

OVERVIEW

Food web perspectives and methods for riverine fish conservation

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Abstract

Food web analyses offer useful insights into understanding how species interactions, trophic relationships, and energy flow underpin important demographic parameters of fish populations such as survival, growth, and reproduction. However, the vast amount of food web literature and the diversity of approaches can be a deterrent to fisheries practitioners engaged in on-the-ground research, monitoring, or restoration. Incorporation of food web perspectives into contemporary fisheries management and conservation is especially rare in riverine systems, where approaches often focus more on the influence of physical habitat and water temperature on fish populations. In this review, we first discuss the importance of food webs in the context of several common fisheries management issues, including assessing carrying capacity, evaluating the effects of habitat change, examining species introductions or extinctions, considering bioaccumulation of toxins, and predicting the effects of climate change and other anthropogenic stressors on riverine fishes. We then examine several relevant perspectives: basic food web description, metabolic models, trophic basis of production, mass-abundance network approaches, ecological stoichiometry, and mathematical modeling. Finally, we highlight several existing and emerging methodologies including diet and prey surveys, eDNA, stable isotopes, fatty acids, and community and network analysis. Although our emphasis and most examples are focused on salmonids in riverine environments, the concepts are easily generalizable to other freshwater fish taxa and ecosystems.

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KEY WORDS

ecosystem management, fisheries, food webs, rivers, watersheds

1 | INTRODUCTION

“To understand the success or failure of populations of particular species, we must, among other things, know their energy and material relationships within the ecosystem within which they live.” (C. E. Warren, 1971).

Food webs describe the complex architecture of species interactions and the flows of energy and nutrients within ecological communities (Elton, 1927; Lindeman, 1942). The abundance, demography, productivity, and persistence of any one species is strongly linked to the broader food web in which it participates, and species-specific responses to perturbations are often filtered through food web interactions (Wootton, 1994). Understanding food web dynamics is an integral component of the successful conservation and management of imperiled species and ecosystems (Vander Zanden et al., 2006). Shifts toward ecosystem-based management approaches incorporating food webs have occurred in marine and lentic ecosystems (e.g., Levin & Lubchenco, 2008), but progress is less apparent in riverine ecosystems despite calls to better integrate food webs to improve fisheries management (Naiman et al., 2012; Wipfli & Baxter, 2010; Woodward et al., 2021).

There is abundant evidence demonstrating the profound influence of food web interactions on riverine fish populations. For instance, fish abundance and productivity have strong links to spatial and temporal variability in prey availability (Chapman, 1966; McCarthy et al., 2009), competition (Bellmore et al., 2013; Sabo & Pauley, 1997), and predation (Frechette et al., 2013). Yet, these processes are frequently overlooked in management approaches, which typically focus on single species and on the direct influence of abiotic habitat factors such as water temperature (Naiman et al., 2012; Piccolo et al., 2014).

Ignoring food web processes can impact the outcomes of management actions. For instance, the concept of carrying capacity (the abundance or biomass of fish a given habitat can support) figures centrally in common approaches to restore depleted fish populations, such as structural habitat restoration and hatchery production. Habitat restoration often implicitly assumes that carrying capacity can be increased through improvements to physical habitat (e.g., increasing pool frequency, constructing off-channel habitat); meanwhile, hatchery production may assume habitats have sufficient carrying capacity to support large numbers of artificially raised fish. Consideration of food webs in these applications is rare, yet the availability of food is a fundamental constraint on fish productivity, and a key determinant of carrying capacity (Chapman, 1966). Food web processes may therefore have a strong bearing on the success or failure of these actions, which involve significant economic investment (Bernhardt et al., 2005; Roni et al., 2008). For example, restoration activities focused on augmenting habitat quantity may have diminishing returns if productivity of a target population is also limited by food availability (Cross et al., 2011; Naman et al., 2018).

Given the large investment in managing riverine fishes (e.g., Pacific salmon) and the proliferation of aquatic food web research, why have food web principles and methods struggled to gain traction in riverine fisheries management? In addition to the perceived simplicity of physical habitat and single-species approaches, we believe that a key barrier is the lack of a clear entry point into the vast food web literature and the rapidly expanding diversity of analytic methods, some of which may appear esoteric or daunting to many practitioners. This review addresses that barrier by providing fisheries professionals with an introduction to perspectives and methods for investigating lotic food webs. First, we outline critical management questions where incorporating food webs can provide key insights to guide management actions; second, we describe alternative perspectives through which food webs are commonly conceptualized; and third, we highlight existing and emerging methods to collect and analyze information about lotic food webs. We focus many of our examples on salmonid fishes and their food web relationships, given the expertise of the authors, the amount of food web related research on these species, and their cultural, economic, and ecological importance. Our intent is not to provide a comprehensive review of food web literature, but instead to highlight the key relevant concepts as an entry point for practitioners.

2 | CRITICAL MANAGEMENT QUESTIONS

Understanding food webs can be highly informative in guiding management and monitoring activities in river ecosystems. Below we highlight several critical management questions and show how a food web approach could provide key insights. These questions are not exhaustive but are commonly asked by fisheries professionals. By applying a food web perspective to these and other common management questions, it is likely that new and unexpected questions and perspectives may emerge that reshape management paradigms.

2.1 | How many fish can a habitat support?

The realization that populations have a “carrying capacity” is a seminal ecological concept that has strongly influenced fisheries research and management (Barber, 1988; Odum, 1953). Numerous approaches have been developed to estimate the limits of fish abundance in rivers, such as fitting statistical models to population data (Barrowman et al., 2003) and quantifying in-stream physical habitat conditions (Beechie et al., 1994; Cramer & Ackerman, 2009). However, regardless of physical habitat, the production of a population cannot exceed the availability of that population's prey and the efficiency at which consumed prey is converted into biomass (Lindeman, 1942). Therefore, food web approaches can be used to estimate the capacity of streams and rivers by quantifying the production and availability of prey that support fish production (Bellmore et al., 2013; Cross et al., 2013; Hayes et al., 2007). These approaches can also be extended to estimate how carrying capacity has changed (or might change) over time due to anthropogenic alteration (e.g., Bellmore et al., 2019).

2.2 | How does habitat alteration influence fish populations?

Habitat alteration (restoration or degradation) directly influences species by changing the quantity and quality of physical habitat attributes such as water depth, velocity, or structural cover (Roni & Quinn, 2001). However, habitat alteration also influences focal fish species indirectly by altering food webs (Vander Zanden et al., 2006; Wipfli & Baxter, 2010). Restoration actions may therefore have unexpected and undesirable outcomes if food web interactions are not considered (Bellmore et al., 2017; Naiman et al., 2012). For example, common restoration actions (e.g., side channel reconnection, wood additions) that increase suitable habitat for a desired fish species will be less successful, and possibly detrimental, if they also reduce suitability for that species' prey or increase suitability for predators and/or competitors.

