

Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds

ABSTRACT: Physical characteristics of riverine habitats, such as large wood abundance, pool geometry and abundance, riparian vegetation cover, and surface flow conditions, have traditionally been thought to constrain fish production in these ecosystems. Conversely, the role of food resources (quantity and quality) in controlling fish production has received far less attention and consideration, though they can also be key productivity drivers. Traditional freshwater food web illustrations have typically conveyed the notion that most fish food is produced within the local aquatic habitat itself, but the concepts and model we synthesize in this article show that most fish food comes from external or very distant sources—including subsidies from marine systems borne from adult returns of anadromous fishes, from fishless headwater tributaries that transport prey to downstream fish, and from adjacent streamside vegetation and associated habitats. The model we propose further illustrates how key trophic pathways and food sources vary through time and space throughout watersheds. Insights into how food supplies affect fishes can help guide how we view riverine ecosystems, their structure and function, their interactions with marine and terrestrial systems, and how we manage natural resources, including fish, riparian habitats, and forests.

Suministros alimenticios que controlan la productividad en peces: modelación del flujo de presas en redes fluviales

RESUMEN: las características físicas de los hábitats fluviales, tales como abundancia de madera, geometría y abundancia de cuerpos de agua, cobertura de vegetación riparia y condiciones de flujo superficial han sido comúnmente consideradas como determinantes de la producción de peces en este tipo de ecosistemas. Alternativamente, el papel del suministro alimenticio (calidad y cantidad) en el control de la producción de peces ha recibido mucha menos atención y consideración pese a que también puede ser un elemento clave en cuanto al control de la productividad. Las clásicas ilustraciones de redes alimenticias de ambientes de agua dulce han dado la impresión de que la mayor parte del alimento de los peces se produce dentro del propio hábitat acuático local, pero los conceptos y el modelo que se presentan en este artículo muestran que gran parte del alimento de los peces proviene de fuentes externas o muy distantes—incluyendo subsidios por parte de los sistemas marinos como el retorno de adultos de peces anádromos, tributarios paralelos que transportan las presas hacia los peces que habitan río abajo, vegetación ribereña y hábitats asociados. El modelo que se propone, además, explica cómo las vías tróficas clave y los suministros alimenticios, varían a través del tiempo y del espacio entre cuencas. El conocimiento de cómo los suministros de alimento afectan a los peces, puede ayudar a mejorar la forma en la que se estudian los ecosistemas fluviales, a entender su estructura y función, sus interacciones con sistemas marinos y terrestres y a optimizar el manejo de los recursos naturales, incluyendo peces, hábitats riparios y forestales.

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Introduction

Freshwater fisheries management programs have traditionally focused on the maintenance or restoration of physical habitat, an approach that assumes local physical habitat structure and quality dictate fish production. In contrast, there has been less investigation on the role of food in sustaining fish populations. Evidence supports the notion that food limits fish production (Matthews 1998; Diana 2005), and is particularly compelling for stream salmonids (Chapman 1966; Mundie 1974; Mason 1976; Elliott 1994). When management programs are not successful it is often because they do not take a sufficiently broad view of watershed drivers (Meffe et al. 2002), including food webs and the processes that regulate food abundance for fishes. In this article, we expand conventional thought of physical controls on fish production, to look more broadly on food resources as a limiting factor on fish production in riverine ecosystems, and further present concepts and a model illustrating how fish food supplies vary through time and space throughout drainage networks.

As it is increasingly recognized that many stream fishes require a mosaic of habitat types throughout a riverine landscape to complete their life cycles (Schlosser 1995; Fausch et al. 2002; Stanford et al. 2005), there is a need to address the diverse array of prey sources that can be important to a fish population. Ecologists' growing focus on prey fluxes across habitat boundaries that "subsidize" recipient consumer populations (Polis et al. 2004) has drawn attention to the variable energy sources, both aquatic and terrestrial, that can fuel

stream fish production (Bilby et al. 1996; Wipfli 1997; Wipfli et al. 2003; Baxter et al. 2005). In addition, there is growing awareness that the “resource sheds” of consumers often exhibit important variation dependent on spatial and temporal context (Power and Rainey 2000; Power and Dietrich 2007).

Here we propose a conceptual model of energy flow to stream fishes that incorporates the importance of multiple pathways and explicitly addresses how their relative contributions may change with season and spatial context within riverine networks. We develop and apply this model in the context of Pacific salmon and their watersheds, intending that it will be of general utility for understanding the array of food sources for other fishes and the processes and pathways that govern food supplies. Our intent in this article is to develop a model sufficiently applicable to ecosystems that contain other salmon species (e.g., Atlantic salmon), other non-salmon anadromous species (e.g., alewives), and systems lacking anadromous fishes across the globe.

Pacific salmon as a model

While most research and management dollars have gone towards understanding and mitigating the effects of habitat loss, hatchery stocks, dams, and salmon harvest in river systems in the Pacific Northwest (NRC 1996), relatively little has focused on the specific trophic processes and pathways that limit the productivity of riverine food webs that sustain production of salmon during their freshwater phase.

Pacific salmon are ideal for demonstrating an approach that explicitly addresses the diversity of energy sources for stream fishes. Though the emphasis of most past research has been on habitat as a limiting

