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The ecological importance of floodplains in montane river networks:

Implications for habitat restoration and salmon recovery

by

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Committee Approval

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Dedication

This dissertation is dedicated to my Father, and our weekend river trips.

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Abstract

Floodplains are heterogeneous and dynamic landscapes, and are considered to be "hotspots" of biological diversity and productivity. Unfortunately, many floodplains have been severely degraded by human development, and as a result, are frequent targets for restoration. Predicting the potential for restoration to succeed, however, requires an adequate knowledge of floodplain structure and function. This dissertation consists of a sequence of studies conducted in the Salmon River of Idaho and the Methow River of Washington that address key gaps in the understanding of floodplain systems within montane river networks. I employ ecosystem and food web approaches to shed light on the biodiversity, productivity, and trophic complexity associated with the aquatic portion of these systems. In addition, this research evaluates the consequences of floodplain degradation on ecosystem structure and function, and the potential for restoration to restore ecosystem integrity and recover endangered Pacific salmon and steelhead. My findings indicate that floodplain segments can support high biodiversity and food web complexity, and may be important in terms of organic matter processing within montane river networks. However, I did not find clear evidence to suggest that floodplains were more productive (in terms of benthic primary and secondary production) than neighboring river segments. Moreover, my results indicate that degradation of floodplain habitats does not necessary translate into lower productivity of the food-base important to fishes. Although my research indicated that restoration might increase food-base productivity, I found little evidence to suggest that juvenile salmon and steelhead were food limited at my study sites. This finding raises the possibility that downstream factors (e.g., ocean conditions and the hydropower system) may be more limiting, and that

relatively small-scale floodplain restoration efforts may do little to assist salmon and steelhead recovery over shorter time-scales. That said, my research showed that floodplain heterogeneity has important consequences for biodiversity, food web complexity and the strength of trophic interactions. Consequently, conserving and/or restoring heterogeneity may be important for maintaining the long-term resilience of biotic communities. Restoration efforts should be preceded by studies that evaluate if and how systems are impaired, and whether restoration is appropriate to alleviate impairment and restore species of interest.

Preface

Ecologists have long recognized that natural landscapes are complex and heterogeneous, and studies have shown that this heterogeneity is important for populations (Hanski 1982), communities (Holyoak et al. 2005), and ecosystems (Polis et al. 2004). In a well known experiment, for example, Carl B. Huffaker (1958) showed that the outcome of a simple predator-prey system was mediated by the complexity of the experimental landscape. In simple landscapes, predators quickly consumed prey and subsequently starved, whereas in complex systems, predator and prey were able to persist. Contrary to the complexity found in nature, however, it is often human nature to simplify, “tame” and control landscapes (Walters et al. 2002). Historically, complex natural landscapes were perceived as messy and inefficient, and landscapes were simplified and homogenized to maximize the exploitation of human good and services (e.g., removal of wood from rivers). The result of this simplification has, however, had negative consequences on ecological good and services (e.g., clean water and air), biodiversity, and species of cultural and economic importance to humans. To balance the short term exploitative needs of human populations with the longer term sustainability and resilience of ecological systems, there has been increasing recognition that intact natural landscapes, including their spatial complexity, should be preserved, and when necessary, restored. The developing practice of ecological restoration is increasingly utilized to restore such “natural” landscapes, and the heterogeneity found therein (Clewell and Aronson 2007). That being said, relatively few studies have evaluated the importance of landscape heterogeneity on ecosystem structure and function at the larger spatial scales that are most relevant to ecological restoration.

Floodplains are often considered to be some of the most biophysically complex and diverse systems on earth (Bayley 1995), making them an ideal location to study ecological communities in the context of complex landscapes. Flood-pulses that redistribute sediment and organic matter create a dynamic mosaic of physical habitat features (Junk et al. 1998, Stanford et al. 2005) within floodplains, which are thought to support diverse and productive biotic communities. Unfortunately river floodplain systems have also been severely altered by human disturbance (Tockner and Stanford 2002). Because broad, unconfined floodplains associated with low gradient reaches of rivers were most attractive for development, rivers were straightened or diked to minimize the threat of flooding, and these modifications led to the disconnection of rivers from their floodplains. The loss of longitudinal, lateral, and vertical connectivity through channel and flow alteration has diminished the biophysical complexity and ecological processes that are thought to make floodplains hotpots of biotic productivity and diversity (Tockner and Stanford 2002). As a result, floodplains are a frequent target of habitat restoration aimed at restoring the structure and function of these systems (Bernhardt et al. 2005). Although there is substantial evidence to indicate that intact floodplains are, in fact, very biodiverse (Ward et al. 1999), there have actually been very few studies that evaluate the importance of floodplains in terms of ecosystem function (i.e., biotic productivity, energy flows, stability, etc.), let alone studies that assess the consequences of floodplain degradation for these functions or the potential for ecological restoration to restore them.

River floodplain segments are also important for sustaining many organisms of economic, cultural and aesthetic interest (e.g., fishes, waterfowl, riparian vegetation, etc.), and restoration efforts are often designed to recover these species (Tockner and Stanford 2002; Bernhardt et al. 2005). In the context of the Pacific Northwest of the United States, floodplains are a frequent target of restoration aimed at the recovery of threatened and endangered anadromous Pacific salmon and steelhead (NRC 1996; Wissmar and Bisson 2003). Although anadromous species utilize many environments (ocean, estuary, large rivers, tributary streams) during their complex life cycle, floodplains are often prioritized for restoration because they are thought to provide physical habitat critical for fish spawning (Montgomery 1999) and rearing (Sommer et al. 2001). However, an under-represented mechanism by which floodplains may be important to these fishes is via enhanced food base productivity (Wipfli and Baxter 2010). Aquatic habitats within floodplains have been shown to support high rates of both autochthonous production (Coleman and Dahm 1990) and allochthonous organic matter inputs, such as leaf litter and terrestrial invertebrates (Gregory et al. 1991; Baxter et al. 2005). Accordingly, floodplain aquatic habitats can support elevated invertebrate secondary production (Smock et al. 1992; Lewis et al. 2001), enhancing the food base that fuels fish production (Sommer et al. 2001; Stanford et al. 2002; Jeffres et al. 2008). However, in the context of the Pacific Northwest of the U.S. where many floodplain restoration efforts are being conducted or proposed, there have been very few measurements of the productivity of river-floodplain systems that sustain anadromous fishes that are the focus of these restoration projects.

My dissertation attempts to fill gaps in the ecological understanding of floodplains, and in so doing, gain a better perspective of the importance of complexity and heterogeneity in ecological systems, the consequences of simplification, and the potential for restoration. In particular, the objectives of my research were to: (1) evaluate the importance of floodplains in terms of community structure, biotic productivity and the flows of energy that sustain productivity, (2) assess the impact of degradation that disconnects floodplain systems, and (3) evaluate the potential for restoration to improve both floodplain function, and salmon and steelhead populations. To accomplish these objectives I employed an ecosystem approach (Odum and Barrett 2005). In the simplest sense, I utilized this approach to measure the production of organic matter at different trophic levels. Although this model has been criticized for being overly simplistic and coarse (Polis and Strong 1996), it has a long and important history in ecology as a heuristic tool, aiding in interpretation and informing the development of more complex and realistic ecosystem models (Lindeman 1942, Odum 1957, Odum and Barrett 2005). I used this simple approach as the basis for constructing food webs, which identify the individual consumer-resource pathways by which energy and materials flow. The strength of these ecosystem approaches lies in the measurement of energy and material flows and transformations, which are rooted in the laws of thermodynamics. Although such ecosystem studies have a long history in ecology, they are often under-represented in assessments of ecological impairment and restoration. In addition to the objectives listed above, my hope is that this research will highlight the strengths of ecosystem studies, and set the stage for future studies that build upon the approaches and findings I present here.

Results and analyses from my dissertation research are described in four chapters. Each chapter is written as a potentially publishable manuscript, thus some repetition occurs. In chapter one I compare floodplain segments to naturally confined river segments in terms of the structure and function of aquatic ecosystems, to gain a better understanding of the importance of river floodplain segments within larger river networks. In chapter two I present a case study that evaluates the impact of floodplain simplification via dredge-mining on these aquatic ecosystem structures and functions, and the food base that fuels the production of anadromous salmonids. The results of this analysis are utilized to discuss the potential for floodplain restoration to succeed at restoring ecosystem function, and recovering threatened and endangered salmon and steelhead populations. These first two chapters discuss the overall productivity and function of floodplain in relation to other river segments (i.e., floodplain versus confined, degraded versus intact). In contrast, chapters three and four evaluate the ecological contributions of different habitat patches within a single floodplain. In chapter three I describe the pathways of energy flow within different habitat patches, and the implications of food web variation among habitats (within floodplains) for anadromous salmonids and floodplain restoration. Chapter 4 evaluates how this mosaic of habitat patches influences biodiversity, food web complexity, and the strength of interactions between fish predators and their invertebrate prey. This final chapter highlights the potential importance of complex floodplain landscapes for the stability of ecological communities and the persistence of aquatic biodiversity, including anadromous salmonids.

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Chapter 1

Effects of geomorphic process domains on the structure and function of aquatic ecosystems: a comparison of floodplain and confined river segments

Abstract

The geomorphic template of streams and rivers exerts strong controls on the structure and function of aquatic ecosystems. However, relationships between stream geomorphology and ecosystem structure and function are not always clear, and have not been equally evaluated at all spatial scales. In montane regions, rivers often alternate between canyon-confined segments and unconfined floodplain segments. Yet, few studies have evaluated how this pattern influences the structure and function of aquatic ecosystems. In this study I pair five confined river segments to five floodplain segments, and measure allochthonous inputs to aquatic habitats, aquatic primary producer and invertebrate production, stream retentive capacity, and the diversity and assemblage structure of aquatic invertebrates. As hypothesized, my results showed that floodplains had a higher retentive capacity, a significantly greater diversity of aquatic invertebrates, and a distinctly different invertebrate assemblage, relative to confined segments. Contrary to my expectations, the magnitude of allochthonous inputs were greater to confined segments, and aquatic primary and invertebrate production followed no consistent pattern between segment pairs. However, results did indicate that floodplains have greater total heterotrophic production (i.e., community respiration) than confined segments. Together, these findings suggest that floodplain and confined river segments do have indeed differ in terms of ecosystem structure and function, but not entirely as expected. Confined segments had greater allochthonous inputs, but a lower capacity to retain those inputs, whereas floodplain segments had a high capacity to retain transported organic matter, and also a more diverse assemblage of invertebrates and higher overall community respiration to “digest” this organic matter. If these finding are correct, then it

would indicate that confined segments are sources for organic matter within river networks, whereas floodplains act as filters, removing and processing organic matter transported from upstream confined segments.

Introduction

Stream ecologists have long recognized that catchments have a strong influence on the structure and function of stream ecosystems (Hynes 1975), and that spatial heterogeneity in catchment geology, topography, vegetation and climate creates spatial variation in hydrologic and geomorphic processes that constrain the structure of habitat in streams (Allan and Castillo 2007). Stream ecologists have generally incorporated such heterogeneity into theoretical frameworks in two ways: either as relatively continuous longitudinal gradients (e.g., Sheldon 1967; Vannote et al. 1980; Minshall et al. 1983) under which discontinuities are treated as departures from theoretical ideals, or as discontinuous patches or domains that occur in a mosaic whose structure is expressed within a hierarchical context (Frissell et al. 1986; Pringle et al. 1988; Montgomery 1999; Poole 2002). For decades ecological studies have been aimed at evaluating whether stream ecosystems conform to the principles of the former, but there have been far fewer tests of the latter.

Process domains are defined (Swanson et al. 1998; Montgomery 1999) as “predictable areas of a landscape within which distinct suites of geomorphic processes govern physical habitat type, structure and dynamics; the disturbance regimes associated with process domains dictate the template upon which ecosystems develop.” Montgomery (1999) describes that coarse differences in ecosystem function and community structure should parallel the distribution of process domains because of the associated variance in disturbance regimes (e.g., floods, landslides, etc.). For instance, at small spatial scales, substrate size within a "patch" of benthic habitat may determine the susceptibility of different sized particles to scour during high flows. In turn, domains at this scale are thought to create distinctive and predictable patterns in benthic community structure (Townsend 1989). Although there has been substantial research demonstrating linkages between patchiness and community structure and ecosystem function at these smaller spatial scales (microhabitats and channel units; e.g., Huryn and Wallace 1987; Pusch 1996; Finlay et al. 2002) and at larger scales (e.g., stream-to-stream comparisons; Minshall et al. 1983; Mulholland et al. 2001; Sabater et al. 2008), there have been fewer investigations of the ecological consequences of heterogeneity at the intermediate scale of reach and segment domains.

In montane regions, stream channels are often set within deep canyons, and it is a common pattern for the river to alternate between canyon "confined" segments, with narrow valley bottoms, and unconfined "floodplain" segments, with broad valley bottoms (Church 1992; Stanford and Ward 1993; Montgomery et al. 1996 [Figure 1]). The extent of channel confinement (i.e., valley bottom width) in these montane river networks is also associated with differences in channel slope, with more confined channels generally having higher gradients. Together, variation in channel confinement and slope define the geomorphic processes that control segment scale differences in disturbance regime and physical habitat (Montgomery and Buffington 1997). In particular, variation in channel confinement and slope influences sediment dynamics, channel avulsion, and how different river segments respond to high flows (see Swanson et al. 1998). For example, in floodplains, high flows can diffuse laterally onto parafluvial and orthofluvial surfaces, whereas confined segments, with narrower valley bottoms, must largely compensate for high discharge by increasing water depth and velocity. As a result, confined segments generally have greater stream power and sediment transport capacity than floodplain segments, which are considered more depositional in nature (Montgomery and Buffington 1997). These differences strongly control stream channel morphology, and ultimately the template upon which biotic communities develop. Floodplain segments, for example, commonly have smaller substrate, deeper alluvial fill and more expansive hyporheic zones than confined river segments (Stanford and Ward 1993; Montgomery and Buffington 1997). In addition, floodplains are more spatially and temporally dynamic and heterogeneous (Junk et al. 1989; Stanford et al. 2005; Naiman et al. 2010), and contain a diverse array of channel types with different levels of hydrologic connectivity to both the main channel and the subsurface hyporheic zone. According to the Process Domain Concept, coarse differences in community structure and ecosystem function should parallel these differences in disturbance regimes and physical habitat structure. Although there has been some empirical research (e.g., Swanson et al. 1998; Thorp et al. 1998; Montgomery et al. 1999; Baxter and Hauer 2000) and modeling (e.g., Power et al 1995) to test this hypothesis, to date there have been few studies that have explicitly identified if and how floodplain and confined river segments differ in terms of ecosystem structure and function in montane river networks.

Although there has been little research that directly evaluates differences in ecosystem function and community structure between floodplain and confined river segments, it is theorized that floodplain segments are hotspots of biological productivity and diversity in river networks (Bayley 1995). In fact, several conceptual models (Junk et al 1989; Stanford and Ward 1993; Stanford et al. 2005) have been developed that highlight mechanisms believed to enhance productivity and diversity within floodplains. That said, much of the empirical research from whence these models are derived is from large temperate and tropical floodplain systems. Although there are notable exceptions (e.g., Flathead River, Montana, USA; Stanford et al 1994), very few studies have evaluated ecosystem structure and function in smaller montane river networks, and none of these studies have compared floodplains to other segment scale geomorphic domains within the river network (but see Gregory et al 1989). In addition, few floodplain studies have included functional ecosystem measurements, such as primary and secondary productivity, ecosystem metabolism, allochthonous organic matter inputs, and organic matter transport and retention, which are necessary to evaluate the productivity of floodplain systems (but see Lewis et al. 2001). Instead, most studies have focused on measurements of community structure (e.g., Arscott et al. 2005), such as species richness, diversity, and assemblage composition, because historically these metrics were easier to evaluate. Although relationships between ecosystem structure and function are strongly rooted in ecological theory (Cummins 1974; Odum and Barrett 2005; Allen and Castillo 2007), studies have shown that community structure can change without a corresponding change in function, and function can change without any apparent change in structure (Woodward 2009). Consequently, in the context of understanding the influence of geomorphic process domains on aquatic ecosystems, measurements of both community structure and ecosystem function may be necessary.

In this study I paired five floodplain segments to five naturally confined river segments and evaluate if and how ecosystem function and aquatic community structure differed between these two geomorphic domains. To assess differences in ecosystem function I focused on measurements of aquatic productivity, including: allochthonous (leaf litter and aquatic invertebrate inputs) and autochthonous (aquatic primary producer biomass and gross primary production [GPP]) organic matter production, the ability of river segments to retain this organic matter, and the heterotrophic productivity fueled by these basal organic matter sources (aquatic invertebrate production and community respiration [CR]). In terms of community structure, I focused on differences in the richness, diversity, and composition of the aquatic macroinvertebrate assemblage. Based on the current floodplain paradigm (e.g., Junk et al. 1989; Stanford and Ward 1993; Bayley 1995), which considers floodplains to be extremely productive and biodiverse, I hypothesized that floodplain segments would have greater allochthonous and autochthonous organic matter contributions, a higher capacity to retain this organic matter, and higher invertebrate production and community respiration relative to paired confined segments. Likewise, I hypothesized that floodplains would have a more rich and diverse, but also distinctly different, macroinvertebrate assemblage compared to confined river segments.

Methods

Study Sites

All study segments were located in tributaries of the Salmon River, in central Idaho, USA. Although there is a legacy of human impacts within the basin, particularly mining and grazing, a majority of the basin is managed by the USDA Forest Service, and contains large tracts of wilderness and road-less areas. As a result, stream ecosystems remain relatively intact, presenting an excellent opportunity to evaluate ecosystem structure and community function in floodplain and confined river segments. I selected five sites from 4th to 6th order streams within the Salmon River (Figure 2). Sites were located in Basin Creek (BC), Camas Creek (CC), East Fork Salmon River (EF), West Fork of the Yankee Fork (WF), and the Yankee Fork Salmon River (YF). At each of these locations, I paired a single unconfined floodplain river segment with a canyon confined river segment (see Figure 1). Floodplain and confined river segments were delineated based on differences in channel slope, width of the valley floor relative to width of the active channel, and channel pattern (Table 1). On average, valley floor width within selected floodplain segments was close to 6X greater than in paired confined segments (Table 1). Furthermore, the width of the active channel, defined as the terrace-bound portion of the valley that is regularly inundated (every 1-2 years) by high flows (see Figure 3), was on average almost 2.5X wider in selected floodplains than paired confined segments. Floodplain segments also had greater channel sinuosity, on average 20% greater, and more channel complexity, with multiple off-channel aquatic habitats (i.e., side channels, spring brooks, and beaver complexes). Confined segments, on the other hand, tended to have larger stream bed substrate than floodplain segments (on average, 2.5X larger), and also higher stream gradients (on average, 69% higher) (Table 1).

Although confined segments usually bound the upstream and downstream ends of floodplains, for this study, confined segments were selected downstream of floodplains (except the EF site, which had an upstream confined segment due to private property downstream) to facilitate accessibility via hiking. To reduce the potential influence (e.g., high nutrient export) of floodplains on confined segment (and vice versa), sampling in confined segments was conducted at least 1.5 river kilometers downstream of floodplains. The rationale for this separation was to reduce the possibility that observed ecosystem function and community structure was the result of labile nutrients and organic matter delivered from upstream floodplain segments (Noe and Hupp 2007; Tockner et al. 1999).

Sampling Design

I utilized a stratified random approach to sample allochthonous inputs, aquatic primary producers, and aquatic macroinvertebrates in both floodplain and confined segments. For each of these variables I established sampling based on the presence, abundance, size, and complexity of different terrestrial vegetation and aquatic habitat patches, which I measured via visual ground surveys during summer base flows and digitized in ArcGIS (Figure 3, Appendix 1a). These digitized habitat patch maps were used to extrapolate point estimates to entire study segments (see *Analysis* section below). Larger and/or more heterogeneous patches received a greater sampling effort than smaller more homogenous patches. In addition, larger and/or more heterogeneous study segments required more sampling effort to account for the higher diversity of habitat patch types. For allochthonous inputs (leaf litter and terrestrial invertebrates) I stratified sampling by dominant riparian vegetation patches, mainly willow (*Salix spp.*), alder (*Alnus spp.*), cottonwood (*Populus trichocarpa*) and conifer. Similarly, I stratified sampling of aquatic primary producers and invertebrates by dominant aquatic patch types. For main channels this included categorizing habitat into riffles and pools/runs. For aquatic habitats found outside of the main channel (hereafter, off-channel habitats) I classified habitat by degree of connection with the main channel at base flow, including side-channels with both up- and downstream connections, spring brooks connected only on the downstream end, and wetlands with no surface connection to the main channel (but connected during high flows).

All sampling was conducted during summer base flow conditions. Due to logistical constraints, however, sampling in floodplain segments and confined segments was not always conducted during the same year. Allochthonous inputs, aquatic primary producers, and aquatic macroinvertebrates were sampled during summer 2006 in floodplains and summer 2007 in confined segments. However, given that floodplains are considered to be extremely diverse and productive systems, I expected that differences between floodplain and confined segments would be much greater than inter-annual variation within a given river segment. Consequently, I did not expect inter-annual variation to strongly affect the outcome of my comparisons. In contrast to the above metrics, field measurements of retentive capacity and stream metabolism (GPP and CR) were collected in tandem for floodplain and confined segments during the same summer.

Habitat Measurements

For each floodplain and confined segment, several habitat variables were measured that are known to influence the ecological metrics I planned to compare. I estimated annual input of solar radiation to aquatic habitats by tracing surrounding features of the landscape and riparian vegetation using a Solar Pathfinder^{TM} (Platts and others 1983) at several locations along the length of the main channel. I measured stream temperature hourly with Onset HOBO$^{®}$ data loggers placed within the main channel at the downstream end of each study segment, from June to October of 2006 and 2007. I measured discharge several times during the summers of 2006 and 2007 using a current meter. I collected three consecutive water samples from the main channel of each segment in June 2007, which were analyzed for total dissolved nitrogen and phosphorus (TDN and TDP), and dissolved organic carbon (DOC). To estimate substrate size, I measured the β (intermediate) axis of 100 to 300 rocks from main channel habitats during summer 2007.

Allochthonous Inputs and Aquatic Primary Producers

I estimated input of allochthonous leaf and woody litter to aquatic habitats with litter baskets (sample area = $0.20\ m^2$) in floodplain and confined segments by randomly dispersing baskets within riparian vegetation patches (see Figure 3) and collecting contents monthly until the final collection following leaf abscission in late October. The number of baskets placed in each segment ranged from 10 to 28, and (as described above) was proportional to complexity and length of the study segment. Litter was defined as allochthonous input if it would have fallen either directly into aquatic habitats or onto terrestrial surfaces within the active channel (i.e., the portion of the valley that is often inundated by annual peak flows). In the lab, I sorted litter inputs by species, and then dried (at 60ºC for 24 hrs) and weighed basket contents.

I estimated the flux of terrestrial invertebrates entering aquatic habitats using pan traps (sample area = 0.21 m^2). Although invertebrate contributions are small compared to other allochthonous inputs (i.e., leaf litter), they are high quality (i.e., labile and high energy density) and can be an important resource for higher level consumers, such as fish (Baxter et al. 2005). Within each segment I placed 10-28 traps, distributed in proportion to the presence of different riparian vegetation patches, at the wetted edge of the stream. I filled traps with approximately 5 cm of water and a few drops of biodegradable soap to reduce water surface tension. Three times in July (after collecting 3-8 days), I removed invertebrates with dip nets (500 µm mesh). In the lab, I sorted samples under a dissecting microscope to remove aquatic taxa, and then dried (60°C for 24 hrs) and weighed the remaining terrestrial invertebrates. I calculated invertebrate flux by multiplying the average input to all traps at a segment ($g\ m^{-2}\ d^{-1}$) by the total wetted area of that segment (m^2).

At each floodplain and confined segment I estimated aquatic primary producer biomass by sampling periphyton, algae, and aquatic vegetation within aquatic habitat patches. In total, I collected 10-45 samples from each segment. In rocky habitats, I sampled periphyton by scrubbing the surface of randomly selected rocks. I then traced the top surface of sampled substrate to determine planar surface area (Bergey and Getty 2006). I sampled epipelon and epiphyton by placing a bottomless bucket (0.053 m^2) over silt/sand and aquatic vegetation, which was then lightly disturbed and a subsample of water taken. I filtered all samples through a glass fiber filter (0.7 µm), placed them in a dark container, and froze them until processing. In the lab, I extracted chlorophyll-*a* from filters with methanol, which I then analyzed with a spectrophotometer following standard methods (Steinman et al. 2006). I sampled vascular aquatic vegetation by placing a bottomless bucket over vegetation and clipping vegetation at ground level. Air- dried vegetation was subsequently oven dried (60°C for 24 hrs) and weighed.

During summer 2010, I measured stream metabolism (GPP and CR) via the open channel, single-station, diel O_2 method (Grace and Imberger 2006). Because of logistical constraints (transporting equipment to backcountry locations), only three floodplain/confined pairs (BC, EF and YF) were included in this analysis. I measured oxygen concentration and temperature in the channel thalweg every five minutes for at least 36 hours with a YSI sonde outfitted with an optical oxygen probe. This technique integrated GPP and CR only for the main channel and off-channel aquatic habitat patches that were highly connected to the main channel during the period of sampling. I calculated atmospheric reaeration using the energy dissipation model (EDM; Tsivoglou and Neal 1976). Daytime CR was corrected to account for temperature dependence following Grace and Imberger (2006). Because stream metabolism is known to be highly variable in time, these short term estimates of metabolism were simply used as a relative index of potential differences in GPP and CR between floodplain and confined river segments.

Retention

I measured the capacity for in-stream retention of organic matter using both "leaf-release" and conservative (i.e., no biological uptake) solute approaches once during summer base flow conditions (Harvey and Wagner 2000; Lamberti and Gregory 2006). Again, due to logistical constraints retentive capacity was only assessed at the BC, EF, and YF sites. I utilized the standard leaf-release method to evaluate the capacity for stream segments to retain coarse particulate organic matter (CPOM). In each segment, I released 1000 strips of construction paper (as a standard surrogate for leaves) with dimensions 10.6 cm X 2.5 cm into the stream. Prior to releasing, I placed a block net at the downstream end of a 500 m reach to collect un-retained particles. One hour after release the number of un-retained paper strips in the block net was quantified. The number of retained paper strips was then counted at 20 m increments upstream from the block net. These data were subsequently plotted to determine the average travel distance of a particle in transport (see Lamberti and Gregory 2006).

Within the same 500 m reaches, I also assessed the relative capacity of segments to retain fine and dissolved organic matter in surface and subsurface storage zones by use of conservative tracers and stream transient storage modeling (Harvey and Wagner 2000). I measured transient storage via pulse releases of a known amount (approximately 23 kg) of salt (NaCl) into the stream (Stream Solute Workshop 1999). Prior to NaCl additions, I placed a YSI sonde outfitted with a conductivity probe (YSI 6560) in the thalweg of the channel at the downstream end of the reach. I utilized these data to model dispersion (D), transient storage zone cross-sectional area (A_s), stream cross-sectional area (A), and the transient storage exchange coefficient (α) via OTIS and OTIS-P (One-dimensional Transport with Inflow and Storage) modeling software (Runkel 1998). To evaluate the importance of transient storage in floodplain and confined segments, I utilized modeled values to calculate A_s/A, the ratio of transient storage cross-sectional area to stream cross-sectional area (Harvey and Wagner 2000).

Aquatic Macroinvertebrates

To estimate the biomass and production of macroinvertebrates, I collected 6-28 samples from each study segment. To sample benthic substrate, I used a Surber sampler (0.096 m^2, 250 µm mesh) in lotic habitats, and a bottomless bucket (0.053 m^2) or mini-ponar (0.027 m^2) in lentic habitats. All samples were elutriated through a 250 µm sieve and preserved in 95% ethanol. To reduce processing time in the lab, I utilized a two-phase sorting approach (after Vinson and Hawkins 1996). In the first phase, I removed all large invertebrates ($\geq$ 10 mm) from the sample. In the second phase, I removed and sorted successive subsamples at 10X magnification until at least 300 individuals were picked. I identified all invertebrates to the lowest taxonomic level feasible (genus or species, except Chironomidae to family), and categorized taxa into functional feeding groups (FFG) (Merritt et al. 2008). I then dried (60°C for 24 hrs) and weighed all insects (to nearest 0.001g) to obtain estimates of biomass.