2.3 | How do species introductions or extirpations affect ecosystems?

Invasive species can significantly alter riverine food webs by rerouting basal resources that support consumers (Moore et al., 2012), altering nutrient cycling (Atkinson et al., 2010; Capps & Flecker, 2013; Heinrich et al., 2021), and competing with and preying upon native organisms (Baxter et al., 2004; Koel et al., 2019). Understanding the impacts of invasive species—and if/how they can be controlled—often necessitates a food web approach. Conversely, the loss of members of a food web (i.e., extinctions or extirpations) can have cascading effects on focal populations (Koel et al., 2019) and key ecosystem processes (Taylor et al., 2006; Tronstad et al., 2015; Whiles et al., 2013).

2.4 | How do environmental contaminants spread and bioaccumulate, and what are the consequences?

The number of known contaminants in freshwaters has dramatically increased over the last century; even environments that are considered pristine frequently have high contaminant levels due to atmospheric deposition (Landers et al., 2010). The growing number of known contaminants has been fuelled, in part, by the increased awareness of the impact of pharmaceutical and personal care products on freshwater organisms. In many cases, contaminants propagate through ecosystems via food web linkages (Macneale et al., 2010; Richmond et al., 2018; Walters et al., 2020). Understanding food web dynamics can help elucidate pathways of contaminant flow, as well as the source(s) of contaminant entry and consequences of contaminants on structure and dynamics of the food web itself.

2.5 | How will climate change affect focal species?

Climate change may significantly alter stream temperatures and flow regimes, as well as the adjacent terrestrial ecosystems through which water, nutrients and organic matter are delivered to rivers (Palmer et al., 2009). Changes in such inputs to streams may also manifest through climate-mediated shifts in terrestrial disturbance regimes, such as wildfire

and associated debris flows (Davis et al., 2013), with attendant positive or negative consequences for fish populations (Harris et al., 2015; Spencer et al., 2003). The realized impacts of these changes on a focal species are often strongly mediated by food webs. For example, responses by fishes to warmer temperatures driven by climate change depend on whether increasing metabolic demands can be met by the productivity of lower trophic levels (Beakes et al., 2014; Brett et al., 1969; Crozier et al., 2010; Railsback, 2021). Climate change also directly affects the phenology and community structure of prey resources, competitors, and predators (Burgmer et al., 2007; Morin & Dumont, 1994). Food webs are therefore a key consideration when projecting how populations of fishes and other freshwater organisms will respond to climate change.

2.6 | How resilient will freshwater communities be to future conditions?

The stability and resilience of biological communities is, in part, determined by the structure and dynamics of food webs. Empirical studies and theory have elucidated various ways that attributes of food webs may promote resilience, biodiversity, and adaptive capacity (Bellmore et al., 2015; Rooney & McCann, 2012). For example, complex food webs with many weak interactions are thought to be more resilient to disturbances than simple food webs with few strong interactions (McCann et al., 1998). Although the underlying mechanisms are not fully resolved, these insights suggest that measures of food web complexity and interaction strength (e.g., Bellmore et al., 2015; Ledger et al., 2012) could help project the resilience and adaptability of entire biological communities in the face of environmental change. This is especially relevant given the continued shift from “single-species” to “ecosystem-based” fisheries management.

3 | FOOD WEB PERSPECTIVES

Since Charles Elton first described food chains and food webs (Elton, 1927) the most basic approach has been to simply observe “who eats whom.” More recently, additional approaches have been pioneered to describe food webs in more detail and from different perspectives. Below, we describe these different food web perspectives with examples of their application to riverine fisheries management. Specifically, we discuss: (1) basic food web description of feeding relationships; (2) metabolic (bioenergetics) models describing an organism’s energetic or food requirements; (3) trophic basis of production approaches for quantifying the strength of food web linkages and potential for food resource limitation; (4) community-based approaches that infer food web structure by evaluating community network structure and comparing the relative body sizes and abundances of different organisms; (5) ecological stoichiometry for examining food webs in terms of prey quality—or the ratio of essential nutrients food resources contain relative to the nutrient requirements of consumers; and (6) mathematical models that simulate the dynamics of food webs through time.

3.1 | Basic food web description

Feeding links between pairs or groups of species can be defined through a range of methods, including lethal or non-lethal gut content sampling, observing behavior, or indirect approaches that trace energy flow. These initial descriptions vary considerably in the level of resolution, comprehensiveness, and spatiotemporal extent. For instance, food web links can be defined qualitatively based on the presence/absence of feeding relationships (Pimm, 1982), or quantitatively based on the relative strengths of predators’ interactions with prey (Paine, 1980; Wootton & Emmerson, 2005). Qualitative presence/absence food webs have a long history, with well-established tools and metrics to define structural food web properties (Bersier et al., 2002). Weighing all feeding linkages equally offers limited insights into underlying energetic or demographic processes (Woodward & Hildrew, 2002). However, qualitative food webs can be highly valuable for management; for instance, by indexing common prey species or identifying carbon sources that fuel production, which can inform about key habitats and processes in need of protection or restoration.

By contrast, quantitative food web description additionally focuses on relative interaction strengths, providing deeper insights into what species and energy pathways are most important. Interaction strengths can be defined in numerous ways, including the demographic impact of consumers on resources (Paine, 1980; Power et al., 2008) or the magnitude of consumption by a predator relative to production of prey populations (Benke, 2018). A compelling case has also been made for including interactions beyond predator-prey connections in stream food webs. In particular,

non-predatory trophic interactions (e.g., parasitism) as well as non-consumptive and positive interactions (e.g., bioturbation, refuge creation, behaviorally mediated interactions) can dramatically influence the structure and function of ecological communities in streams (Albertson et al., 2021; McIntosh & Townsend, 1996). Detecting these important non-predatory interactions requires a robust understanding of a system's natural history and ecology and may require experiments to supplement observational studies (e.g., Sato et al., 2012).

Regardless of how feeding links are defined, basic food web description provides important information about the trophic roles of focal species and the architecture of feeding relationships. It is the basis for many other food web perspectives (see below) and is also useful in itself as a diagnostic tool if food webs are described repeatedly over environmental gradients or dynamics (e.g., Cross et al., 2011; Morley et al., 2020).

