organism’s digestive tract, and either be assimilated or excreted.</td>
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<tr>
<td>Gut capacity</td>
<td>The mass or volume of food that an organism can retain in its digestive tract at any one time.</td>
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<tr>
<td>Metabolic rate</td>
<td>The amount of energy expended by a consumer over a specific time period. For fishes this has almost always been measured as O₂ removal from the water. Using O₂ accounts only for aerobic energy production, the primary metabolic pathways in fishes (see Nelson 2016). Types of energy use include the standard metabolic rate (a measure of the energy required to maintain essential functions), activity costs (e.g., “swimming costs”), and the energy used for digestion, excretion, and gonad production (Fry 1947, Brett and Groves 1979).</td>
</tr>
<tr>
<td>Feeding rate</td>
<td>The amount of food consumed over a period of time. In fishes, this can vary with multiple factors including fish size, water temperature, food abundance and size, competition, and perception of risk (fear).</td>
</tr>
<tr>
<td>Physiological growth potential</td>
<td>The growth rate that would be possible if only a consumer’s physiological constraints and behaviors were considered. These constraints include metabolic costs such as standard metabolic rate and energy expenditure due to activity. They also include the consumer’s maximum feeding rate, digestion rate and capacity and assimilation efficiency. Physiological growth potential describes the scope for growth (Fry 1947, Brett and Groves 1979) predicted by traditional bioenergetics models, but does not integrate the ecological dynamics of food abundance or accessibility.</td>
</tr>
<tr>
<td>Ecological growth potential</td>
<td>The maximum growth rate a given consumer could achieve in a patch of the foodscapes mosaic, as a function of food abundance, food accessibility, and physiological growth potential (see box 1).</td>
</tr>
<tr>
<td>Life history diversity</td>
<td>Variation in how animals balance trade-offs among survival, growth, and reproduction. We emphasize one aspect of life history diversity: the different ways that animals move through the foodscapes to exploit patterns of ecological growth potential through time (see box 2).</td>
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In addition to the abundance and quality of these different food sources, an individual’s growth also depends on food accessibility (table 1). Food accessibility can change with abiotic conditions; for example, high velocities preclude drift foraging for small fish in larger mainstem rivers, and high turbidity may reduce foraging efficiency of visual predators (Sweka and Hartman 2001, Harvey and Railsback 2014). Some prey items are not as available in the water column to drift foraging fishes (Rader 1997) or have structural defenses that preclude consumption or assimilation (Wootton et al. 1996). Prey accessibility (sensu lato, Railsback et al. 2005) for a given forager depends on prey morphological and behavioral traits (which may change over space and time), abiotic factors, and trade-offs between prey quality and foraging risks (e.g., predation). Finally, growth is also mediated by a consumer’s physiological growth potential (table 1), including the metabolic costs of foraging, such as those incurred while swimming between different foraging habitats (i.e., activity costs), and other endogenous factors, such as feeding rate, prey assimilation, and digestion rate, which ultimately influence growth (e.g., Fausch 1984, Hughes and Dill 1990). Traditionally, bioenergetic models (such as drift foraging models) have not accounted for the ecological dynamics of food abundance and food accessibility (but see Rossi et al. 2022 or Rhoades et al. 2023), nor have they been applied at spatial and temporal scales relevant to the life history of many mobile freshwater fishes.

Each component of growth potential is influenced by environmental conditions that fluctuate spatially and temporally in watersheds. For salmonids and other stream-dwelling organisms, water temperature influences each of three determinates of growth: food abundance, food accessibility, and physiological growth potential (table 1, box 1). For example, water temperature can influence gross primary productivity (Davison 1991), as well as aquatic invertebrate growth rates, emergence, and fecundity (Bonacina et al. 2023). Salmonids are poikilotherms, and their basal metabolic costs increase exponentially with temperature, whereas their physiological capacities (e.g., activity, gut capacity, or feeding rate) typically exhibit a hump-shaped relationship (Fry 1947, Brett and Groves 1979). Ecological factors determine where fish fall on these curves. Specifically, fish in the wild generally feed at a small fraction of their assimilative capacity, suggesting they are limited by food availability (Armstrong and Schindler 2011), and activity levels interact with hydraulic conditions (e.g., velocity, turbulence) to elevate metabolic rates, reducing how much energy from consumption is left over for growth (Oldham et al. 2019).
Collectively, food abundance, food accessibility, and a consumer’s physiological growth potential all vary across space and time (box 1) creating a dynamic mosaic of asynchronous growth hotspots that mobile consumers can exploit. However, it is a mosaic in which growth potential is balanced against the risks of predation, death from dangerous environmental conditions (e.g., stranding or hypoxia), and access to and competition for foraging habitats. In the present article, we synthesize the spatiotemporal dynamics of food abundance, food accessibility, and a consumer’s physiological growth potential into the concept of foodscape—the shifting mosaic of growth potential that mobile consumers exploit across a patchy environment (box 2). Although a growing body of work illustrates the emerging value of a foodscape perspective in salmon ecology and management (e.g., Searle et al. 2007, Wipfli and Baxter 2010, Bellmore et al. 2013, Rossi 2020, Armstrong et al. 2021, Cordoleani et al. 2022, Sturrock et al. 2022), we are unaware of any studies that have attempted to quantify the foodscape at spatiotemporal scales that match consumer life histories. For salmonid fishes, ecological growth potential—that is, physiological potential constrained by the ecological dynamics of food abundance and accessibility (figure 1)—has not been estimated in any system at the riverscale (e.g., headwaters to sea) throughout the complete annual cycle. In addition, although the importance of growth potential and food for mobile consumers is well recognized, there is no holistic framework that integrates the mechanisms underlying growth potential with the concepts of resource tracking and life history diversity.