To estimate secondary production of aquatic invertebrates, I multiplied the biomass of each taxon by a taxon specific annual production to biomass (P/B) value derived from the literature (method described by Benke 1984). I then summed taxon specific production values to determine total aquatic invertebrate production. I used published P/B values from the region whenever possible (Gaines and others 1992; Robinson and Minshall 1998), but if these did not exist for a taxon, I applied values from outside the region. If multiple values existed for individual taxa, I used the lowest P/B value. When no literature values could be found, I applied a P/B value of five (Benke and Huryn 2006). Such an approach results in secondary production values that are relatively coarse. In the context of this study, however, absolute accuracy of secondary production estimates for a given segment was less important than generating estimates that would allow for relative comparisons between floodplain and confined segment pairs. Of course, similar taxa could have different P/B values between floodplain and confined segments. However, in terms of estimating total invertebrate secondary production, I assumed that uncertainty associated with taxon specific P/B would be relatively minor compared to measured differences (and associated uncertainty) in the composition and biomass of invertebrates between study segments.

Analyses

Samples of aquatic primary producers, litter inputs, and aquatic invertebrates were used to generate total estimates ($\hat{Y}_{total}$) and standard errors (SE) for each segment as:

$$\hat{Y}_{total} = \sum A_p \times \hat{Y}_p$$

$$SE(\hat{Y}_{total}) = \sqrt{\sum A_p^2 \times \frac{S_p^2}{n_p}}$$

Where $\hat{y}_p$ is the mean value for the p^{th} patch, A_p is the area of the p^{th} patch, s_p^2 is the variance in the p^{th} patch and n_p is the number of samples taken in the p^{th} patch (Snedecor and Cochran 1967). I then divided total estimates and associated standard errors by segment length, which resulted in units of mass per meter of valley length (e.g., g/m) (*sensu* Gladden and Smock 1990), instead of the typical mass per unit area (e.g., g/m^2). Linear units were more appropriate in this comparison because I expected differences between floodplain and confined segments would be driven in part by differences in the amount of aquatic habitat or active channel surface per length of river valley (see Table 1), rather than differences in density or concentration. Aerial metabolism estimates (g C

m^{-2} d^{-1}) were converted to linear estimates (g C m^{-1} d^{-1}) by multiplying aerial values by channel sinuosity, and channel wetted width. For the purposes of this calculation, channel wetted width excluded disconnected off-channel aquatic habitats (i.e., wetland), which likely had little influence on DO measurements taken in the main channel. Although linear estimates (mass per unit of valley length) for each metric are reported here, for comparison, aerial estimates (mass per unit area) are also presented in Appendix 1b. Overall, however, results of the comparison of segment types were not strongly sensitive to the standardization approach.

I analyzed differences between paired floodplain and confined segments using paired *t*-tests. I square-root transformed non-normal data, but if transformation failed to normalize data, I conducted paired sample Wilcoxon signed-rank tests. I did not conduct statistical analyses on metabolism and retention data due to low sample size (n=3). I analyzed the structure of the aquatic macroinvertebrate community via estimates of taxa richness and diversity, and also non-metric multidimensional scaling (NMDS) ordination techniques. In this study, richness was calculated as the total number of aquatic invertebrate taxa identified within each segment, and also the total number of taxa within each FFG. FFG information was utilized to evaluate potential functional differences in the invertebrate assemblage between segment types. Diversity was calculated for each segment using the Shannon index ($\overline{H} = -\sum p_i \times \ln p_i$), where p_i represented the total biomass of each individual taxon. Compositional analyses on the invertebrate assemblage were conducted using Primer, Version 6 (Clarke and Gorley 2006). I utilized NMDS to generate a visual representation of the differences in invertebrate community structure, between floodplain and confined segments, based on invertebrate biomass data.

Prior to conducting this analysis, I normalized and then square-root transformed invertebrate biomass data to reduce the weight of high biomass taxa. I tested for differences in community structure between floodplain and confined segments using analysis of similarity (ANOSIM, 999 permutations, Primer 6). I then utilized the similarity percentages analysis (SIMPER, Primer 6) to identify those taxa that most strongly contributed to observed differences.

Results

Habitat Measurements

Differences in stream temperature and nutrients (DOC, TDN, and TDP) were generally minimal between floodplain and confined segments (Table 1). A notable exception was the EF site, where the confluence of a tributary resulted in a large increase in discharge (200%) and a large decrease in total dissolved nitrogen (60%) in the downstream floodplain segment. As a result of reduced shading from both canyon walls and the vegetation canopy, solar radiation inputs were, on average, 46% higher in floodplains than in paired confined segments ($t = 3.60$, $P = 0.02$).

Ecosystem Function

Contrary to my hypothesis, confined segments had, on average, 127% more leaf litter inputs than paired floodplain segments (Figure 4a), a difference that was found to be marginally significant ($t = -2.24$, $P = 0.089$). In terms of the composition of these inputs, confined segments had greater contributions (by mass) of conifer needles (55%) than floodplain segments (20%), whereas floodplains had a greater proportion of deciduous inputs (55%), mainly comprised of alder and willow leaves, relative to confined segments (23%). Other inputs represented woody structures, such as small twigs and cones, which, on average, had proportionally similar contributions to floodplain (25%) and confined (22%) segments. Also contrary to expectations, the input of terrestrial invertebrates was significantly higher (on average 83%) in confined versus floodplain river segments ($t = -2.84$, $P = 0.046$; Figure 4b).

I detected no differences between floodplain and confined segments with respect to the biomass of chlorophyll *a* (Figure 4c; $S = 1.5$, $P = 0.41$). Although some floodplain segments had higher chlorophyll *a* biomass than paired confined segments (EF and YF sites), the pattern was not consistent. Floodplain segments did have significantly higher biomass of aquatic vegetation ($S= 7.5$, $P = 0.031$). Vegetation biomass ranged from 0.01 to almost 1.5 kg/m in floodplains segments, whereas aquatic vegetation was virtually absent in confined segments. Comparisons of GPP estimates for main channel habitats were inconsistent. Two of three sites had much higher GPP in floodplain segments (up to 9X more), whereas there was no detectable difference in GPP between floodplain and confined segments at the BC site (Table 2).

As expected, I found that floodplain segments had a higher capacity to retain organic matter than paired confined segments (Table 2). CPOM releases showed that the average travel distance for a particle in transport at confined segments was 1.4, 3.7 and 3.9 times the travel distance in paired floodplains segments for the BC, EF, and YF sites respectively. Modeled parameters from OTIS also indicated that floodplains had a higher potential to retain particulate and dissolved organic matter in surface and subsurface transient storage zones. Modeled values of transient storage area (A_s), along with the ratio of the storage zone area to the advection zone area (A_s/A) were on average 72% and 45% higher in floodplain segments, respectively (Table 2).

Total organic matter (>250 um) collected during benthic sampling (BOM), was higher (268% higher on average) within floodplains than confined segments for four of five pairs (Figure 5a), but this difference was not significant (t = 1.36, *P* = 0.25) because one confined segment (the WF site) had very high BOM that corresponded with a landslide that occurred upstream two months prior to sampling.

Contrary to my hypothesis, there were no consistent differences between floodplain and confined segments in terms of either the total biomass (t = 0.67, *P* = 0.54) or production (t = 0.67, *P* = 0.54) of benthic macroinvertebrates (Figure 5b and 5c). However, in the three sites (BC, EF and YF) where metabolism measurements were conducted, CR was on average 2.6X higher in floodplains (Figure 4), indicating higher overall heterotrophic productivity within floodplain segments, relative to paired confined segments, at these locations.

Community Structure: Aquatic Macroinvertebrates

Consistent with my hypothesis, total taxa richness (t = 4.96, *P* = 0.008) and Shannon diversity (t = 6.60, *P* = 0.003) were significantly higher in floodplain than in confined segments (Table 3). On average, total taxa richness was 58% higher and diversity was 17% higher in floodplain river segments. Greater overall taxa richness in floodplains was principally a result of significantly higher numbers of taxa in collector/gatherer (t = 3.65, *P* = 0.022), predator (t = 7.80, *P* = .004), and shredder (t = 5.58, *P* = 0.005) functional feeding groups. Ordination analysis also showed that floodplain and confined segments differed in their macroinvertebrate assemblages (Figure 6a), and that they were statistically distinct groups (ANOSIM Global R = 0.26, *P* = 0.04). The taxa that contributed the most to the dissimilarity between floodplain and confined segments were: Sphaeriidae, Limnephilidae, Ostracoda and Chironomidae (higher relative biomass in floodplains), and Perlidae, Pteronarcyidae, Hydropsychidae and Simuliidae (higher relative biomass in confined segments). The NMDS also showed that the main channels of both floodplain and confined segments, along with side channel habitats, grouped together in multivariate invertebrate assemblage space, whereas other off-channel habitats showed a separate grouping (Figure 6b). ANOSIM results indicated that the composition of these off channel habitats were significantly different from main channel and side channel habitats (ANOSIM, Global R = 0.808, *P* = 0.001). The taxa that contributed the most to the differences between these habitat types were: Pelocypoda, Ostracoda, Chironomidae and Limnephilidae (higher relative biomass in off-channel habitats), and Perlidae, Ephemerellidae, Heptageniidae and Hydropsychidae (higher relative biomass in main channel habitats).

Discussion

The Process Domains Concept holds that spatial variability in geomorphology governs geomorphic processes and disturbance regimes, which in turn influences ecosystem structure and function (Montgomery 1999). In this study I found that coarse differences in valley confinement in a montane river network do indeed influence the structure and function of stream ecosystems, although not exactly as I hypothesized. In terms of ecosystem function, floodplain river segments had higher retentive capacity and community respiration (which is principally driven by microbes) than confined segments. Opposite my hypothesis, however, I found that allochthonous inputs were higher within confined segments. In addition, although floodplains are generally thought to contain extremely productive aquatic systems, I did not observe consistent differences between segment types in terms of the biomass and production of aquatic primary producers and aquatic macroinvertebrates. This result questions whether the concepts, on which my hypotheses were based (e.g., flood pulse concept, Junk et al. 1989), are applicable to small montane river networks, like the ones in this study. Segments did, however, differ markedly in terms of aquatic macroinvertebrate community structure, and floodplains had higher overall invertebrate richness and diversity than confined segments, a finding which illustrates that community structure can change without associated changes in function (i.e., invertebrate production).

My results showed that floodplain and confined segments were functionally distinct in terms of the input and retention of organic matter. As I hypothesized, floodplain segments had a higher capacity to retain organic matter, but contrary to my expectation, floodplain segments had less allochthonous leaf litter and invertebrate inputs relative to confined segments. I expect that this functional disparity in organic matter dynamics is due to differences in the physical structure (e.g., narrow versus wide valley bottoms) and disturbance regimes of stream habitats between canyon confined river segments and unconfined floodplain river segments. For example, in this study, floodplain river segments generally had higher sinuosity, lower slope, greater active channel width, and more complex channels (i.e., more off-channel habitats) than confined river segments. These attributes control how much power the stream has to do work, which has a direct affect on the transport, mobilization and deposition of both sediment and organic matter (Leopold et al. 1964). As is well known in the context of sediment dynamics (Montgomery and Buffington 1997), my findings suggest that floodplain segments may act as depositional zones for organic matter, whereas confined segments act as transport zones. Although retention measurements were only taken once during low flow, it is likely that incorporating measures at higher flows would have only amplified differences in retention, due to the differential response of floodplain and confined segments to flooding. Floodplains can dissipate flow laterally, providing lower velocity storage zones lateral to the main channel, whereas confined segments cannot dissipate flow laterally, and respond to high flows largely by increasing velocity and depth, further reducing retentive capacity (Montgomery and Buffington 1997).

I hypothesize that the differences in processes at high flows in floodplain versus confined segments impact riparian vegetation and the associated input of allochthonous organic matter and terrestrial invertebrates. I found that floodplain segments often had sparse vegetation both adjacent to and within the active channel, whereas confined segments had thick bands of vegetation adjacent to the stream that would often overhang the channel (Figure 2). Because confined segments only have minimal lateral expansion during flooding, riparian vegetation can persist adjacent to the channel. In contrast, my observations suggest that in the high energy river environments of this montane setting, the lateral expansion of high water in floodplains suppresses the growth and development of vegetation on the surface of the active channel (see Naiman et al 2010). Consequently, not only do confined segments have higher organic matter input, but those inputs are more likely to fall directly into the stream, instead of on a floodplain surface where they may not be directly incorporated into aquatic habitats until high water events, such as spring snowmelt.

Given previous research which shows that floodplain systems generally receive substantial organic matter subsidies from adjacent floodplain forests (e.g., Goulding 1980, Cuffney 1988, Junk et al. 1989), it was surprising to find that in this study, floodplains actually received less lateral input of organic matter than confined river segments. However, the large temperate and tropical systems where a majority of previous floodplain research has been conducted (e.g., Amazon, Orinoco, Mississippi, etc.) generally have flood events that are highly predictable and long in duration, which is hypothesized to allow adaptation by organisms to utilize aquatic/terrestrial transition zones (Junk et al. 1989). In contrast, the timing, magnitude and duration of peak flows for the streams in this study are generally more variable (Emmett 1975). In addition, flash flood events associated with rain-on-snow and/or severe thunder storms are highly unpredictable, and can occur at almost any time of year. Moreover, smaller montane floodplains are usually higher gradient and have greater erosive power during flood events relative to larger tropical and temperate floodplains (Tockner et al. 2000). As a result, few riparian vegetation species may be adapted to survive within the active channel of these floodplains, resulting in fewer inputs of allochthonous organic matter compared to larger floodplain systems from whence much of the floodplain literature and concepts have been derived.

Contrary to the input and retention of organic material, I was unable to detect consistent differences in the biomass and production of aquatic primary producers and invertebrate consumers between floodplain and confined segments. Although no other studies have explicitly tested for differences in aquatic productivity between floodplain and confined river segments, this finding was very surprising because it is generally believed that floodplains are hotspots of productivity within river networks. Instead, my findings indicate that simple single-channel confined segments may be just as productive as more complex multi-channel (i.e., off-channel habitats) floodplain segments, at least in terms of algae and aquatic macroinvertebrates. That said, the sampling techniques I utilized likely under-represented or completely overlooked meiofauna and hyporheic invertebrates, both of which are known to be abundant in floodplain segments (Stanford and Ward 1988, 1993; Gladden and Smock 1990, Lewis et al. 2001), and, if included, would likely increase invertebrate production well above what is reported in this study. Estimates of primary production, from open-channel metabolism calculations, were also limited in spatial (did not include disconnected off-channel habitats) and temporal scope (36 hours), and may not be representative of total aquatic primary production on an annual basis. For example, these estimates did not incorporate floodplain primary production that occurred within disconnected off-channel habitats, where vascular aquatic vegetation (i.e., aquatic macrophytes, grasses, sedges, rushes) was often found.

Although I did not detect differences in invertebrate production between floodplain and confined river segments, aquatic invertebrates generally represent only a small portion of total heterotrophic productivity in stream ecosystems. The most abundant and productive heterotrophic organisms in streams are microorganisms (Allen and Castillo 2007), such as bacteria and fungi, and floodplain segments are likely to have much greater microbial production than confined river segments. In addition to having greater above ground wetted area, glacially influenced floodplains like the ones in this study usually have voluminous hyporheic zones that provide orders of magnitude more interstitial space for microorganisms to grow. In fact, studies have shown that depending on the volume of the hyporheic zone, subsurface production can be just as great, if not much than benthic production (Fellows et al. 2001; Craft et al. 2002). Although I did not measure microbial respiration within hyporheic and some off-channel aquatic habitats (habitats disconnected during time of sampling), my estimates of metabolism still indicate that floodplain segments have higher community respiration than confined river segments. Consequently, floodplains likely have greater overall heterotrophic productivity than confined segments, and hence, greater respiration of organic matter.

As I hypothesized, floodplain segments had significantly higher aquatic invertebrate taxomonic richness and diversity. This finding is consistent with the idea that floodplains are more biodiverse because they are physically complex and heterogeneous landscapes (e.g., Sheldon et al. 2002, Arscott et al. 2005; Stanford et al. 2005). Unlike confined segments, in which all wetted habitats are contained within the main-channel, the floodplains in this study had numerous types of off-channel aquatic habitats (beaver complexes, wetlands, spring-brooks, side-channels, etc.). In fact, the main channels of floodplains had invertebrate composition very similar to the main channel of confined segments. It was the distinctly different invertebrate assemblage found in off-channel aquatic habitats (more lentic type invertebrate taxa; e.g., Pelocypoda, Ostracoda, Chironomidae and Limnephilidae) that produced the higher richness and diversity observed within floodplain segments. The habitat complexity supporting the high diversity in floodplain segments is a direct result of the ability of the river channel to migrate laterally. Channel migration and flooding creates and maintains a dynamic and diverse mosaic of habitat types within floodplains (Stanford et al. 2005), within which a gradient of hydrologic connectivity exists with the main channel. This creates habitats that differ in terms of water velocity, solar inputs, substrate, temperature, and hyporheic connectivity, all of which are known to influence aquatic invertebrate assemblages directly or indirectly (Allen and Castillo 2007). In addition, the quality of basal organic matter sources may differ between floodplain habitat patches, which may also influence the diversity and composition of invertebrates. In fact, my results show that floodplains had a higher richness of both shredder and collector-gather FFGs, indicating that floodplain segments may contain a greater standing crop and diversity of leaf litter and other types of low quality organic matter (i.e., wood, vascular aquatic vegetation) that are often associated with higher abundances of these two FFGs (Allen and Castillo 2007; Merritt et al. 2008).

Together, the results of this study provide insight into the potential function and process-based interaction of floodplain and confined segments within montane river networks. Specifically, my findings suggest that floodplain and confined segments act as “digesters” and “transporters” of organic matter, respectively. Confined segments have similar algal biomass and higher allochthonous organic matter inputs compared to floodplain segments but have relatively low retentive capacity. Consequently, organic matter is more likely to be transported downstream in confined segments prior to being incorporated into the aquatic food web. Conversely, floodplain river segments are highly retentive, and are likely to retain a greater proportion of organic matter produced *in situ* or delivered from upstream. High microbial respiration, combined with a diverse invertebrate community with floodplain aquatic habitats, may subsequently facilitate the efficient “digestion” of retained organic matter. In the context of montane river networks, where floodplain segments are juxtaposed with confined river segments, this might indicate that a large portion of aquatic respiration in floodplain segments is fueled by organic matter subsidies from upstream confined segments. In a simple model, confined segments would uptake labile energy sources, while transporting more refractory materials (e.g., terrestrial litter, wood, etc.) downstream. Within floodplain segments, the residence time of this organic material would be extended, allowing digestion via a combination of invertebrate consumption, and both aerobic and anaerobic microbial respiration (see Battin et al. 2008). In a reciprocal fashion, digestion of organic matter within floodplain river segments may also provide transformed organic matter and nutrients to downstream ecosystems (see Tockner et al. 1999). More intensive measures of organic matter and nutrient dynamics, along with ecosystem metabolism, are needed to evaluate these potential segment scale interactions.

This study shows that floodplain and confined river segments not only represent different geomorphic process domains, but that these domains influence both the structure and function of aquatic ecosystems. Furthermore, my findings suggest that floodplain and confined segments have different, but perhaps complementary functions. Confined segments, which are often a dominant feature of montane networks, appear to be source habitats for organic matter, whereas the occasional floodplain segment may act as a filter, removing and processing organic matter transported from upstream (see Battin et al. 2008). Although concepts have highlighted how lateral (e.g., Junk et al. 1989) and vertical (e.g., Stanford and Ward 1993; Boulton et al. 1998) connectivity are important in fueling productivity in floodplain segments, these results indicate that longitudinal connectivity (Vannote et al. 1980) between different segment scale geomorphic domains might also be important, at least in montane river systems. If true, these findings would indicate that floodplain restoration efforts that focus solely on lateral floodplain reconnection may not be successful if longitudinal connectivity is not also addressed. Additional studies are needed that more directly focus on the potential interactions between floodplain and confined river segments, and their implications for patterns and processes throughout river networks.

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Tables

Table 1. Habitat characteristics of floodplain and confined river segments measured during summer 2007. D50 = median substrate size, TDN = total dissolved nitrogen, TDP = total dissolved phosphorus, and DOC = dissolved organic carbon.

	BC		CC		EF		WF		YFR	
Segment Character	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
segment length (m)	2,940	2,800	5,420	16,100	1,970	1,890	5,600	2,005	1,015	3,155
base flow discharge (L/s)	0.6	0.7	1.4	1.5	2.2	1.1	1	1.1	0.9	1.1
avg valley floor width (m)	108	20	129	40	174	25	180	40	151	17
avg active channel width (m)	28	15	46	25	55	19	36	18	58	16
avg wetted width (m)	9	8	13	15	18	10	10	8	14	7
channel slope (m/m)	0.016	0.012	0.008	0.023	0.011	0.014	0.011	0.016	0.009	0.020
D50 (cm)	5	5	5	14	8	8	5	20	5	20
sinuosity	1.27	1.02	1.12	1.01	1.13	1.01	1.26	1.01	1.19	1.00
presence of off-channel habitat	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
avg summer water temp (°C)	9.9	10.3	11.7	12.0	10.4	11.6	9.4	10.0	9.4	9.5
solar radiation (kWh $m^{-2}year^{-1}$)	1261	1170	1422	1225	1301	625	1235	789	1500	1051
TDN (µg/L)	7.2	7.3	9.2	8.8	17.4	42.2	4.8	5.7	7.8	7.1
TDP (µg/L)	6.9	7.6	6.2	5.0	3.8	3.9	4.7	6.9	43.1	38.8
DOC (mg/L)	1.6	1.6	1.6	1.7	0.8	0.9	1.2	1.1	1.9	1.9

Table 2. Results from leaf release (CPOM) experiments, transient storage modeling, and stream metabolism measurements in three floodplain/confined segment pairs during summer 2007. Average CPOM travel distance represents the average distance particles from leaf-releases traveled before being retained. Transient storage parameters were modeled from salt pulse data (using OTIS); and metabolism values were calculated from 36 hour (2 nights and 1 day) dissolved oxygen and temperature measurements from the main channel following single station metabolism methods (see details in text). D = dispersion, A = stream cross-sectional area, A_s = storage zone cross-sectional area, α = transient storage exchange coefficient, CR = community respiration, and GPP = gross primary production.

			Transient Storage					Metabolism (g C m^{-1} d^{-1})	
Site	Segment	Avg CPOM Travel Dist (m)	D (m^2 s^{-1})	A (m^2)	A_s (m^2)	α (1/s)	A_s/A	CR	GPP
BC	floodplain	60	0.136	1.656	0.653	0.003	0.394	12	3
	confined	222	0.211	1.421	0.342	0.003	0.241	9	3
EF	floodplain	173	2.792	3.345	0.853	0.002	0.255	142	77
	confined	230	0.498	1.591	0.391	0.003	0.245	69	12
YFR	floodplain	66	0.808	1.431	0.462	0.003	0.323	26	9
	confined	260	0.294	2.246	0.430	0.003	0.191	6	1

Table 3. Aquatic invertebrate diversity and richness in floodplain and confined segments, calculated from benthic samples taken in summer 2006 and 2007. Diversity numbers represent Shannon-Weiner diversity calculated on invertebrate biomass values. Richness values are separated by functional feeding group, coll/gath = collector/gathers. * denotes statistically significant differences at the 0.05 level.

			Richness					
Site	Segment	Diversity*	Coll/Gath*	Filters	Predators*	Scrapers	Shredders*	Total*
BC	floodplain	2.29	38	7	26	9	9	89
	confined	1.95	23	7	10	5	2	47
CC	floodplain	2.22	37	9	28	6	10	90
	confined	1.74	19	7	10	6	6	48
EF	floodplain	2.62	26	6	18	9	7	66
	confined	2.4	22	6	10	8	5	52
WF	floodplain	3.26	29	8	21	7	10	75
	confined	2.74	23	7	13	9	5	57
YFR	floodplain	3.06	27	7	27	8	11	80
	confined	2.77	20	5	14	7	5	51

Figures

Figure 1. Photographs of a typical floodplain river segment (top), and canyon confined river segment (bottom) compared in this study.

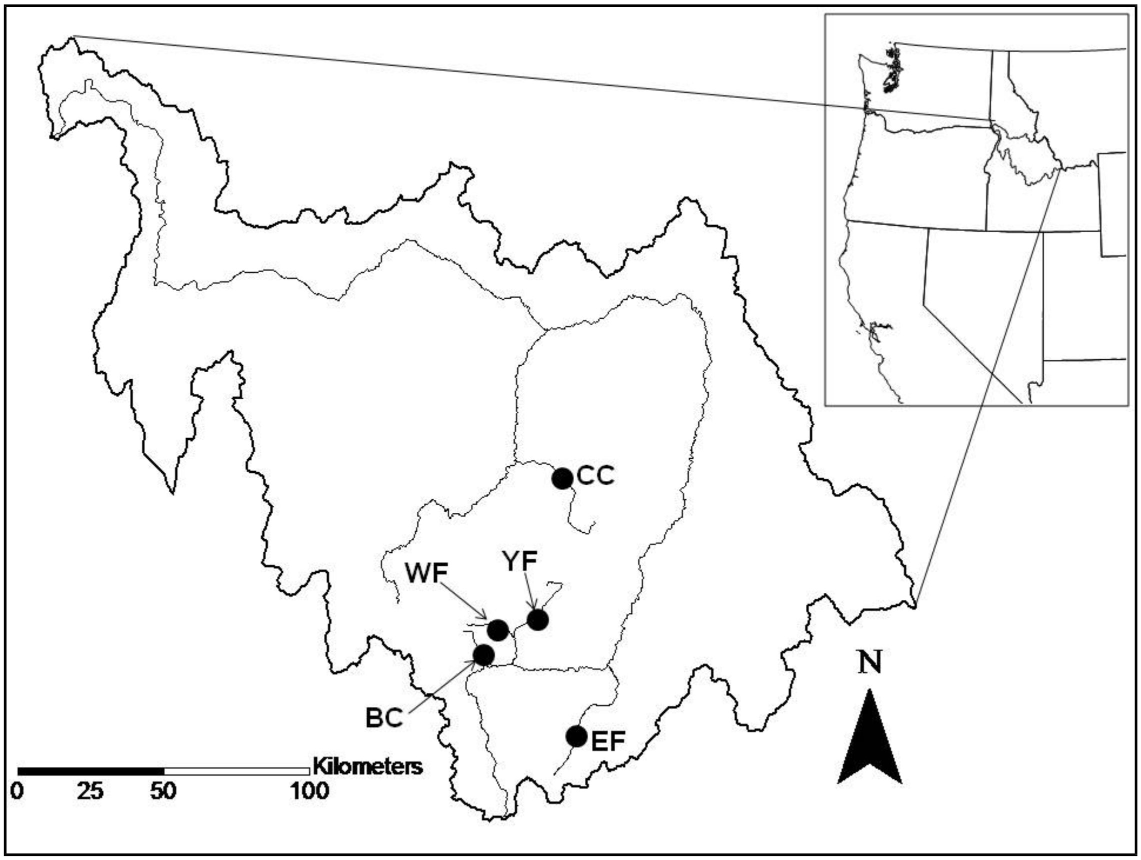

Figure 2. Map of the Salmon River basin, Idaho, with study sites labeled; BC = Basin Creek, CC = Camas Creek, EF = East Fork Salmon River, WF = West Fork Yankee Fork, and YF = Yankee Fork Salmon River.