3.2 | Metabolic (bioenergetics) models

Bioenergetics models describe how individual organisms budget the energy they consume into growth, reproduction, and metabolic demands. These models are based on physiological relationships between body size, temperature, and maximum consumption rate that have been developed for a wide range of fish species through laboratory studies (e.g., Beauchamp et al., 1989; Stewart et al., 1983). Bioenergetics models have a long history of use in fisheries biology, largely through the Wisconsin Bioenergetics Software platform (Deslauriers et al., 2017; Hanson, 1997). While they do not describe food webs per se, bioenergetics models can be used to estimate energy flows from prey resources to consumers. Thus, when combined with additional information, bioenergetics models can help address management questions through a food web perspective. For example, bioenergetics models are often combined with descriptive food web information (e.g., diet composition) to quantify fluxes of energy, organic matter, and nutrients through food webs, or reciprocally, to calculate how much fish production could be supported given available food resources (McCarthy et al., 2009) or how fish may respond to shifts in environmental conditions (Falke et al., 2019). Bioenergetics models have also been linked with foraging theory to describe the energetic profitability of habitat conditions for drift-feeding fishes (Hughes & Dill, 1990). These drift-foraging bioenergetics models are increasingly being applied to inform metrics of stream habitat quality (Jenkins & Keeley, 2010; Rosenfeld et al., 2014; Urabe et al., 2010), carrying capacity (Wall et al., 2016), and ecological responses to flow alteration (Caldwell et al., 2018; Rosenfeld & Ptolemy, 2012).

3.3 | Trophic basis of production

The trophic basis of production approach is a technique for quantifying flows of resources along food web pathways, the strength of food web interactions, and trophic efficiency of consumer–resource relationships in rivers (Benke, 2018; Benke & Wallace, 1980). This approach combines estimates of consumer diets, energy assimilation efficiencies, and population-level production to construct “quantitative flow food webs,” whereby food web linkages are scaled to the magnitude of organic matter flowing along a given pathway (Benke, 2018). These quantitative flow food webs can be used to determine which linkages are most important for fueling consumer production over a given time interval (typically seasonally or annually) and can be linked across trophic levels to quantify energy flows from basal resources (periphyton and terrestrial litter) up to fish (Cross et al., 2011). This approach has been used to examine the energy flow pathways that support both aquatic invertebrate (Benke & Wallace, 1980; Hall et al., 2001; Nelson et al., 2020), and fish production (Bellmore et al., 2013; Marcarelli et al., 2020) in rivers, and to derive numerous management-relevant metrics such as food limitation of fishes, top-down control on invertebrate prey populations, interspecific competition for food, and carrying capacity (Box 1; Cross et al., 2011; Bellmore et al., 2013). In addition, the trophic basis of production approach can be used to map pathways of nutrient (Cross et al., 2007) or contaminant (Runck, 2007; Walters et al., 2020) flow through food webs if the stoichiometry or contaminant concentration of predators and prey are known.

3.4 | Ecological community description

Ecological community description represents a suite of approaches that elucidate food web structure using commonly collected population data, such as the size, abundance, and assumed trophic relationships of organisms (Cohen

BOX 1 Food web studies and adaptive management of the Colorado River, Grand Canyon, USA

Food web investigations have informed adaptive management of Glen Canyon Dam and the Colorado River in Grand Canyon. First, quantification of the trophic basis of production of both invertebrates and fishes (Figure A) showed that food resources (especially insect prey), were likely limiting fish populations, including imperiled native fishes like the U.S. Endangered Species Act-listed humpback chub and a prized non-native rainbow trout fishery in the dam's tailwater (Cross et al., 2011, 2013)—the latter of which had also been implicated in declines of native fishes downstream and were a focus of removal efforts (Yard et al., 2011). Second, these studies bracketed an experimental high flow release, and when an unanticipated burst of rainbow trout production occurred following the high flow, results showed that this was attributable to increases in the availability of insect prey that fuelled juvenile trout in the tailwater. The food web of the tailwater segment was simplified relative to the segments downstream of tributary inputs, dominated by flows from algae, and characterized by strong trophic interactions—all of which made animal populations more likely to exhibit dramatic fluctuations. These and other subsequent food web studies (e.g., Behn & Baxter, 2019; Kennedy et al., 2016) have informed flow management in the Colorado River system.

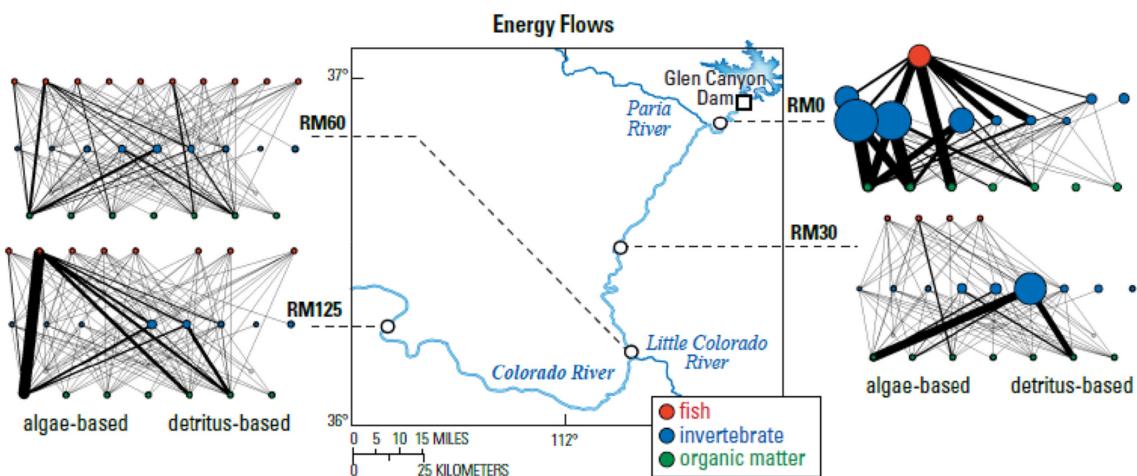


FIGURE A Food webs for four segments of the Colorado River downstream of Glen Canyon Dam. Widths of connecting lines reflect the magnitude of organic matter flows along different food web pathways (algae vs. detritus) from organic matter (green points in bottom row of diagrams) to invertebrates (blue points middle row) and to fishes (red points top row). Reprinted with permission from Cross et al. (2013). Courtesy of the U.S. Geological Survey

et al., 2003; Jonsson et al., 2005). From this information, various emergent properties of food webs can be calculated such as trophic generality and vulnerability, predator-prey body size allometry, and abundance-body size allometry. These approaches are conceptually simple to characterize yet offer insight into higher-level ecosystem properties (i.e., structure and function; Trebilco et al., 2013; Sprules & Barth, 2016). They also provide a synthetic metric for environmental monitoring that may be more sensitive than traditional fish community or population metrics (de Kerckhove, 2014; Woodward et al., 2021) and can be used to compare food webs across sites (Thompson et al., 2018) or through time (Yurista et al., 2014). The theory underlying this approach is simple: constraints on an ecosystem's energy supply (i.e., basal resource pools) combined with the laws of thermodynamics translates into progressively less energy available to support organisms living at higher trophic levels. Since body size tends to correlate with trophic position, an orderly progression from small-many to large-few is expected moving up the "food chain." Ecological community description has been used to assess several important fisheries management issues, including acidification in streams (Gray et al., 2014; Box 2), habitat restoration with large wood additions (Thompson et al., 2018), and climate change impacts to marine and freshwater fish assemblages (Dantas et al., 2019).