Conceptualizing watersheds as foodscape raises new questions about the factors that control the distribution, abundance, and life histories of mobile consumers. We propose the foodscape framework specifically to address questions such as what causes foraging and growth hot spots and hot moments of food availability to appear and disappear over space and time, how do mobile foragers such as migratory salmonids make use of dynamic patterns of food availability across the watershed habitat mosaic, and how closely do mobile consumers track spatiotemporal peaks in growth potential seasonally and through their life histories and what constrains their ability to do so as they grow, transform, and move through watersheds? Finally, we address how humans can detect, predict, and repair or manage foodscape to benefit mobile consumers such as salmon, and the socioecological systems they support.

We begin by defining the foodscape concept and explain how it can be specifically applied to better understand the distribution, abundance, movement, and life history diversity of salmonids, as well as other mobile consumers. We next present case studies from California to Alaska that reveal local foodsca pes and illustrate, in the aggregate, the utility of the foodscape perspective in understanding salmon ecology. We provide a brief review of how foodscape concepts could apply to mobile foragers in other landscapes (terrestrial and ocean). We then discuss approaches to evaluate foodscape and identify knowledge gaps that currently limit our capacity to measure, model, and manage foodsca pes for salmon and other mobile consumers. Finally, we consider approaches to restore, recover, and steward foodscape and tools managers can use to incorporate a foodscape perspective into salmonid conservation and recovery planning.

What is the foodscape?

The foodscape is a mosaic of linked habitats with different growth potential phenologies as seen through the eyes of a mobile consumer, or a population of mobile consumers, that moves among these habitats. The foodscape concept explores how foraging conditions and growth potentials vary across landscapes throughout the annual cycle. Specifically, it considers the shifting mosaic in food abundance, food accessibility, and physiological growth potential (box 1), which, in turn, provide diverse foraging and ecological growth (table 1) opportunities for mobile consumers across the landscape (box 2).

To assess a foodscape, we must delineate foraging patches in the mosaic, a task that draws partly artificial but conceptually meaningful boundaries across landscapes or riverscapes (e.g., Tansley 1935). How patches are defined may depend on the resolution and the specific goals of each foodscape assessment. Foodsca pes consider both the vital source areas that generate food (i.e., resource sheds, table 1; Power and Rainey 2000), as well as in situ physiochemical conditions that shape physiological growth potential in the foraging patch (box 1). Foodsca pes can be defined for the entire landscape that supports a consumer through its life or some portion of it (e.g., the freshwater phase of anadromous salmon, see also supplemental 1). Foodscape can also be described as ranging across a spectrum of ecological resolution, from generalized foodscape suites of similar consumers to individualized foodscape for single individuals. Generalized foodsca pes define broad seasonal spatial patterns in the determinants (box 1) or estimates (figure 2, shaded) of ecological growth potential for populations or functional groups of organisms with similar growth responses to prey abundance, prey accessibility, and abiotic factors. An individual foodscape is a time series of ecological growth potential across space (figure 2, solid lines), defined for an individual organism as it passes through successive life history stages or size classes. Individualized foodscape can be used to evaluate the different ways that consumers can exploit a foodscape through the expression of diverse life histories (e.g., figure 2).

While ecological growth potential is expressed for an individual (box 2), the concept also has implications for populations. The spatiotemporal dynamics of growth potential within a foodscape provide opportunities for diverse life histories within populations to exploit the complement of foraging and growth opportunities in different ways (e.g., the third case study below and figure 2). In turn, the diversity of life history patterns within a population, supported by a dynamic foodscape, may contribute to the productivity and stability of that population (Hilborn et al. 2003, Schindler et al. 2010, Flitcroft et al. 2016). Although relating foodscape dynamics to the expression of consumer life histories is a central theme of this article, we recognize that to fully addres s the population consequences of foodscape, practitioners will also have to consider how density dependence, habitat capacity and the risk of mortality (i.e., the deathscape) change temporally within each patch of the foodscape. These issues are not covered in this article but are fertile ground for future investigations.

To address the four questions posed in the introduction, we developed three hypotheses that frame the foodscape concept, which are presented in the Case Studies section below. The fourth question is discussed in the “Restoration, recovery, and stewardship of foodscape” section.