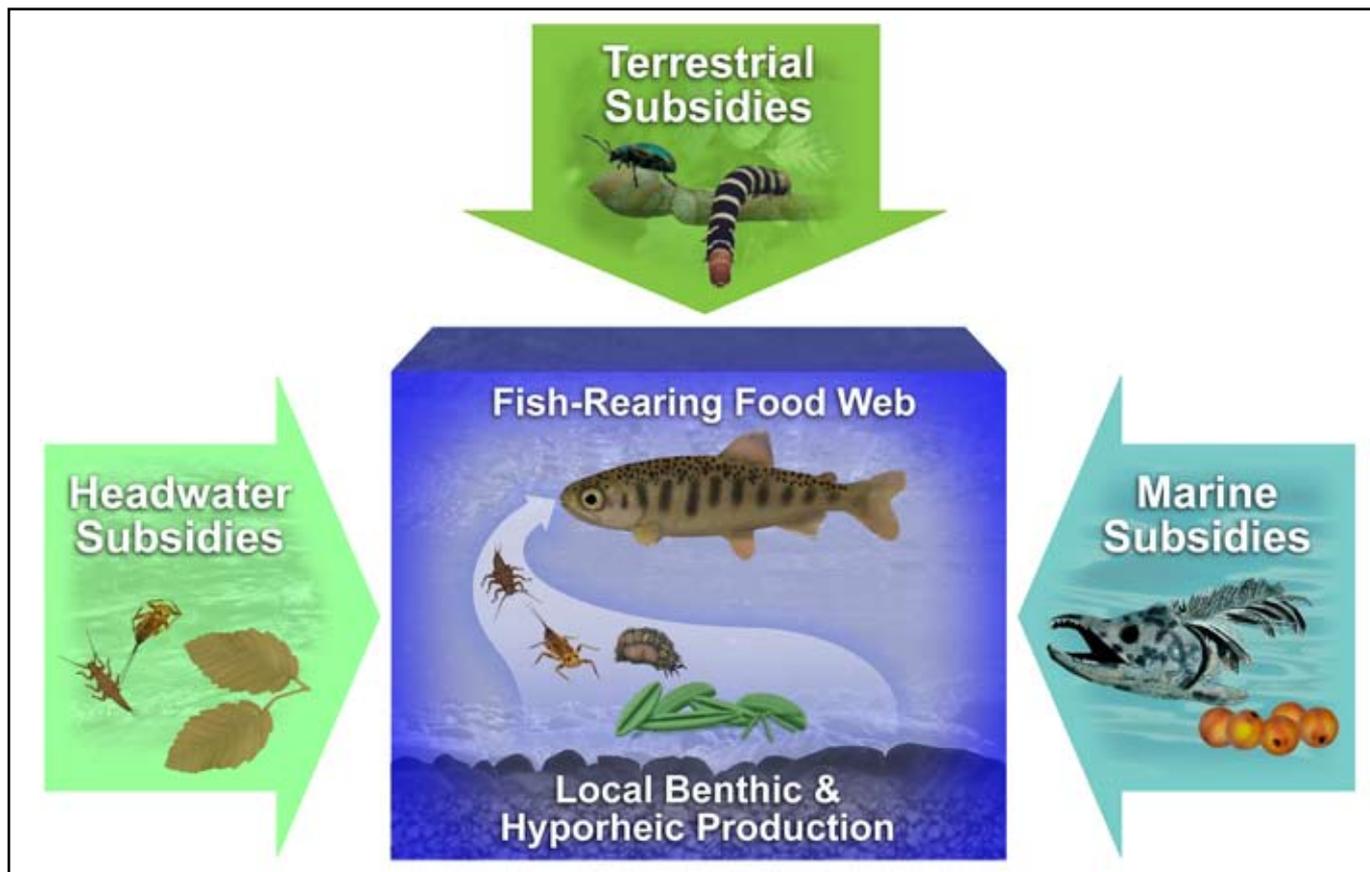
factor, there have been decades of research on the diets of salmonid fishes. In addition, our knowledge of energy pathways and function in the freshwater ecosystems they inhabit and the fluxes from adjacent terrestrial habitats has been improving. Many of these ecosystems also receive (or historically received) immense quantities of marine-derived biomass each year as adults migrate from the ocean to freshwater to spawn, a process whose importance is now better understood (Juday et al. 1932; Mathisen et al. 1988; Piorkowski 1995; Stockner 2003). Moreover, we now have increased information on the timing and spatial distribution of such fluxes in salmon streams, providing the basis for a model that addresses multiple cross-habitat subsidies whose importance varies through time and space.

Food sources for Pacific salmon in freshwater

Local production of benthic invertebrates

Fishes are often the top aquatic predators in riverine food webs and receive energy from multiple sources. For salmonid fishes, the most studied and widely recognized sources of prey in freshwater are benthic invertebrates that are produced locally, within the stream reach where fish occur (Allen 1951; Hynes 1970; Matthews 1998). In turn, the production of stream invertebrates is fueled by a combination of smaller prey (in the case of those that are predators) and organic matter synthesized by primary producers in streams, but also by small prey and organic matter which may be imported from ter-

Figure 1. Resource subsidies fueling fish-rearing food webs.



restrial, hyporheic, or marine habitats (Figure 1). Annual benthic invertebrate production in streams ranges widely, from ~2 to > 100 g dry mass/m², with the majority of estimates being < 20 g dry mass/m², depending upon the stream and geographic locale (Huryn and Wallace 2000; Benke and Huryn 2006). However, most studies conducted in salmon-bearing streams of the Pacific Northwest have measured only densities or standing crop biomass of benthic invertebrates, and estimates of secondary production rates have been rare. Duncan et al. (1989) estimated 1 g dry mass/m²/y in southeastern Alaska streams, whereas estimates from the Columbia Basin in Oregon and Idaho range from similarly low rates (Speir and Anderson 1974) to as high as 50 g dry mass/m²/y (Minshall 1978; Robinson and Minshall 1998). Several studies have reported salmonid growth or abundance is greater when benthic invertebrate prey availability is higher (Cada et al. 1987; Peterson et al. 1993; Boss and Richardson 2002). Studies that have attempted to quantify and balance energy budgets for salmonid-bearing streams have repeatedly found that local benthic invertebrate production alone does not account for the associated fish production (Allen 1951; Waters 1988; Huryn 1996), suggesting other energy sources are also important. At the same time, at least a small surplus of benthic invertebrate production appears in these streams. It has long been posited that the only way to balance such budgets and provide a solution to what has been termed "Allen's Paradox" (Hynes 1970) is to include other prey sources in a more comprehensive approach (Allan 1995; Huryn 1996).

Tributary subsidies

Tributary streams, most notably those that are fishless, are sources of invertebrate prey to predatory fishes in recipient downstream habitats (Figure 2). Although numerous authors have shown that organic matter and nutrients originating upstream can fuel secondary production in downstream habitats (Vannote et al. 1980; Wallace et al. 1997), few investigations have focused on the transport of invertebrate prey down stream networks and little is known regarding the extent to which fishless tributary streams subsidize downstream fish-bearing food webs via the fluvial transport of invertebrates (Wipfli et al. 2007). Wipfli and Gregovich (2002) showed that fishless headwaters are a year-round source of invertebrates to fish habitats lower in drainages within the rainforests of coastal Alaska. They calculated that within a typical southeastern Alaska watershed, subsidies from fishless headwaters (163 mg dry mass of invertebrates per stream per day; 10.4 g dry mass of detritus per stream per day) are at levels that could theoretically support 0.2 to 2.0 young-of-the-year coho (*Oncorhynchus kisutch*) fry per m² of stream reach meters to kilometers downstream. In addition, Piccolo and Wipfli (2002) reported headwater subsidies of both invertebrates and leaf litter were strongly mediated by upland forest management and riparian vegetation type. In terms of an annual prey budget, Wipfli and Musslewhite (2004) suggested delivery of invertebrate prey from tributary streams is small relative to local, in-stream production and subsidies of terrestrial invertebrates. However, prey from headwater sources may be seasonally important at fishless-fish habitat interfaces, as some fish species may seek out these specific habitats during certain times of the year (Bramblett et al. 2002; Bryant et al. 2004), and may partly explain the high fish densities often seen at tributary junctions (Benda et al. 2004).

Terrestrial subsidies

Ecologists have long recognized the importance of terrestrial inputs of nutrients, dissolved organic carbon, and plant matter to basal productivity and invertebrate production in streams (Cummins 1974; Vannote et al. 1980). While these nutrients and energy may indirectly feed higher consumers such as fishes, terrestrial invertebrates that fall into streams are a relatively high quality food source directly available to fish. Terrestrial invertebrate subsidies to streams can be substantial during the plant growing season, with annual inputs in forested temperate streams as high as 11 g/m²/y (see Baxter et al. 2005 for a review), dependent in part on the extent and composition of riparian vegetation (Mason and MacDonald 1982; Edwards and Huryn 1995; Romero et al. 2005). Terrestrial invertebrates can comprise more than half of energy ingested by stream fishes (Wipfli 1997; Allan et al. 2003) and are often the preferred prey of juvenile salmonids (see reviews by Hunt 1975; Baxter et al. 2005). Wipfli (1997) found terrestrial prey inputs averaged 10 mg dry mass/m²/d but at times were as high as 39 mg dry mass/m²/d. Further, in small streams in northern Japan, terrestrial invertebrates have been shown to comprise roughly half of the annual prey ingested by salmonids (Kawaguchi and Nakano 2001; Nakano and Murakami 2001), with significant consequences for fish growth and abundance (Kawaguchi et al. 2003; Baxter et al. 2007).