BOX 2 Food web networks as an indicator of recovery and invasion: The case of Broadstone Stream, UK

Broadstone Stream is an intensively studied, headwater tributary of southeast England that has slowly recovered from anthropogenic acidification over several decades. Along with the stream's recovery, researchers collected long-term data on aquatic macroinvertebrate and fish composition using the "ecological community description" approach described in this review. Since the 1970s, invertebrate taxa that were tolerant to extreme acidity gradually decreased as expected, with variations in pH forming the sideboards for which taxa colonized or became established (Woodward et al., 2002). However, signs of biological recovery—as measured by invertebrate abundance—did not appear to be as prevalent as expected with increasing pH. The ecological community description approach makes use of the numerical abundance, body mass, and known or assumed feeding relationships among members of a biological community. Researchers concluded that increased pH allowed a non-native top predator (brown trout, *Salmo trutta* L.) to invade this stream. Coupled with other evidence, brown trout were implicated in suppressing the abundance of aquatic invertebrates even after recovery of pH in Broadstone Stream (Layer et al., 2011; Figure B).

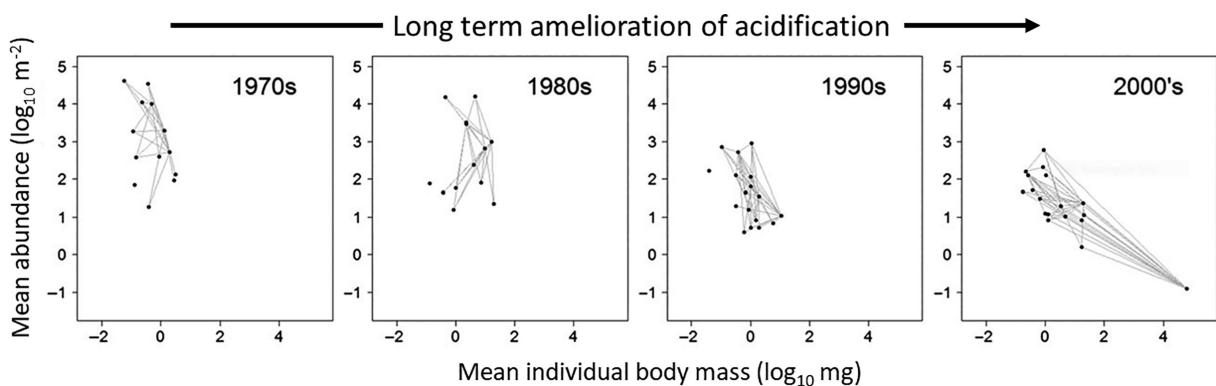


FIGURE B Broadstone stream food webs plotted as species log abundance versus log body mass data, with links between nodes representing feeding interactions. The abundance of invertebrates declines despite improving environmental conditions, as top-down effects intensify. Reprinted with permission from Layer et al. (2011)

3.5 | Stoichiometric approaches

Although food webs are generally viewed through an energetic lens, that is, how much energy or carbon is transferred from prey to predators, they also represent flows of nutrients and chemical compounds essential to sustain life. Ecological stoichiometry focuses on factors shaping the balance of nutrients within different ecosystem compartments; for instance, between consumers and food resources, or primary producers and nutrients (Sterner & Elser, 2002). Stoichiometric approaches are widely used to investigate lentic food webs, and they offer similar promise for understanding riverine organisms and ecosystem processes (Atkinson et al., 2017; Woodward & Hildrew, 2002). While stoichiometric approaches have traditionally focused on the "Redfield elements" (i.e., C, N, and P) due to their nutritional and functional significance to individuals and ecosystems, the discipline has broadened considerably in recent years to include micronutrients, stable isotopes, and more complex molecules such as fatty acids (Torres-Ruiz & Wehr, 2020; Twining et al., 2017). These developments have enhanced the ability of stoichiometry to improve upon traditional food web metrics, such as trophic connections and linkages (van Oevelen et al., 2010). A particularly promising application of stoichiometric approaches is assessing how fish populations could be limited by stoichiometric imbalances with their prey (McIntyre & Flecker, 2010; Závorka et al., 2021).

BOX 3 Modeling food web responses to the removal of dams on the Elwha River, USA

Between 2011 and 2014, two dams were removed from the Elwha River in northwest Washington State. A food web simulation model was used (Aquatic Trophic Productivity model; (Bellmore et al., 2017; Whitney et al., 2019) to explore responses directly downstream of the removed dams for fish, aquatic invertebrates, periphyton, and instream detritus. The model was parameterized with observed changes in channel morphology, water turbidity, and nutrient concentrations, which influenced the dynamics of the modeled food web via several pathways. Shortly following the initiation of dam removal in 2011, the model showed a dramatic decrease in fish, aquatic invertebrate, and periphyton biomass (Figure C). Simulated declines were largely due to the combined effects of high turbidity that limited light availability and periphyton growth, and deposition of finer and more mobile sediments unsuitable for benthic organisms. Biomass values remained low until mid-2014, at which point turbidity decreased to levels that allowed periphyton growth to rebound. Modeled detrital biomass was high during dam removal, reflecting the pulse of detritus from within stored sediments and restored connectivity to the upstream river network. These simulations illustrate the value of food web models for generating hypotheses about river ecosystem responses to dam removal (see Bellmore et al., 2019 for further details).

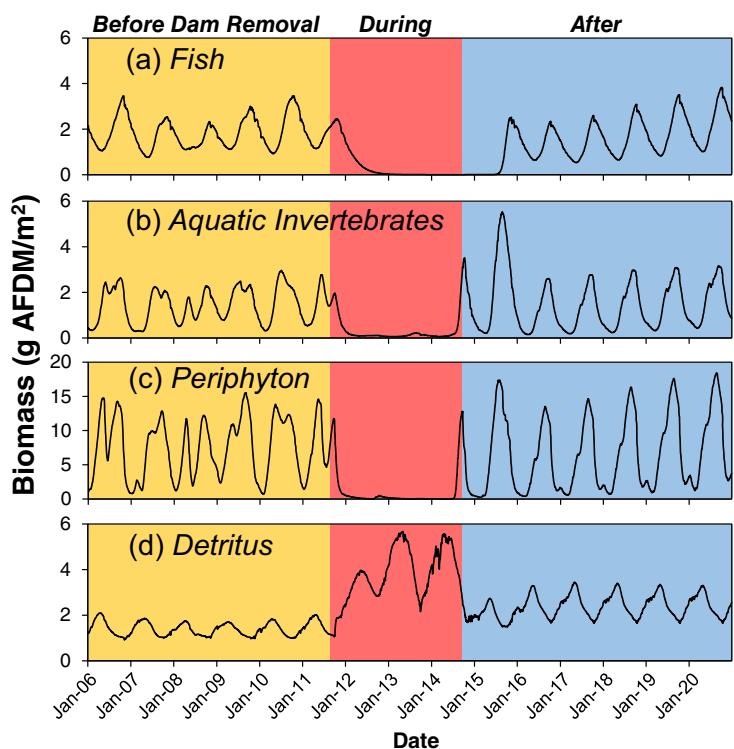


FIGURE C Outputs of the food web simulation model show fish (a), aquatic invertebrate (b), periphyton (c), and detritus (d) biomass responses to dam removal on the Elwha River (Washington State, USA). Reprinted with permission from Bellmore et al. (2019)