We suggest that these hypotheses are a useful starting point for any foodscape inquiry. Below, we present three case studies focused on salmonid fishes that address each of these hypotheses and highlight their importance to the foodscape concept.
Box 1. The spatial phenologies of three foodscape determinants.

Below we present a conceptual illustration of how temporal patterns of food abundance, food accessibility, and physiological growth potential might vary across habitats of a coastal, rainfall dominated riverscape in California (Figure 1). These patterns would differ in snowmelt-fed, spring-fed, or arid river systems. Collectively, patterns in food abundance, food accessibility, and physiological growth potential represent the determinants of ecological growth potential (Figure 1 inset). Ecological growth potential is the traditional scope for growth, constrained by a consumers maximum consumption rate (Cmax), and basal metabolic rate (Brett and Groves 1979) and further constrained by ecological factors that control food abundance (e.g., resource subsidies and in situ production), food accessibility (e.g., velocity, turbidity, and the structural or behavioral defenses of prey species), and the consumer’s physiological response to the foraging environment. We note that bioenergetic models commonly applied to salmonids typically consider a narrow range of the foraging environments that salmonids exploit (e.g., lentic habitats, floodplains, and large mainstem rivers are rarely modeled) and a narrow suite of energetic constraints (e.g., the energetic consequences of factors such as dissolved oxygen, turbidity and light are rarely parameterized). A foodscape perspective encourages a broader view of the ecological determinants that control ecological growth potential across time and space in the ecosystem.

Whether to lump or split suites of similar species in a generalized foodscape will depend on the purpose of the analysis. We suggest that grouping species with similar diets and life histories may often be beneficial for resource managers evaluating the major factors that constrain food production for groups of similar species. Broad patterns of food availability may often trump smaller differences in factors that constrain consumer physiology, because fish in the wild are often food limited (e.g., they generally feed at a small fraction of their assimilative capacity, Armstrong and Schindler 2011).

Figure 1. The three foodscape determinants highlighted here (food abundance, food accessibility, physiological growth potential) can be defined for varying levels of spatial and temporal resolution (e.g., the full range of a consumer’s occupied habitat or some subset of it). In addition, these determinants can be defined in a generalized way for suites of similar species, or as an individualized foodscape for a specific consumer (or functional groups) with well-defined physiological growth potential. A generalized foodscape for similar species, such as coho salmon and steelhead trout, may have identical patterns of food abundance (as they eat the same prey species), but only share broad patterns of food accessibility and physiological growth potential, because each species has unique endogenous energy budgets and behaviors. For example, in this illustration physiological growth potential in mainstem rivers becomes negative in late summer because of warm temperatures, which, in many systems, may be true for coho salmon but not for steelhead trout. Therefore, generalized foodscape may reflect only general periods of high growth potential (box 2) rather than discrete timeseries of growth potential (box 2).
Box 2. Consumer life histories interact with foodscapes to create complex growth trajectories.

Seasonal cycles in food availability, food accessibility, and physiological growth potential (box 1) result in asynchronous patterns of ecological growth potential across the riverscape (Figure 2a–2e), which, in turn, support distinct growth trajectories (Figure 2f) for fish that rear in these habitats at different times and for different durations. The individualized growth phenologies used in this heuristic simulation (figure 2) were informed by measurements of seasonal and habitat-specific growth of Oncorhynchus mykiss in several coastal, rainfall-dominated streams of the Pacific Northwest (Stillwater 2007, Hayes et al. 2008, Tattam et al. 2016, Thompson and Beauchamp, 2016, and Rossi et al. 2022), as well as the authors’ experiences. However, we could find no comprehensive estimates of seasonal spatial growth patterns in any single river system. The four life history trajectories (figure 2f) were broadly taken from Shapovalov and Taft (1954), Erman and Hawthorne (1976), and Hayes and colleagues (2008). These included two life histories of fish that reared for 1 year in their natal tributary, a third in which fish dispersed early to an upper mainstem habitat to rear, and a fourth in which year-of-the-year fish immediately moved to lower mainstem and estuarine habitat to rear (figure 2f). Growth trajectories (figure 2f) were simulated by combining seasonal growth potentials (figure 2a–2e) with bioenergetic modeling that accounted for allometric effects on fish metabolism. As fish moved between different habitats, daily mass-specific growth (g(t)) was a function of growth rates specified for the occupied habitat i at time t (ghabitat(i,t)); figure 2a–2e corrected for shifting allometric constraints on growth as fish size changed through time:

\[ g(t) = \frac{g_{\text{Max}_{\text{size}}}}{\frac{\text{Max}_{\text{size}}}{\text{Max}_{\text{size}}}} \times \frac{\text{Habitat}}{\text{Max}_{\text{size}}} \]

Habitat specific growth rates (ghabitat(i,t)) were divided by the maximum growth potential of an average size juvenile steelhead gMaxsize (assumed to be 4.5 grams), at 16 degrees Celsius and maximum ration (proportion of Cmax = 1), using bioenergetic model equations parameterized for O. mykiss (Hanson et al. 1997). The resulting quotient represents the proportion of maximum growth achieved in habitat i at time t. Observed growth potential patterns shown in figure 2a–2e represent those of an average size fish. This value was multiplied by the size-corrected maximum growth potential calculated for fish at time t (gMaxsize), a value that was recalculated each day in the bioenergetic model as fish grew. Total growth was calculated by multiplying mass-specific growth rates (g(t)) by fish mass (grams) at time t. All simulations were run on a daily time step with a fish mass of 0.3 grams on the first day of the simulation (approximate weight of emergent steelhead fry).