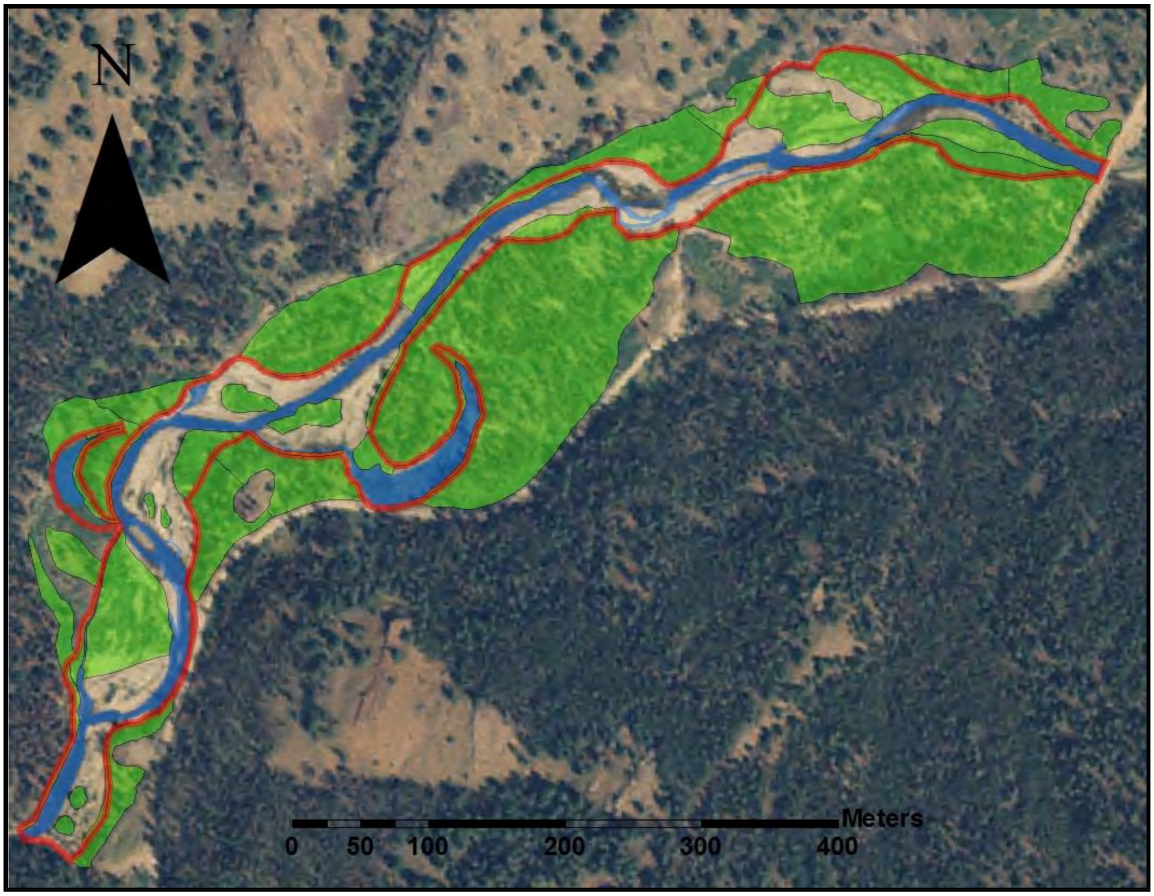

Figure 3. Unconfined river floodplain segment with the active channel delineated (red line), and aquatic (blue) and terrestrial vegetation (green) patches digitized. Similar maps were constructed for all study segments from visual ground surveys, and were utilized to stratify sampling effort (see text for details).

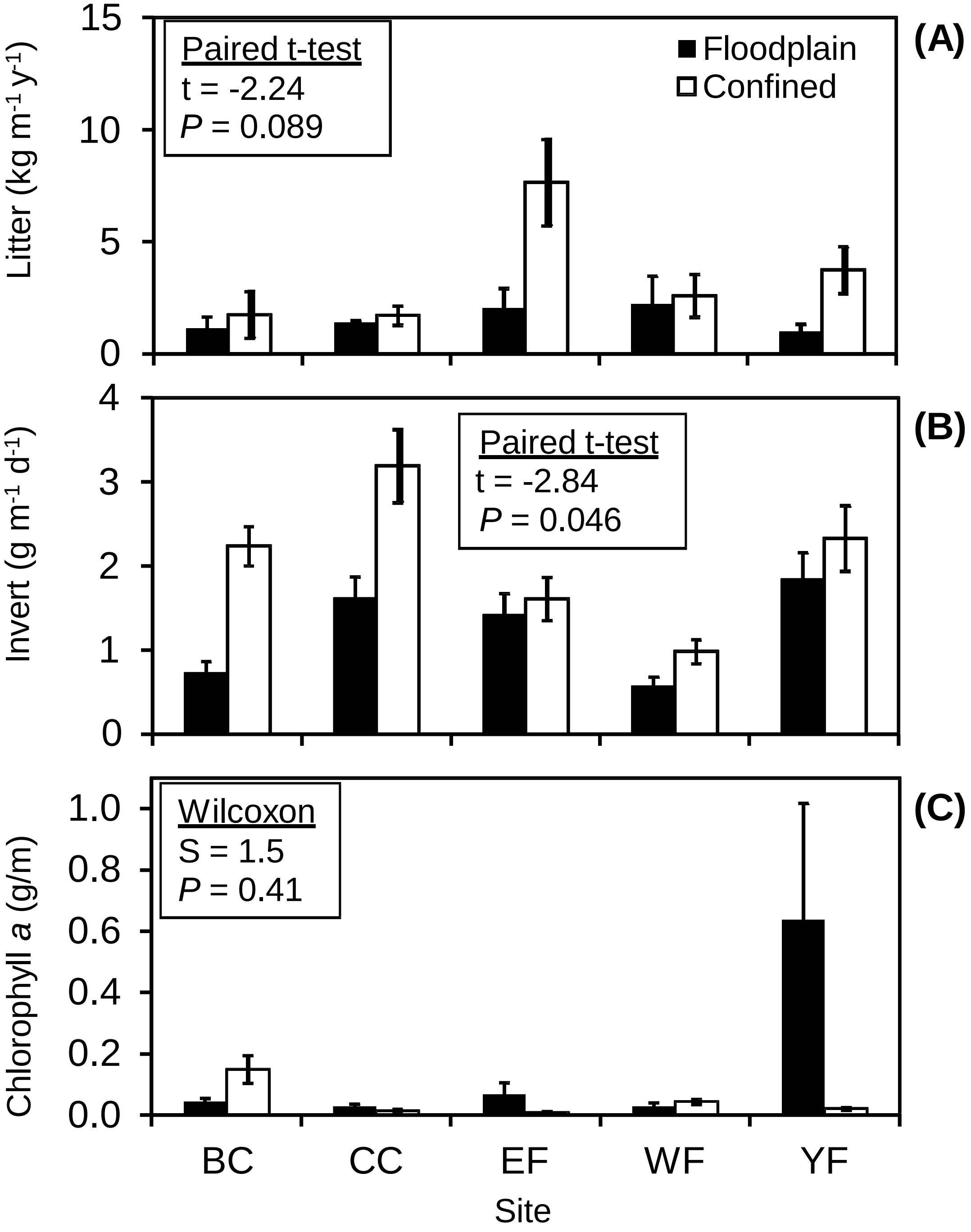

Figure 4. For each floodplain and confined segment: estimated annual input (dry mass) of leaf litter to aquatic habitats (A), average daily terrestrial invertebrate input (dry mass) to aquatic habitats during summer (B), and estimated chlorophyll *a* biomass for all aquatic habitats during summer (C), ± 1 SE. Boxes within figures shows test statistic and associated P-value.

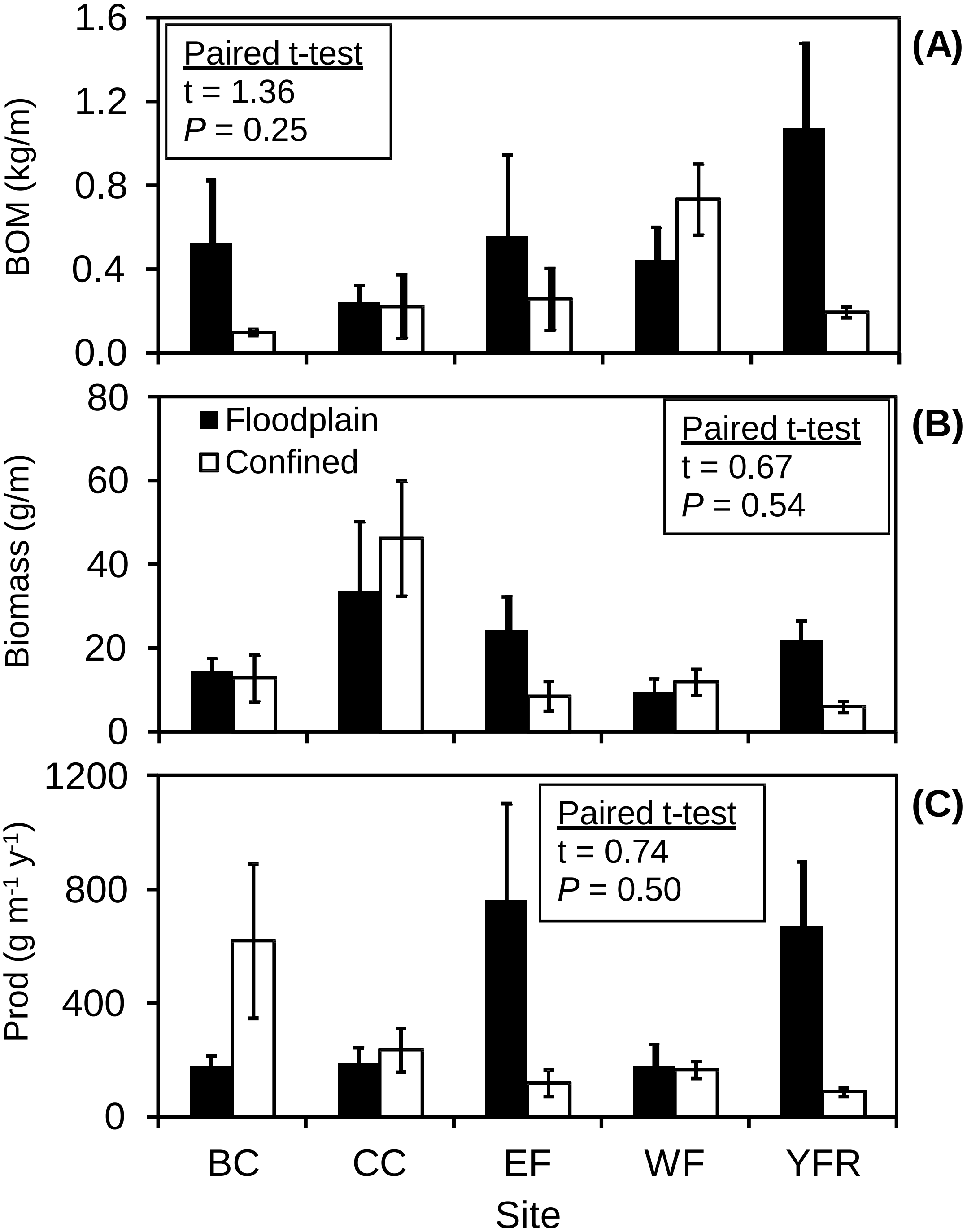

Figure 5. Benthic organic matter standing crop (A), aquatic invertebrate biomass (B), and total annual aquatic invertebrate production (C), for each floodplain and confined river segment, ± 1 SE. All values calculated from summer benthic sampling. Boxes within figures shows test statistic and associated P-value.

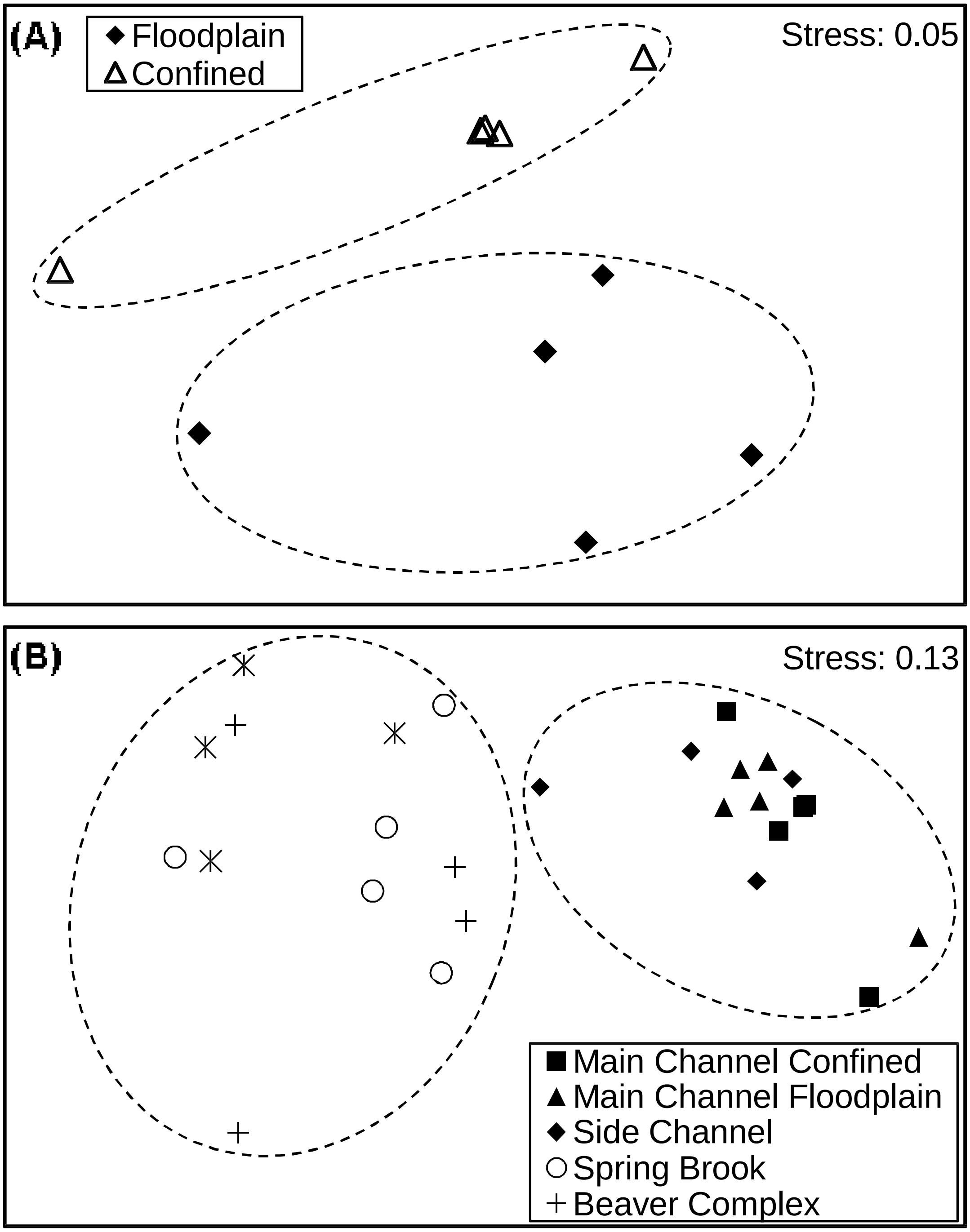

Figure 6. Nonmetric multidimensional scaling (NMDS) plots for (A) floodplain and confined segments and (B) habitat types within segments based on standardized family-level aquatic invertebrate biomass data. Dashed ovals within plots delineate statistically distinct groups (ANOSIM, *P* < 0.05).

Appendix

Appendix 1a. Segment length, total aquatic habitat area, and the proportion of total aquatic habitat within each aquatic habitat patch type, measured via visual ground surveys during base flows in summer 2006 and 2007 (see Figure 2 for definitions of acronyms).

				Proportion of Total Aquatic Habitat					
Site	Segment	Segment Length (m)	Aquatic Habitat Area (m^2)	Beaver Complex	Pool/Run	Riffle	Side Channel	Spring Brook	Wetland
BC	floodplain	2,940	26,113	0.07	0.08	0.69	0.05	0.02	0.09
	confined	2,800	22,344	-	-	1	-	-	-
CC	floodplain	5,420	68,670	0.01	0.10	0.82	0.03	0.03	0.01
	confined	16,100	248,683	-	-	1	-	-	-
EF	floodplain	1,970	35,169	0.11	0.06	0.73	0.09	0.01	-
	confined	1,890	19,391	-	0.03	0.97	-	-	-
WF	floodplain	5,600	58,368	0.04	0.14	0.67	0.08	0.04	0.02
	confined	2,005	16,488	-	-	1	-	-	-
YF	floodplain	1,015	14,703	-	0.12	0.60		0.08	0.21
	confined	3,155	22,551	-	-	1	-	-	-

Appendix 1b. Summary of parameter estimates and associated standard errors for each segment as well as aquatic habitat units within each segment. For comparison, values are presented in both mass per unit valley length (e.g., g/m), and mass per unit area (e.g., g/m^2). CR = community respiration, GPP = gross primary production, and BOM = benthic organic matter.

			BC		CC		EF		WF		YF	
Parameter	Units	Aquatic Habitat Type	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
litter inputs	kg/m^2	All	0.13 ± 0.06	0.22 ± 0.13	0.11 ± 0.01	0.11 ± 0.03	0.11 ± 0.05	0.75 ± 0.19	0.21 ± 0.12	0.32 ± 0.12	0.07 ± 0.02	0.52 ± 0.15
	kg/m	All	1.14 ± 0.51	1.74 ± 1.04	1.41 ± 0.09	1.71 ± 0.43	2.04 ± 0.88	7.64 ± 1.92	2.23 ± 1.24	2.60 ± 0.96	1.00 ± 0.33	3.74 ± 1.05
invert. inputs	g/m^2	All	0.082 ± 0.016	0.280 ± 0.029	0.128 ± 0.020	0.206 ± 0.028	0.080 ± 0.014	0.157 ± 0.025	0.055 ± 0.010	0.120 ± 0.017	0.127 ± 0.022	0.326 ± 0.055
	g/m	All	0.73 ± 0.14	2.24 ± 0.23	1.62 ± 0.25	3.19 ± 0.44	1.42 ± 0.25	1.61 ± 0.26	0.57 ± 0.11	0.98 ± 0.14	1.84 ± 0.32	2.33 ± 0.39

Appendix 1b continued.

Parameter	Units	Aquatic Habitat Type	BC		CC		EF		WF		YF	
			Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
CR	g m^{-1} d^{-1}	Main Channel	14	9	--	--	163	68	--	--	35	6
	g m^{-2} d^{-1}	Main Channel	1.2	1.1	--	--	8	6.7	--	--	2.1	0.9
GPP	g m^{-1} d^{-1}	Main Channel	3	3	--	--	88	12	--	--	13	1
	g m^{-2} d^{-1}	Main Channel	0.3	0.4	--	--	4.3	1.2	--	--	0.8	0.1

Appendix 1b continued.

			BC		CC		EF		WF		YF	
Parameter	Units	Aquatic Habitat Type	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
BOM	kg/m^2	Beaver Comp.	0.305 ± 0.237	--	0.12 ± 0.026	--	0.197 ± 0.166	--	0.308 ± 0.191	--	--	--
	kg/m^2	Pool	0.015 ± 0.002	--	0.027 ± 0.012	--	0.007 ± 0.002	0.033 ± 0.025	0.027 ± 0.002	--	0.011 ± 0.008	--
	kg/m^2	Riffle	0.018 ± 0.007	0.012 ± 0.002	0.012 ± 0.003	0.014 ± 0.01	0.008 ± 0.003	0.025 ± 0.014	0.015 ± 0.001	0.089 ± 0.021	0.007 ± 0.001	0.027 ± 0.004
	kg/m^2	Side Ch.	0.017 ± 0.006	--	0.045 ± 0.016	--	0.023 ± 0.012	--	0.025 ± 0.007	--	--	--
	kg/m^2	Spring Brk	0.188 ± 0.112	--	0.086 ± 0.07	--	0.037 ± 0.015	--	0.209 ± 0.11	--	0.129 ± 0.046	--
	kg/m^2	Wetland	0.221 ± 0.109	--	0.19 ± 0.026	--	--	--	0.276 ± 0.099	--	0.324 ± 0.073	--
	kg/m^2	All	0.059 ± 0.034	0.012 ± 0.002	0.019 ± 0.006	0.014 ± 0.01	0.031 ± 0.022	0.025 ± 0.014	0.043 ± 0.015	0.089 ± 0.021	0.083 ± 0.021	0.027 ± 0.004
	kg/m	All	0.525 ± 0.301	0.097 ± 0.014	0.242 ± 0.08	0.223 ± 0.152	0.555 ± 0.391	0.257 ± 0.148	0.444 ± 0.158	0.734 ± 0.17	1.198 ± 0.299	0.195 ± 0.026

Appendix 1b continued.

			BC		CC		EF		WF		YF	
Parameter	Units	Aquatic Habitat Type	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
chloro. *a*	g/m^2	Beaver Comp.	14.5 ± 4.87	--	--	--	17.2 ± 8.91	--	19.0 ± 15.5	--	--	--
	g/m^2	Pool	3.48 ± 1.30	--	3.55 ± 1.60	--	1.00 ± 0.05	2.35 ± 1.15	3.91 ± 0.24	--	6.89 ± 4.69	--
	g/m^2	Riffle	1.62 ± 0.47	18.7 ± 5.63	1.40 ± 0.24	0.88 ± 0.33	2.10 ± 1.43	0.80 ± 0.17	1.01 ± 0.39	5.30 ± 0.10	2.11 ± 0.41	2.85 ± 0.73
	g/m^2	Side Ch.	11.1 ± 5.36	--	4.99 ± 2.09	--	2.19 ± 0.92	--	0.93 ± 0.23	--	--	--
	g/m^2	Spring Brk	3.36 ± 0.50	--	3.07 ± 1.33	--	6.01 ± 2.83	--	15.3 ± 4.90	--	6.59 ± 3.12	--
	g/m^2	Wetland	19.0 ± 3.64	--	45.0 ± 20.8	--	--	--	2.78 ± 0.93	--	200 ± 122	--
	g/m^2	All	4.78 ± 1.37	18.7 ± 5.63	2.21 ± 0.68	0.88 ± 0.33	3.78 ± 2.16	0.85 ± 0.20	2.73 ± 1.10	5.30 ± 0.10	44.0 ± 26.4	2.85 ± 0.73
	g/m	All	42.7 ± 12.2	149 ± 44.9	28.0 ± 8.62	13.6 ± 5.15	67.4 ± 38.5	8.72 ± 2.05	28.4 ± 11.5	43.6 ± 8.19	637 ± 382	20.3 ± 5.21

Appendix 1b continued.

			BC		CC		EF		WF		YF	
Parameter	Units	Aquatic Habitat	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
invert. biomass	g/m^2	Beaver Comp.	5.46 ± 3.52	--	3.01 ± 1.49	--	6.06 ± 1.60	--	0.57 ± 0.19	--	--	--
	g/m^2	Pool	0.41 ± 0.07	--	0.57 ± 0.09	--	0.55 ± 0.09	0.56 ± 0.12	1.12 ± 1.11	--	0.72 ± 0.44	--
	g/m^2	Riffle	0.37 ± 0.06	1.61 ± 0.71	2.89 ± 1.42	2.98 ± 0.89	0.47 ± 0.04	0.91 ± 0.26	0.72 ± 0.29	1.44 ± 0.38	0.43 ± 0.12	0.84 ± 0.19
	g/m^2	Side Ch.	1.86 ± 0.65	--	2.58 ± 1.06	--	1.47 ± 0.54	--	0.84 ± 0.26	--	--	--
	g/m^2	Spring Brk	5.38 ± 4.09	--	3.35 ± 0.99	--	4.11 ± 2.18	--	3.05 ± 0.54	--	1.26 ± 0.73	--
	g/m^2	Wetland	8.26 ± 2.37	--	2.64 ± 0.92	--	--	--	2.15 ± 0.24	--	5.21 ± 1.40	--
	g/m^2	All	1.63 ± 0.62	1.61 ± 0.71	2.65 ± 1.25	2.98 ± 0.89	1.23 ± 0.28	0.91 ± 0.26	0.92 ± 0.41	1.44 ± 0.38	1.52 ± 0.47	0.84 ± 0.19
	g/m	All	14.47 ± 5.46	12.87 ± 5.63	33.58 ± 15.89	46.18 ± 13.75	21.9 ± 5.07	9.23 ± 2.62	9.55 ± 4.27	11.86 ± 3.13	22.01 ± 6.8	5.97 ± 1.36

Appendix 1b continued.

			BC		CC		EF		WF		YF	
Parameter	Units	Aquatic Habitat	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf	Flood	Conf
invert. prod.	g/m^2	Beaver Comp.	41.02 ± 13.52	--	17.38 ± 7.04	--	292.3 ± 103.4	--	9.48 ± 3.46	--	--	--
	g/m^2	Pool	6.44 ± 1.15	--	8.98 ± 0.99	--	9.28 ± 1.83	12.25 ± 1.46	13.51 ± 13.5	--	7.68 ± 4.65	--
	g/m^2	Riffle	4.02 ± 0.62	77.60 ± 34.02	13.42 ± 3.79	15.22 ± 4.94	7.11 ± 0.60	13.44 ± 3.97	15.72 ± 9.3	20.17 ± 3.62	6.67 ± 3.08	12.33 ± 2.16
	g/m^2	Side Ch.	44.74 ± 14.46	--	44.26 ± 13.13	--	29.50 ± 7.63	--	9.43 ± 3.62	--	--	--
	g/m^2	Spring Brk	53.34 ± 33.93	--	30.43 ± 9.79	--	171.1 ± 148.9	--	54.52 ± 24.18	--	10.42 ± 4.29	--
	g/m^2	Wetland	115.3 ± 25.77	--	67.44 ± 22.66	--	--	--	44.76 ± 11.63	--	196.1 ± 85.80	--
	g/m^2	All	20.15 ± 5.21	77.60 ± 34.02	15.03 ± 4.20	15.22 ± 4.94	42.76 ± 14.06	13.41 ± 3.88	17.05 ± 9.95	20.17 ± 3.62	46.33 ± 20.49	12.33 ± 2.16
	g/m	All	179.0 ± 46.27	619.2 ± 271.5	190.6 ± 53.15	235.8 ± 76.51	763.3 ± 250.9	137.5 ± 39.8	177.7 ± 103.7	165.8 ± 29.73	671.1 ± 296.9	88.09 ± 15.45

Chapter 2

Assessing the potential for salmon recovery via floodplain restoration: a multitrophic level comparison of dredge-mined to reference segments

Abstract

Pre-restoration studies typically focus on physical habitat, rather than the food-base that supports aquatic species. However, both food and habitat are necessary to support the species that habitat restoration is frequently aimed at recovering. Here I evaluate if and how the productivity of the food-base that supports fish production is impaired in a dredge-mined floodplain within the Yankee Fork Salmon River (YFSR), Idaho (USA); a site where past restoration has occurred and where more has been proposed to help recover anadromous salmonids. Utilizing an ecosystem approach, I found that the dredged segment had comparable terrestrial leaf and invertebrate inputs, aquatic primary producer biomass, and production of aquatic invertebrates relative to five reference floodplains. Thus, the food-base in the dredged segment did not necessarily appear impaired. That being said, previous restoration in the dredged segment that connected several ponds to the main channel still increased invertebrate production by an additional 58%. However, using a simple bioenergetics model, I estimated that the invertebrate food-base was at least 4X larger than present demand for food by fish in both dredged and reference segments. In the context of salmon recovery efforts, this observation questions whether additional food-base productivity provided by habitat restoration would be warranted in the YFSR. Together, my findings highlight the importance for studies that assess the aquatic food-base, and emphasize the need for more robust ecosystem models that evaluate factors potentially limiting fish populations that are the target of restoration.

Introduction

Over the last several decades habitat restoration has been increasingly utilized as a strategy to recover and conserve threatened and endangered species in river ecosystems (Bernhardt and others 2005), especially stream fishes. However, the success of habitat restoration is often highly uncertain (Wissmar and Bisson 2003), and researchers and practitioners have emphasized the importance of pre-restoration studies that evaluate potential for projects to succeed, as well as monitoring to evaluate responses post-restoration (e.g., Ebersole and others 1997; Palmer and others 2005). Although monitoring and evaluation studies are now commonly conducted in stream and river ecosystems prior to restoration, the majority of these assessments focus on physical habitat condition, largely neglecting any evaluation of the food base that supports aquatic species (Wipfli and Baxter 2010). This approach assumes that either (1) physical habitat structure dictates habitat quality for species of interest, or (2) that food base productivity directly mirrors physical habitat condition. However, both food and habitat are necessary to sustain biological populations, and assessment of physical habitat alone may not be adequate to define food base productivity. In addition, the successful restoration of physical habitat does not guarantee that restoration will succeed at restoring either the productivity of the aquatic food base, and/or the target species at which the effort may be aimed.