3.6 | Mathematical food web simulation models

Food web simulation models are mathematical representations of food webs, where the structure and parameterization of the models may be informed by empirical studies, but the food web relationships themselves are described by equations (e.g., Lotka-Volterra predator-prey equations) or qualitative interaction matrices (e.g., Montaño-Moctezuma et al., 2007). They range from highly complex, such as Ecopath-Ecosim models (Christensen & Walters, 2004) that frequently include numerous predator and prey populations (Harvey & Kareiva, 2005; Warren et al., 2014), to relatively simple food chain models (Atlas & Palen, 2014; Doyle, 2006; Power et al., 1995). Food web simulation models can be used to explore how river ecosystems might respond to a variety of management actions, from direct manipulations of the food web (e.g., salmon carcass addition), to alterations of the physical template upon which food webs emerge (Box 3). For example, Bellmore

et al. (2017) and Whitney et al. (2020), used a food web model to illustrate how the structure of river food webs, specifically the presence of invasive species, can mediate responses to restoration across a river network. A strength of these models is their ability to generate testable hypotheses, which in turn can support decision making and management experiments within an adaptive management context. Although model results may be imprecise, subsequent monitoring can help refine model parameters, the structure of the model, and even the underlying knowledge and assumptions on which the model is based (Power, 2001). Despite these benefits, food web simulation model applications in riverine ecosystems are rare relative to marine systems where they are widely used (e.g., Christensen & Pauly, 1992).

4 | FOOD WEB METHODS

There are a range of methods used to inform the different food web perspectives. Some are well established among fisheries professionals (e.g., gut content sampling) while others are rapidly emerging (e.g., community size-abundance analysis). Each method has advantages and drawbacks in terms of inferences provided about food web structure and dynamics, as well as their complexity and labor and financial requirements. We outline several key existing and emerging methods to empirically describe food webs (Figure 1). While we cannot do justice to the many procedures, technical considerations, and assumptions associated with each approach, we refer readers to key literature containing more detailed information.

4.1 | Direct diet and prey sampling/surveys and eDNA

Direct sampling of consumer diets is the most straightforward approach to measure feeding relationships and often the first step taken in describing food webs. Gut content sampling is well established and offers practical appeal as it can be

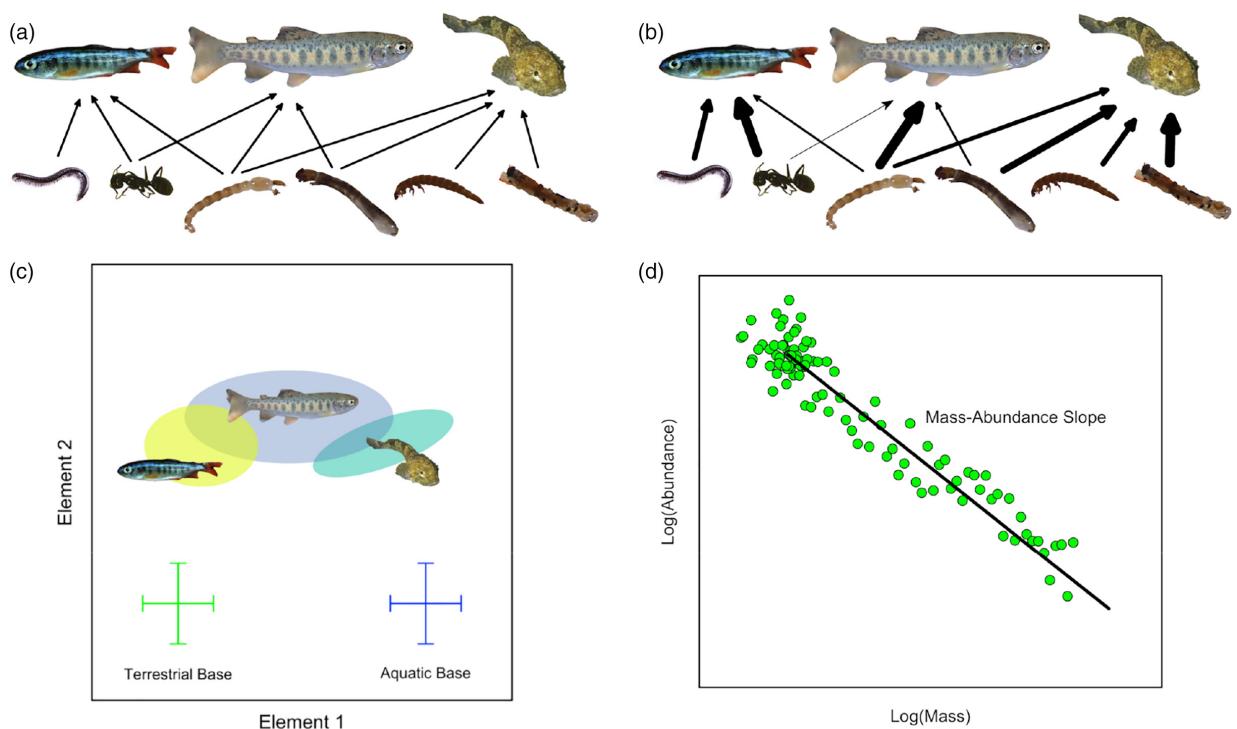


FIGURE 1 Simplified representation of how alternative methodologies can inform different food web perspectives. (a) Direct sampling of stomach contents can illuminate basic feeding links and can be used to construct qualitative connectance food webs; (b) if diet sampling is combined with measures of prey production and estimates of prey consumption, a production-based interaction strength can be estimated (represented by arrow thickness) and more quantitative food webs can be constructed (e.g., trophic basis of production); (c) inferences regarding energy sources and flows can be drawn from more indirect methodologies using chemical tracers - for instance, stable isotopes could be used to trace the flows of terrestrial vs. aquatic derived carbon (variation along element 1) and infer trophic position of fish consumers (variation along element 2); (d) food web structure can also be inferred from information on the abundance and body sizes of individuals in communities

done non-lethally for many fish species and does not require expensive analytical procedures (Chipp & Garvey, 2006). Diet analysis is the basis for qualitative food webs based on presence/absence of prey in the diet, as well as more quantitative perspectives (bioenergetics or trophic basis of production analyses) based on the abundance and/or biomass of prey in the diet and the growth of fish or other consumers (Box 1).