Figure 2. Ecological growth potential curves (a)–(e) were estimated for steelhead (Oncorhynchus mykiss; individualized, solid lines) or suites of similar species (generalized, shaded areas) from empirical observations for California coastal riverscapes. Growth trajectories (f) were modeled for four steelhead freshwater life histories using a simple bioenergetic growth model. The colored segments along each simulated growth trajectory (f) reflect the time spent and growth attained in each part of the watershed from fry emergence to ocean entry. We constrained the model so that fish entered the ocean at 175 millimeters to illustrate how different habitat use patterns and associated growth trajectories could lead to complexity in the age and timing of ocean entry. In reality, size and timing at ocean entry vary, and the number of individuals that each life history supports would be a product of the habitat capacity (space) and mortality risks associated with each life history pathway, which are not shown on this figure. This heuristic simulation illustrates how a complex portfolio of growth trajectories can emerge from asynchronous patterns of growth, which may promote population stability (Hilborn et al. 2003, Schindler et al. 2010).
Case studies of foodscapes for salmon in river networks

Hypothesis 1: Growth potential hotspots arise in different habitats at different times because of asynchronous events and cycles determining local food abundance, accessibility, and physiological constraints

The Sacramento River flows through California’s Central Valley, a highly modified landscape with flow alteration by upstream reservoirs and floodplain disconnection by a large system of levees. Few locations with river–floodplain connection remain. One of these is the Yolo Bypass, a 24,000-hectare flood bypass that routes floodwaters around the city of Sacramento. This habitat is a mosaic of agricultural fields and managed wetlands during the nonflood season. Following major precipitation events in the winter and spring months, flows overtop managed levees or weirs, generating lentic habitat with warmer temperatures and high nutrient availability that support abundant zooplankton (figure 3). Juvenile salmon exploiting these habitats grow rapidly and become much larger than individuals that remain in the mainstem (Sommer et al. 2001, Katz et al. 2017, Jeffres et al. 2020). In addition to in situ food production for juvenile salmon, this floodplain exports prey to downstream mainstem habitats during flood events (Sturrock et al. 2022). In turn, rapid growth and large body mass prior to ocean entry greatly enhance survival and early marine rearing of juvenile salmon (Woodson et al. 2013), indicating that rapid growth on inundated floodplains may have population consequences. Floodplain habitats are an example of ephemeral but exceptionally productive habitat that can contribute to the portfolio of successful life history strategies for juvenile salmonids.

The work on managed floodplain habitats in California’s Central Valley highlights that hotspot of food resources (e.g., eggs of spawning fish, synchronous insect emergences) can vary drastically across space and may be only briefly available. Many river systems have seasonal floodplains and off-channel habitats that are dry or disconnected much of the year. When inundated, however, these habitats can provide a variety of highly productive trophic pathways (table 1) for mobile consumers. As flood water fills terrestrial habitats, terrestrial invertebrates trapped by rising
water can be flushed back into the main channel. Reduced floodplain velocities settle suspended sediments, increasing light penetration and stimulating primary production (Ahearn et al. 2006). In turn, floodplain primary production frequently supports lentic-adapted zooplankton and macroinvertebrate populations, which fuel fish growth via unique trophic pathways not found at other locations in river foodscapes (Bellmore et al. 2013, Jeffres et al. 2020). Prolonged floodplain inundation can also sustain productive heterotrophic food web pathways supported by dissolved and particulate organic carbon liberated from inundated soils (Jeffres et al. 2020). Both primary production and liberation of heterotrophic carbon give rise to prolific densities of zooplankton and macroinvertebrates, an important food resource to juvenile salmonids (Sommer et al. 2001, Jeffres et al. 2008, Jeffres et al. 2020). Moreover, downstream movement of migratory fish such as juvenile salmon (from headwater habitats) frequently coincides with seasonal productivity peaks on floodplains, allowing fish to actively or passively move into these productive off-channel habitats when mainstem productivity is low (box 2; Sommer et al. 2001, Jeffres et al. 2008).