One case in which more in-depth evaluations of restoration potential are needed is the on-going effort to recover Endangered Species Act (ESA)-listed anadromous Pacific salmon and steelhead populations in the United States (U.S.). Each year millions of dollars are spent in attempts to restore or enhance freshwater spawning and rearing habitat used by these fish (NRC 1996; Bernhardt and others 2005). In this effort, the selection of specific restoration sites is frequently based on the outcome of watershed-level assessments which evaluate the structure and function of different river segments in terms of their hydrologic and geomorphic habitat character (Roni and others 2002; Pess and others 2003). These assessments identify restoration potential based on the detection of impaired physical habitat and/or processes (e.g., sediment dynamics, pool area, hydrologic connectivity, etc.). However, they do not evaluate if and how the food base (e.g., primary and secondary productivity) that fuels the freshwater production of anadromous salmonids is impaired (Wipfli and Baxter 2010). At the same time, there is increasing concern that reductions in the abundance of returning adult spawners has significantly diminished an important source of nutrients and organic matter to rearing habitats that are often oligotrophic (Gende and others 2002), potentially reducing the food base for juvenile anadromous fish well below historic levels (but see Moore and Schindler 2004). To understand the potential for habitat restoration (and nutrient supplementation) to recover and preserve species of interest, such as Pacific salmon and steelhead, there is a need for studies that complement physical habitat assessments, by focusing on the food base that fuels the production of target species.

A frequent target of habitat restoration efforts are river floodplains (Bernhardt and others 2005). These are river segments in which the channel is relatively unconfined and where over-bank flooding, alluviation and channel migration create a heterogeneous and dynamic mosaic of terrestrial and aquatic habitat patches (Stanford and others 2005) important to many kinds of terrestrial and aquatic organisms (Ward and others 1999). In the Pacific Northwest of the U.S., floodplain restoration is often aimed at the recovery of

Pacific salmon and steelhead, in large part because floodplains are thought to provide physical habitat critical for spawning (Montgomery 1999; Isaak and Thurow 2006) and juvenile rearing (Beechie and others 1994, Sommer and others 2001). Although there is evidence to support the importance of physical habitats in floodplains to anadromous salmonids, an under-represented mechanism by which floodplains may be important to these fishes is via enhanced food base productivity (Copp 1989; Junk and others 1989; Stanford and others 2002). Aquatic habitats within floodplains have been shown to support high rates of both autochthonous production (Coleman and Dahm 1990) and allochthonous organic matter inputs, such as leaf litter and terrestrial invertebrates (Cuffney 1988; Gregory and others 1991; Baxter and others 2005). Accordingly, floodplains can support elevated invertebrate secondary production (Smock and others 1992; Lewis and others 2001), enhancing the food base that fuels production of both resident and anadromous fishes (Sommer and others 2001; Stanford and others 2002; Jeffres and others 2008). However, in the context of the Pacific Northwest of the U.S., where many floodplain restoration efforts are being conducted or proposed, there have been very few measurements of the productivity of river-floodplain systems, or their role in supporting anadromous fishes that are the focus of these projects.

Unfortunately, river-floodplain systems have also been severely altered by human disturbance (Tockner and Stanford 2002). Some of the most dramatic examples of floodplain alteration have resulted from in-stream placer mining (i.e., dredge mining), and there are few places where these impacts are more striking than in the Yankee Fork Salmon River (YFSR) in central Idaho, USA. A 10 km segment of this river and its floodplain were extensively dredge-mined for gold in the 1930s and 1950s. Once complete, the combined effect of dredge-mining and associated road building effectively reduced the river to a single channel confined between dredge piles, and restricted riparian vegetation to the dredge piling-stream interface. In addition, dredging hampered processes, such as channel migration and cut and fill alluviation, which enhance connectivity between the main channel and the adjacent floodplain by creating and maintaining a diverse array of off-channel aquatic habitat types (i.e., side channels, spring brooks, etc). The desire to recover ESA-listed populations of spring Chinook salmon and summer steelhead in the YFSR, which currently measure only a fraction of their historic magnitude, has made this disturbed floodplain an obvious target for habitat restoration. In 1988 several isolated ponds that were created via the dredge-mining process (Fig. 2) were connected to the main channel of the YFSR by removal of dredge pilings (Richards and others 1992), in an attempt to increase rearing habitat for Chinook salmon and steelhead. However, recovery goals for anadromous fish have still not been met in the YFSR, and additional restoration is being proposed to further reclaim connectivity with floodplain habitats in the dredge segment.

Although degradation of physical habitat, such as that wrought in the YFSR, is often visually apparent, consequences for the aquatic food base may not be simply inferred. Given that floodplains are thought to be very productive features in river networks, I would expect floodplain degradation to have reduced the productivity of the food base that fuels fish production in the dredged segment. Yet, surprisingly little research has been completed to date that evaluates how floodplain degradation and channel confinement affects biotic productivity across trophic levels (but see Power and others 1995), and the potential implications for fish populations. Thus, though habitat in the dredged segment of the YFSR appears substantially altered, the consequences of this physical degradation on the productivity of the aquatic food base are not understood, and an assessment of previous habitat restoration on food base productivity has not been conducted. To understand how further habitat restoration might impact populations of anadromous salmonids in the YFSR studies are needed that evaluate the food base that supports these species.

In this study I utilize an ecosystem approach to evaluate if and how the food base that fuels fish production is impaired in the dredged segment of the YFSR. My research objectives were to: (1) determine if and how the food base (allochthonous inputs, aquatic primary producers, and aquatic invertebrates) that provides energy to feed both resident and anadromous fishes differs between the dredged segment of the YFSR and reference condition floodplain segments, (2) assess potential food base consequences of the 1988 restoration effort in the dredged segment that connected isolated ponds to the main channel, and (3) investigate the possible food base consequences of further floodplain restoration. In addition, I conduct a simple bioenergetic modeling exercise, whereby I compare the productivity of the existing food base to the demand for food by the fish assemblage, an approach which has been employed in other systems to evaluate how closely fishes track food resources (e.g., Allen 1951; Waters 1988; Huryn 1996, 1998). I utilized this modeling exercise to aid in interpreting results of my food base assessment, generate hypotheses regarding food limitation of fish in the YFSR and other systems of its kind, and provide a starting point (including identification of complexities and important uncertainties) for developing ecosystem models to be used in river restoration assessments.

Methods

Study Design

To evaluate the impact of dredging on food resources for resident and anadromous fishes in the YFSR, I used a space-for-time substitution approach. I compared the dredged segment to five reference-condition river-floodplain segments, located nearby in the Salmon River basin (Fig. 2c). Segments were compared in terms of: (1) allochthonous inputs of organic matter and invertebrates, (2) the biomass of aquatic primary producers and (3) the biomass and production of aquatic invertebrates. Measuring multiple reference segments provided a range of values for the characters I measured, wherein the historic potential of the YFSR dredged segment may lie (Ebersole and others 1997). In the dredged segment and reference segments within the YFSR sub-basin, I employed a relatively simple production/demand model that has been utilized in trout streams worldwide (e.g., Waters 1988; Huryn 1996, 1998). This approach requires estimating the production and associated food demand of the fish assemblage at a segment and comparing that to the invertebrate prey base, which includes both aquatic invertebrate production and inputs of terrestrial invertebrates. Although this approach provides only a coarse assessment of the potential degree to which a fish population tracks food resources, it has a long and important history in ecology as a heuristic tool, aiding in interpretation and informing the development of more complex and realistic ecosystem models (Lindeman 1942, Allen 1951, Odum 1957, Odum and Barrett 2005).

Study Site

All study segments were located in the Salmon River basin, Idaho (U.S.) drainage area 36,260 km^2), which is set within a highly mountainous region, and was historically one of the most productive salmon streams in the Columbia basin (Petroski and others 2001). However, populations have declined over the last century, resulting in the ESA-listing of spring/summer Chinook salmon (*Oncorhynchus tshawytscha*), and summer steelhead (*Oncorhynchus mykiss*). The YFSR is a major tributary of the upper Salmon River (drainage area 493 km^2). The dredged segment is ca. 10 km in length and 400 m wide between hill-slopes. More than 30 isolated ponds of various size and depth remain from dredging. During the 1988 restoration effort in the YFSR, channels were excavated through dredge piles, connecting four pond series (with multiple ponds per series) to the main channel (Richards and others 1992; Fig. 2b). The potential impact of this restoration on the food base in the dredged segment is evaluated in my results, and abbreviated as “RST” (Restored) in subsequent tables and figures.

Reference floodplain segments were selected based on proximity to the dredged segment (YFD), floodplain and stream size, and the relative absence of human disturbance. Two reference floodplain segments were selected within the YFSR: one 6.5 km upstream from the dredged segment (YFR) and one in the West Fork of the Yankee Fork (WF). Three other floodplains segments were chosen outside the YFSR, one in Camas Creek (CC), one in Basin Creek (BC), and another in the East Fork Salmon River (EF; Fig. 1). Given the range of possibilities, I chose reference segments that best represented the historic potential of the dredged segment (*sensu* Ebersole and others 1997). Though all had some level of human disturbance (i.e., roads, campgrounds, minor grazing, trails, etc.), they were the best available, and I reasoned that these impacts were small in comparison to the changes wrought in the dredged segment.

Sampling Design

To represent the complex and heterogeneous habitats in river-floodplain systems, a stratified random sampling approach was used to sample allochthonous inputs, aquatic primary producers, and aquatic invertebrates. Sampling effort was established based on the presence, abundance, and size of riparian vegetation and aquatic habitat patches, which were measured via visual ground surveys and later digitized in ArcGIS. Larger and/or more heterogeneous patches received a greater sampling effort than smaller, more homogenous patches. Likewise, larger and/or more heterogeneous segments required more sampling effort to represent the higher diversity of patch types. Sampling of allochthonous inputs (leaf litter and terrestrial invertebrates) was stratified by dominant riparian vegetation, mainly willow (*Salix spp.*), alder (*Alnus spp.*), cottonwood (*Populus trichocarpa*) and conifer. Similarly, sampling of aquatic primary producers and invertebrates was stratified by aquatic habitat. Aquatic habitat in main channels was divided into riffles and pools/runs based on visual surveys during base flow (see Hawkins and others 1993). Pools were grouped with runs because they represented a very small proportion of total habitat area (< .05%), and because they were generally too deep for my sampling equipment. Habitat patches located outside of the main channel (hereafter, off-channel habitat patches) were classified by degree of connection with the main channel at base flow, ranging from side-channels with both up- and downstream connections, spring brooks connected only on the downstream end, and wetlands with no surface connection to the main channel during base flow (but connected during high flows). Aquatic habitat patches that remained disconnected during high flow events were not included in my estimates, as they were inaccessible to fishes.

Habitat Measurements

To aid in interpretation of results from my comparisons, several habitat variables were measured at each study segment that are known to influence biotic productivity. Stream temperature was measured hourly with Onset HOBO® data loggers from June to October of 2006 and 2007. Annual input of solar radiation was estimated by tracing surrounding features of the landscape and riparian vegetation using a Solar Pathfinder™ (Platts and others 1983), which incorporates stream aspect and latitude to calculate radiation flux for a site. Discharge was measured several times during the summers of 2006 and 2007 using a current meter. In order to provide a snapshot of potential differences in the nutrient status of study segments, total dissolved nitrogen and phosphorus (TDN and TDP), and dissolved organic carbon (DOC) were measured via three consecutive water samples from the main channel during June 2007. Substrate size and embeddedness was estimated for the main channel during summer 2007 by measuring the β (intermediate) axis of 100 to 300 rocks and qualitatively evaluating the percentage of each particle that was embedded in a matrix of smaller particles.

Allochthonous Inputs and Aquatic Primary Producers

Inputs of allochthonous leaf and woody litter into aquatic habitat were estimated with baskets (sample area = 0.20 m^2). In summer 2006, baskets were randomly dispersed within riparian vegetation patches in each segment. Baskets were collected monthly through leaf abscission in late October. The number of baskets placed in each segment ranged from 14 to 28, and (as described above) was proportional to complexity and length of the study segment. Baskets were placed at the wetted edge of the stream but also at other locations within the active channel, which was defined as the area of floodplain inundated annually and delineated by evidence of scour and deposition of flood debris. Litter was defined as potential allochthonous input if it would have fallen either directly into aquatic habitat or onto the active-channel. In the lab litter was identified, dried at 60ºC for 24 hrs and weighed.

Pan traps (sample area = 0.21 m^2) were used to sample terrestrial invertebrate flux. During July 2006 I distributed 10-28 traps, in proportion to the presence of different vegetation patches, at the wetted edge of the stream in each segment. Traps were filled with 10 cm of water and a few drops of biodegradable soap to reduce surface tension. Invertebrates were collected three times in July (after collecting 3-8 days). Adult aquatic taxa were separated from terrestrial taxa with a dissecting scope. Terrestrial invertebrate contributions were dried at 60°C for 24 hrs and weighed.
Invertebrate flux was calculated by multiplying the average input to all traps at a segment ($g\ m^{-2}\ d^{-1}$) by the wetted area of that segment (m^2).

Aquatic primary producer biomass was estimated for each study segment by sampling algae and aquatic vegetation in each aquatic habitat patch. Most sampling was conducted in summer 2006, with additional samples collected in summer 2007 to increase sample size in off-channel habitat patches. Biomass of chlorophyll-*a* was used as a surrogate for biomass of periphyton and attached algae. Between 21 and 45 samples were collected in each study segment. In rocky benthic habitat, periphyton was sampled by scrubbing the surface of randomly selected rocks, and surface area of rocks was determined by tracing their top surface (Bergey and Getty 2006). To sample epipelon a bottomless bucket (0.053 m^2) was placed over the silt or sand, which was then lightly disturbed and a subsample of water taken. Samples were filtered (0.7 μm), placed in a dark container, and frozen until processing. Chlorophyll-*a* was extracted with methanol and analyzed with a spectrophotometer following standard methods (Steinman and others 2006). Vascular aquatic vegetation was sampled by placing a bottomless bucket over vegetation and clipping vegetation at ground level. Air-dried vegetation was subsequently oven dried for 24 hrs at 60°C, and weighed.

Aquatic Invertebrates

Standing crop biomass of aquatic invertebrates in each study segment was estimated by collecting 14-28 benthic samples from habitat patches in each segment. Sampling was conducted in summer 2006, with additional sampling in summer 2007 to increase sample size in off-channel habitat patches. In lotic habitat patches a Surber sampler (0.096 m^2, 250 μm mesh) was used, whereas lentic habitat patches were sampled with a bottomless bucket (0.053 m^2) or mini-ponar (0.027 m^2). Drift nets (250 μm) were pulled across lentic patches to sample known volumes of water for pelagic invertebrates, such as zooplankton. However, this is likely to have resulted in an under-estimate of the presence of many zooplankters (e.g., *Daphnia*) that were smaller than the mesh size of my nets (< 250 μm). Samples were preserved in 95% ethanol. A two-phase sorting approach was utilized to reduce processing time. First, all large invertebrates (≥ 10 mm) were removed from the sample, then, successive subsamples were removed and sorted at 10X magnification until at least 300 individuals were picked. Invertebrates were identified to the lowest taxonomic level feasible (genus or species, except for Chironomidae), dried at 60°C for 24 hrs, and weighed.

The annual secondary production of invertebrates was calculated by utilizing a common approach whereby the biomass of each taxon was multiplied by taxon specific annual production to biomass (P/B) values derived from the literature (described by Benke 1984). Taxon specific production values were summed to determine total aquatic invertebrate production. Published P/B values from the region were used when possible (Gaines and others 1992; Robinson and Minshall 1998), but if these did not exist, I applied values from outside the region. If multiple values existed for a taxon, the lowest published P/B value was used. When no literature values could be found a P/B value of five was applied (Benke and Huryn 2006). I assumed that invertebrate standing crop biomass in the summer approximated the average annual invertebrate biomass for each taxon. Although this assumption was not directly evaluated, peak emergence is usually in late-spring/early-summer in the Salmon Basin (Malison and Baxter 2010), prior to my invertebrate sampling effort. Therefore, my snap-shot of invertebrate biomass was likely an underestimate of the average annual biomass for many taxa, which means that estimates of invertebrate production are probably low. Standard errors for my production estimates were based on variation in summer invertebrate biomass samples.

Food Production to Fish Demand Model

Fish production for the dredged segment and both reference segments in the YFSR (WF and YFR) was calculated for 2007 and 2008 using data from routine annual multi-pass electro-fishing surveys conducted by the Shoshone-Bannock Tribes. Within each study segment, 2-6 main channel reaches (~100 m long) were block netted, and 3-4 consecutive electro-fishing passes were conducted, whereby all captured fish were removed and fish abundance for all species (except sculpins, *Cottus spp*., which are not efficiently captured by this technique) was estimated via the depletion method (White and others 1982). Weights and lengths were collected on all captured fish and were used to determine the total biomass (g/m^2) of fish by multiplying the estimated abundance of each species and size class by average fish weight. Wet mass was converted to dry mass by multiplying by 0.25 (Elliot 1976). Similar to invertebrate production, fish production was calculated by multiplying wet mass by annual growth rates via the instantaneous growth method (Benke and Huryn 2006). For steelhead trout, annual growth was calculated from the fish survey data for each segment, using size-frequency histograms to infer growth between sampling years. For all other species, I was unable to infer growth with size-frequency histograms, and published annual growth rates from nearby basins were applied (Bjornn 1978; Overton and others 1978). . Of course, fish could have different P/B values among floodplain segments. However, potential differences in annual growth rates are likely to be relatively minor compared to measured differences (and associated uncertainty) in fish abundance and biomass between study segments. Estimates of food demand were obtained by multiplying annual fish production by the reciprocal of gross production efficiency (GPE), which is the product of assimilation efficiency and net production efficiency (*sensu* Waters 1988; Huryn 1996, 1998; Cross and others 2011). Because ecological efficiencies were not measured in this study, a GPE of 0.15 was applied, which is at the low end of GPE values utilized in other studies (e.g., Waters 1988; Huryn 1996, 1998). I chose this conservative value because in my model I did not want to underestimate the demand for food by fish.

The total invertebrate food base was calculated as the sum of annual aquatic invertebrate production and terrestrial invertebrate inputs. Contributions from off-channel aquatic habitat patches were not included in these estimates, because no fish data was available for these areas. In addition, taxa that are known to be invulnerable to predation by salmonids (e.g., gastropods and bivalves) were removed. Annual terrestrial invertebrate input was calculated by multiplying the daily flux (g m^{-2} d^{-1}) from summer samples by the 92 days in June, July and August. Though the majority of terrestrial inputs in this region occur during summer (see Baxter and others 2005), this approach probably underestimated the total input of terrestrial invertebrates because it did not include fluxes during spring and autumn.

Analysis

Samples of aquatic primary producers, litter inputs, and aquatic invertebrates were used to generate total estimates ($\hat{Y}_{total}$) and standard errors (SE) for each segment as:

$$\hat{Y}_{total} = \sum A_p \times \hat{Y}_p$$

$$SE(\hat{Y}_{total}) = \sqrt{\sum A_p^2 \times \frac{S_p^2}{n_p}}$$

Where $\hat{y}_p$ is the mean value for the p^{th} patch, A_p is the area of the p^{th} patch, $s_p{}^2$ is the variance in the p^{th} patch and n_p is the number of samples taken in the p^{th} patch. Total estimates and associated errors were then standardized by dividing total values by segment length, which resulted in units of mass per meter of valley length (e.g., g/m), instead of the typical mass per unit area (e.g., g/m^2). Linear units were more appropriate in this comparison because I expected differences between the dredged and reference segments would be driven in part by the amount of aquatic habitat or floodplain surface per length of valley, rather than differences in biotic productivity on a per area basis. However, I also present aquatic invertebrate production in mass per unit area (g m^{-2} y^{-1}) to facilitate comparison with other literature values. In comparing segments, it was also important to account for differences in stream size (i.e., discharge and drainage area; Table 1) because it likely affects the amount of wetted habitat per length of floodplain. For example, I would expect larger streams to have larger main-channel wetted width and also larger off-channel complexes (i.e., larger channel units), which could support a higher biomass of aquatic biota per valley length. Differences in stream size were incorporated by dividing estimates for aquatic primary producers and invertebrates in each reference segment by a stream size correction ratio (Table 1); the ratio of drainage area upstream of reference segments to the drainage area above the dredged segment.

The state of the dredged segment was evaluated by comparing estimates in the dredged segment to the range of estimates in reference segments. If the dredged segment fell below the range defined by reference segment estimates and associated errors (±1SE), then it was considered to be "impaired" with respect to that metric. However, in the context of the proposed restoration project, I wanted to minimize the chance of incorrectly defining the dredged segment as unimpaired. Therefore an additional evaluation was employed whereby the error in each metric was disregarded, and estimates for the dredged segment were compared to the range of estimates in reference segments without error. If the dredged segment fell outside the range of reference values it was considered to be "possibly" impaired relative to reference conditions. To evaluate the consequences of the 1988 restoration effort, I added estimates of food base contributions from the connected dredge ponds to those for the main-channel of the dredged segment (labeled "RST" in figures). Potential differences in food production and fish demand were assessed by visually comparing approximate 95% confidence intervals (±2SE; e.g., Bradford and others 2005). Means with non-overlapping confidence intervals were interpreted as significantly different.

To assist in interpreting differences in food base productivity (or a lack thereof) between the dredged and reference segments, Pearson's correlation analysis was used to compare habitat (i.e., drainage area, floodplain length, substrate size, solar radiation and stream nutrients) and biotic variables (i.e., allochthonous inputs, chlorophyll-*a* biomass, and invertebrate biomass and production). When necessary, data were square-root transformed to meet the assumption of normality. Spearman's rank correlation was used when assumptions for parametric analyses were not met. All significant correlations ($\alpha \leq 0.05$) are reported in the results.

Results

Habitat Measurements

Values for habitat measurements in the dredged segment were generally within the range found in reference segments (Table 1). Concentrations of TDN, TDP and DOC were generally low in all segments (Table 1), with the exception of the higher values of TDP found in the YFR (43 μg/L) and YFD (20 μg/L) segments. Of the habitat variables measured in the dredged segment, only segment length and substrate size had values outside the reference segment range. The dredged segment was 8 km in length, whereas reference segments ranged from 1 km to 6 km in length. Main channel substrate size (D50) was larger in the dredged segment (median particle size was 13 cm) than at reference segments (range = 5-8 cm). Substrate embeddedness was highest in the EF segment, where 35% of particles were at least 50% embedded in a matrix of smaller substrate (mostly packed silt and sand), followed by 30% that were similarly embedded in the dredged segment, and 4-19% in the remaining reference segments.

Allochthonous Inputs and Aquatic Primary Producers

Total input of riparian leaf litter and wood to the active channel in the dredged segment was 2.26 kg/m, which was slightly higher than the range of estimates from reference segments (0.998 – 2.23 kg/m; Fig. 3a). Inclusion of off-channel habitat patches in the dredged segment that had been connected to the main channel in the 1988 restoration action (labeled as “RST” in figures) raised the estimate of litter input to 2.51 kg/m. The composition of inputs varied considerably between segments (Fig. 3a). The input of alder leaves was highest in the dredged segment, where it comprised 58% of total inputs, compared to an average of 17% among reference segments (range of 0% to 47%). Conifer and willow input in the dredged segment comprised 2.5% and 10% of the composition, respectively, and were well below the reference segment averages of 25% and 23%. Variation among segments in the magnitude of litter inputs was not correlated with any of the habitat variables we measured.

Average daily input of terrestrial invertebrates to the dredged segment was 1.26 g m^{-1} d^{-1}, which was within the range of values measured at reference segments (0.57 – 1.84 g m^{-1} d^{-1}; Fig. 3b). Inclusion of connected areas from the 1988 restoration effort in the dredged segment raised the estimate to 1.53 g m^{-1} d^{-1}. Input of terrestrial invertebrates exhibited a strong positive correlation with total solar radiation flux to the stream (Pearson's correlation, $r = 0.88$, $P = 0.02$), but was not associated with any other measured variable.

Total chlorophyll-*a* biomass corrected for segment length and drainage area varied widely among reference segments, ranging from 21 to 691 mg/m (Fig. 3c). In the dredged segment chlorophyll-*a* biomass was 219 mg/m, which was higher than all the reference values except for that of the YFR segment. High chlorophyll-*a* biomass in the dredged segment was due to much greater biomass in the main channel of the dredged segment compared to main channel habitat patches in reference segments. This pattern was reflected in the significant positive correlated between chlorophyll-*a* biomass and substrate size (Spearman's rank correlation, $r = 0.88$, $P = 0.02$). Chlorophyll-*a* biomass was not associated with any other variable. Off-channel habitat patches contributed substantially (between 32 – 89%) to total chlorophyll-*a* estimates and were responsible for much of the variation among reference segment values (Fig. 3c). The inclusion of connected off-channel habitat patches from the 1988 restoration effort in the dredged segment raised the chlorophyll-*a* value over three times, to 692 g/m. The inclusion of restored habitat patches also raised the biomass of vascular aquatic vegetation from zero to 37.9 g/m in the dredged segment, which was within the wide range of estimates for reference segments (ranging from 12.7 to 3600 g/m).

Aquatic Invertebrates

Total corrected aquatic invertebrate biomass in the dredged segment was 32.6 g/m, which was within the range for reference segments, 25.5 – 69.5 g/m (Fig. 4a). Reference segments with the highest total biomass (BC and YFR) possessed large contributions from off-channel habitat patches (Fig 4a). In the dredged segment, inclusion of off-channel habitat patches connected by the 1988 restoration effort increased invertebrate biomass to 42.4 g/m. The main channel of the dredged segment had higher invertebrate biomass than main channels in any of the reference segments (Fig. 4a). High invertebrate biomass in the main channel of the dredged segment was driven by high densities of the large-bodied, filter feeding caddisfly *Arctopsyche grandis* (Hydropsychidae), which comprised 24% of the total biomass. In main channel habitat, biomass densities (g/m^2) of aquatic invertebrates were also positively correlated with average summer water temperature (Pearson's correlation, $r = 0.84$, $P = 0.04$). Invertebrate biomass was not associated with any other variable.

Aquatic invertebrate production was highly variable among reference segments, ranging from 113 – 1640 $g\ m^{-1}\ y^{-1}$ (Fig. 4b). As was the case for biomass, segments with the highest production (BC, EF and YFR) had large contributions from off-channel habitat patches. Production in the dredged segment was 216 g m^{-1} y^{-1}, and 341 g m^{-1} y^{-1} with the inclusion of off-channel habitat patches connected by the 1988 restoration. Main channel habitat in the dredged segment had higher invertebrate production than main channels in reference segments (Fig. 4b), principally due to high densities of midges (Chironomidae) and blackflies (Simuliidae), which have high P/B ratios (Table 2). Invertebrate production in off-channel habitat varied considerably among reference segments (Fig. 4b), ranging from 2% of the total production in CC to 90% of production in the YFR segment. Habitat patches connected by 1988 restoration contributed 25% to total production in the dredged segment. Aquatic invertebrate production was not correlated with any of the habitat variables I measured.

Food Production to Fish Demand Model

The dominant fish species present in surveyed study segments were rainbow trout (mostly juvenile steelhead), juvenile Chinook salmon and mountain whitefish (*Prosopium williamsoni*); rare taxa included bull trout (*Salvelinus confluentus*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; Table 2). The dredged segment had higher fish abundance, biomass, and production than surveyed reference segments (Table 3). Total estimated fish production in the dredged segment in 2008 was 1.9 g m^{-2} y^{-1} of dry mass, whereas values for reference segments were 0.24 g m^{-2} y^{-1} in the YFR segment and 0.34 g m^{-2} y^{-1} in the WF segment. In 2007, fish production in the dredged segment was 1.7 g m^{-2} y^{-1}, and 0.06 and 0.73 g m^{-2} y^{-1} in the YFR and WF segments respectively. In both 2007 and 2008 the higher fish biomass and production in the dredged segment was driven by a greater abundance of rainbow trout and adult mountain whitefish (Table 3). In general, mountain whitefish had larger average body mass (211 g) than juvenile steelhead (22.4 g) and Chinook (6.24 g).

Our model calculations yielded estimates of total food demand by the fish assemblage in 2008 of 12 g m^{-2} y^{-1} of dry mass in the YFD segment, 2.3 in the WF segment and 1.6 in the YFR segment (Fig. 5). Estimates for 2007 were 11 g m^{-2} y^{-1} in the YFD segment, 4.9 in the WF segment and 0.39 in the YFR segment. Although food demand in 2007 and 2008 was similar in the YFD segment, in the WF segment 2007 food demand was approximately double that of 2008, and in the YFR segment 2007 demand was less than 25% of that calculated for 2008.