Marine subsidies

Marine inputs from adult anadromous fishes returning to freshwater habitats to spawn can be a major energy and nutrient subsidy to riverine ecosystems during parts of the year (Elliott 1997; Schmidt et al. 1998; Wipfli et al. 1998; Cederholm et al. 1999). Salmon typically range 2–25 kg each, depending upon species and gender, and often return by the millions in many of the large drainages around the Pacific Rim (Groot and Margolis 1991). Subsidy levels can range broadly from just a few spawners per stream to very high, local densities (Groot and Margolis 1991). Even very small watersheds can experience large returns of salmon. During and after salmon runs, marine carbon and nitrogen are sequestered at multiple trophic levels in freshwater and terrestrial systems (Kline et al. 1990; Chaloner et al. 2002a; Hicks et al. 2005), and these subsidies often dramatically influence community productivity and demographics. Wipfli et al. (1998, 1999) observed that biofilm mass and invertebrate density increased up to 25 times in Alaska stream systems with spawning salmon, and more salmon led to increased responses, up to a threshold. Aquatic invertebrates colonize and consume salmon carcasses (Piorkowski 1995) and can be found in high densities on and around dead salmon soon after the run (Minakawa and Gara 1999; Chaloner and Wipfli 2002; Claeson et al. 2006). Chaloner et al. (2002b) showed invertebrate growth rates increase in the presence of salmon carcasses in Alaska streams, although it remains unknown how much invertebrate biomass is produced from a given amount of salmon tissue. That will vary depending upon many factors, including invertebrate species present and whether carcasses remain reasonably intact and in place rather than flushing downstream or becoming buried or excessively fragmented (Chaloner and Wipfli 2002). Through invertebrate prey production, these increases can be translated to stream-resident salmonids, though fish also ingest salmon tissue and eggs directly (Bilby et al. 1996).

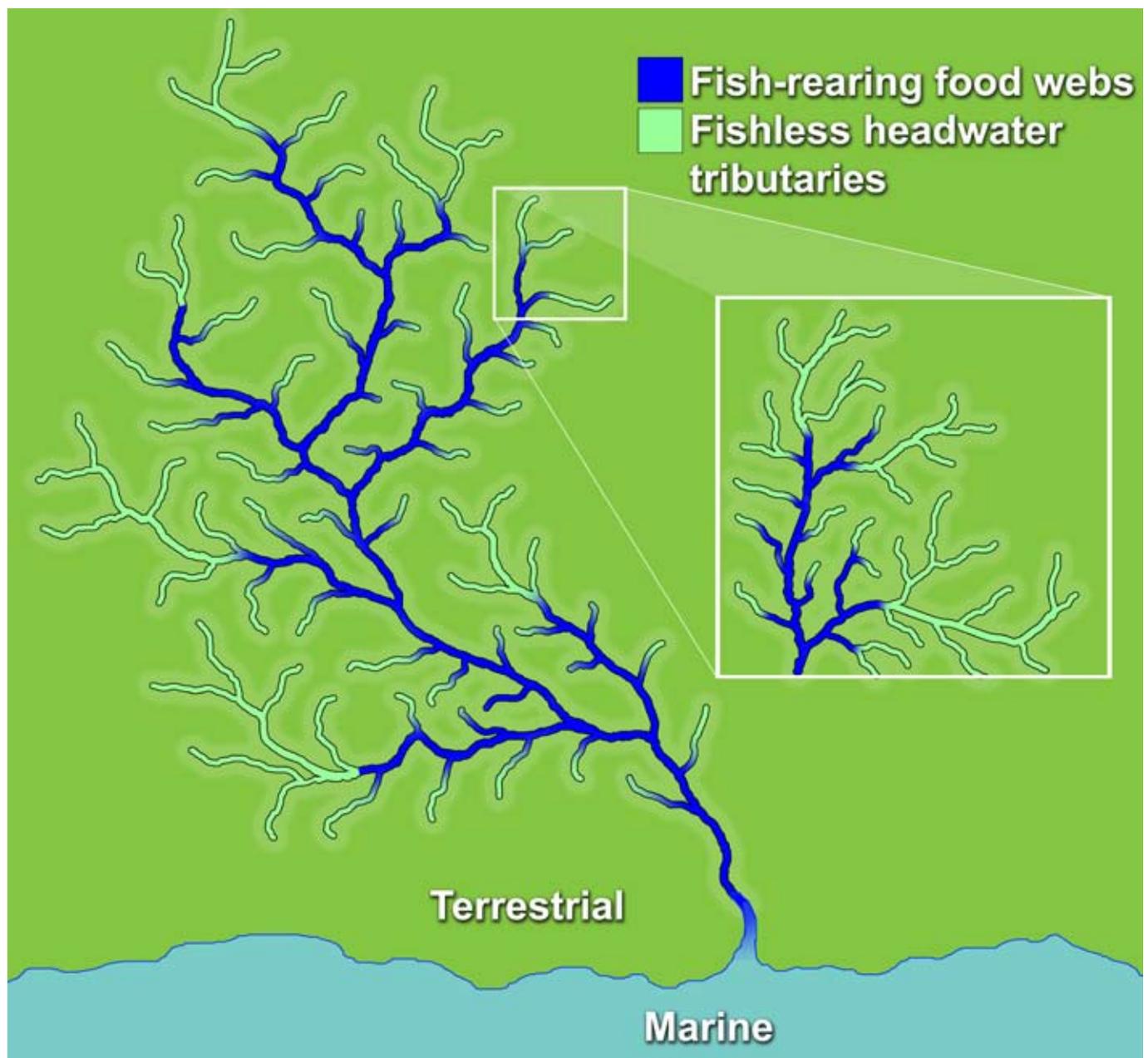
Wipfli et al. (2003) showed that stream-resident salmonids grew much faster and larger in southeastern Alaska streams enriched with salmon carcasses and eggs. Similarly, in selected Washington streams, juvenile salmonid growth increased in response to artificially-added salmon carcasses (Bilby et al. 1996, 1998). Responses to marine subsidies can vary though (Chaloner et al. 2004), with some stream communities showing no or even possible negative effects, possibly due to the lack of nutrient limitation in some streams (Wilzbach et al. 2005) or localized physical disturbance (Moore et al. 2004; Monaghan and Milner 2009). Nonetheless, the amount of adult salmon biomass actually available for ingestion by fish (directly via salmon eggs or fragmenting tissue, or indirectly through ingesting invertebrates that assimilate carcass tissue) is probably a very small fraction (est. 0.1–1%) of what enters freshwater systems, after accounting for removal by ver-

tebrates (Cederholm et al. 1989; Gende et al. 2004) and other 'losses' from flushing, fragmentation, physical adsorption, or burial (Cederholm et al. 1989; Bilby et al. 1996; Gende et al. 2002; Moore et al. 2004).