**Hypothesis 2: Fish can profit by tracking peaks in growth potential across riverscapes**

Upper Klamath Lake is large (approximately 270 square kilometers), shallow, and hypereutrophic. In summer, water temperatures exceed 25 degrees Celsius and massive cyanobacteria blooms create hypoxic conditions and associated fish kills. However, radio telemetry of adult redband trout revealed that these large-body fish migrate to the lake during spring, when dissolved oxygen and pH are suitable, and temperatures were near optimal for growth. In the lake, redband trout gorged on abundant chub and sculpin, feeding near their assimilative capacity (Hahlbeck et al. 2022). The fish then moved to cool tributaries during summer, where their condition declined as they switched to invertebrate prey and failed to fully meet their metabolic demands (figure 4). The fish again took advantage of foraging opportunities in the lake during fall, then moved to tributaries to spawn in the winter, presumably incurring another period of energy loss. Therefore, seasonally warm habitats fueled most trout production, despite the fact that the lake was inhospitable for several months of the year. This example illustrates how nonanadromous salmonids can track optimal growth conditions across large spatial scales (tens to hundreds of kilometers) and how fluctuation in water quality may mediate access to productive foraging habitat. The lake likely offers abundant food year-round, but positive physiological growth potential in salmonids occurs only as pulses in spring and fall, as the lake is transitioning between suboptimally cold and warm temperatures (Hahlbeck et al. 2022).

There are several other examples of stream-dwelling fishes tracking resources across multiple habitat scales (Power 1984, Ruff et al. 2011, Armstrong and Schindler 2013). The temporal component of a habitat’s growth potential for salmonids may vary seasonally (Rossi et al. 2022) or over much shorter time frames (Armstrong et al. 2013, Baldock et al. 2016), particularly when there are trade-offs between food abundance and physiological suitability. Salmonid behaviors such as habitat cycling (e.g., feeding forays over minutes to hours) can alleviate these trade-offs. For example, juvenile coho salmon foray into suboptimally cold shallows to feed on abundant salmon eggs (Armstrong et al. 2013, Fitzgerald et al. 2023) or benthic invertebrates (Baldock et al. 2016) and then move to warmer floodplain or beaver-meadow complex habitat to assimilate their food at faster rates. Fish similarly make forays into food-rich habitat that is overly warm (Munson et al. 1980, Sims et al. 2006) or hypoxic (Rahel and Nutzman 1994). To reduce physiological stress, individuals may exploit diel variation and enter foraging...
habitats during more favorable periods (Sims et al. 2006) or may tolerate harsh conditions but leave before physiological costs accrue (Rahel and Nutzman 1994). Similarly, diel vertical movements of juvenile sockeye salmon in lakes track intermediate light levels (the antipredation window), and the fish adjust their cyclical movements as day lengths and light penetration vary intraseasonally (Scheuerell and Schindler 2003). At coarser timescales, salmonids may move seasonally between refuge and foraging habitats. For example, lake trout are cold-water specialists restricted to deeper pelagic habitat during summer (Martin 1952, Guzzo et al. 2017). However, in spring and fall, when lake conditions are relatively isothermal and cool, these fish exploit productive littoral habitats. Indeed, water bodies that could be lethal to salmonids in summer may fuel a substantial fraction of fish production, as was demonstrated by the work from Klamath Lake described above (figure 4; Hahlbeck et al. 2022).

Hypothesis 3: Diverse foodscapes beget diverse life history strategies for mobile consumers that use the spatial complement of habitats and food webs in different ways

In the Gulf of Alaska, coastal watersheds contain a mosaic of glacial-, snow-, and rain-fed tributaries (figure 5a) that have distinct, and frequently asynchronous seasonal flow, temperature, and nutrient regimes (Hood and Berner 2009). These pronounced physicochemical differences drive divergent seasonal cycles of production and availability of aquatic resources that support juvenile salmon (Fellman et al. 2023), creating foraging and growth hotspots at different times of the year (figure 5b). In model simulations, Bellmore and colleagues (2022) showed that these seasonal asynchronies in food availability may allow juvenile salmon to express a broader range of growth trajectories by cycling between glacial-, snow-, and rain-fed streams, tracking energetically favorable foraging and growth opportunities as they shift through time across the river network (figure 5c, 5d). With climate warming, however, glaciers and snow disappear from the landscape and watersheds will become more hydrologically and thermally homogeneous (Barnett et al. 2005). This homogenization could shrink collective foraging and growth opportunities as seasonal patterns of resource availability across the foodscapes become more synchronous, narrowing the range of habitat use options, associated growth trajectories, and life history strategies that juvenile salmon can express (figure 5d).

Life history diversity is key to the resilience of Pacific salmon (Schindler et al. 2010, Carlson and Satterthwaite 2011, Moore et al. 2014). Pacific salmon life history diversity is most frequently associated with variation in the age, timing, and size of transitions between life stages (i.e., smolting and maturation; Quinn 2007), which has been shown to stabilize population dynamics via portfolio effects (Hilborn et al. 2003, Schindler et al. 2010). In the present article, we emphasize that different movement patterns—and their associated habitat use patterns—contribute to the success of different life histories that salmon and trout have been shown to exhibit during their freshwater life stages (box 2; Koski 2009, Bourret et al. 2016). These can influence their growth, survival, and subsequent reproductive success. Variation within a watershed in the availability of mainstem, tributary, floodplain, and estuary habitats provide numerous permutations of habitat use, foraging opportunities, and growth potentials in foodscapes, differentiating growth trajectories in ways that may promote life history diversity and population resilience (see box 2). As this case study illustrates, hydrologic heterogeneity within watersheds, such as tributaries with different runoff patterns,
may also promote life history diversity (see also Dralle et al. 2023).