For food webs expressed in terms of interaction strengths, either a small subset of focal interactions may be quantified via experimental manipulations (Paine, 1980; Power et al., 2008), or sampling the abundance of prey communities—often aquatic and terrestrial invertebrates—is required to estimate production-based interaction strengths (i.e. the proportion of a prey population's production consumed by various predators for entire communities of organisms; e.g., Cross et al., 2011). The former approach is aligned with the idea that although there may be many interactions in food webs only a few of these are strong and these are the ones that need to be understood (Power et al., 1996). By contrast, the latter approach allows for a more explicit focus on the potential importance of weak trophic interactions and various metrics of food web complexity to the stability of particular populations and/or biodiversity as a whole (Bellmore et al., 2015; McCann et al., 1998).

Though direct diet and prey sampling is straightforward, there are challenges that warrant consideration (reviewed in Chipp & Garvey, 2006). First, there can be significant labor involved in collecting, sorting, and identifying diet and prey availability samples in the field and laboratory, especially if large portions of diet and prey are composed of invertebrates or a wide array of animal and other organic matter sources. Each sample may contain hundreds, or thousands of individuals of many different prey taxa and large sample sizes are often required to detect patterns (Weber et al., 2017). Second, estimating the identity and mass of partially digested prey individuals in the gut can be difficult and may lead to biases despite a wide range of methods available (Benke et al., 1999; Hyslop, 1980). For example, more sclerotized prey will typically be over-represented relative to soft-bodied prey that are easily digested. Third, gut contents reflect only a snapshot of a consumer's diet (hours to days). Consequently, the importance of a given prey can be overestimated or important feeding relationships can be missed; for example, if short pulses of prey like salmon eggs are critical to a species' production (e.g., Armstrong et al., 2010) but fall outside of the sampling window(s). This issue can be addressed with repeated sampling or complementing gut contents with longer term, integrative indicators of diet composition like stable isotope composition (discussed below). Indeed, repeated sampling (using gut contents and/or stable isotopes) may be necessary not only to provide a “representative sample” of the overall diets of fishes, but because the variability in time of these diets is itself a phenomenon of interest (Behn & Baxter, 2019; McMeans et al., 2016; Winemiller, 1990).

Environmental DNA metabarcoding (eDNA) is an emerging tool for diet and prey availability sampling that may address issues with high labor requirements and identification challenges associated with traditional sampling techniques. eDNA sampling extracts genetic material from water or digested stomach contents and references that mixture to a database to identify what species are present (Rees et al., 2014; Yoccoz, 2012). eDNA sampling can be completed faster and at less cost than traditional diet and prey availability sampling and laboratory processing (McInerney & Rees, 2018). Yet, it is not without limitations. Most notably, eDNA has primarily been used to provide information on presence/absence rather than biomass and abundance. As a result, eDNA sampling alone currently has limited utility for more quantitative food web perspectives. However, eDNA methodology is rapidly advancing toward more quantitative estimation of population abundance and biomass (Doi et al., 2016; Traugott et al., 2021).

4.2 | Stable isotopes

The use of stable isotopes to infer freshwater food web attributes and energy sources supporting consumers has been steadily increasing due to reduced costs over time and advancements in analytical approaches (Layman et al., 2012). Stable isotopes in an organism's tissues generally reflect the isotopic composition of their diet, after accounting for isotopic fractionation and trophic discrimination (Nielsen et al., 2018; Peterson & Fry, 1987). A key advantage of stable isotopes is that they integrate the portion of the diet that has been assimilated over time (rather than what has been ingested), and tissues with different turnover times can be selected to reflect diet over weeks (e.g., mucus), months (e.g., muscle tissue), or even years (e.g., otoliths) depending on the question and time period of interest (e.g., Heady & Moore, 2013). They also have a well-established array of associated analytical tools (see Phillips et al., 2014).

The most common stable isotopes used to investigate freshwater food webs are those of nitrogen (^{15}N) and carbon (^{13}C), although deuterium (^2H), sulfur (^{34}S), and others are also used (Jeffres et al., 2020; Layman et al., 2012; Nielsen et al., 2018). Nitrogen is particularly useful to determine trophic position and ontogenetic diet shifts (Anderson &

Cabana, 2007; Post, 2002). For example, by examining relationships between bull trout (*Salvelinus confluentus*) length and $\delta^{15}\text{N}$, Lowery and Beauchamp (2015) identified what size a shift to piscivory occurred. Nitrogen is also useful in quantifying the flow of marine-derived nutrients through freshwater food webs, as anadromous species typically have enriched ^{15}N signatures that can be used as a tracer (Bilby et al., 1996; Box 4). Carbon and deuterium are commonly used to trace the flow of energy from basal food resources, such as distinguishing relative contributions of allochthonous (terrestrial-derived) and autochthonous (aquatic-derived) carbon fueling stream food webs following landscape change (Spencer et al., 2003; Thorp & Delong, 2002; Wootton, 2012). Combining multiple isotopes and advanced mixing models (e.g., Moore & Semmens, 2008; Stock et al., 2018) may allow for more detailed evaluation of diet contributions to consumers as well as isotope-based metrics of emergent food web properties (e.g., dietary overlap, dietary niche breadth, trophic diversity; Jackson et al., 2011). For example, using multiple isotopes, Rubenson et al. (2020) found little overlap in the dietary niches of northern pikeminnow (*Ptychocheilus oregonensis*), smallmouth bass (*Micropterus dolomieu*), and juvenile Chinook salmon (*Oncorhynchus tshawytscha*), suggesting that predation and competition among these species was likely low.

However, stable isotope analyses have important limitations. First, they provide coarse detail and usually do not allow for delineation of actual feeding pathways (i.e., who eats whom). To draw reliable inferences, it is important that there is clear discrimination in the isotopic composition of diet sources to avoid misleading estimates of contributions to consumers, and this often restricts analysis to a few classes of resources (e.g., aquatic vs. terrestrially derived C, marine vs. freshwater derived N). Second, high temporal or spatial variation in food resources may require more intensive sampling (Brett et al., 2017; Finlay et al., 2002). Third, results can be highly sensitive to variable isotope fractionation rates across trophic levels, which are difficult to assess in field settings (Vander Zanden & Rasmussen, 2001). Emerging stable isotope methods such as compound-specific stable isotope analysis (e.g., amino acids; Thorp & Bowes, 2017) can bypass some of these issues and allow more detailed inference into different prey sources. However, these techniques are in earlier stages of development (Liew et al., 2019; Nielsen et al., 2018).