A model incorporating multiple food sources for stream fishes

The importance of food from the four sources described above (local production, and tributary, terrestrial, and marine subsidies) can be better understood by addressing the relative contribution of each (Figure 3). The quantity and nutritional quality of these energy inputs can vary dramatically across time and space in riverine networks. A model incorporating these multiple food sources,

Figure 2. Headwater streams comprise the vast majority of total stream network length in watersheds.



and applied in a spatially explicit manner to fish-bearing food webs, would provide insight into food web function, energy fluxes, processes that govern fluxes, and the spatially local and distant conditions that influence these processes. Here we develop such a model, based on literature-derived parameters for Pacific salmon in streams of Alaska and the Pacific Northwest.

The amount of food (F) entering fish habitat from the four sources (Figures 1 and 3) is characterized by

$$F = L + H + T + M,$$

where F = food (total food amount),

L = local food production,

H = headwater (tributary) food subsidies,

T = terrestrial food subsidies, and

M = marine food subsidies.

Incorporating annualized empirical data from typical salmonid-rearing streams (~2–5 m active channel width) in southeastern Alaska for these four independent variables:

L = 2.7 mg prey dry mass/m²/d (Duncan et al. 1989),

H = 1.2 mg prey dry mass/m²/d (Wipfli and Gregovich 2002),

T = 5.8 mg prey dry mass/m²/d (Wipfli 1997), and

M = 1.5 mg ingestible salmon dry mass/m²/d (derived from pink salmon (*O. gorbuscha*) adults at 1 spawner/m² at 0.1% availability described above; Groot and Margolis 1991; Wipfli et al. 2003) gives:

$$F = L + H + T + M,$$

$$= (2.7 \text{ mg prey dry mass/m}^2/\text{d}) + (1.2 \text{ mg prey dry mass/m}^2/\text{d}) +$$

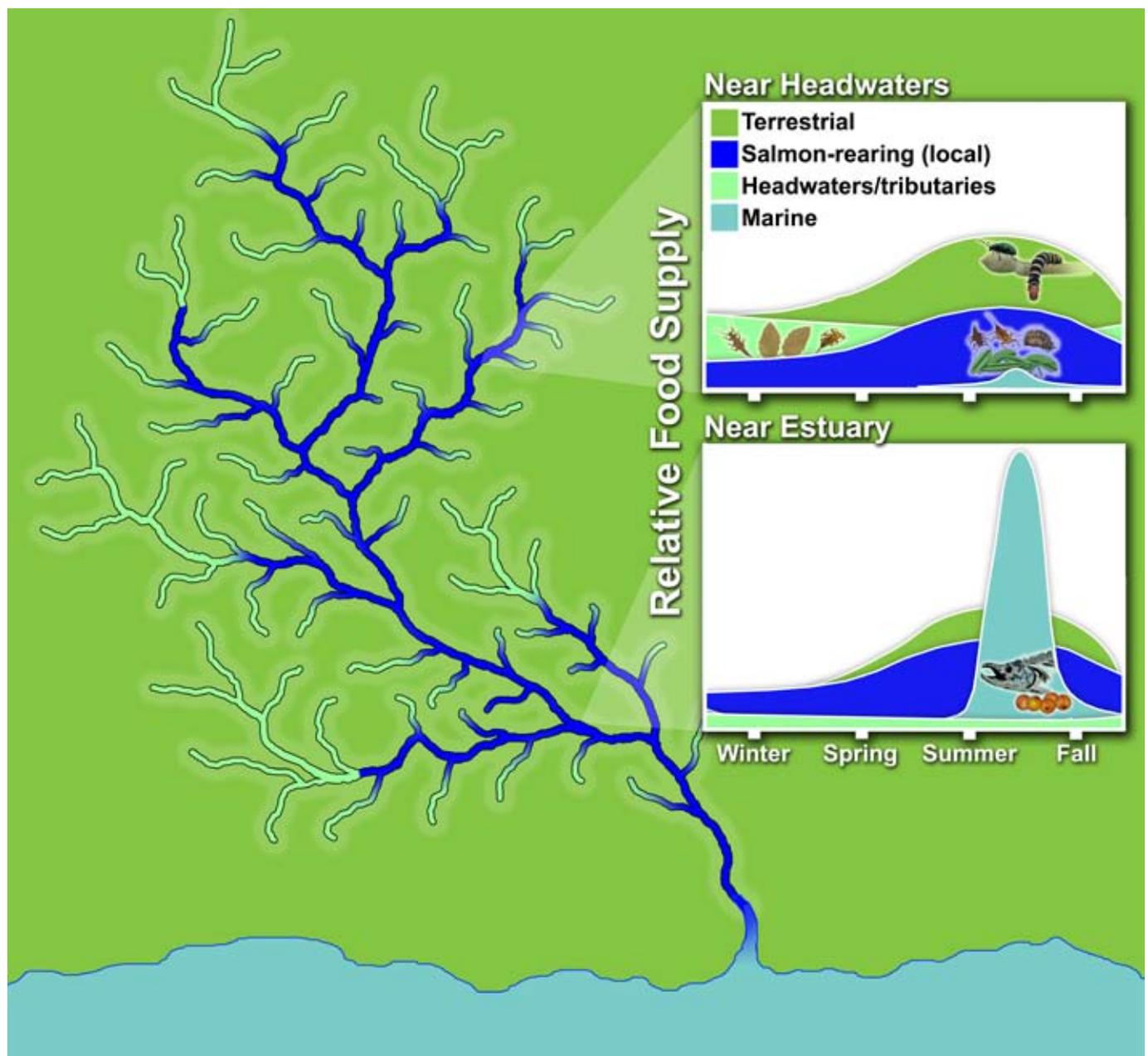
$$(5.8 \text{ mg prey dry mass/m}^2/\text{d}) +$$

$$(1.5 \text{ mg ingestible salmon dry mass/m}^2/\text{d}),$$

$$= 11.2 \text{ mg dry mass/m}^2/\text{d}$$

coming from all four sources on a mean annual basis.

Figure 3. Seasonal and temporal flux of food supplies in fish-rearing salmonid food webs.