We estimated that the total invertebrate food base ranged from 18 g m^{-2} y^{-1} in the YFR segment to 56 g m^{-2} y^{-1} in the YFD segment, with terrestrial invertebrates comprising only 14% of the food base in the dredged segment and as much as 64% in the YFR segment (Fig. 5). The total measured invertebrate food base (aquatic invertebrate production minus taxa known to be invulnerable plus terrestrial invertebrate inputs) was significantly larger than the modeled calculations of demand by fish (based on 95% confidence intervals; Fig. 5). Food base estimates were approximately four times larger than calculated fish demand at the dredged segment, six times larger at WF and 30 times larger at YFR. One exception to this pattern occurred in 2007 at the WF segment; although the food base was larger than demand, 95% confidence intervals overlapped slightly.

Discussion

In this study I evaluated restoration potential by assessing the food base that supports fish production via an ecosystem approach. The results of this study provide little evidence to support proposed floodplain restoration in the YFSR based strictly on a goal of increasing food base productivity to fuel population recovery of anadromous salmonids. I did find that off-channel habitat patches can contribute substantially to productivity to river segments and that past restoration in the YFSR dredged segment has increased food resources across multiple trophic levels, and it is reasonable to predict that future restoration might do the same. However, measured food base productivity in the dredged segment was within the range of that found in reference segments, and compared to estimates of invertebrate food production from other systems, production in the dredged segment and reference segments within the YFSR would not be considered low. Thus it remains unclear if further food production provided by habitat restoration would have any impact on the recovery of target salmon and steelhead populations. My findings demonstrate a simple lesson: while it is usually possible to identify a form (or forms) of "improvement" that might result from restoration, the true potential for a project to restore a target population cannot be assessed without evaluating whether or not restoration will address a factor that is limiting population recovery (see Budy and Schaller 2007).

Though I did not observe differences in terms of productivity, my study did not represent a comprehensive analysis of ecological degradation in the dredged segment of the YFSR, nor did I explore how changes in species composition or biodiversity may occur as a consequence of floodplain restoration. If proposed restoration is to proceed in the YFSR, I submit that additional analyses are necessary to provide a clear rationale that identifies in what manner the dredged segment is impaired, how this is linked to factors limiting anadromous salmon and steelhead populations in the YFSR, and how floodplain restoration will address these concerns. For example, although my study found high food productivity in the dredged segment, physical habitat conditions (see Fausch 1984; Statzner and others 1988), and/or biotic interactions and complexities (see Fraser and Gilliam 1992; Fraser and Metcalfe 1997; Power 1992) could still limit the ability of fish to utilize these resources.

Food base: Dredged versus Reference Segments

Despite the fact that major differences in physical habitat between reference segments and the dredged segment of the YFSR are evident even to the casual observer, I did not observe strong differences with respect to the aquatic food base. Aggregate estimates for allochthonous inputs, aquatic primary producers and aquatic invertebrates in the dredged segment were within the range of that found in reference segments. That said, the range among reference segments was large, owing mainly to differences in productivity between habitat patch types, not all of which were present in every segment. These findings were surprising, given that intact floodplains are thought to be hotspots of productivity in river networks (Junk and others 1989; Stanford and others 2005). One explanation might be that floodplain segments studied here were relatively small, and possibly less productive, compared to those of larger temperate and tropical rivers where much productivity arises from longer and spatially extensive inundation (Junk and others 1989; Lewis and others 2001). In addition, estimates of productivity alone do not represent the full function of floodplain features in river networks. The identity of organisms involved in production, the role of floodplain habitat structure in organism life histories, and overall contributions to biodiversity are functional aspects of these habitats that were not the explicit focus of this study. Nevertheless, my results highlight that consequences of habitat degradation for aquatic productivity are not always straightforward, as has been demonstrated in other contexts (e.g., riparian logging can increase stream productivity, Noel et al. 1986; tailwaters below dams can be highly productive, Blinn and Cole 1991; etc.).

Explanations for the seemingly counterintuitive findings of my study may be found in the characteristics of the study segments themselves. For example, I found that leaf litter inputs to the area of the floodplain inundated on an annual basis in the dredged segment were slightly higher than the range of values at reference segments, which might seem surprising given that portions of the dredged segment appear to be completely lacking riparian vegetation (Figure 2). However, a thick band of alder and willow lines the majority of the wetted edge of the channel in the dredged segment, whereas in reference segments, vegetation is often set-back away from the wetted edge of the main channel. I hypothesize that the incised channel and consequent lack of scouring overbank flow in the dredged segment allows these thick bands of vegetation to persist. In addition, a large portion of these inputs likely fall directly into the stream, instead of onto a floodplain surface, where they may not be incorporated into aquatic habitat until the following spring runoff. Input of terrestrial invertebrates was also similar between the dredged and reference segments. However, contrary to the findings of other studies (see Baxter and others 2005), invertebrate flux did not appear to be associated with riparian vegetation, but was instead positively associated with the amount of solar radiation reaching the water's surface, which is higher in segments with more open riparian canopies. The mechanism behind this association is unclear; however, one explanation (which would require compositional analysis not conducted here) might be that invertebrate input during the time frame of my study was dominated by aerial invertebrate taxa that are more abundant in open canopy stream segments.

Our observations of aquatic primary producers were initially surprising as well, in that estimated chlorophyll-*a* biomass in dredged segment was higher than all but one of the reference segment values. However, as with leaf litter inputs, plausible explanations arise upon closer examination. The elevated biomass of chlorophyll-*a* in the dredged segment was correlated with the larger substrata found in its main channel. I hypothesize that the larger, embedded substrata in the dredged segment are not as easily mobilized and scoured during high flows. Lack of substrate mobilization and scouring might facilitate the accumulation of high standing crops of aquatic primary producers, particularly large mats of filamentous algae that were frequently observed in the dredged segment, and which contrasted to the diatom-dominated periphyton of reference segment main channels. This explanation is supported by results from another study in the region, which also identified an association between substrate mobility/scouring and periphyton standing crops (Myers and others 2007). That said, higher chlorophyll-*a* biomass in the main channel dredged segment may not translate to higher primary production. In a pilot study during summer 2007, I used open-channel metabolism techniques and found gross primary production was actually slightly less in the dredged segment compared to one reference segment, suggesting that algal communities in the dredged segment may have slower turnover rates (Bellmore and Baxter 2009). In addition, the reference segments had a greater biomass of vascular aquatic vegetation.

The relatively high biomass and production of aquatic invertebrates in the dredged segment also appeared to be driven by physical characteristics of the dredged segment. Filter-feeding invertebrates (principally Hydropsychidae and Simuliidae), which have been shown to be important to the diets of fishes like those found in the YFSR (Angradi and Griffith 1990, Northcote and Ennis 1994, Sommer and others 2001), were much more productive in the dredged segment, compared reference segments. One explanation for the high abundance of filter-feeding invertebrates may be that higher velocity, lower retention streams like the dredged segment provide optimal foraging habitats for these taxa (Georgian and Thorp 1992). In a parallel study, I found that the dredged segment had higher water velocity and reduced capacity for retention of organic matter compared to reference segments (Bellmore and Baxter 2009). In addition, the large immobile substrate in the dredged segment might provide secure microhabitats for Hydropsychidae to construct their stationary retreats (Georgian and Thorp 1992). That being said, my approach to sampling aquatic invertebrates is likely to have under- represented components of aquatic invertebrate production, such as zooplankton and hyporheic invertebrates, which are likely to be more abundant in reference floodplain segments.

Though some findings of this study were contrary to expectations under the current floodplain paradigm (Junk and others 1989; Stanford and others 2005), I did find that off-channel aquatic habitat patches contributed up to 90% to total primary and secondary productivity. These findings are consistent with other floodplain studies that have reported high primary and secondary production in lateral floodplain habitats (e.g. Lewis and others 2001), as well as with the flood-pulse (Junk and others 1989) and shifting habitat mosaic (Stanford and others 2005) concepts that emphasize the importance of hydrologic connectivity with lateral habitats in fueling river-floodplain productivity. In addition, my results showed that the connection of off-channel habitat patches in the dredged segment as part of the 1988 restoration effort increased aquatic invertebrate production by 58%. This finding indicates that floodplain restoration aimed at enhancing connectivity with lateral habitat in the dredged segment does have the potential to increase floodplain productivity and the aquatic food base that fuels fish production.

Food Production to Fish Demand Model

Our estimates of food base production in the YFSR are some of the first derived for a salmon bearing stream, and provide no evidence that the food base that supports fish populations is depleted in the YFSR. Estimates of benthic invertebrate production in the main channel of my study segments ranged from 7 to 48 g m^{-2} y^{-1}. Although there are currently no other total invertebrate production estimates from salmon-spawning streams to which I can compare, these values would be considered moderate to high when compared to those from elsewhere (see Huryn and Wallace 2000). Similarly, total terrestrial invertebrate inputs ranged from 5 to 12 g m^{-2} y^{-1} in the main channel of my study segments, values also at the moderate to high end of published estimates (Baxter and others 2005). When I combined terrestrial and aquatic prey into an estimate of total invertebrate food production, I found that the food base was at least four times larger than my modeled calculations of demand for food by the fish assemblage at segments within YFSR. This was surprising given that results from a majority of the other trout streams where similar production/demand approaches have been utilized have shown that food production is insufficient to account for estimated demand for food by fish (see review by Waters 1988). This discrepancy, known as the "Allen Paradox" (Allen 1951), was only resolved after all potential invertebrate prey resources were included in the budget, including terrestrial inputs and hyporheic invertebrate production (Huryn 1996, 1998). Thus, the literature illustrates that some stream fish populations apparently have the capacity to utilize a majority of the invertebrate food base, whereas in the YFSR my model indicates that fish populations may not do so.

If the results of my comparison hold, there are numerous reasons why fish populations may not closely track food resources in the YFSR, including the following likely candidates. First, portions of the invertebrate food base, other than those I removed as invulnerable to predation (e.g., gastropods, bivalves), may be unavailable to fish (Power 1992). For example, most salmonids have a high propensity to feed from the drift, which means that some portion of benthic invertebrate production that does not drift may be less available (Rader 1997). Second, fish populations may be limited by physical habitat. In a bioenergetics framework, numerous studies and models have shown that physical habitat mediates how efficiently food resources can be consumed by fish and what proportion may be allocated to growth versus maintenance (Fausch 1984, Hanson 1997). Likewise, such models (e.g., Railsback and Harvey 2002, Guensch and others 2001) show that if appropriate rearing habitat is limiting, fish populations may be unable to efficiently acquire invertebrate prey. This may be particularly true in the dredged segment, which has high velocities, few pools, and limited refugia (e.g., under-cut banks, log-jams). Third, biotic interactions such as competition and predation, or risk of predation, may limit population size, and reduce foraging efficiency (Hearn 1987). If competition or predation is high, then fish spend more time and energy defending foraging territories and/or evading predators, and less time foraging (Fraser and Gilliam 1992; Fraser and Metcalfe 1997). Fourth, fish populations may currently be too small to utilize available food resources. Historically salmon and steelhead were much more abundant in the YFSR, and one hypothesis is that not enough adult spawners are returning to fully capitalize the food base. If true, this would indicate that factors outside of the YFSR (e.g., ocean conditions, hydropower, etc.) might be responsible for limiting population size (see Budy and Schaller 2007). Finally, my estimates of food production and modeled calculations of fish demand are likely not completely accurate. In a modeling exercise such as I conducted it is common (see Waters 1988, Huryn 1996) to use literature derived values (e.g., fish production efficiency, and invertebrate P/B values), make many assumptions (e.g., similar production efficiencies across sites) and even leave out factors of potential importance for which data do not exist (e.g., I could not estimate production and food demand by sculpin, which are potentially numerous). The question then becomes whether improved accuracy would alter the outcome of the comparisons. It is possible that it would, which begs for such efforts to be undertaken.

Although my simple production/demand model is admittedly coarse, and may be inaccurate for a number of reasons, the outcome of this heuristic exercise emphasizes the need to more rigorously evaluate the role food may play in limiting fish populations. In many river systems alternative management and restoration strategies are applied founded on assumptions, often implicit, about food limitation. This is particularly evident in the Pacific Northwest, where multiple strategies, often with contrasting assumptions about food limitation, are utilized in the name of recovering anadromous salmonids (Williams and others 1999, ISAB 2011). For example, habitat restoration is implemented based on the assumption that food and/or habitat limit freshwater production of anadromous fish. Similarly, nutrient and salmon carcass analog additions are proposed under the same assumption. In contrast, hatchery supplementation is used as a tool in recovery, based on the assumption that ample resources (including food) exist to sustain supplemented fish. Without some measure of when and where, and to what degree food limits populations, a key piece of the ecological rationale is missing for prioritizing alternative recovery actions for anadromous fishes. Consequently, there is a need to develop new tools, which can quantitatively evaluate food base productivity and limitation.

The simple production/demand model presented here represents a first heuristic step in developing and parameterizing more complex and realistic ecosystem and food web models that can be utilized in assessments of food limitation. For example, combining estimates of invertebrate production and fish demand with species specific diet information provides the data necessary to construct quantitative flow food webs (Benke and Wallace 1980, Hall and others 2000, Cross and others 2011), which can be utilized to evaluate interaction strengths and food limitation along individual predator- prey pathways. This type of information also sets the stage for parameterizing fairly complex ecosystem models, such as Ecopath with Ecosim (Christensen and Pauly 1993). When production/demand and dietary information are collected in a temporally and spatially explicit fashion, these more complex and realistic models can be utilized to model how trophic interactions change under different management and restoration scenarios. For example, Cross and others (2011) used a quantitative flow food web approach to show how a controlled flood on the Colorado River altered production of particular invertebrates and increased production by nonnative rainbow trout. Although those types of food web models are relatively complex, a prerequisite to such analyses are estimates of the productivity of the food base and fish production and demand, and often still require assumptions like those I made. If more rigorous ecosystem models are to be developed and applied to the science of salmon recovery and river restoration, simple energetic models (*sensu* Lindeman 1942, Allen 1951, Odum 1957, Odum and Barrett 2005), such as the one I construct here, may be a necessary stepping stone.

Conclusions

We found little evidence to support proposed floodplain restoration in the YFSR based strictly on a goal of increasing food base productivity. If proposed restoration is to proceed in the YFSR, I submit that additional analyses are necessary in order to provide a clear rationale that identifies in what manner the dredged segment is impaired, how this is linked to factors limiting anadromous salmon and steelhead populations in the YFSR, and how floodplain restoration will address these concerns. This study demonstrates how an ecosystem level approach can be utilized to evaluate restoration potential, and in so doing, emphasizes the need for pre-restoration studies that assess the aquatic food base in addition to physical habitat. The strength of this type of approach lies in the quantitative assessment of impairment based on measures of aquatic productivity (i.e., allochthonous organic matter and invertebrate inputs, aquatic primary and secondary production). Although physical habitat assessments are a necessary component of pre-restoration studies, this study reveals that consequences of physical habitat condition for the aquatic food base may not be simply inferred. In addition, my simple production/demand model emphasizes the need to evaluate assumptions regarding food limitation in river ecosystems, and sets the stage for development of more rigorous ecosystem models that can be used to evaluate restoration potential for stream fishes.

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Tables

Table 1. Background habitat variables measured for each segment. “Upstream drainage area” is the area of the drainage upstream of each study segment, and the “stream size correction ratio” is the ratio of reference segment drainage area to dredged segment drainage area (see text for further explanation). TDN = total dissolved nitrogen, TDP = total dissolved phosphorus, DOC = dissolved organic carbon, and D50 = median substrate size.

Segment	Upstream Drainage Area (km^2)	Stream Size Correction Ratio	Segment Length (m)	Base Flow Discharge (L/s)	Avg. Summer Water Temp (°C)	Solar Radiation (kWh m^{-2} year^{-1})	TDN (µg/L)	TDP (µg/L)	DOC (mg/L)	D50 (cm)
YFD	477	1.00	7760	1800	10.9	1423	8	20	1.49	13
BC	99	0.21	2940	600	9.9	1261	7	7	1.56	5
CC	628	1.32	5420	1500	11.7	1422	9	6	1.72	5
EF	392	0.82	1970	2000	10.4	1301	17	4	0.79	8
WF	132	0.28	5600	800	9.4	1235	5	5	1.25	5
YFR	194	0.41	1015	900	9.4	1500	8	43	1.88	6

Table 2. Annual invertebrate production and associated literature derived P/B (production to biomass) values for the dominant taxa in the dredged and reference segments (DM = dry mass). The 'Restored' dredge segment (RST) includes both main channel habitats and habitats connected to the main channel as part of the 1988 restoration effort, while YFD represents only main channel habitats. Values are calculated from benthic invertebrate sampling in summer 2006 and 2007 and converted to production using annual P/B values. Production values for all additional taxa are listed as "other."

				Production (DM g m^{-2} yr^{-1})						
Order	Family	*Genus*	Annual P/B	BC	CC	EF	WF	YFR	YFD	RST
Diptera	Chironomidae		88	9.11	4.95	35.14	5.79	31.63	21.30	29.35
	Simuliidae	*Simulium*	55	0.79	0.79	0.21	6.42	0.78	15.33	12.61
	Tipulidae	*Hexatoma*	4.5	0.23	0.02	0.33	0.29	0.13	0.84	0.69
Ephemeroptera	Baetidae	*Baetis*	24	0.79	0.28	0.71	0.27	1.33	2.82	2.35
	Ephemerellidae	*Serratella*	6	0.03	0.05	0.07	0.02	0.06	0.74	0.62
Plecoptera	Perlidae	*Hesperoperla*	7	0	0.40	0.46	0	0	0.27	0.22
	Perlidae	*Claassenia*	1.2	0	1.11	0	0	0	0.04	0.03
	Pteronarcyidae	*Pteronarcys*	1.2	0	0.87	0	0	0	0	0
Tricoptera	Limnephilidae	*Dicosmoecus*	5	0	0	0	0.40	0.02	0.56	0.46
	Hydropsychidae	*Arctopsyche*	7.5	0.07	0.03	0.06	0.59	0.18	4.12	3.39
Copepoda			14.5	0.08	0.02	0.11	0.01	1.41	0	0.03
Hydracarina			5	0.12	0.55	0.08	0.14	0.09	0.23	0.27
Ostracoda			40	3.86	0.36	7.59	0.50	4.45	0	0.13
Pelocypoda			3	2.53	0.05	0.46	0.13	0.15	0	0.94
Other			1-13	2.30	2.24	2.05	1.82	3.32	2.49	2.51
Total				19.91	11.73	47.27	16.39	43.55	48.74	53.59

Table 3. Main channel fish abundance, biomass, and annual production (mean ± SE) by species in 2007 and 2008 for the dredged segment (YFD), and the West Fork (WF) and Yankee Fork (YFR) reference segments (DM = dry mass). Species classified as "other" include cutthroat trout, bull trout, and brook trout. Values with no standard errors represent species and locations where we were unable to calculate error due to low catches and/or inadequate electro-fishing depletions.

Segment	Year	Species	Abundance (#/m^2)	Biomass (DM g/m^2)	Production (DM g m^{-2} yr^{-1})
YFD	2007	Chinook	0.0097 ± 0.0006	0.015 ± 0.0009	0.0275 ± 0.0017
		Rainbow	0.0881 ± 0.0035	0.214 ± 0.0106	0.8222 ± 0.0408
		whitefish	0.0096 ± 0.0002	0.5208 ± 0.0098	0.8333 ± 0.0157
		Other	0.0012	0.0044	0.0133
		Total	0.1085 ± 0.0043	0.7542 ± 0.0214	1.6963 ± 0.0582
	2008	Chinook	0.0053 ± 0.0003	0.0091 ± 0.0004	0.0168 ± 0.0008
		Rainbow	0.0657 ± 0.0049	0.1169 ± 0.0165	0.4492 ± 0.0633
		whitefish	0.0146 ± 0.0007	0.8657 ± 0.0425	1.3851 ± 0.068
		Other	0.0006 ± 0.0001	0.0102 ± 0.0013	0.0256 ± 0.0033
		Total	0.0862 ± 0.0059	1.002 ± 0.0607	1.8767 ± 0.1354
WF	2007	Chinook	0.0058 ± 0.0003	0.0074 ± 0.0004	0.0136 ± 0.0007
		Rainbow	0.0933 ± 0.0101	0.1759 ± 0.014	0.6759 ± 0.0538
		whitefish	0.0005	0.0008	0.0012
		Other	0.0011 ± 0.0002	0.0137 ± 0.0026	0.0412 ± 0.0079
		Total	0.1007 ± 0.0106	0.1978 ± 0.017	0.732 ± 0.0624
	2008	Chinook	0.0085 ± 0.0015	0.0139 ± 0.0024	0.0256 ± 0.0044
		Rainbow	0.0579 ± 0.004	0.0453 ± 0.0035	0.1742 ± 0.0135
		whitefish	0.0015	0.0679	0.1086
		Other	0.0005	0.0128	0.0319
		Total	0.0685 ± 0.0054	0.1399 ± 0.0059	0.3403 ± 0.0179
YFR	2007	Chinook	0.0152 ± 0.0019	0.0213 ± 0.0027	0.0392 ± 0.0049
		Rainbow	0.0016 ± 0.0001	0.0033 ± 0.0003	0.0127 ± 0.0011
		Other	0.0004	0.0017	0.0052
		Total	0.0171 ± 0.002	0.0264 ± 0.003	0.0571 ± 0.0061
	2008	Chinook	0.0176 ± 0.0027	0.023 ± 0.0035	0.0424 ± 0.0064
		Rainbow	0.0206 ± 0.0033	0.0322 ± 0.0029	0.1238 ± 0.0112
		Other	0.0026 ± 0.0006	0.0296 ± 0.0071	0.0741 ± 0.0176
		Total	0.0409 ± 0.0066	0.0849 ± 0.0134	0.2402 ± 0.0352

Figures

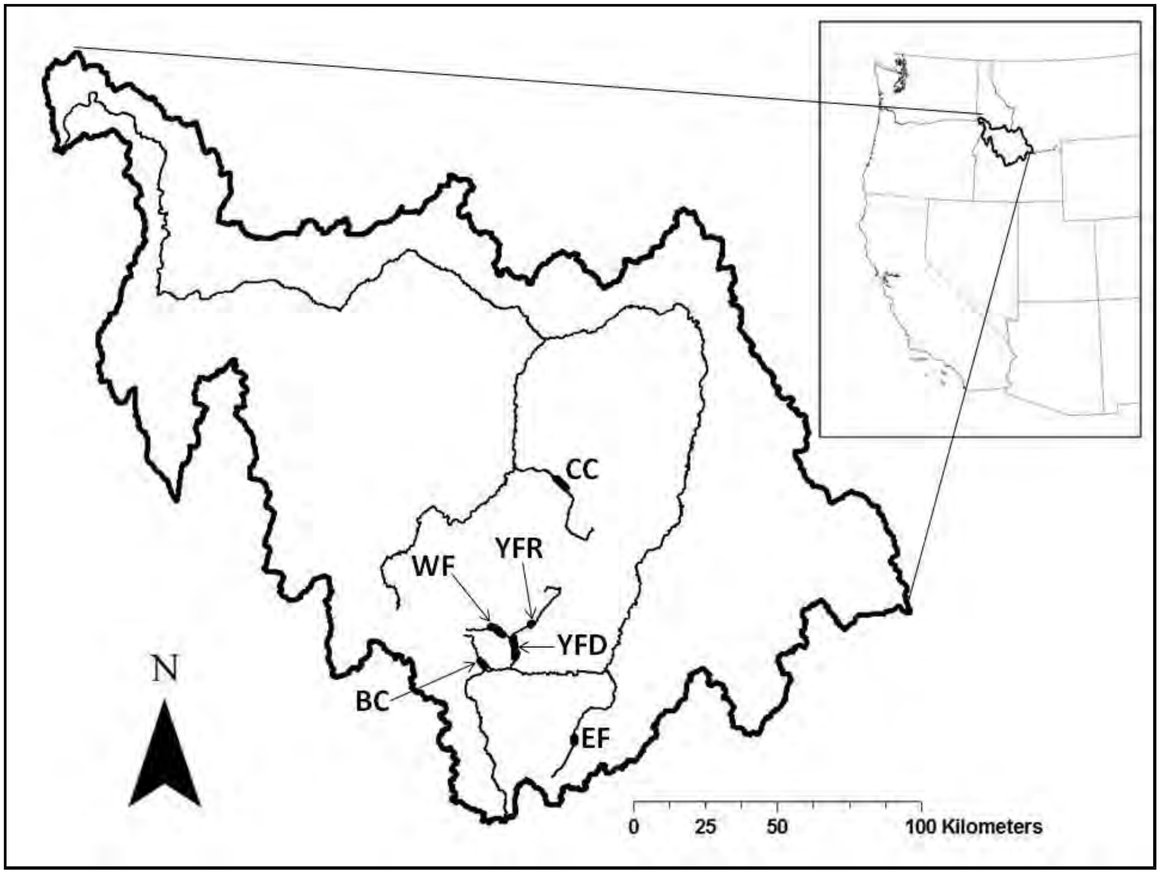

Figure 1. Map of the Salmon River basin, Idaho, with labeled study segments; BC = Basin Creek, CC = Camas Creek, EF = East Fork Salmon River, WF = West Fork Yankee Fork, YFD = Yankee Fork Dredged segment, and YFR = Yankee Fork Reference segment.

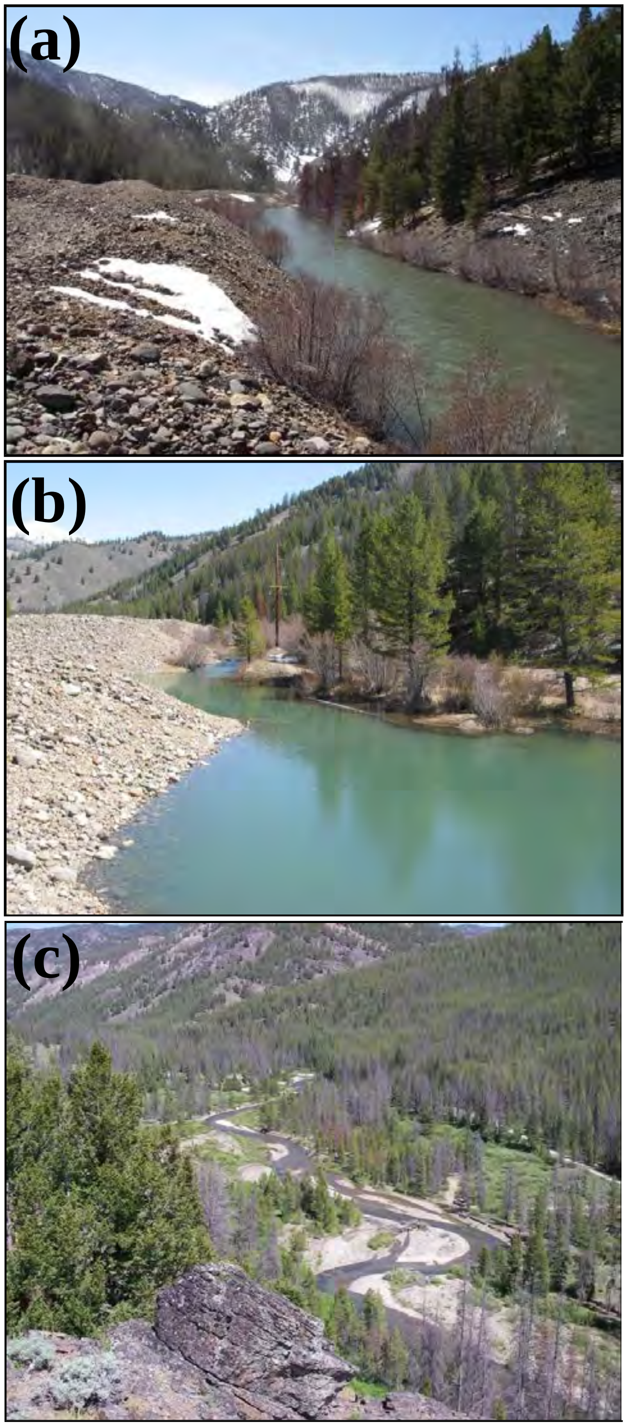

Figure 2. Photographs of (a) the dredged segment of the Yankee Fork Salmon River with associated dredge piles, (b) a remnant dredged pond that was connected to the main channel as part of the 1988 restoration effort, and (c) a typical intact reference condition floodplain.