4.3 | Fatty acids

Like stable isotopes, fatty acids (FA) are biomarkers that can be used to infer feeding relationships and the flows within food webs of both energy and these critical compounds themselves. FA has been used less in riverine systems but may be preferable to stable isotopes in some situations. For instance, because FA analysis uses more markers than stable isotopes, it provides more dimensional space to discriminate diet composition among consumers (i.e., more diet sources can be evaluated). Additionally, certain FAs are indicative of specific taxa at the base of the food web, providing more detail about the flow of energy from basal organisms (e.g., bacteria, fungi, aquatic algae, terrestrial plants, etc.). Fatty acids can also be used as a measure of food quality, as a number of essential fatty acids are important for fish growth, health, and survival (Rinchard et al., 2007).

However, the use of FA in riverine ecosystems has largely been restricted to lower trophic levels (e.g., invertebrates and their food resources; Twining et al., 2017), with few studies focused on wild populations of vertebrate predators (but see Fujibayashi et al., 2019; Heintz et al., 2010). Further, the use of FA has been relatively qualitative, whereas mixing models used in stable isotope analysis provide quantitative estimates and error of proportional contributions of diet items to a consumer. However, quantitative FA approaches are advancing. Quantitative FA signature analysis (QFASA) infers diet composition using a weighted mixture of FA stores in putative prey sources that most closely match the FA signature of a consumer (Iverson et al., 2004). FA profiles can be modified from prey to consumer, and it is important to account for these changes prior to analysis (Happel, Stratton, Kolb, et al., 2016). Currently, this restricts the application of this method to consumers with a simple prey composition (Happel, Stratton, Patridge, et al., 2016). Because FA are currently largely qualitative, coupling FA with other approaches such as stable isotopes and direct diet analysis can be more informative (e.g., Fujibayashi et al., 2019; Rubenson et al., 2020).

4.4 | Ecological community description and analysis

Ecological community description involves collecting data on taxa present in the food web (“nodes”), inferring the trophic relationships between them (“links”), developing a table of who eats whom (“predation matrix”), and optionally coupling this information with estimates of individual body mass and abundance (Box 3). Mass–abundance (M–N)

BOX 4 Food web responses to carcass additions in the Northeast Oregon

In regions with suppressed anadromous fish runs, managers commonly add inorganic nutrients, salmon carcasses, or salmon carcass analogs to streams to compensate for losses of marine-derived nutrient subsidies and stimulate food web productivity. Understanding how food webs respond to these actions is critical to evaluating their effectiveness and impact on target species (Collins et al., 2015). Researchers added carcasses to sections of the upper Grande Ronde River in northeastern Oregon and utilized stable isotopes and diet sampling to evaluate how these subsidies were incorporated into the food web (Kaylor et al., 2021). Stable isotopes revealed that carcass nitrogen was broadly incorporated into food webs, including biofilm, numerous macroinvertebrate groups, and a diverse assemblage of native fish species (Figure D). However, juvenile salmonids showed much greater assimilation of carcass nitrogen than other taxa, suggesting that they could not have obtained this enriched nitrogen directly from lower trophic level prey. Diet analysis confirmed that juvenile salmonids were consuming large amounts of carcass tissue and eggs, whereas other taxa were not. Thus, combining stable isotope analysis and diets revealed the mechanism driving higher carcass nutrient assimilation by juvenile salmonids, suggesting that retaining eggs within carcasses is critical to maximize the impact of this management action

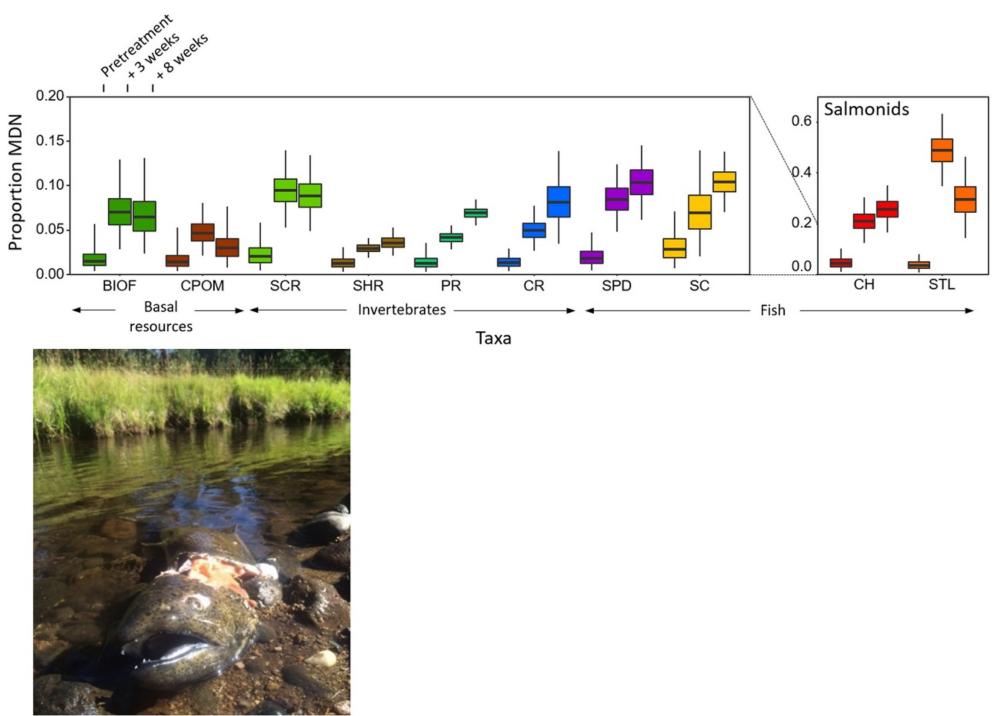


FIGURE D The estimated proportion of nitrogen that was assimilated by taxa from carcasses (MDN) before (first box) and 3 and 8 weeks after carcass additions (second and third boxes). BIOF, biofilm; CH, juvenile Chinook salmon; CPOM, leaf litter (alder); CR, crayfish; PR, invertebrate predators; SC, sculpin; SCR, invertebrate scrapers; SHR, invertebrate shredders; SPD, speckled dace; STL, juvenile steelhead. Reprinted with permission from Kaylor et al. (2021)

relationships or size spectra methods may be particularly useful to fisheries biologists given that body size and abundance (absolute or relative) data are typically collected during routine field sampling (White et al., 2007). The insight gained from $M-N$ relationships depends on the nature of field data, as well as the statistical methods used to fit models. Unbiased estimates of abundance (or abundance indices like catch per unit effort) are needed for all taxa and size classes of interest, which may necessitate multiple sampling methods or data corrections to account for taxa- and

size-selectivity. Whether $M-N$ relationships will encompass one (e.g., piscivores) or multiple trophic levels (e.g., primary consumers, secondary consumers, etc.) should be considered before sampling commences, so that mass and abundance is accurately characterized for all relevant members of the biological community. There are also a range of statistical methods for characterizing mass-abundance relationships that are still very much a subject of active research and discussion (see Edwards et al., 2017; Sprules & Barth, 2016).