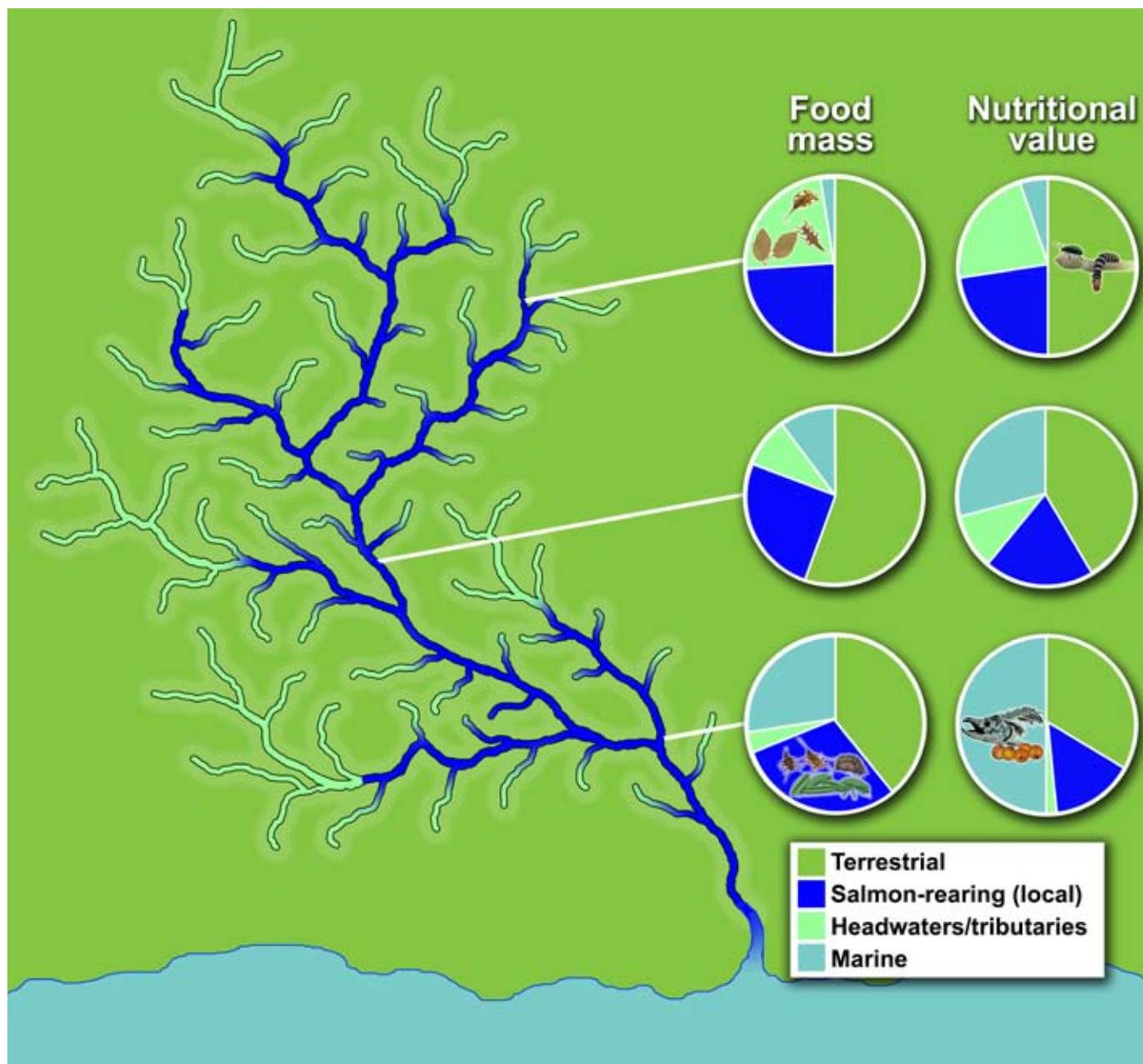


This translates to roughly 25% of the total from local production, 10% from headwater inputs, 50% from terrestrial sources (immediately adjacent streamside), and 15% from marine sources during the summer (Figure 4). These proportions match closely with the diets (aquatic v. terrestrial prey) of salmonids in small salmonid-rearing streams in southeastern Alaska (Wipfli 1997), where cutthroat trout (*O. clarkii*) and juvenile coho salmon ingested about 50–60% terrestrially-derived prey, and Dolly Varden char (*Salvelinus malma*) in northern Japan (Kawaguchi and Nakano 2001; Nakano and Murakami 2001) ingested about half of that during the summer. At any point in time, food is delivered to a fish's feeding space from some or all of these sources. Over time (e.g., one year), assuming salmonid-bearing habitats receive

salmon or other anadromous runs, fish can acquire food from all four sources.

The conceptual model described above provides the basis for identifying and partitioning prey sources that serve as the trophic basis for production of salmonid and other fishes. To gain a more thorough perspective on fish demand for prey and the flow of resources that fuel production for a species or an assemblage of fishes, such information must be integrated into the framework of a bioenergetics model. The demand for prey by fish is frequently estimated using a bioenergetics model like that developed by Hanson et al. (1997) that incorporates information on prey energy content and is parameterized for the particular species and habitat of interest (e.g., Koehler et al. 2006, McCarthy et al. 2009). A somewhat coarser, "trophic basis of production" approach that has long been utilized by stream

Figure 4. Food subsidies incorporating both food quantity and its nutritional value.



invertebrate ecologists (e.g., Benke and Wallace 1980, 1997) may also be useful for fish in cases for which such a bioenergetic model may not be available. The approach requires estimates of production for each prey source and proportions of each prey type in fish diets as described above, but also assimilation efficiencies (commonly derived from the literature) for each prey type, and the production rate of the fish themselves. The method of Benke and Wallace (1980) calculates the trophic basis of production as follows:

1. Determine the fraction of production attributed to food type i (B_i),
 $B_i = (G_i \times AE_i) / \sum G_i = 1, \dots, n$
2. Estimate the flow of organic matter via food type i to consumer j (F_{ij}),
 $F_{ij} = (B_i \times P_j) / (AE_i / NPE)$

where G_i is the percent of each food type, AE_i assimilation efficiency (the fraction of the organic matter the consumer is able to assimilate) of food type i , P_j is the secondary production of consumer j (in this case fish) in $g/m^2/y$, and NPE is the net production efficiency—the proportion of assimilated organic matter used to produce fish tissues (also commonly derived from the literature; e.g., Huryn 1996). With this approach, estimates of the contribution of different prey sources to the production of fish can be obtained, and actual flows from each prey type to the fish consumer can be calculated that provide the means for constructing a quantitative food web involving the fish and their prey. Incorporating temporal and spatial variation in prey source availability is the next step in developing a more comprehensive picture of the trophic basis for fish production.

Incorporating temporal variation in food availability

Annual and seasonal fluctuations affect the amount of food delivered from any of the sources described above to fishes at any given time (Figure 3). Water and air temperature play a role in determining the amount of invertebrate prey supplied from either aquatic or terrestrial sources (Price 1997). Though benthic production is usually higher in the warmer seasons (Huryn and Wallace 2000), insect life histories often dictate that the standing crop biomass of benthic invertebrate prey is greatest during late winter and early spring (e.g., Nakano and Murakami 2001). Subsidies of invertebrate prey from headwater streams might be expected to follow similar seasonal patterns, but few studies have investigated their temporal variation. Wipfli and Gregovich (2002) showed they can be temporally variable but still a reliable source throughout the year.

Terrestrial invertebrate inputs and marine-derived fluxes are both markedly seasonal sources. Peaks in terrestrial prey inputs can occur any time during late spring, summer, or early autumn, and vary strongly in magnitude from year to year (Baxter et al. 2005). As described by Nakano and Murakami (2001), the seasonal asynchrony in availability of benthic vs. terrestrial invertebrate prey may be an important factor sustaining fish productivity and diversity in many streams inhabited by salmonids. Likewise, marine-derived subsidies exhibit dramatic seasonal variability, and usually occur during summer and fall when the standing crop of benthic invertebrates and fluxes of terrestrial invertebrate prey are at their lowest, thus providing fish a timely energy source prior to overwintering (Wipfli et al.