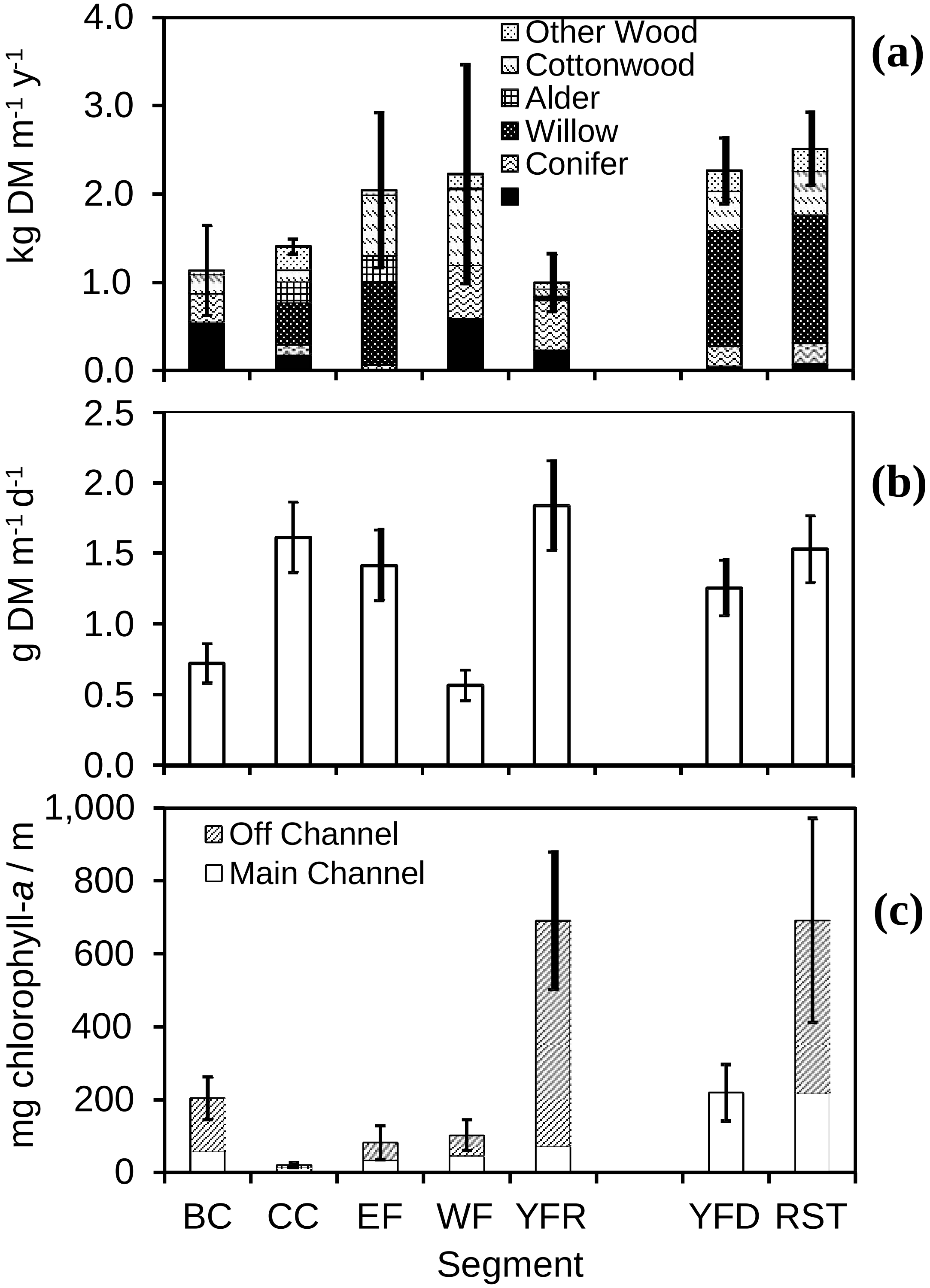

Figure 3. Basal allochthonous and autochthonous organic matter resources for the dredged segment and each reference segment (mean ± 1SE). (a) Annual litter inputs and

composition to aquatic habitats from summer 2007 sampling (DM = dry mass), (b) average daily terrestrial invertebrate flux into aquatic habitats from summer 2007 sampling, and (c) total corrected chlorophyll-*a* biomass for main channel and off-channel aquatic habitats, calculated from samples taken in summer 2006 and 2007. The 'Restored' dredge segment (RST) includes both main channel habitats and habitats connected to the main channel as part of the 1988 restoration effort.

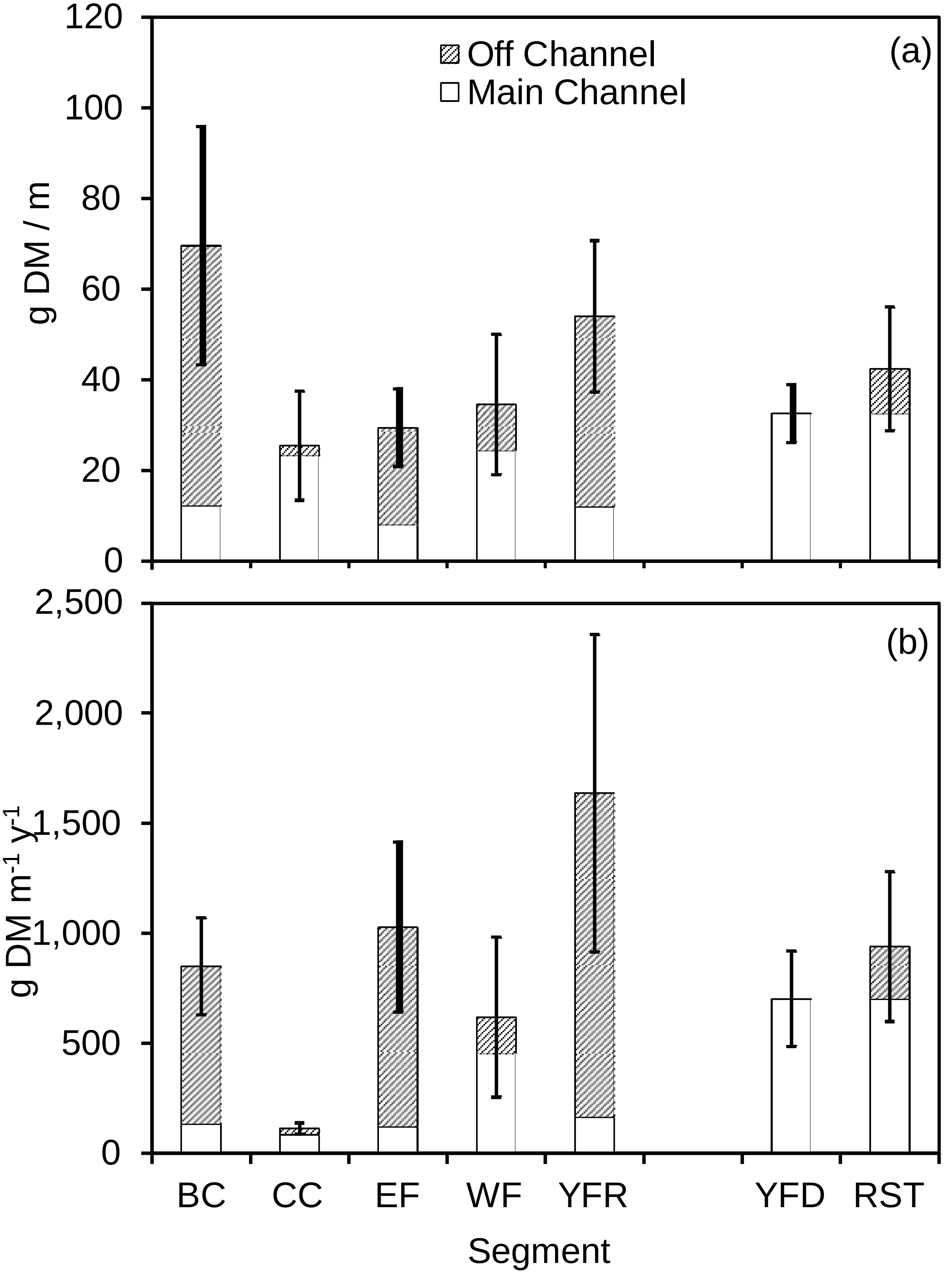

Figure 4. Total corrected estimates (mean ± 1SE) of aquatic invertebrate biomass (a) and annual production (b) for main and off-channel habitats in the dredged segment (with

and without restored habitats from the 1988 restoration effort) and each reference segment (DM = dry mass), calculated from samples taken in summer 2006 and 2007.

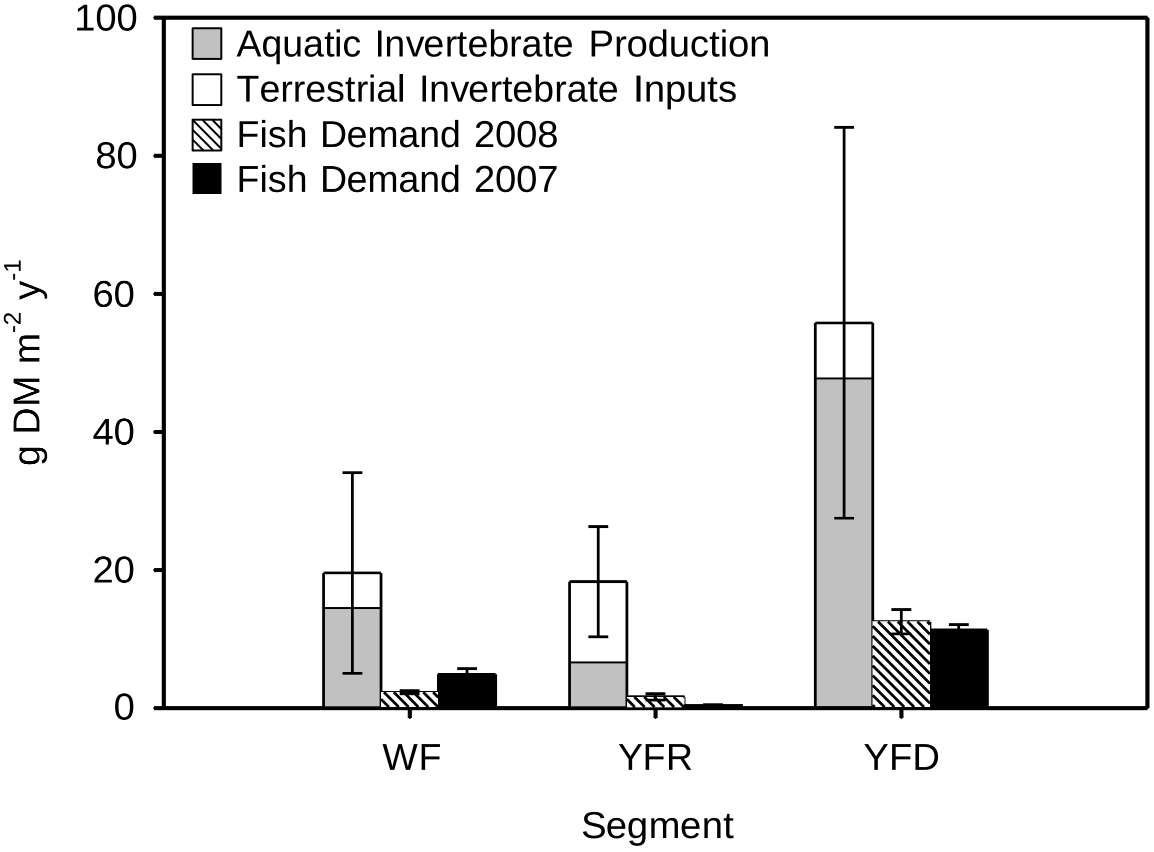

Figure 5. A comparison of total invertebrate prey base (aquatic invertebrate production + terrestrial invertebrate inputs) to fish food demand in the main channel of the dredged segment and both reference segments within the Yankee Fork Salmon River for both 2007 and 2008 (mean ± 95% confidence intervals; DM = dry mass)

Chapter 3

The floodplain food web mosaic: a study of its importance to Pacific salmon and steelhead with implications for their restoration

Abstract

Although numerous studies have attempted to place species of interest within the context of food webs, these attempts generally occur at small spatial scales or disregard potentially important spatial heterogeneity, and may be inadequate to describe the complex landscapes within which these species are embedded. If food web approaches are to be employed to help manage species, studies are needed that evaluate the multiple habitats and associated webs of interactions in which these species participate. In this study I describe the food webs that sustain freshwater production of Pacific salmon and steelhead within a floodplain landscape in the Methow River, Washington, USA, a location where restoration has been proposed to reconnect/recreate side channels in an attempt to recover anadromous fishes. I combine fish production and food demand estimates with fish dietary information, and invertebrate food base production to evaluate food webs within the main channel and five different side channels. For each habitat, this study (1) identifies pathways and magnitudes of energy flow that sustain both target and non-target fish species, (2) quantifies interaction strengths between fish predators and their prey, (3) estimates competition coefficients between fish species based on dietary overlap and food availability, and (4) models total salmon and steelhead production that could be supported given available food resources. I found that habitat patches within the floodplain landscape hosted very different local food webs. Juvenile Chinook salmon and steelhead utilized all of these patches, indicating that these species are flexible enough to exploit a wide range of food resources across a variety of habitats. This flexibility may be particularly important in the Methow River, where my results showed that non-target fish species (i.e., mountain whitefish and sculpin) consume a majority of

the prey base in the main channel, resulting in potentially high competition for available food. In contrast, side channels had a larger portion of energy flowing toward Chinook salmon and steelhead. In addition, side channels appeared to be under-seeded with respect to the invertebrate prey base, indicating that much higher salmon and steelhead production could be sustained in these habitats. I suggest that efforts to recover anadromous fish in the Methow would benefit from preserving and restoring the processes that create and maintain habitat complexity, rather than restoration aimed at actively recreating/reconnecting particular types of floodplain habitats.

Introduction

Food webs describe the pathways by which energy and materials move through ecosystems, and provide insight into the complex, multi-species assemblages within which organisms of interest grow, survive and reproduce (Elton 1927; Polis and Winemiller 1996). Although most natural resource science has traditionally focused on the population dynamics of single species of interest (Pikitch et al. 2004), the importance of food webs is now well recognized, and there are numerous examples of studies that describe the food webs within which focal species occur (e.g., Christensen and Pauly 1993; Vander Zanden et al. 2003; Frank et al. 2005). However, many of these studies occur at small spatial scales, or do not incorporate potentially important spatial heterogeneity, and therefore may be inadequate to describe the complex landscapes within which species are embedded (Woodward 2002). Landscape ecology, on the other hand, focuses on spatial heterogeneity and its consequences for organisms at larger spatial scales (Wiens 2002), but has rarely addressed food webs. Instead of only describing food webs for single habitats, or integrating food web information over heterogeneous landscapes, it may be important to bridge the gap between food web and landscape ecology, and in so doing evaluate food webs across the variety of different habitats used by species of interest.

River floodplains are often considered to be among the most biophysically complex and diverse landscapes on earth (Bayley 1995; Tockner and Stanford et al. 2005). Flood-pulses that redistribute sediment and organic matter create a dynamic mosaic of aquatic and terrestrial habitats in floodplains (Junk et al. 1998; Stanford et al. 2005) that are important to many species. The aquatic portion of this riverine landscape encompasses a spectrum of hydrologic conditions, ranging from main channel habitats, to small isolated side channels fed mainly by groundwater (Stanford et al. 2005). As a result of these differences in hydrologic connectivity, aquatic habitats in floodplain segments can vary widely in terms of water velocity, temperature, nutrient and oxygen content, sediment dynamics, and organic matter sources (i.e., allochthonous versus autochthonous) (e.g., Lewis et al. 2000). Although this mosaic of aquatic habitats can be thought of in aggregate as a single, larger food web for a floodplain segment, differences in biophysical characteristics among habitat patches are likely to create numerous spatially distinct sub-webs across the landscape (Winemiller 2004). In the context of natural resource management, the structure of food webs in these different patches may have important implications for sustaining species of interest (Winemiller 2004).

Unfortunately, many river-floodplain systems have been severely altered by human disturbance (Tockner and Stanford 2002). Because broad floodplain surfaces were most attractive for agricultural and urban development, rivers have been straightened, diked and their flows regulated to minimize the threat of flooding and bank erosion. These modifications have led to the disconnection of river channels from associated floodplains. This loss of longitudinal, lateral, and vertical connectivity through channel and flow alteration has diminished the physical processes that create and maintain aquatic habitat heterogeneity in floodplains (Tockner and Stanford 2002), which is deemed to be important to many species of economic, aesthetic or cultural interest (e.g., amphibians, mammals, birds and fish). This degradation, coupled with the desire to recover and preserve species of concern, has resulted in increasing numbers of habitat restoration projects aimed at floodplain reconnection (Bernhardt et al. 2005). That said, floodplain reconnection often requires intensive active (e.g., dike removal) and passive (e.g., beaver reintroduction) techniques, which can be quite expensive (Bernhardt et al. 2005). Consequently, studies are needed to evaluate the potential for proposed projects to succeed in recovering focal species.

In the Pacific Northwest of North America, floodplain restoration is often targeted at the recovery of threatened and endangered Pacific salmon and steelhead (*Oncorhynchus spp.*) populations (Roni et al. 2002). Although anadromous salmon and steelhead may utilize many environments during their complex life-cycle (ocean, estuary, large rivers, and headwaters), floodplains are often targeted for restoration because they are thought to contain important spawning and rearing habitats for these fish. In comparison to more confined river segments, floodplains have been shown to have more microhabitats (substrate, flow, depth and temperature combinations) suitable for spawning and egg deposition (Montgomery et al. 1999; Isaak et al. 2006). Furthermore, the mosaic of habitat patches within floodplain landscapes are thought to be important rearing areas for juvenile salmon and steelhead (Beechie et al. 1994; Sommer et al. 2001; Ebersole et al. 2003; Jeffres et al. 2008). Side channel habitats are thought to be especially important to rearing fishes by providing better energetic conditions for growth, via enhanced food base production, lower water velocities, and moderated water temperatures (Sommer et al. 2001, Ebersole et al. 2003). Hence, the reconnection and recreation of side channel habitats is often a key priority in floodplain restoration efforts aimed at salmon and steelhead recovery (Roni et al. 2002). That said, side channel habitats are themselves very diverse (e.g., ranging from large, highly connected channels to small, more isolated channels), and are likely to contain food webs that are distinct from one another, as well as the main channel (Winemiller 2004). Understanding how food webs vary across the floodplain mosaic may be important to evaluating the importance of individual habitat patches to salmon and steelhead, and to assessing how overall riverine landscape heterogeneity influences their populations.

Pre-restoration studies are now commonly conducted to evaluate the potential for these types of salmon and steelhead recovery projects to succeed (e.g., Beechie et al. 2008). However, these studies have generally focused on evaluations of physical habitat (e.g., sediment, pool area, temperature, etc.) and fish abundance (e,g., redd surveys). Few of these studies include any evaluation of the food base that supports fish production (Wipfli and Baxter 2010). Moreover, past assessments have generally focused on one or two fish species when in reality most anadromous salmonids spawn and rear in the context of complex food webs that include entire assemblages of fishes with whom they have evolved, as well as, more recently, exotic species. Although these assessments do provide valuable information, neglecting to include assessments of the food base that sustains these species and the food web webs in which they are embedded can result in high uncertainty, the implementation of inappropriate management actions, and unexpected consequences following restoration (Link 2002, Walters et al. 2005, ISAB 2011). Consequently, there is a need for the development and implementation of new approaches to evaluate restoration potential in terms of the complex freshwater food webs within which salmon recovery occurs (ISAB 2011).

In this study I utilize food web and ecosystem approaches to evaluate the mosaic of floodplain habitats utilized by salmon and steelhead in the Methow River, Washington (USA; Figure 1). Floodplain reconnection has been identified as a priority for recovery of anadromous fishes in the Methow, and pre-restoration assessments are needed to evaluate the potential for proposed restoration to positively affect target species. The objectives of my study were to: (1) quantify the productivity of the invertebrate food base (aquatic and terrestrial invertebrates) that fuels fish productivity in the main channel and five existing intact side channel habitats, (2) estimate the demand for prey taxa by members of the fish assemblage in these habitats, and (3) build quantitative flow food webs for each habitat to evaluate how prey productivity is distributed among members of the fish assemblage. This approach allowed us to (a) elucidate dominant pathways of material flow in different floodplain habitats, (b) assess the potential for food limitation of Chinook salmon and steelhead populations, (c) evaluate the potential for interspecific competition between target and non-target fishes, and (d) quantify the relative importance of different habitats to sustaining salmon and steelhead production. Together, our results highlight the importance of utilizing more holistic food web approaches to understand the role of landscape heterogeneity in the ecology of species of conservation and management concern.

Methods

Study Site

The Methow River is a fifth order tributary (4662 km^2) of the Columbia River, located in north-central Washington, USA (Figure 1). The headwaters drain east and south from an elevation of 1700 m in the Cascade Mountains, to 240 m at the confluence with the Columbia River. Precipitation is variable, ranging from 200 cm along the crest of the Cascades, to 25 cm at the confluence with the Columbia River. A majority of the precipitation falls in the winter in the form of snow. The hydrograph of the Methow River is typical of snow-melt dominated systems, with peak flows occurring in May and June, and peak discharges often exceeding 300 cubic meters per second (CMS) at the river mouth. Mean annual discharge for the period of record (1959 – present) is 43 CMS, with a base flow of 5 CMS (USGS discharge data). Forests, composed primarily of Douglas fir (*Pseudotsuga menziesii*) and pine (*Pinus spp*.), cover much of the basin, with shrub-steppe communities common at elevations less than 1,200 meters. Floodplain valley bottoms in the lower river are dominated by black cottonwood (*Populus trichocarpa*) and aspen (*P. tremuloides*).

Prior to European settlement, the Methow River supported large runs of Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*). Today, runs of anadromous fish have been significantly depressed by a history of dams and impoundments, water diversions, overfishing, exotic species and habitat degradation. Currently, spring Chinook salmon are listed as endangered and summer steelhead as threatened under the endangered species act (ESA). Coho salmon, which were extirpated in the 1920s, have recently been reintroduced, and small numbers have begun to spawn naturally in the Methow. The resident (non-anadromous) fish assemblage of the Methow includes: Westslope cutthroat trout (*O. clarkii*), bull trout (*Salvelinus confluentus*), resident rainbow trout (*O. mykiss*), mountain whitefish (*Prosopium williamsoni*), longnose dace (*Rhinichthys cataractae*), bridge lip sucker (*Catostomus columbianus*) and several species of sculpin (*Cottus bairdi, C. confusus*, and *C. rhotheus*; hereafter referred to as 'sculpin'). Other fish species present in the Methow are native Pacific lamprey (*Lampetra tridentata*), and non-native brook trout (*S. fontinalis*), brown bullhead (*Ameiurus nebulosus*), and smallmouth bass (*Micropterus dolomieu*). However, these species were rare at study sites at the time of my study, and were not included in my analysis. In addition, because I could not distinguish between anadromous and resident rainbow trout, hereafter I refer to all rainbow trout as 'steelhead.'

Habitat restoration has been part of the continued strategy to help recover ESA-listed fish in the Methow basin, and the reconnection of river floodplain habitats is now considered a priority. The floodplain segment that has been targeted for restoration is located on the mainstem Methow, between the confluences with the Twisp and Chewuch Rivers. This 13.5 km long segment has been developed for agricultural and residential use, and sections have been diked (i.e., rip-rapped banks) to protect private property, leading to the disconnection of the river from the floodplain. This development is believed to have hampered the ability of the river to create and maintain aquatic habitats outside of the main channel.

To evaluate the importance of side channels of different types, I quantified fish and invertebrate prey production and constructed quantitative flow food webs in both the main channel of the proposed restoration segment and in five intact side channel habitats, which varied naturally in their level of hydrologic connectivity to the main channel. Three of the five side channel habitats were located within the restoration segment and two were located upstream (Figure 1). During spring run-off (April-June), all side channels had both an upstream and downstream surface water connection to the main-channel, allowing aquatic organisms, including juvenile salmon and steelhead, to move between side channels and the main channel. As flows receded, three of the channels became disconnected from the main channel and were eventually reduced to one or more isolated pools, whereas two habitats retained some level of surface water connection to the main channel year-round (Figure 2). For convenience, I refer to the five side channels according to their level of hydrologic connectivity with the main channel under low flow conditions during the period of my study (2009-10): '*con updwn*' refers to the side channel that retained both up and downstream surface water connections; '*con dwn*' is the side channel with only a downstream surface water connection; '*discon lrg*' is disconnected from the main channel but retained one relatively large pool; '*discon sml*' is disconnected and mainly represented by one small pool; and '*discon noscr*' is disconnected with large pools, but in contrast to the other side channels, its bed was not scoured by high flows during the study period (Figure 2). Together, these side channels represented a range of hydrologic conditions (i.e., connectivity and disturbance history), physical character (e.g., temperature) and habitat dimensions (Table 1).

Habitat Measurements

Habitat surveys of each side channel were conducted approximately monthly during 2009 and 2010. Surveys measured the area (lengths and widths), average and maximum depth, and proportion of different habitat types (e.g., pools, riffles, glides, etc.) present. The area and proportion of different channel units present in the main channel were determined from a single survey completed in summer 2009. Stream temperatures were recorded year-round in the main channel and each side channel using Onset HOBO® data loggers (P. Connolly & Bureau of Reclamation, unpublished data).

Invertebrate food base productivity

I sampled benthic habitats for invertebrates seasonally in the main channel and each side channel in June, August and October of 2009 and March 2010. June sampling occurred while all side channels were still connected to the main channel. On each date, I collected at least three replicate samples from each habitat, and in August I collected five samples. Each replicate sample represented a composite of several sub-samples (n = 3-11), which I collected in proportion to the different unit types present (e.g., riffles, pools, etc.) within each habitat. When combined, sub-samples incorporated the perceived habitat variation within each habitat, for each sampling date. I sampled all habitats with a modified Surber sampler (0.26 m^2, 250 μm mesh) attached to a shovel handle, which was used for stabilization when sampling deep and/or high velocity habitats. One person held the sampler in place, while another disturbed substrate to a depth of ~10 cm. I elutriated all samples through a 250 µm sieve and removed as much of the inorganic material as possible, the remaining sample was preserved in 95% ethanol. In the lab, a two-phased sorting approach was utilized (after Vinson and Hawkins 1996). In the first phase, all large invertebrates (≥ 10 mm) were removed from the sample. In the second phase, successive subsamples were removed and sorted at 10X magnification until at least 500 individuals were picked. I identified all invertebrates to genus or species, except for Chironomidae, which I split into Tanypodinae and non-Tanypodinae. All invertebrates were then dried at 60°C for 24 hrs, and weighed. I used these seasonal data to calculate the mean annual biomass of each taxon at each habitat. I calculated 95% confidence intervals for mean biomass estimates via bootstrapping (see Benke and Huryn 2006), whereby the biomass of each taxon for each habitat on each date was resampled with replacement 10,000 times to generate 10,000 separate estimates of mean annual biomass.

In order to estimate invertebrate secondary production, I collected a single composite sample from the main channel and one side channel (*discon noscr*) at approximately monthly intervals (June 2009 to June 2010). I processed these samples following the same methods outlined above, except that I measured the lengths of all individual invertebrates to the nearest 0.5 mm. The biomass of each taxon was then calculated using literature-based length-weight relationships (Benke et al. 1999). I then estimated secondary production for all common taxa using the size-frequency method (Benke and Huryn 2006), corrected for my best estimate of cohort production interval from size-frequency data (see Benke and Huryn 2006). Two additional estimates of non-Tanypodinae chironomid production were calculated using the instantaneous growth method, based on the size- and temperature-specific equations of Huryn (1990) and Walther et al. (2006). The three separate estimates of non-Tanypodinae chironomid production were averaged for use in this study. I calculated production to biomass (P:B) ratios by dividing production by the average taxon biomass for that habitat. Production at all habitats was then calculated by multiplying P:B estimates by mean annual biomass of each taxon within each habitat, including the four habitats where monthly secondary production samples were not collected. For rare taxa, I estimated secondary production using published annual P:B ratios. When available, I used P:B ratios from nearby production studies (Gaines et al. 1992, Robinson and Minshall 1998). Total annual benthic invertebrate production was calculated as the sum of taxon specific production.