5 | FURTHER CONSIDERATIONS AND CONCLUSIONS

We intended this review to provide a starting point and initial guidance to fisheries researchers and practitioners addressing critical management questions, or who are considering integrating food webs for guiding management actions and restoration activities. This broad scope meant that we could not cover all the nuances of each approach; in particular, we did not discuss many computational and statistical considerations. Interested readers should therefore consult the references highlighted in each section for further details. In addition to these key articles, user friendly software for tackling these analyses is increasingly available; for instance, there are free open-source programs and packages to implement bioenergetics analysis (Deslauriers et al., 2017; Naman et al., 2020), ecological community description (Hudson et al., 2013; Permado, 2015), diet composition using stable isotopes (Stock et al., 2018), and whole food web simulations (Whitney et al., 2020). We encourage interested readers to investigate these tools and their documentation, which are rapidly increasing the accessibility of food web approaches.

Ultimately, there is no “one size fits all” approach to assessing food webs, nor is there a cookbook method for choosing which approach is most appropriate for a given problem. Each has advantages and limitations that are best applied to particular management questions (Figure 2). Approaches can also be complementary when used simultaneously (Rine et al., 2016), providing a more accurate picture of food webs and their dynamics. Important considerations include what metrics to use (e.g., single species vs. emergent whole food web properties), the level of detail desired (e.g., qualitative vs. quantitative food web links), how much field and laboratory effort is feasible, and the required analytical expertise.

The value of any food web investigation will also depend on the rigor of the study design. In particular, inferences into cause and effect will be strengthened when food web properties are integrated into experiments. While manipulative food web experiments (e.g., Morley et al., 2020; Nakano & Murakami, 2001; Power, 2001; Suttle et al., 2004) may not always be tractable, mensurative experiments taking advantage of natural contrasts in environmental conditions

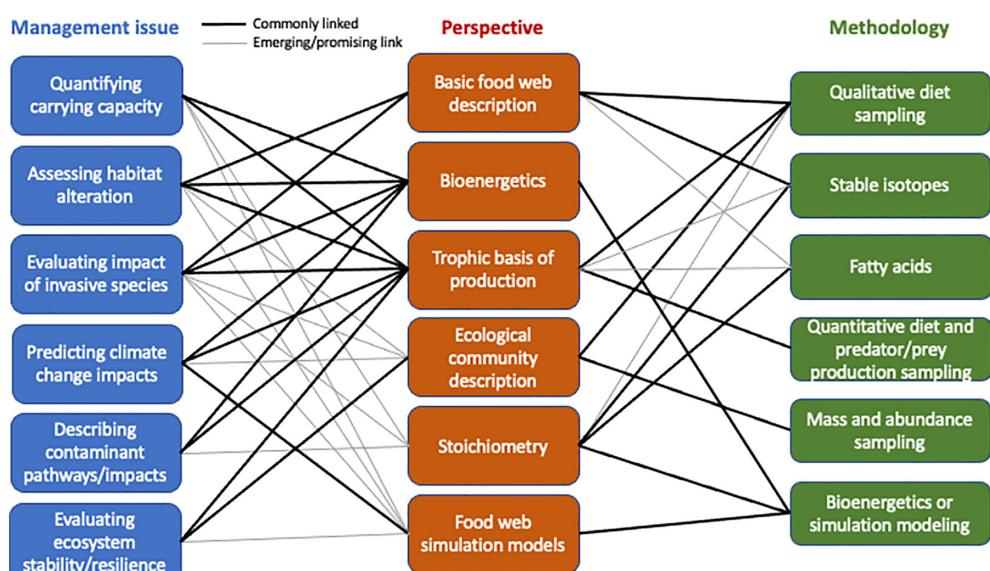


FIGURE 2 Critical management questions are commonly linked to certain food web perspectives, which in turn are informed by distinct methodologies. Dark lines represent “common” linkages, that is, where there are abundant examples in the literature. Gray lines represent “emerging” links, where there may be strong conceptual association between compartments but few example applications to date. Note, these links are based on the collective experience of the authors, not a formal bibliometric analysis

can be a powerful tool in many management situations. Further, management actions themselves, such as physical habitat manipulation or invasive species removal, can act as quasi-experimental treatments (Konrad et al., 2011). Careful measurement of food web parameters around these actions can provide deeper insights into the processes underlying ecological responses and be highly informative for adaptive management decisions (Cross et al., 2011).

Scale is also a critical consideration and challenge for any food web investigation. While food web studies are often applied at relatively small spatial scales (e.g., stream reaches) and over short timeframes, many fishes complete their life histories at larger spatial and temporal scales throughout riverscapes, and these are the scales at which fisheries managers may have the most need for understanding (Fausch et al., 2002; Torgersen et al., 2021). Thus, efforts to quantify food webs at larger scales throughout river networks (Power & Dietrich, 2002) and/or river-floodplain mosaics are needed, but are still relatively nascent (but see: Bellmore et al., 2015; Jeffres et al., 2020; Laske et al., 2019; Uno & Power, 2015).

Riverine fisheries management and conservation can benefit from the incorporation of food web perspectives, and food web investigations are increasingly identified as a critical priority for restoring depleted populations, for example, Pacific salmon in the Columbia River (Naiman et al., 2012; White et al., 2021) and Atlantic Salmon in Europe (Woodward et al., 2021). In stark contrast to approaches focused only on physical habitat, these insights suggest integrating food web perspectives is paramount to the success or failure of critical and costly management actions such as habitat restoration, invasive species removal, or climate mitigation strategies. This incorporation of food webs is inherently challenging and will face continued barriers; however, the wide ranging and evolving array of conceptual and methodological approaches we described offer an important and exciting opportunity to better address these existing and emerging management issues through a food web lens.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Sean M. Naman: Conceptualization (lead); writing – original draft (lead); writing – review and editing (lead). **Seth M. White:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **J. Ryan Bellmore:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Peter A. McHugh:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Matthew J. Kaylor:** Conceptualization (supporting); writing – original draft (equal); writing – review and editing (equal). **Colden V. Baxter:** Conceptualization (equal); writing – original draft (supporting); writing – review and editing (equal). **Robert J. Danehy:** Conceptualization (equal); writing – review and editing (equal). **Robert J. Naiman:** Conceptualization (equal); writing – review and editing (equal). **Amy L. Puls:** Conceptualization (equal); writing – review and editing (equal).

DATA AVAILABILITY STATEMENT

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

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