2003; Heintz et al. 2004; Wipfli et al. 2004). Salmon runs often last for several weeks, sometimes months (Groot and Margolis 1991). Though escapement peaks can be short-lived for given salmon species, the presence of multiple salmon species or stocks with variable run timings can increase the period over which this annual marine subsidy takes place, possibly stretching biomass flux out over half the year. Yet, regardless of the magnitude of this flux, its timing with respect to high flows can affect how much of this input is incorporated into freshwater production or is flushed out to the estuary (Cederholm et al. 1989; Wipfli et al. 1998; Chaloner et al. 2002b).

Superimposed on the gross seasonal patterns described, the timing of food delivery relative to consumer physiology, movement patterns, and behavior are also important temporal considerations. Consumers must be positioned (e.g., physically, physiologically, behaviorally) to take advantage of prey resources when available. Fishes often exhibit movement whose purpose may be to occupy habitats with greater prey availability during different times of the year or stages of their life history. For instance, seasonal fish migrations between mainstem and tributary or floodplain habitats often appear to track availability of terrestrial prey sources and differences in timing of benthic invertebrate prey availability (e.g., Northcote 1997; Winemiller and Jepsen 1998; Lucas and Baras 2001). Likewise, they may move to upper reaches or tributary confluences in part to capitalize on headwater tributary subsidies of prey (Bramblett et al. 2002), or they may follow the spawning migrations of salmon to take advantage of opportunities to feed on their eggs or carcasses (Gende et al. 2002).

Yet, just because food is in a stream does not mean it is truly available. Being visual drift feeders, most salmonid fishes prey upon drifting invertebrates or emerging adult insects, whose availability is partially affected by drift timing and propensity to drift (Brittain and Eikeland 1988). Because invertebrates generally drift at higher densities at night (Waters 1962; Groot et al. 1995), and salmonids are generally believed to forage mostly during daylight, much of the prey that originates in headwaters may go uningested by these fishes (Brittain and Eikeland 1988; Groot and Margolis 1991; Allan 1995), a pattern that may also be induced by spikes in turbidity. The terrestrial food (T) category and total food (F) would both be lowered. Moreover, even if prey is available, it may not be used by fish. For example, extreme water temperatures can negatively affect the foraging rates of salmonid fishes (Matthews 1998), even if prey abundance is high. This would not affect the model, but would affect the amount of food assimilated.

Incorporating spatial variation into food availability

The location of a given reach of fish habitat within a drainage will strongly influence the relative amount of prey that habitat receives from each of the four sources described above (Figures 3 and 4). The estimates of inputs from the four sources are those that might be expected throughout mid-watershed reaches (Figure 4). The relative contribution from each source should change predictably with position in a drainage network, though channel complexity in floodplain segments (Figure 5) would modify some of these expectations. This channel complex-

ity, particularly characteristic of natural floodplains, will greatly contribute to the amount of water-land boundary (Stanford et al. 2005), and in terms of prey exchange between land and water, make these highly complex habitats behave more like headwater channels with their high stream margin-to-water volume ratios relative to larger channels. Local, in-stream production of benthic invertebrates often varies predictably from headwaters to mouth (Grubaugh et al. 1997; Rosi-Marshall and Wallace 2002), but could be elevated in highly braided floodplains, relative to reaches with less complexity. However, such changes are likely to be smaller relative to spatial variation in marine, terrestrial, and tributary inputs, because these are more influenced by the extent of penetration of salmon into drainages and stream margin to stream volume ratios (Vannote et al. 1980; Polis et al. 2004). Thus, relative to other sources, the contribution of in-stream production to fish energy budgets is expected to be more consistent throughout the basin (Figure 4).

Subsidies of invertebrates from headwater tributaries likely would be greatest immediately downstream of the fishless-fish

interface, because prey from this source have not yet been exposed to predation by fishes, and they are most proximal. As invertebrates are transported downstream through fish habitat, they may be consumed or leave the stream via adult emergence. Fish habitats downstream, farther from the highest density of fishless tributary sources, would be predicted to receive increasingly less prey from headwaters (Figure 4).

Regarding terrestrial invertebrate prey inputs, river continuum theory (Vannote et al. 1980) predicts that headwaters with their high stream margin-to-water volume ratios receive more allochthonous inputs than larger downstream reaches. Thus, small headwater streams should receive more riparian inputs of prey per stream surface area than larger streams nearer the coast (Figures 3 and 4). However, highly braided floodplains might have similar stream margin-to-water-volume effects, increasing prey inputs to streams per unit surface area (Baxter et al. 2005; and see Figure 5). In addition, inputs of terrestrial invertebrates can be affected by spatial patchiness in the type of riparian vegetation present (Wipfli 1997; Kawaguchi and Nakano

Figure 5. Floodplain habitat complexity increases amount of water-land interface in watersheds. Naturally functioning floodplains not impacted by human development provide immense off-channel habitats for rearing fishes and other freshwater-dependent species. Consumers in these complex off-channel habitats can benefit from high levels of both terrestrial subsidies and marine subsidies.



2001; Allan et al. 2003), with deciduous species generally housing more insects than conifers (Southwood 1961; Mason and MacDonald 1982; Ober and Hayes 2008).

In river systems with anadromous fish runs, habitats close to the ocean immediately upstream of saltwater often (but not always) receive the largest marine subsidy, simply because this area would usually receive the highest concentration of spawners, typical of those systems with strong chum (*O. keta*) and pink salmon runs that often spawn lower in drainages (Groot and Margolis 1991). Thus, in these areas and other reaches containing more concentrated aggregations of spawners, model inputs should shift towards a larger relative marine contribution (Figure 4). Progressing upstream, or other parts of the drainage where fewer spawners aggregate, marine subsidies would be expected to generally decline, dwindling to low spawner densities, and eventually becoming zero in headwaters (Figure 4). Sockeye (*O. nerka*), Chinook (*O. tshawytscha*), and coho salmon likely deliver the largest marine subsidies to fish habitats nearer the headwaters, as they generally swim farther up basins to spawn than chum and pink salmon and, though they usually exhibit lower spawner densities, at least Chinook salmon are also much larger sized (Groot and Margolis 1991). Exceptions to this general pattern clearly exist, as many spawning populations aggregate in drainage sections far from saltwater (Quinn 2004). For example, sockeye typically aggregate and spawn above and below lakes. Further, superimposed on general longitudinal patterns, spatial patchiness in carcass retention and nutrient storage mechanisms such as the amount of large wood or the size of floodplains and hyporheic zones may affect the extent to which this subsidy stays in streams and rivers versus being exported to saltwater (Cederholm et al. 1989).

Food quality

As is emphasized in the equations for calculating trophic basis of fish production and in models of bioenergetics in general, food quality is also an important consideration in the flow of energy to and assimilation by consumers. Quality is frequently expressed in terms of energy content of the food, but is also a function of a consumer's efficiency in digesting and assimilating a food resource. Caloric content of invertebrates varies, with consequences for energy assimilation (Cummins and Wuycheck 1971). Many invertebrates are highly sclerotized (e.g., bark beetles) or contain distasteful or poisonous biochemicals (e.g., rove beetles), which would be expected to affect digestibility and energy assimilation by fishes (Gerking 1994). In addition, prey size matters. Large prey are more profitable than small prey, all other factors being equal. Hence, both caloric content and digestibility will ultimately influence prey profitability.