**Foodscapes for other mobile consumers**

Although our conceptual models (e.g., boxes 1 and 2) are developed for riverine ecosystems and focus on salmonids as the consumer, the topics we integrate into foodscapes are active areas of research in other ecosystem types, and this modeling framework could easily be adapted to inform terrestrial or marine ecology. For example, the green wave hypothesis for terrestrial herbivores inspired much of the contemporary work on phenological tracking of food resources across a variety of taxa from fig wasp to blue whales (e.g., Kjellberg et al. 1988, Abrahms et al. 2019). Accelerometers and GPS collars have provided rich data on the energetic constraints of terrestrial vertebrates and other taxa, particularly in the topic of energy landscapes, that are often focused on how costs of locomotion explain patterns of animal movement across landscapes (Wilson et al. 2012). Finally, there is much interest in how prey accessibility mediates predator energy gain. Although functional response models emphasize how prey abundance mediates predation rates (Holling 1959), empirical studies suggest habitat-mediated prey vulnerability can have equally large effects (e.g., Hopcraft et al. 2005). These topics could be integrated to define foodscapes across ecosystem boundaries. For example, Armstrong and colleagues (2020) considered how prey accessibility and phenological variation (e.g., Deacy et al. 2017) combine to shape foraging opportunities for brown bears feeding on sockeye salmon. This work showed that habitats with relatively low salmon abundance contribute disproportionately to bear energy gain, because they offer early runs of vulnerable salmon.

**Knowledge gaps in foodscapes to support riverine consumers**

Certain aspects of the foodscapes can be measured and modeled using established methods. For example, process-based and statistical approaches used to estimate key variables controlling growth potential are rapidly expanding, including models to predict water temperature (e.g., Fullerton et al. 2018), channel hydraulics, and light inputs across whole watersheds and seasons (e.g., Bachiller-Jareno et al. 2019). Advances in biologging tags are improving estimates of metabolic costs (e.g., Lennox et al. 2019). Modeling approaches that estimate food availability and growth potential from known channel and riparian conditions are also emerging (Bellmore et al. 2017), which could be expanded to network scales (e.g., Bellmore et al. 2022). Other aspects of foodscapes are less well understood and difficult to estimate. Below, we outline key knowledge gaps that, if they can be filled, would help us better understand and quantify foodscapes.

**Watershed-scale estimates of food availability and quality**

Prey abundance is often measured at small spatial (e.g., reach) and narrow temporal (e.g., seasonal, or single sampling event) scales, limiting our understanding of prey abundance dynamics across larger scales of time and space. Because of the effort required for macroinvertebrate sampling and processing, studies focused on capturing spatial patterns of prey abundance often do so at the cost of temporal replication, and vice versa. Until very recently, few studies have attempted to quantify prey availability across a range of available habitats and over time (but see Nakano and Murakami 2001, Bellmore et al. 2013, Cordoleani et al. 2022, Rossi et al. 2022, or Scholl et al. 2023a), and none have encompassed the full spatial range of the consumer. In addition, empirical information on food abundance and production is often descriptive, resulting in fewer predictive tools to estimate prey relative to physical parameters such as water temperature (but see Bellmore et al. 2017). We refer readers to Ouellet et al. (2024; forthcoming) which provides a comprehensive review of the current tools and limitations in assessing prey abundance and availability in foodscapes.

There is also increasing evidence that food quality (nutritional content) is critical for growth and development of consumers (Twining et al. 2021). Emerging techniques using fatty acid profiles suggest that differences in prey quality, especially between aquatic and terrestrial prey sources, could impose important nutritional bottlenecks on fish (Zavorka et al. 2021). Declines in the abundance and accessibility of prey rich in fatty acids such as salmon eggs (Fitzgerald et al. 2023) or coastal marsh-dwelling amphipods (Jiménez-Prada et al. 2018) may have outsized effects on foraging fish. Furthermore, the quality of prey (independent of quantity) may influence foraging and movement decisions by consumers in ways that aren’t fully understood (Twining et al. 2021), for instance, fishes could make directed movements to habitats where prey abundance is low but nutritional quality is high. Although prey quality is clearly an essential part of foodscapes, very little is currently known about how prey quality varies over space and time, making this an important frontier for future research.