I measured terrestrial invertebrate flux to the main channel and each side channel monthly ($n = 3$) during summer 2009. I placed 10-12 pan traps (0.21 m^2) at the wetted edge of the stream at each habitat. Pans were distributed in proportion to the presence of different riparian vegetation types, because invertebrate inputs are known to vary with riparian vegetation (Baxter et al. 2005). Traps were filled with approximately 5 cm of water and a few drops of biodegradable soap to reduce water surface tension. After collecting for three days, invertebrates were removed with dip nets (500 μm mesh). In the lab, I sorted samples under a dissecting microscope to remove aquatic taxa. The remaining terrestrial invertebrates were identified to order, dried at 60°C for 24 hrs and weighed. I calculated total summer inputs by multiplying average daily fluxes by the number of days in each month.

Fish Abundance, Biomass and Production

Fish abundance in both the main channel and side channels was estimated using a combination of snorkeling and electro-fishing. In side channels, the abundance of all salmonids was calculated seasonally (June, August, and October 2009, and March 2010), using the depletion method (White et al. 1982). Block nets were placed at the upstream and downstream of individual channel units (riffles, pools, glides, etc.) within each side channel, and multiple electro-fishing passes were completed until an adequate regression was achieved (following Connolly 1996). Mark-recapture and/or snorkeling were utilized in channel units that were too wide and/or deep to allow adequate depletions. Captured fish were measured for length and weight, and implanted with a passive integrated transponder (PIT) tag. Although these surveys were targeted at salmonids, the numbers of non-salmonids (dace, sculpin, and sucker) were also recorded, and several individuals of each species were captured to obtain lengths and weights. To estimate the abundance of non-salmonids, I first calculated the capture efficiency for the first pass of fishing surveys, obtained by dividing the number of salmonids captured on the first pass by the total salmonid population estimate for that channel unit, which was approximately 0.5 for pools, 0.6 for riffles and 0.9 for glides/runs. I then multiplied these capture efficiencies by the number of individuals of each non-salmonid species observed in different channel unit types. Error for these estimates was calculated by propagating the error associated with the salmonid electro-fishing depletions with the variance in capture efficiency for different channel unit types.

In the main channel, downstream snorkel surveys were conducted monthly (except in winter) to estimate the abundance of larger fish (>150 mm) during 2009 and 2010. Briefly, four snorkelers would float downstream over an 8 km section of the main stem and enumerate fish by species and size class (size classes: 150-300 mm, 300-500 mm, and >500 mm). Error of snorkel estimates was determined by conducting three consecutive downstream surveys over a three day period. To account for observation efficiency, I divided snorkel abundance estimates by 0.25 for adult fish (> 150 mm) following Thurow and Peterson (2006). To estimate the abundance of juvenile salmonids (< 150 mm), the stream margin of three 400 to 800 m main channel segments were single-pass electro-fished once in March, July and October 2009. I estimated sculpin abundance in the main channel by sampling three randomly selected riffles and three runs, within which I collected three quantitative sub-samples by electro-fishing within the metal quadrat of the Surber sampler (0.26 m^2). Because none of these methods were appropriate for estimating the abundance of longnose dace, I assumed dace abundance was similar to that observed in the side channels where dace were present. Bridge lip suckers were rare in the main channel, and were not included in my analysis for that habitat. I converted all fish abundance estimates to aerial biomass (g/m^2), by multiplying by the average weight (g) of each species within each habitat and then dividing by habitat (or sample) area (m^2). I converted wet biomass to dry mass (DM) by assuming 80% water content for juvenile fish and 75% water content for adult fish and sculpin (see Warren and Davis 1967; Elliot 1976; Berg and Bremset 1998).

I estimated annual secondary production of each fish species using the instantaneous growth rate method (Hayes et al. 2007), whereby I multiplied the average annual biomass of each species and age class, by size- and habitat-specific annual growth rates (or annual P:B ratios). For all salmonids and bridge lip suckers, growth rates were determined from recapture of marked individuals (P. Connolly, USGS Columbia River Research Laboratory, unpublished data). For mountain whitefish, I calculated size-specific growth rates from length at age data, which were determined by analyzing scales from approximately 80 fish (range: 190 – 500 mm fork length). For sculpin, I conducted multi-pass electro-fishing depletions within one run and one riffle in the *con updwn* and *con dwn* habitats, which allowed me to calculate production for these locations using the size-frequency method (Hayes et al. 2007). These production estimates were subsequently divided by sculpin biomass in these habitats to estimate annual P:B ratios. Sculpin production in all habitat types was then calculated by multiplying P:B ratios by average annual sculpin biomass. I estimated longnose dace production by applying a P:B ratio derived from the literature (Neves and Pardue 1983). Error in production estimates was calculated by propagating the standard errors associated with fish biomass and growth rate, and then multiplying by 1.96 to represent approximate 95% confidence intervals.

Gut Content Analysis

I collected gut content samples from all but the rarest members of the fish assemblage seasonally in the main channel and each side channel (total $n = 375$). Diet samples for side channels were collected during electro-fishing surveys. Diets were collected for the main channel using a combination of techniques, including trammel and gill netting, electro-fishing, and angling. At each habitat on each date, I attempted to collect at least five diet samples from all salmonid species, four from sculpin and three from longnose dace and juvenile bridge lip suckers. I stratified steelhead sampling by age 0 and 1+. For salmonids > 75 mm and sculpins, I collected diets via gastric lavage and preserved contents in 70% ethanol. For dace and suckers, individuals were sacrificed, preserved in 95% ethanol, and diets were later extracted by removing the first 10% of the digestive tract. In the laboratory, I identified and measured the length and head width of all prey items in fish diets. Invertebrate prey items were identified to the family level and fish found in diets were identified to species. Invertebrate lengths and head widths were converted to biomass using published regressions (Benke et al. 1999). Fish lengths were converted to biomass from length-weight regressions developed within the Methow (P. Connolly, USGS Columbia River Research Lab, unpublished data). Dietary proportions were based on the proportion that each food item contributed to total weight of gut contents. Diet proportions were averaged across all individuals of each species at each site on both a seasonal and annual basis.

Trophic Basis of Production and Flow Food Webs

I quantified organic matter flows to fish using the trophic basis of production (TBP) method, which estimates (a) contributions of different food resources to animal production and (b) rates of resource consumption that support measured rates of animal production (Benke and Wallace 1980). The relative fraction of annual production attributed to each prey type (F_i) was calculated as:

$$F_i = G_i \times AE_i \times NPE$$

where G_i = proportion of prey type i in fish diet, AE_i = assimilation efficiency of prey type i, and NPE = net production efficiency. The proportion of fish production attributedto each prey type (PF_i) was then calculated from the relative fractions (F_i) as:

$$PF_{ij} = \frac{F_i}{\sum_{i=1}^{n} F_i}$$

Lastly, annual flows from each prey type i to consumer j (FC_{ij} measured in g DM m^{-2} year^{-1}) was calculated as:

$$FC_{ij} = \frac{PF_{ij} \times P_j}{AE_i \times NPE}$$

where P_j = annual secondary production (g DM m^{-2} y-^{1}) of fish j.

Assimilation efficiencies for all salmonid species were: 0.75 for aquatic invertebrates, 0.70 for terrestrial invertebrates, and 0.95 for fish tissue (see Warren and Davis 1976, Warren 1971, Brocksen and Bugge 1974, Elliot 1976). Diets of non-salmonids consisted almost entirely of aquatic invertebrates and assimilation efficiencies were set at: 0.90 for dace, 0.85 for sucker, and 0.82 for sculpin (see Davis and Warren 1965, Atmar and Stewart 1972, Eiriksdottir 1974). Net production efficiency values were set at 0.125 for adult fish (CTT, RBT2+, BLT, MWF), while a production efficiency of 0.250 was used for juvenile salmonids (< 150 mm) and all non-salmonid species (Donner

2011; Cross et al. 2011). This was done to account for the allometric relationship between fish consumption and growth with fish size (i.e., larger, older fish spend proportionately more energy on maintenance than on growth). Although assimilation and production efficiencies are size and species specific, and vary with temperature, I assumed that differences in fish production across habitat types would outweigh any relatively small differences in assimilation and production efficiencies.

Interaction Strength, Interspecific Competition, and Carrying Capacity

To quantify the strength of interactions between fish predators and invertebrate prey, I calculated 'interaction strengths' (I) for each prey item as:

$$I_i = \frac{FC_i}{PP_i}$$

where FC_i = total annual consumption of prey type i (g DM m^{-2} y^{-1}) by the fish assemblage, and PP is the annual production of prey type i. This metric is a unit-less value, ranging from 0 to 1, which represents the proportion of annual prey-specific production consumed by the fish assemblage. Values greater than 1 (i.e., fish are consuming more than is being produced) are energetically impossible, and indicate potential errors in my estimates of invertebrate production, fish production, and/or fish dietary proportions. In my results, however, values >1 are simply reported as 1 (i.e., prey production = consumption). In a few cases, it appeared that discrepancies between production and demand were the result of dietary proportions skewed by individual fish that may have been feeding outside of study sites. These individuals were identified by diet compositions dominated by prey taxa that appeared to be rare or absent at the location where they were sampled. In total, I identified only three of these individuals, which I removed from the analysis. Although individual fish may accrue production outside of the habitats where they were sampled, I assumed that this was balanced by fish movement and foraging both inside and outside of each habitat.

To evaluate potential for interspecific competition between each fish species *j* and the rest of the fish assemblage *h* I calculated 'competition coefficients' (CC) as:

$$CC_j = \sum_{i=1}^{n} \frac{FC_{ih}}{PP_i} \times PF_{ij}$$

where FC_{ih} = total annual consumption of prey type *i* (g DM m^{-2} y^{-1}) by all members of the fish assemblage except for the species of interest *j*, and PF_{ij} is the proportion of annual production for species *j* derived from prey item *i*. This index incorporates both the availability of each prey type in the environment, after consumption by the rest of the fish assemblage *h*, and the importance of each prey item to the production of the species of interest *j*. The output of this index is a unit-less value ranging from 0 to 1 that represents the proportion of prey items important to the species of interest *j* that are consumed by all other members of the fish assemblage (*h*).

Finally, I utilized the output of the CC index to estimate the potential level of Chinook salmon and steelhead production (g DM m^{-2} y^{-1}) that could be sustained (*PotenP*) per area within each habitat. This was calculated as:

$$PotenP_j = \sum_{i=1}^{n} \left(\left(PP_i - FC_{ih} \right) \times AE_{ij} \times NPE_j \times PF_{ij} \right)$$

where AE_{ij} and NPE_j are assimilation and net production efficiencies for prey type i by fish j. This metric assumes: (1) that the dietary proportions of the fish assemblage remain static, (2) that production by all other members of the fish assemblage remains the same, and (3) that Chinook and steelhead are able to perfectly track the production of their prey. Although these assumptions may not be realistic in all cases, these assumptions were imperative for deriving a relative estimate of the carrying capacity for juvenile Chinook salmon and steelhead, in terms of food.

Statistical Analysis

To evaluate differences in fish production, prey production, and prey production versus fish demand, I visually compared percentile 95% confidence intervals. Means with non-overlapping confidence intervals were interpreted as significantly different. I analyzed trophic basis of production data via nonmetric multidimensional scaling (NMDS), followed by multiresponse permutation procedures (MRPP) to test for significant differences in TBP among different sites and species (Mielke and Berry 2001). In addition, I utilized permutation-based nonparametric MANOVAs to evaluate the amount of variation in TBP data explained by both site and species (Anderson 2001).

Results

Fish Production, Prey Production and Total Consumption by Fishes

Estimated fish production in the main channel was 1.85 g DM m^{-2} y^{-1}, and was significantly greater (non-overlapping 95% CIs) than fish production on a per area basis in side channels, which ranged from 0.12 to 0.63 g DM m^{-2} y^{-1} (Figure 3a). Approximately 95% of the production in the main channel was by sculpin and whitefish. The composition of fish production varied greatly among side channels that differed in connectivity with the main channel. At the three habitats that were disconnected from the main channel at low flow, a larger number of species contributed more evenly to total fish production, with 50 to 85% being comprised of salmonids, principally juvenile steelhead, along with juvenile coho and Chinook salmon. On the other hand, production in the two side channels that remained connected to the main channel was dominated by sculpin. Absolute production per area by Chinook and steelhead was generally highest in disconnected side channel habitats (Figure 3a). Mountain whitefish, bull trout and cutthroat trout were rarely encountered in side channels.

Total aquatic invertebrate production was higher in the main channel (14.1 g DM m^{-2} y^{-1}) than most side channels (4.7 to 18.8 g DM m^{-2} y^{-}1; Figure 3b). In contrast, the input of terrestrial invertebrates was generally higher in side channels (2.9 to 20.8 g DM m^{-2} y^{-1}) than in the main channel (4.7 g DM m^{-2} y^{-1}), but was highly variable among habitats (Figure 3b). When terrestrial inputs were added to benthic invertebrate production, total invertebrate prey production did not differ between sites, except for in *discon noscr*, which had significantly higher prey production than the two other disconnected habitats (Figure 3c).

Invertebrate food demand by fishes (i.e., consumption) in the main channel was not significantly different (non-overlapping 95% CIs) than invertebrate prey production. In contrast, prey production in side channels was consistently higher (on average 16X higher) than demand by the fish assemblage. In particular, the two connected side channels had approximately 25X more prey production than estimated fish demand.

Trophic basis of production

In the main channel, nearly 80% of the production by the entire fish assemblage was fueled by only four prey taxa: Chironomidae, Brachycentridae, Ephemerellidae, and Tipulidae (Figure 4). In contrast, across all side channels, a comparable proportion of fish production was fueled by at least 6 and up to 13 prey taxa (Figure 4). The contribution of more lentic taxa (e.g., *Daphnia*, Amphipoda, Isopoda, Leptophlebiidae) was highest in the less connected side channels (*discon lrg*, *discon sml*, and *discon noscr*), sustaining between 16% and 63% of total fish production. Fish production in the two side channels that were more connected (*con dwn* and *con updwn*) was derived from more lotic taxa, though the contributions were more evenly distributed among prey than was the case in the main channel. Fish production derived from terrestrial invertebrates in side channels ranged from 3.2% to 17% and was always at least double that of the main channel (1.6%).

Within each habitat, the production of different fish species was largely derived from similar prey taxa (Figure 5). In the main channel, Chinook and steelhead had the most similar TBP (Figure 5a). However, at least 45% of production for all fish species in the main channel, except for cutthroat and bull trout, was sustained by the same five taxa: Chironomidae, Brachycentridae, Ephemerellidae, Tipulidae, and Lepidostomatidae. In contrast, cutthroat and bull trout production was derived from much higher proportions of terrestrial insects (32%) and fish (>99%), respectively.

In the two most connected side channels, Chinook, steelhead and sculpin all had similar TBP (Figure 5b and c), although sculpin production generally lacked contributions from terrestrial invertebrates. Over 40% (and up to 67%) of production by Chinook, steelhead and sculpin within these habitats was attributable to the same six taxa: Chironomidae, Ephemerellidae, Lepidostomatidae, Limnephilidae, Baetidae, and Heptageniidae. In the disconnected side channels that had scoured during high flows (*discon lrg* and *discon sml*), the proportion of fish production sustained by each prey item was highly variable between species (Figure 5d and e). That said, between 30% and up to 100% of production for each fish species was attributed to the same six prey taxa: Chironomidae, Leptophlebiidae, *Daphnia*, Baetidae, Limnephilidae, and Heptageniidae. At both sites, bridge lip sucker derived all of their production from only two prey taxa—Chironomidae and *Daphnia*. In the side channel that did not scour during high flows (*discon noscr*), all five fish species had very similar TBP, with at least 50% of production by each species sustained by only four prey items: Chironomidae, Amphipoda, Isopoda and Limnephilidae.

Variation in the composition of fish TBP among habitats reflected differences in the level of hydrologic connectivity with the main channel (Figure 6a). The NMDS ordination for each species-habitat combination, which explained 64% of the variation in TBP, showed almost complete separation between side channels connected to the main channel versus those that were disconnected at low flow (MRPP, A = 0.145, $P<0.001$). Connected side channels and the main channel were separated in the ordination from disconnected side channels along axis 2, which explained 32% of the variation in TBP. Differences were most strongly driven by contribution to TBP by Perlidae (Pearson's r =

0.73), Perlodidae (0.59), Lepidostomatidae (0.59), and Ephemerellidae (0.58), which were more important to fish in connected side channels and the main channel, and Amphipoda (-0.60) and Isopoda (-0.59), which were more important to fish in disconnected habitats. Although both species and habitat were significant factors in explaining total variation in the TBP data (perMANOVA, $P<0.05$), habitat explained 2.5X more variation than species (35% versus 14%).

Flow Food Webs

The structure of organic matter flows between fish and their prey differed between the main channel and side channels, and also among side channels (Figure 7). The overall magnitude of organic matter flow to fishes (i.e., consumption) was highest in the main channel (13.8 g DM m^{-2} y^{-1}) and lowest in the connected side channels (*con updwn* = .69 and *con dwn* = .60), reflecting differences in fish production (Figure 3a). In the main channel, nearly 95% of all invertebrate flows were to whitefish and sculpin (Figure 7a). The highest magnitude flows in the main channel were from Brachycentridae to mountain whitefish (4.2 g DM m^{-2} y^{-1}), Chironomidae to sculpin (2.3) and whitefish (1.4), Ephemerellidae to sculpin (1.0), and Tipulidae to sculpin (0.72). In the two connected side channels, *con updwn* and *con dwn*, approximately 63 and 55% of invertebrate flows were to sculpin respectively (Figure 7b and c). At the c*on updwn* habitat, the five highest magnitude flows were all to sculpin, including: Limnephilidae (0.09 g DM m^{-2} y^{-1}), Chironomidae (0.76), Baetidae (0.06), Perlidae (0.06), and Perlodidae (0.05). At the *con dwn* habitat the largest flows were from Ephemerellidae to sculpin (0.08 g DM m^{-2} y^{-1}), Chironomidae to sculpin (0.07), Heptageniidae to sculpin (0.04), Lepidostomatidae to juvenile steelhead (0.04) and Perlidae to sculpin (0.04).

In contrast to the connected side channels and the main channel, invertebrate flows in the disconnected side channels were more evenly distributed among fish species (Figure 7d – f). In particular, flows of invertebrates to Chinook were on average 15X greater, whereas flows to sculpins were 96% lower than in connected habitats. At the *discon lrg* habitat, 38% of invertebrate flow was to Chinook, 37% to suckers, and 17% to steelhead (Figure 7d). The largest magnitude flows were: Chironomidae to suckers (0.43 g DM m^{-2} y^{-1}) and Chinook (0.19), Heptageniidae to Chinook (0.10), *Daphnia* to sucker (0.08), and Baetidae to Chinook (0.05). Similar to the *discon lrg* habitat, 39% of invertebrate flows at the *discon sml* habitat were to Chinook, 29% to sucker and 18% to steelhead (Figure 7e). The five largest magnitude flows were from *Daphnia* to sucker (0.53 g DM m^{-2} y^{-1}), Chironomidae to sucker (0.44) and Chinook (0.49), Leptophlebiidae to Chinook (0.30), and terrestrial invertebrates to Chinook (0.16). At the *discon noscr* habitat just over 75% of all invertebrate flows were to steelhead (51%) and coho (24%), with the largest magnitude flows from Amphipods to steelhead (0.32 g DM m^{-2} y^{-1}) and coho (0.20), Isopods to steelhead (0.21) and coho (0.20), and terrestrial invertebrates to steelhead (0.32) (Figure 7f).

A small portion of organic matter flow, generally less than 5% at each habitat, occurred along piscivorous pathways (Figure 7). The largest magnitude piscivorous fluxes were consumption of steelhead by sculpin at the *con updwn* habitat, the consumption of suckers by steelhead at the *discon noscr* habitat, the consumption of sculpin by other sculpin at the *con dwn* habitat, and consumption of dace by cutthroat trout in the main channel. Although bull trout in the main channel consumed nearly 100% fish (Figure 5a), their production and associated food demand was small (Figure 3a and c), and as a result, the total piscivorous flux to bull trout was low (Figure 7a).

Interaction Strength, Competition Coefficients and Carrying Capacity

Values of interaction strength, which represent the proportion of taxa-specific prey production consumed by the fish assemblage, revealed that fish interacted more strongly with their prey in the main channel than in any of the side channels (Figure 8, left panel). Of the top 15 prey taxa consumed by fish in the main channel, 9 had interaction strengths ≥ 0.9, indicating that the fish assemblage consumed a majority of production by those prey (Figure 8a). In contrast, the two connected side channels combined had only two interaction strengths that were ≥ 0.9 (Figure 8b, c). The number of strong interactions (> 0.9) in the three disconnected side channels was intermediate to that found in the main channel and connected side channels: 4 in *discon lrg*, 6 in *discon sml* and 2 in *discon noscr* (Figure 8d, e, f).

Competition coefficients, which represent the proportion of prey important to the TBP of a selected fish species that is consumed by other members of the fish assemblage, reflected general differences in interaction strengths among habitats (Figure 8, right panel). In general, fish in the main channel had the highest competition coefficients, ranging from 0.23 for whitefish to 0.76 for dace (Figure 8a). Connected side channels had the lowest values, ranging from: 0.05 for sculpin to 0.11 for steelhead in *con updwn*, and 0.07 for sculpin to 0.14 for Chinook in *con dwn* (Figure 8b, c). Disconnected side channels had values intermediate to those in the main channel and connected side channels, ranging from: 0.08 for sucker to 0.20 for steelhead and coho in *discon lrg*; 0.7 for sucker to 0.53 for steelhead in *discon sml*; and 0.09 for steelhead to 0.27 for sculpin in *discon noscr* (Figure 8d, e, f).

Based on our estimates of existing food resources, the potential amount of Chinook or steelhead production that could be supported on a per area basis in each habitat type was on average 25X higher than measured production levels for Chinook and 5.5X greater for steelhead (Figure 9a, b). These findings indicate that most habitats could potentially support additional Chinook and steelhead production. That being said, within the *Discon lrg* and *Discon sml* habitats, both juvenile Chinook and steelhead appeared to be at or approaching estimated carrying capacity. For both Steelhead and Chinook, I estimated that the highest levels of fish production could be supported in the *Discon noscr,* followed by the *Con updwn* habitat. The lowest carrying capacities values were found in the main channel for Chinook, and the *Discon sml* habitat for Steelhead.

Discussion

Consistent with the paradigm that floodplains are hotspots of biophysical complexity (Junk et al. 1989, Bayley 1995, Tockner and Stanford et al. 2005), my research indicates that floodplains are also hotspots of food web complexity. Food web variability in the Methow River floodplain paralleled the diversity of different habitat patches within the floodplain landscape. In particular, variation in hydrologic connectivity between the main channel and different side channels appeared to be associated with distinct food web structures. Endangered Chinook salmon and steelhead utilized all of these habitats, indicating that these species are flexible enough to exploit a wide range of food resources across a variety of habitat types. This flexibility may be particularly important in the Methow River, where my results suggest that non-target fish species (i.e., mountain whitefish and sculpin) consume a large fraction of the prey base in main channel habitats. That being said, carrying capacity estimates for both the main channel and side channels indicate that Chinook salmon and steelhead are currently under-seeded with respect to the available prey base. If true, this finding would indicate that the floodplain segment of the Methow River studied here could potentially support much greater anadromous salmonid populations.

This study is the first to empirically quantify the organic matter flows that sustain salmon and steelhead within a heterogeneous floodplain landscape. In contrast to connectance based food webs, which assign equal weight to all food web links, I quantified both the magnitude and strength of interactions between fish predators and their invertebrate prey. To quantify these links, I utilized two approaches that have been commonly applied in stream ecosystem and food web studies, but have rarely been combined (but see Entrekin et al. 2007, Cross et al. 2011): the 'trophic basis of production' (TBP; Benke and Wallace 1980, Benke and Huryn 2010), and production-demand (e.g., Waters 1988, Huryn 1996) approaches. Although the TBP approach is now commonly utilized to quantify predator-prey food web links, it does not account for the availability of prey in the environment. Consequently, the ability to evaluate the impact of predators on their prey and to assess the potential that individual prey items might limit predator populations is hindered (Hall et al. 2000, Woodward and Hildrew 2002). To address this weakness, I estimated interaction strengths for each prey item by comparing the annual demand for each invertebrate prey item to its annual secondary production (see also Wootton 1997). Although this type of production-budget approach has been commonly utilized to compare gross estimates of invertebrate production and fish demand (Allen 1951; Waters 1988; Huryn 1996, 1998), very few studies have evaluated production-demand on a prey-specific basis (but see Cross et al. 2011), as I have done here. Together, this combination of food web and ecosystem production- budget approaches provided the basis for evaluating food web structure, interspecific competition in terms of food availability, and the potential production of Chinook salmon and steelhead that could be supported in different floodplain habitats.

Dissimilarities in food web structure among habitats were primarily driven by differences in fish assemblage composition and production. For example, habitats with the highest magnitude organic matter flows (i.e., consumption) also had the highest levels of fish production. In particular, the distribution and abundance of mountain whitefish and sculpin strongly controlled organic matter flow. Sculpin were the most productive fish species in both the main channel and connected side channels and dominated organic matter flows in these habitats. In contrast, sculpin were much less productive in the more lentic/disconnected habitats, and represented only small proportion of organic matter flow. Although other studies have shown that sculpin can be very abundant in lentic habitats (e.g., Eggers et al. 1978), it is likely that the sculpin species present in the Methow are better adapted to flowing waters (Wydoski and Whitney 2003). This is supported by my observation that sculpin abundances were generally higher in riffles versus runs and pools (J. R. Bellmore, unpublished data). Similar to sculpin, mountain whitefish were also very abundant in main channel habitats but were virtually absent from side channels, which is not surprising given their propensity for larger streams and rivers (Northcote and Ennis 1994). In addition, mountain whitefish spawn during the fall, when many side channels are disconnected.

The potential for non-target fish species, such as sculpin and mountain whitefish, to compete with Chinook and steelhead populations was principally dependent on food availability. For example, even though sculpin dominated organic matter flows in the two connected side channels, their estimated impact on anadromous salmonids via exploitative competition was low because production for shared prey items was generally well above consumption. As a result, overall potential competition for food (i.e., competition coefficients), or the proportion of prey items important to Chinook or steelhead consumed by other species, was low. In the main channel, however, sculpin and mountain whitefish consumed a majority of the prey base, resulting in high levels of potential exploitative competition with Chinook and steelhead. In disconnected habitats, where non-target fish production was low, potential competition for food was intermediate between the main channel and connected side channels, and was largely attributable to competition between Chinook and steelhead. Overall, however, my findings indicate that juvenile anadromous fishes were generally under-seeded with respect to the available food base, in both the main channel and side channels. This could mean that much higher overall Chinook and steelhead production could be supported in these habitats with minimal density-dependent affects (i.e., growth, condition, and survival) on individuals.

An unanticipated finding revealed via the use of my food web approach was that the TBP for all fish species (except bull trout) was attributable to a relatively similar suite of invertebrate prey. Because salmon and trout are thought to be primarily drift feeders

(Zaroban et al. 1999), many competition studies in streams have focused solely on competition among salmon and trout populations (see Hearn 1987), largely neglecting potential competition with benthic foraging species such as mountain whitefish, suckers, dace and sculpin. These studies generally assume, whether explicitly or not, that (1) other members of the fish assemblage eat different prey items and/or (2) interference competition among drift feeders is more important than exploitative competition between fishes with different foraging strategies. In contrast, my results emphasize that fish species that forage differently may still consume similar prey items. Although my approach did not evaluate the potential for interference competition (see Hearn 1987), my findings indicate that benthic foraging species such as mountain whitefish and sculpin can have a substantial impact on the availability of food for drift feeding fish. In fact, there is the potential that resident mountain whitefish and sculpin may actually have 'filled the niche' per se, left by the diminished populations of anadromous fishes in the Methow. In other words, the production of mountain whitefish and sculpin could have at least partially replaced that of Chinook, coho, and steelhead, which historically were much more abundant. My results also demonstrate that juvenile suckers in the Methow are insectivores, not herbivores or detritivores as is often assumed (Zaroban et al. 1999), and given the right conditions (i.e., high population size) these species could also affect target salmonids.