Salmon eggs and certain other salmon tissues have a very high nutritional value, given their relatively high lipid content (Gende et al. 2004), and are often consumed by young salmonids (Wipfli et al. 2003; Bilby et al. 1996; Heintz et al. 2004). Juvenile salmon that consume salmon carcass tissues high in lipids sequester these in their own bodies, often resulting in increased freshwater and marine survival (Groot et al. 1995). Given the high nutritional quality of salmon eggs and other salmon tissues compared to the nutritional value of other food items (e.g., various species of insects), the relative trophic value

of the marine subsidy would be much larger than predicted by the basic food quantity model. If food quality (e.g., measured as calories or assimilation efficiencies) is taken into account, relative inputs (weighted for quality) for the model shift towards a larger role for the marine subsidy (Figure 4). Balancing food nutritional quality, abundance, and seasonal availability will help put into perspective the true value of individual prey sources to fish production.

Interactions among food sources and indirect trophic linkages

It is also important to consider that the four prey sources we have described are often interactive, and can contribute to fish production through indirect as well as direct pathways. For example, as mentioned above, tributary, terrestrial, hyporheic, and marine sources of materials and organisms can all affect local production of benthic invertebrate prey for fishes. Perhaps the strongest illustration of such interactive effects may be via marine subsidies, which not only fuel fish production directly through consumption of eggs and tissue, but also through multiple indirect trophic pathways (Wipfli et al. 1998). Because much of the marine input is used by lower trophic levels (i.e., microbial production, and invertebrates), and fragmented and dissolved salmon tissue is stored within the hyporheic zone and released later, fishes may be benefiting indirectly as well as directly (Bilby et al. 1996; Stanford et al. 2002; Wipfli et al. 2003). Taking this marine storage and higher local secondary production into account, proportional inputs for the trophic model would shift towards an even larger marine influence (Figure 4), with some incremental increase in local production being an indirect result of marine subsidies (Wipfli et al. 1998; Minakawa and Gara 1999; Chaloner and Wipfli 2002). Moreover, these estimates do not take into account that terrestrial invertebrates may graze on riparian plants fertilized by salmon-derived nutrients (Wipfli 1997; Ben-David et al. 1998). Changes in plant growth and forage quality from fertilization by salmon could have profound effects on nutritional quality and abundance of terrestrial invertebrates (Slansky and Rodriguez 1987; Price 1997) that fall prey to fishes (Wipfli 1997; Allan et al. 2003; Baxter et al. 2005). Reciprocally, inputs of terrestrial invertebrates that feed juvenile salmon could affect their survival to adulthood, thus indirectly mediating the potential for return of marine-derived energy and nutrients to the system.

Food, habitat, and their interactions

A more comprehensive understanding of the ecological processes that regulate fish production in freshwater ecosystems will require a balanced consideration of food resources, physical habitat, and the interactions between them, as well as interactions with predators and competitors. Physical habitat structure may set the stage that constrains the extent to which food resources can regulate fish (or any consumer's) production in freshwater. A stream with ample prey resources, but with little suitable fish habitat, is not likely to support above average salmonid populations (Naiman and Bilby 1998). Alternatively, ideal salmonid habitat lacking ample food (i.e., oligotrophy, no marine subsidies, dense conifer young-growth riparian forest providing little riparian inputs and local productivity, and negligible headwater inputs) will also not sup-

port high salmonid production (Wipfli and Gregovich 2002; Allan et al. 2003). Freshwater ecosystems with reliable, suitable habitat and food supplies will undoubtedly support higher fish densities and in turn produce more fish biomass. Further, interactions between habitat and food are also important. For example, researchers have pointed out that wood in streams helps retain salmon carcasses, keeping this energy and nutrient subsidy available longer for assimilation by riverine food webs (Cederholm et al. 1989; Gregory et al. 1991; Gurnell et al. 1995). Also fish behavior itself may enhance retention, for example by salmonids seeking more quiescent waters (Piorkowski 1995). Likewise, the occurrence of optimal habitats (e.g., velocity refuges) and conditions (e.g., water clarity) for drift feeding influence the ability of fish to utilize prey resources that are present. Gaining a better understanding of the relative roles of food and habitat and their interactions in governing freshwater food webs will help us evaluate where and when fish populations are limited by food, habitat, or both.

Effects of resource management on food resources

Resource management activities at scales from local to global have the potential to strongly affect the quantity and quality of prey sources for stream fish such as Pacific salmon. Management practices that result in stressors such as habitat homogenization, pollution, or loss of water can drive reductions in local benthic invertebrate production (Rosenberg and Resh 1993; Carlisle and Clements 2005; Chadwick and Huryn 2005). Sedimentation in streams, from logging, road building, glacial melt, or other causes, will also impact local and headwater invertebrate prey sources (Waters 1995). Fish in food-limited habitats will probably be most vulnerable to the consequences of such prey loss. However, the assumption that high benthic invertebrate production follows from management for high quality trout and salmon habitat may lead to confounded efforts. For example, at the scale of channel units within stream reaches, pools are known to be sites of high salmonid abundance, whereas riffles are the locations that exhibit greatest invertebrate production. Drifting invertebrates originating in riffle habitats are thought to subsidize fish in pool habitats (e.g., Cooper et al. 1990). Consequently, attempts to manage for dramatic increases in pool density may come at the expense of prey availability for drift-feeding fish. Even where habitat restoration actions (e.g., large wood addition) may initially appear to increase fish numbers, these may be driven by redistribution of fish (e.g., Gowan and Fausch 1996) rather than increased local production of fish.

Likewise, management practices may directly or indirectly alter or reduce terrestrial or marine subsidies to stream fishes. Streamside forest management affects the amount and composition of riparian vegetation, with consequences for terrestrial subsidies of invertebrate prey (Wipfli 1997; LeSage et al. 2005; Richardson et al. 2005). Streams whose riparian forests have been removed or overgrazed will have reduced input of terrestrial invertebrate prey (Edwards and Huryn 1996; Kawaguchi and Nakano 2001) with likely consequences for salmonid populations (Mason and MacDonald 1982; Saunders and Fausch 2007). In contrast, headwater streams with riparian forest patches of red alder, often a consequence of past timber harvesting, can contribute more invertebrates to fish-bearing streams than those with conifer-dominated riparian forests

(Piccolo and Wipfli 2002; Wipfli and Musslewhite 2004; Romero et al. 2005). Wildfires in headwater subcatchments can also dramatically alter the composition and increase the flux of insect prey from streams to surrounding habitats, for several years post-fire (Mellon et al. 2008; Malison and Baxter 2010). Regarding marine subsidies, commercial, sport, and subsistence fishing, as well as impediments to upstream salmon migration such as dams or road crossings, may block or severely reduce adult salmon returns into drainages. For instance, the Columbia River Basin presently receives a small fraction of its historical salmon runs, before resource management in the form of dams, urbanization, and fishing impacted returns, dramatically reducing marine nutrient and carbon subsidies to a vast landscape (Baker et al. 1996; NRC 1996; Lichatowich 1991). Loss of wood in and along streams, from past logging for example, diminishes carcass retention (Cederholm et al. 1989), in turn allowing carcasses and nutrients to more easily flush downstream, reducing nutrient and carbon availability and flux into riverine food webs. If prey quality is as important in aquatic food webs as that seen in southeastern Alaska (Wipfli et al. 2003; Heintz et al. 2004; Wipfli et al. 2004), lack of marine subsidies could have major consequences for the productivity of these food webs and associated fish assemblages. On top of these effects, climate change is predicted to push ocean salmon populations northward (Welch et al. 1998), further reducing marine subsidies to freshwater ecosystems in the more southern regions of current salmon occurrence, but potentially enhancing returns and subsequent effects in northern ecosystems.