Work on fish foraging has not yet explored the full range of feeding conditions fish encounter in the foodscape. First, most of the focus has been on drift foraging by salmonids (e.g., Piccolo et al. 2014). Although this is the dominant strategy in flowing water, salmonids frequently forage in other ways (Nakano et al. 1999, Rossi et al. 2021), especially in more lentic habitats such as floodplains (Jeffres et al. 2020) or low velocity pools (Harvey and Raiselback 2014, Naman et al. 2018) and lakes. Factors that constrain prey accessibility and energetic costs in these habitats are less understood and would benefit from a similar level of attention that has been given to drift foraging. Second, foraging observations have been almost entirely constrained to smaller habitats accessible to humans. Foraging in larger mainstem rivers is understudied, despite well-documented occurrences of fish in these habitats (e.g., Bradford and Taylor 1997). How fish “make a living” in these bigger systems in the face of harsh hydrologic conditions, often high turbidity, warm summer temperatures, and possibly higher predation risk is a key gap in our understanding of the foodscape. Third, studies characterizing foraging behavior in streams have largely been limited to summer and low flows (but see Nakano et al. 1999, Nielsen 1992), which does not represent the full range of conditions they experience. High flow conditions may provide important foraging opportunities for some species by expanding inundated environments and entraining terrestrial and aquatic prey into the water column (Fitzgerald et al. 2023). Finally, fish foraging behaviors are highly context dependent, influenced by food availability but also by a suite of other factors that vary across the riverscape and over time, including physical habitat quality, predation risk, and inter- and intraspecific competition (White et al. 2014). Expanding empirical studies and theory to include more of the foraging conditions fish actually experience in watersheds is critical to better understanding the foodscape.

A central tenet of the foodscapes concept is that fish can, and often do, track spatiotemporal variation in growth potential. Although there is evidence to support this (e.g., Power 1984, Ruff
et al. 2011, Armstrong and Schindler 2013), the mechanisms underlying resource tracking are less understood. What cues do fish use to track resources? Over what spatiotemporal scales does this occur? And what are the life history, population, and food web consequences of resource tracking? Although broader ecological theory has advanced mechanistic understanding of these processes (e.g., Abrahms et al. 2021), applications to aquatic ecosystems are limited (Johnson and Rice 2014).

Fish have neither omniscient knowledge of their environments nor perfect access to the best available habitat at any time, so resource tracking is imperfect. Understanding when and why resource tracking fails (and the consequences for consumers) is critical for understanding foodscape dynamics. A particularly important question for management is how anthropogenic alterations to watersheds affect resource tracking. For example, physical habitat alteration could disrupt important cues fish use to acquire and process information about their environments, creating ecological traps where low-quality habitats are perceived as preferred and high-quality habitats are avoided (e.g., Jeffres and Moyle 2012). Streamflow alteration, for instance, may limit access (connectivity) and distort hydraulic cues that fish use to track food resources (Freeman et al. 2022), and alter food availability (e.g., Rhoades et al. 2023). Invasive species can also seize or alter the relationships between consumers and their prey through fear or competition (Baxter et al. 2004) that may alter resource tracking. Human impacts on the fish themselves could also affect resource tracking. For instance, human-induced selection through increasing hatchery supplementation could misalign behavioral traits or spawning distributions or timing (Hoffnagle et al. 2008) with growth hotspots. Hatchery effects are poorly understood but could severely reduce the ability of fish to exploit shifting growth opportunities, given rapid declines in many wild populations (e.g., Price et al. 2020).

Resource tracking by mobile consumers may also contribute to food web stability. Mobile consumers “crop” resource peaks that could destabilize local food webs, and move nutrients and organic matter across watershed networks. Ecological theory suggests that these meta–food web links could benefit both mobile and sessile organisms by stabilizing food web dynamics (McCann et al. 2005, Bellmore et al. 2015, Scholl et al. 2023b). Conversely, reducing the extent of resource tracking could lead to destabilizing effects, e.g., via resource “escape” (Ryser et al. 2021). Further empirical study is needed to test these theoretical predictions.

Restoration, recovery, and stewardship of foodscape

Climate warming and land use activities are driving rapid change in salmon-bearing watersheds (e.g., Pitman et al. 2020), with many systems already significantly degraded by humans (Bilby et al. 2024). A foodscape perspective expands our view of salmon watershed restoration, recovery, and stewardship to encompass the sources, phenology, and pathways of key food resources. It also focuses our attention on the conditions that allow populations of salmonids to track and exploit feeding opportunities across the riverscape (White et al. 2014). Collectively, these foodscape components are important dimensions of ecological resilience, and therefore critical management considerations in an era of rapid change (Beechie et al. 2023). In relatively intact watersheds, defining foodscape can illuminate the key trophic pathways and spatiotemporal patterns of foraging and growth potential that support fish populations (e.g., Bellmore et al. 2022), which can inform planning and climate vulnerability assessments (e.g., Wade et al. 2017). For heavily affected systems, foodscape can provide a novel lens to consider how alternative restoration actions promote diverse and connected foraging and growth opportunities for fish (e.g., Cordoleani et al. 2022).

Restoration objectives for salmon species are often based on population targets and physical habitat suitability metrics, but these approaches may fail to protect vital ecological processes and favor heavily managed solutions that can result in unnatural static conditions (Trush et al. 2000). Process-based restoration has emerged as an alternative paradigm that addresses these concerns. Process-based restoration aims to “reestablish normative rates and magnitudes of physical and ecological processes that sustain river and floodplain ecosystems” (Beechie et al. 2010). However, in practice, process-based restoration has primarily emphasized reestablishment of physical (typically channel and riparian) processes, assuming—often with little evidence—that food web and consumer recovery will necessarily follow (Whitney et al. 2020). We suggest that more explicit focus on the spatiotemporal dynamics of food webs that sustain salmon, and factors that prevent mobile consumers from capitalizing on those food webs (e.g., foodscape), would benefit the field of process-based restoration.

In many cases, physical process-based restoration may address the impairments to foodscape dynamics (e.g., the three determinants in box 1). But, working to restore physical processes without explicitly considering the full suite of mechanisms that control growth potential could lead to missed recovery opportunities. For example, the production and acquisition of food is often mediated by ecological interactions (species interactions) such as resource subsidies (terrestrial and marine resource fluxes), migrations of prey species, or behaviors that are cued by the actions of conspecifics (e.g., Bett and Hinch 2015). These types of interactions may benefit from process-based restoration of the physical habitat template, but it’s not guaranteed, because the target species depend on each other as much as they do on the landscape processes that facilitate their interaction (Bilby et al. 2024). In another example, introduced exotic species rewire food web interactions and energy flows (Jackson et al. 2017), or alter habitat selection and prevent consumers from tracking food resources across space (Baxter et al. 2004). In these cases, physical process restoration may not fully restore the lost growth potential (or potential expression of life history diversity) to native consumers and a more direct form of invasive species management may be necessary in addition to process-based restoration. Finally, all restoration, including process-based restoration, is limited by funding and requires prioritization or sequencing efforts. When loss of growth potential and life history diversity is considered a primary recovery goal, core foodscape management questions (defined above) can help focus restoration prioritization efforts.

Foodscape restoration can be framed within process-based restoration by explicitly emphasizing the processes and interactions that control the growth of mobile consumers across the riverscape and through time. The central question of foodscape restoration is how the multiscale processes affecting food abundance, food accessibility, and physiological growth potential (box 1) have been degraded and how they can be recovered. More focused questions follow from this such as whether there are important trophic pathways that have been impaired, which could help reestablish critical consumer populations and life histories if restored and how consumers might track resources across the landscape (or riverscape) if the foodscape was healthy. Both of these questions presuppose some reference state—a shared understanding of how an intact or healthy foodscape
functions. Although returning to a reference foodscape may not be practical or even possible in many cases (because of shifting baseline conditions, species invasions, etc.), comparing the reference foodscape to current conditions can inform restoration actions aimed at recovering (or replacing) foraging and growth opportunities necessary to support productive populations.

We acknowledge that quantifying current patterns of food production, food availability, energetic costs, and salmon life histories at a riverscape scale requires intensive sampling effort, and a suite of food web sampling methods and modeling (Naman et al. 2022, Ouellet et al. 2024; forthcoming), some of which have yet to be developed (see “Knowledge Gaps in Foodscares”). Estimating how patterns of growth potential have been altered by human modification may require a combination of all these methods along with estimates of unimpaired physiochemical and biotic conditions, and local and Indigenous knowledge (Quaempts et al. 2018, Atlas et al. 2021). However, we suggest that the determinants of reference foodscape patterns can be reasonably estimated (at least for well-studied taxa such as Pacific salmon) using a conceptual model framework (box 1) and then quantified and tested using a nested, iterative approach of modeling, monitoring, and experimentation (Power et al. 1998). Conceptual foodscape models should link a suite of predicted salmon life histories with the phenologies of growth potential at the riverscape scale (e.g., box 2). Conceptual foodscape models can be developed on the basis of a combination river food web ecology and existing knowledge about common life histories of focal prey and consumer species and how they interact with hydrology and stream type. These models help focus subsequent field work to resolve critical uncertainties, and expand inferences to broader ranges of climatic, hydrologic, and human-imposed conditions. Even with imperfect foodscape models, contrasting existing conditions with a reference foodscape may reveal new insights and testable hypotheses about what is limiting the capacity, diversity, and recovery of salmon populations.

Conclusions

The foodscape is a mosaic of linked habitats with different growth potential phenologies that are exploited by mobile consumers. Although the constituent themes of the foodscape concept are well established (e.g., riverscapes, food webs, resource tracking), this is among the first efforts to synthesize them, particularly at spatial scales that encompass a significant part of the life history of mobile consumers. In the present article, we describe the foodscape using salmonids as a focal organism, but the concept is generalizable to any mobile consumer that can track fluctuating patterns of growth potential across time and space (e.g., Sinclair and Beyers 2021). Foodscape also offer a holistic framework to integrate food web considerations into watershed management and salmon recovery, an increasingly recognized knowledge gap. We hope the foodscape framework offers fertile ground to generate testable hypotheses, and ultimately actions to guide the recovery and stewardship of watersheds and freshwater organisms.

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Supplemental Material

Supplementary 1 – The concept of foodscares presented as a song.

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