Implications for other food webs, consumers, ecoregions and geomorphologies

Multi-prey source models such as the one we have developed here are likely to look different for other freshwater food webs that contain different fishes, are in other climatic regions, or are underlain by different geology, but the basic premises and processes will apply. For example, models for fishes that exhibit non-anadromous migrations or are herbivores, detritivores, or piscivores would focus on trophic pathways we have not emphasized here (e.g., Goulding 1980; Winemiller 1990; Taylor et al. 2006). Moreover, there is important variation in the prey sources we included even among stream systems occupied by invertivores like salmonids. Many streams outside of southeastern Alaska are substantially more productive for benthic invertebrates (Benke and Huryn 2006; Duncan et al. 1989; Huryn and Wallace 2000), and fish in these systems would likely depend more heavily on this food source, and proportionately less on the subsidies we have described. Fish in streams that are predominantly fed by ground water, with little runoff through stream networks, will undoubtedly rely very little if at all on invertebrate subsidies from headwater tributaries. It is also possible that in more arid landscapes fishless tributaries may be ephemeral and less reliable sources of invertebrate prey, assuming tributary hyporheic production is also minimal. Focused studies would help assess the contribution of this prey source to the trophic basis of production for stream fishes. Regarding marine subsidy, this component would not be included in the multi-source model for those systems that either never did receive marine subsidies, or no longer receive marine subsidies and are unlikely to be restored. Likewise, food webs that

are not nutrient or food-limited are likely to respond much differently to variation in prey subsidies. For example, salmon carcasses added to tributaries draining into Lake Ontario had little noticeable effect on stream food webs, likely a result of ample ambient levels of nutrients, carbon, and prey (Rand et al. 1992).

Actual vs. apparent food availability

Several critical assumptions are being made in our multi-prey source model, and certainly need to be recognized and researched, to help improve the accuracy, reliability, and applicability of the model. One major set of assumptions revolves around the 1 pink salmon spawner/m²/y used in the model, and how much material gets assimilated into the food web. Salmon densities can range from 0 to several fish per m² (and even higher immediately downstream of waterfalls and other barriers to upstream salmon migrations; Wipfli et al. 1998) and there are four other species of Pacific salmon that enter these watersheds (chum, sockeye, coho, and Chinook), all of which are larger, usually travel farther upstream, and occur at different densities than pink salmon (Groot and Margolis 1991; Quinn 2004). Also assumed is that all sources of food are available for consumption once they enter fish habitat (but clearly not all food items are eaten, due to low light, turbidity, predator avoidance tactics, etc.). While Bilby et al. (1996) found rearing salmonids consume salmon eggs and adult carcass tissue, how much of this biomass is ingested by young fish needs to be determined, relative to other sources. A very small fraction probably gets consumed by fishes, relative to what enters the system, with most “lost” to vertebrate predators, floods and flushing, physical fragmentation and chemical leaching, burial in stream sediments, and biological processing and uptake (Cederholm et al. 1989; Bilby et al. 1996; Wipfli et al. 1998; Gende et al. 2004). Watershed characteristics (e.g., vertebrate scavenger species present, gradient, woody debris and other physical structures, pool frequency and depth, stream flow) will dictate how much salmon tissue is actually available for consumption in streams. In addition to direct consumption, Wipfli et al. (1998) documented that aquatic invertebrate production apparently increases in streams with salmon, but it is unknown how much of the adult salmon biomass is actually converted into secondary invertebrate production, and how much of that gets ingested by fishes. Food quality (e.g., caloric content) also rapidly decreases from the time a salmon enters freshwater to post-spawning, which will also play an important role in energy uptake by consumers (Mathisen et al. 1988).

Current understanding, knowledge gaps, and research needs

This multi-prey source model helps illustrate what we know, what we think we know, and what we do not know about the sources of energy to stream food webs that support stream fish, especially salmonids. It also sheds light on the importance of broader ecosystem and watershed processes and connectivity. Although salmonid protection and restoration over the last few decades has largely focused on fish habitat, hatcheries, hydroelectric dams, and harvest (NRC 1996; Naiman and Bilby 1998), gains in understand-

ing food web dynamics and trophic processes affecting salmonid production have been made (Richardson 1993; Nakano et al. 1999; Wilzbach et al. 2005). Our model helps synthesize and organize current understanding on this topic, and should also help stream ecologists further resolve the Allen paradox (Allen 1951; Hynes 1970; Hurn 1996). It points to three food sources (i.e., local, terrestrial, marine) as being most important, with headwater subsidies potentially less so, and highlights the need to incorporate food quality in food web analyses. However, the model represents only a step toward developing a more holistic understanding of the various prey fluxes to fish. Integrating knowledge of prey sources, fish diets, and prey assimilation efficiencies allows the trophic basis of fish production to be estimated, and when fish production is known as well, the trophic pathways that fuel it can be depicted in a quantitative food web. The seasonal and longitudinal models we have presented should serve as heuristic tools for attempts to more precisely describe how multiple prey fluxes vary in quantity and quality through time (daily, annual) and space (within and among drainages), under different riparian, headwater, local stream, and marine conditions. At larger spatial scales, modifying the model to fit other food webs characterized by different apex consumers (e.g., other fishes, amphibians, birds, etc.) will help expand the utility of the model and help us understand how such trophic pathways vary across regions. For example, how well does the model predict responses to other marine subsidies from species such as Atlantic salmon, smelt, or lamprey in other parts of the world? Also, are there other important sources of subsidies in other places? Undoubtedly so.

Informed management of stream fish populations will require that decision-making explicitly address the consequences of human actions for the complex trophic pathways that fuel fish production. To that end, ecosystem and food web studies are needed that directly assess the effects of management practices on these multiple trophic pathways, not simply their consequences for physical habitat characteristics. At present, relatively little is known about how multiple prey resources are affected by land management regimes or species invasions, either aquatic or terrestrial (but see Baxter et al. 2004; Baxter et al. 2007; Saunders and Fausch 2007). Our model was developed with data from a setting of relatively pristine, old-growth, temperate rainforests in southeastern Alaska. How do food pathways differ in a drainage like the Columbia River Basin that receives 6% of its historic salmon run, contains much more urbanization, irrigation, and agriculture, and has seen decades of fish habitat alteration (NRC 1996; Lichatowich 1999; McClure et al. 2003; Gresh et al. 2000)? The model should be expanded to predict effects of dominant agents of global environmental change, including aquatic and terrestrial habitat alteration, nonnative species introductions, and climate change. This will strengthen the model so that it can become an effective tool that provides insight and improves the way we study and manage fish, as well as riverine ecosystems and the land and seascapes to which they are connected.

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