Although fishes generally had similar TBP within a habitat type, TBP between habitat types was highly variable, and was driven by differences in the composition of the invertebrate prey base. In particular, as side channels became more disconnected from the main channel, the trophic basis of production of the fish assemblage shifted to more lentic type invertebrate taxa. This finding parallels results of many studies that have shown significant variation in aquatic invertebrate assemblages across floodplain landscapes (e.g., Arscott et al. 2005). In addition, these results indicate that fish species in the Methow River, especially Chinook and steelhead, are flexible enough to exploit resources from a wide variety of habitat types. This flexibility has been extensively outlined for rainbow trout (see Behnke 2002), and is believed to be one of the primary mechanisms behind the world-wide success of rainbow introductions and invasions (Welcomme et al. 1992, Nislow 2001, Juncos et al. 2011). Chinook salmon are also known to utilize a variety of freshwater habitats across their range (see Groot and Margolis 1991, Quinn 2005), and studies indicate that in some circumstances side channels may offer enhanced growing conditions for these fish (Sommer et al. 2001, Jeffres et al. 2008). Of all salmon species, however, coho appear to have the greatest affinity for side channels (Beechie et al. 1994, Morley et al. 2005), and may even be better morphologically adapted to utilize more lentic conditions (Bisson et al. 1988). In addition, studies have shown that coho can out-compete similar sized Chinook and steelhead for food and optimal foraging habitat (Hartman 1965, Stein et al. 1972, Hearn 1987). Although coho are not currently very abundant in the Methow River, intensive reintroduction efforts are ongoing. If coho populations continue to grow, it is possible that the abundance of coho in side channels may eventually exceed that of Chinook and steelhead, which could have consequences for their growth and survival.

Despite the fact that fish TBP was highly variable across habitat types, gross prey production was relatively consistent among both side channels and also between side channels and the main channel. This finding contrasts to empirical reports (e.g., Bayley

1988; Lewis et al. 2001) and conceptual models (e.g., Junk et al. 1989) of floodplain systems, which have frequently emphasized the disproportionate importance of side channel habitats to overall floodplain productivity. One explanation for this inconsistency is that the Methow River is much smaller and has different hydrologic characteristics compared to the larger tropical (e.g., Amazon and Orinoco Rivers) and temperate (e.g., Mississippi River) rivers where much floodplain research has been conducted. Nevertheless, in large part due to this research, it is often assumed that side channels utilized by salmonids have enhanced food base productivity and therefore are more favorable rearing habitats for these fish. However, this assumption has never been adequately tested in salmon bearing streams. Although a few studies have calculated the density or standing crop biomass of the food base in these habitats (e.g., Morely et al. 2005), this is the first study to undertake the additional efforts necessary to calculate secondary invertebrate production, terrestrial invertebrate fluxes, and to evaluate the magnitude of prey item consumption by fish.

My research shows that the importance of side channels in the Methow is not a function of enhanced food base productivity within those habitats. Instead, my findings indicate that side channels offer reduced competition for available prey. Moreover, these habitats appear to provide some level of refuge from larger more piscivorous species like bull trout and cutthroat trout, which were generally absent from side channels. That said, this study was not targeted at quantifying organic matter flows along piscivorous pathways; larger sample sizes would be needed to evaluate these temporally discrete but potentially important events. Predation along alternative pathways, however, may be greater in side channels. Research suggests that as flows recede and habitats become shallow and isolated, the risk of predation by terrestrial predators, such as birds and mammals, is likely to increase (Power 1987, Schlosser 1991). That said, lower water velocities reduce energetic costs associated with swimming (Fausch 1984), and depending on the availability of food may be particularly beneficial to rearing salmon and trout (Rosenfeld et al. 2005). Temperature is also likely to play a key role in the relative success of fish in different habitats. Channels with extensive hyporheic connections generally have less variable temperatures during the winter and summer (Torgersen et al. 1999, Baxter and Hauer 2000, Ebersole et al. 2003), which may be more energetically favorable for growth. Habitats with limited surface or groundwater connectivity may result in water freezing solid during the winter and/or exceeding critical temperatures during the summer. In addition, many floodplain habitats completely disappear during low flow periods, stranding fish on the floodplain surface. Overall, this heterogeneity in food web structure and physical conditions creates a mosaic of different habitat patches across the floodplain landscape. Consequently, choosing the best or most energetically favorable habitat would require fish being able to respond to differences and trade-offs among numerous physical and biotic variables.

Although particular habitats may be identified as favorable at any single point in time, the mosaic of different aquatic habitats and associated food web structures within floodplain systems is likely to be more important to sustaining resilient and productive populations, and the overall stability of the biotic community over longer temporal scales (Groot and Margolis 1991; McCann 2000; Hilborn et al. 2003; Bisson et al. 2009). As climate and hydrology change over shorter (e.g., El Nino/Southern Oscillation and Pacific Decadal Oscillation) and longer (e.g., climate change) time scales, the potential for different patches across the landscape to sustain fish productivity is likely to shift. Moreover, having a mosaic of habitats that encompasses distinct physical and biotic conditions may help sustain multiple salmonid life-history strategies (Groot and Margolis 1991, Reeves et al. 1995). Consequently, maintaining a diverse portfolio of habitats across the floodplain landscape increases the chance that at least one habitat or life-history strategy will be favored as environmental conditions change. For example, Hilborn and others (2003) found that biophysical complexity in the Bristol Bay region of Alaska supported a wide array of sockeye salmon life-histories, which helped maintain the productivity of the population, despite major changes in climate conditions.

In the Methow River, one potential mechanism by which biophysical complexity might help maintain resilient populations of salmonids and overall community stability maybe by providing the context for diverse food web structures, with variable interaction strengths between fish predators and their prey. McCann and others (1998) showed that strong predator-prey interactions destabilize model communities, and that strong interactions need to be coupled to many weak trophic interactions to maintain diversity. These weak interactions appear to dampen oscillations between predators and prey, stabilize the ecosystem, and reduce the risk of extinction for members of the community. Although not explicitly tested here (but see Chapter 4), floodplain landscapes such as the Methow, which contain many structurally distinct but spatially connected foods, might contribute more weak predator-prey interactions that are hypothesized to stabilize communities. If this is the case, floodplains may not only be diverse and productive systems in river networks, but also ‘nodes of resilience’ for endangered species like Chinook salmon and steelhead.

Implications for Habitat Restoration

My results show that side channels are important habitats for juvenile rearing Chinook salmon and steelhead in the Methow River. In particular, side channels had lower levels of inter-specific competition for food with other non-target fishes (e.g., sculpin and mountain whitefish), and on a per area basis, appeared to have a greater capacity to sustain production of Chinook salmon and steelhead. Although floodplain reconnection efforts often assume that creating side channels that remain fully connected to the main channel year-round would have the largest benefit to salmonids, my findings do not show any correlation between hydrologic connectivity and productivity. Instead, they suggest that habitat restoration efforts should focus on maintaining current floodplain complexity, and when and where necessary, restoring the ability of the river to create and maintain this complexity (e.g., removing dikes, restoring large woody debris dynamics, etc.) (*sensu* Reeves et al. 1995, Ebersole et al. 2003, Stanford et al. 2005). That said, I present some evidence that existing habitats may be substantially under-seeded, which might indicate that insufficient numbers of spawning adults are returning to fully utilize these habitats.

This study presents an example of how quantitative ecosystem and food web approaches can be combined to address problems of direct relevance to natural resource management. This combined approach allowed us to quantify: (1) primary organic matter flow pathways that sustain fish production, (2) prey-specific food limitation, and (3) potential for interspecific competition for food. My findings demonstrate that the pathways of organic matter flow that sustain target species are widely variable among habitats, and that non-target fish species can have an overwhelming influence on organic matter flows; a finding which calls into question the validity of assessments focused on single species alone. Overall, this study demonstrates that landscape heterogeneity is associated with the occurrence of a mosaic of food webs in river floodplain systems, all of which are utilized by salmon and steelhead, and all of which maybe important to their recovery and long-term persistence. Future investigations are needed to quantify the basal organic matter sources (i.e., primary producers) that are the primary food for invertebrate prey, and organic matter flows along piscivorous pathways. Together, this information would provide the basis for conducting food web modeling that could be used to evaluate the implications of alternative management scenarios (e.g., habitat restoration, nutrient additions, etc.), species introductions, and environmental changes (e.g., climate change) on salmon and steelhead populations in this and other similar river systems.

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Tables

Table 1. Habitat characteristics of the six habitats sampled in this study for 2009, including: whether or not habitats had surface water hydrological connectivity during low flows, whether or not the habitats were scoured during high flows; approximate habitat area during high and low flows, habitat length during high flows when all habitat were fully connected to the main channel; and average daily water temperatures for summer, fall, and winter. Y = yes, N = no, and USGS = United Stated Geological Survey.

			Surface Water Connection?			Habitat Area (m^2)			Temperature °C		
Habitat Type	Habitat Name	USGS Name	Downstream	Upstream	Bed Scour?	High Flow	Base Flow	Length (m)	Summer	Fall	Winter
Main channel	Main ch	M2	Y	Y	Y	-	760000	17000	15.2	-	-
Side channel	Con updwn	Heath	Y	Y	Y	3550	2875	310	13.6	6.9	5.4
Side channel	Con dwn	Stansbury	Y	N	Y	13975	6325	690	11.4	6.7	5.1
Side channel	Discon lrg	Bird	N	N	Y	6425	2200	490	14.9	7.4	5.4
Side channel	Discon sml	Dike	N	N	Y	7500	1100	605	16.1	4.7	-
Side channel	Discon noscr	Habermyl	N	N	N	6150	3400	582	13.2	4.9	1.4

Figures

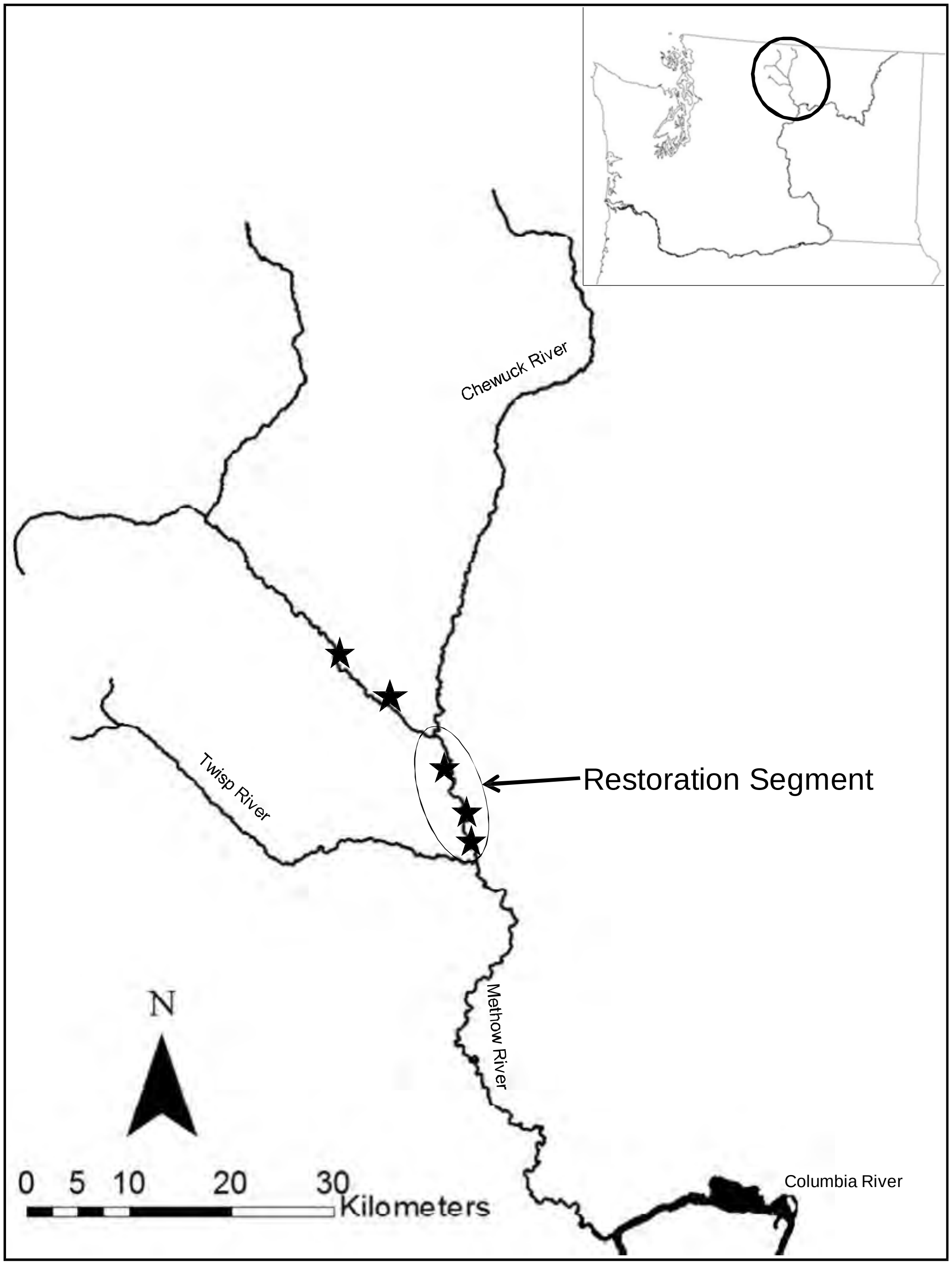


Figure 1. Map of the Methow River, Washington, showing the location of the proposed habitat restoration segment. Stars indicate the location of the five side channel sites sampled in this study. Inset shows the location of the Methow River in Washington State.

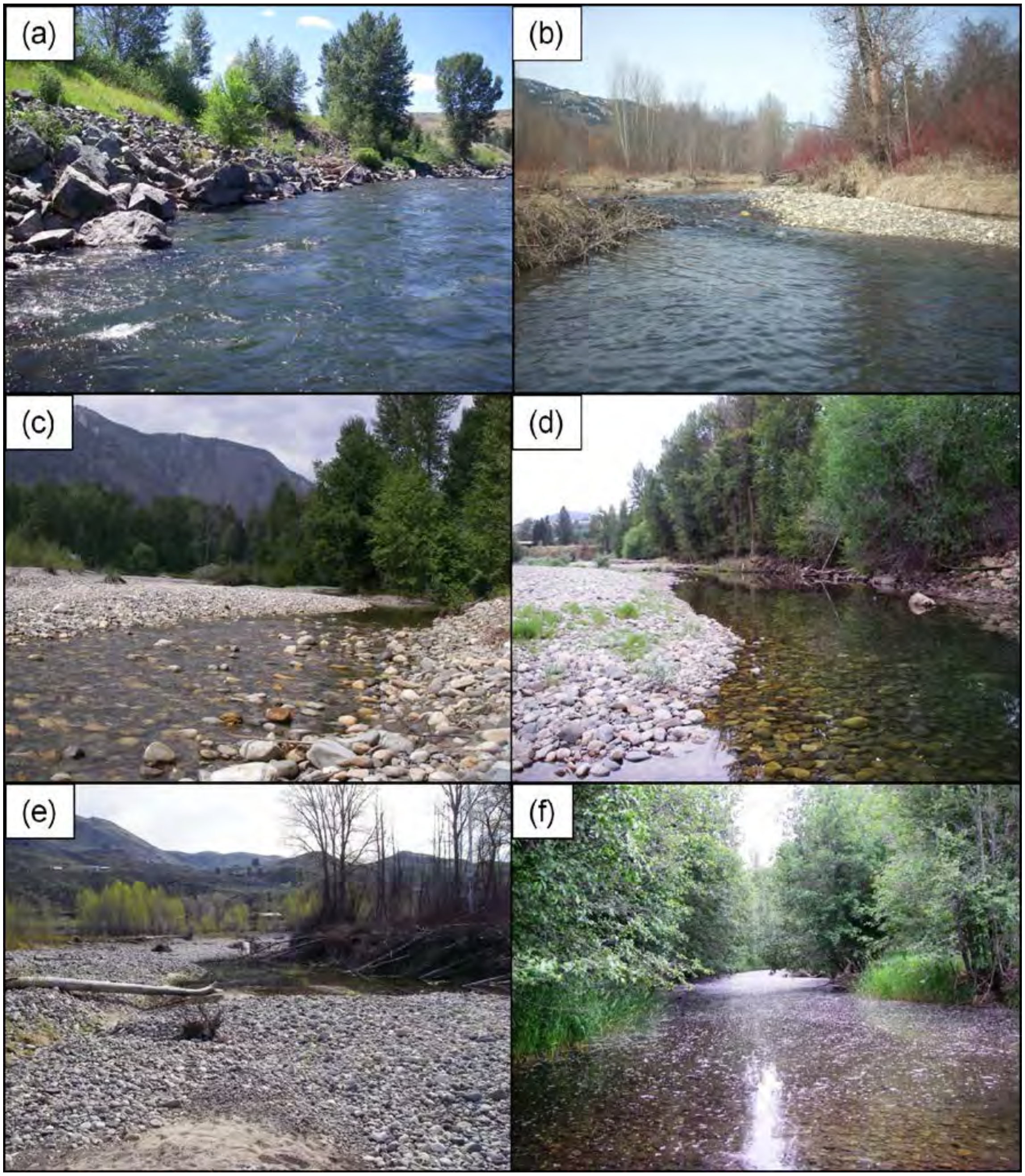


Figure 2. Photographs of a rip-rapped bank along main channel Methow River (A), and the five side channel sites included in this study. Side channels, described by their level of hydrologic connectivity, include: (B; '*con updwn*') retains upstream and downstream surface water connection with main channel throughout year, (C; '*con dwn*') retains downstream connection with main channel, (D; '*discon lrg*') disconnected from main

channel during base flow, but retains large pool; (E; ‘*discon sml*’) disconnected with only one small pool, and (F; ‘*discon noscr*’) disconnected from main channel and in contrast to channels D and E, does not scour during high flows.

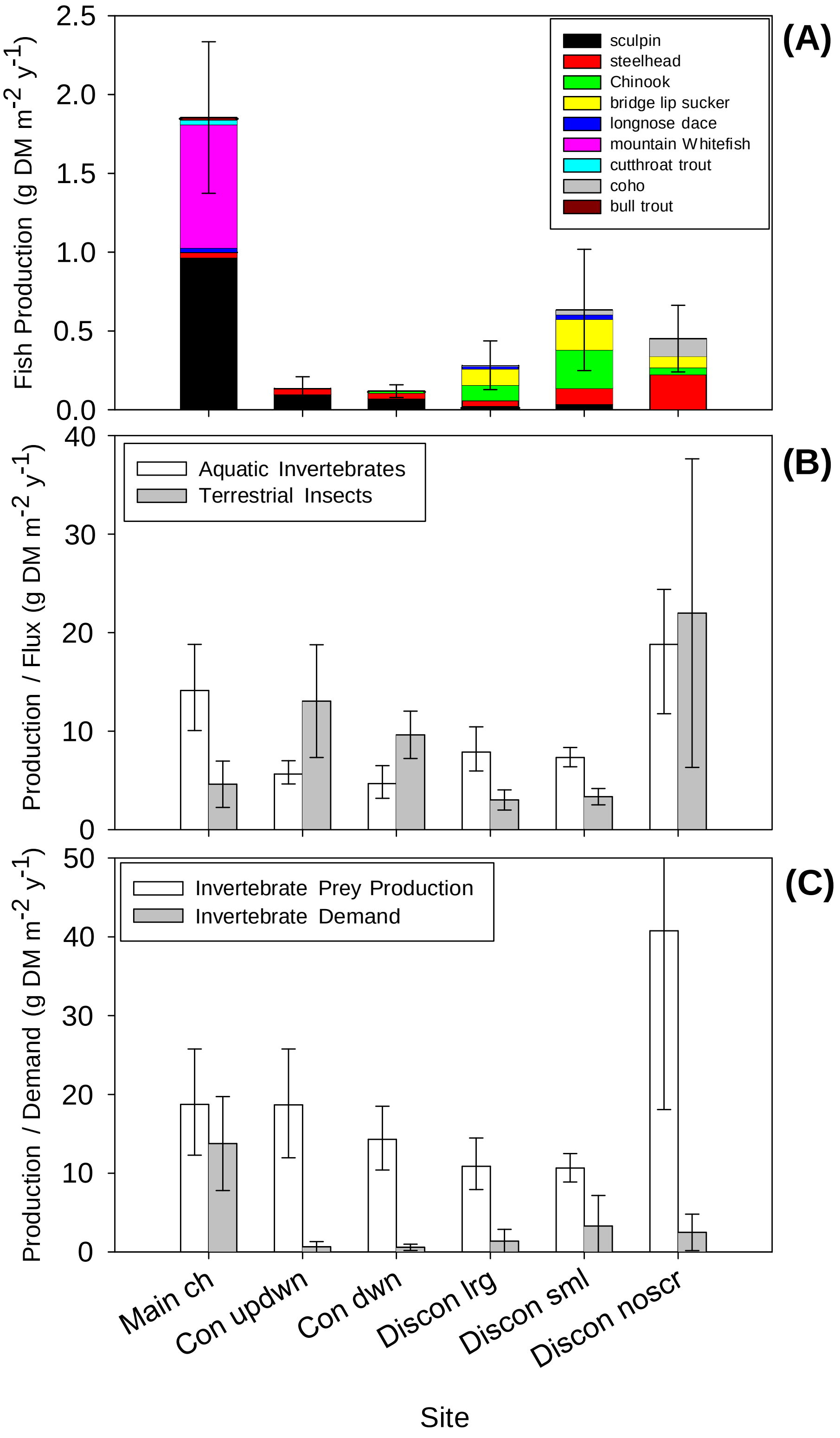


Figure 3. Per area estimates of fish production by species (A), aquatic invertebrate production and terrestrial insect flux to aquatic habitats (B); and comparisons of total

invertebrate prey production (aquatic + terrestrial contributions) to invertebrate prey demand by the entire fish assemblage (C) for the main channel and each side channel in 2009-10. Error bars represent 95% confidence intervals.

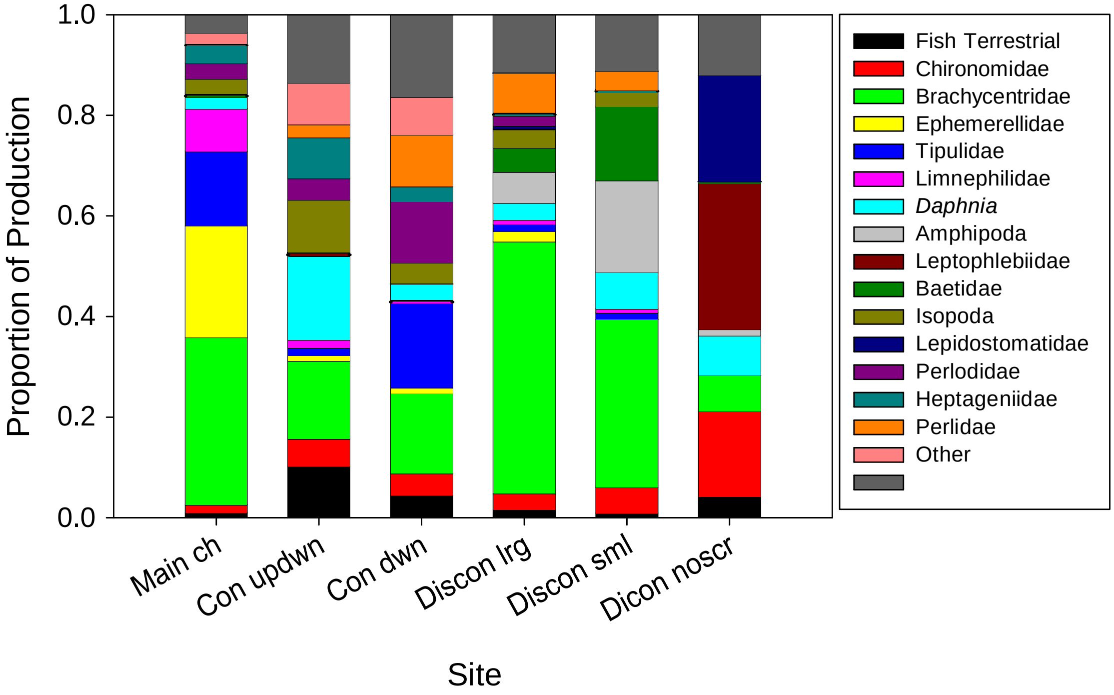


Figure 4.Trophic basis of production figure that shows the proportion of total fish production at each site derived from different prey items during 2009-10.

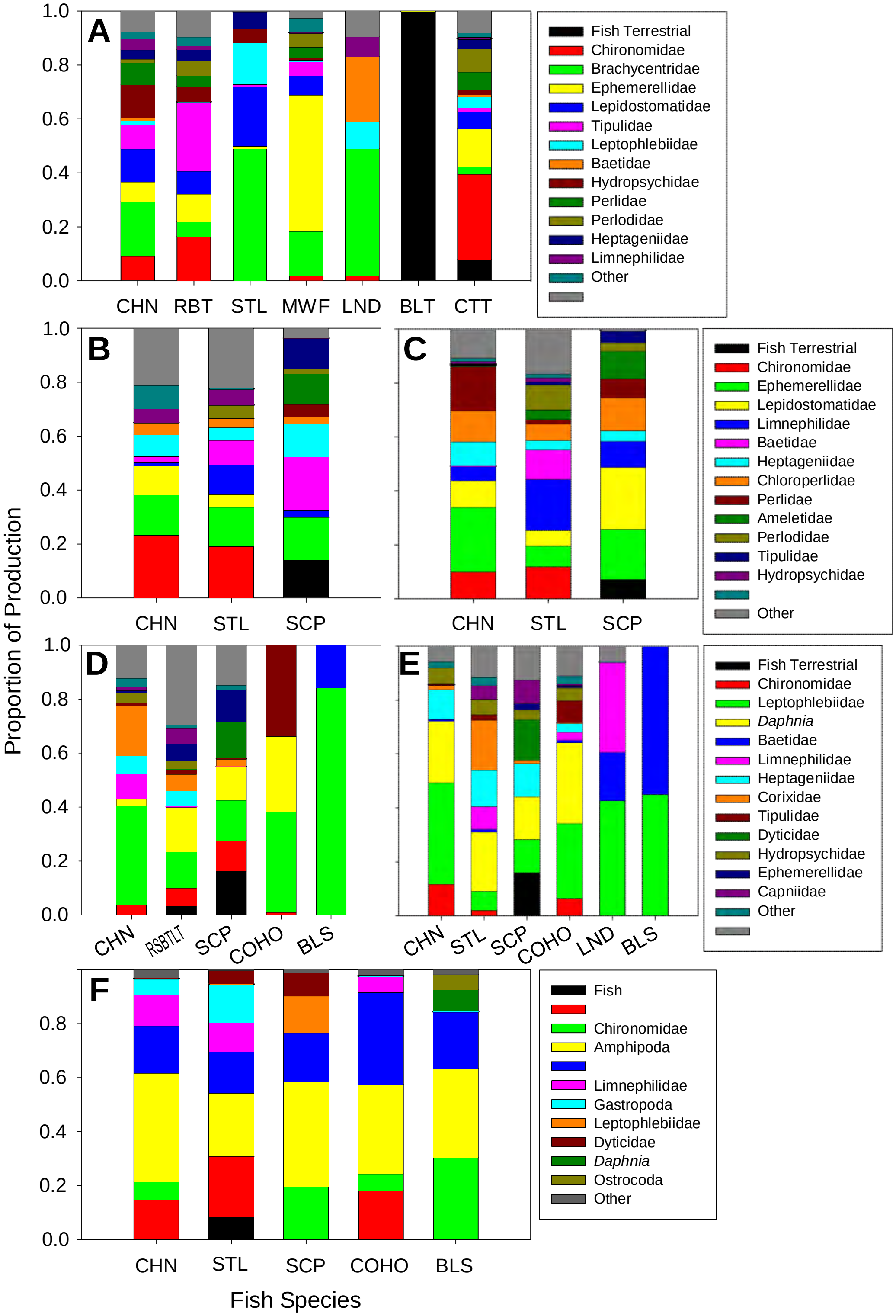


Figure 5. Trophic basis of production figures that shows the proportion of fish production derived from different prey items during 2009-10 within the main channel Methow River

(A) and side channel sites: (B) *con updnw*, (C) *con dwn*, (D) *discon lrg*, (E) *discon sml* and (E) *discon noscr*. BLT = bull trout, CHN = Chinook, LND = longnose dace, BLS = bridge lip sucker, STL = steelhead, CTT = cutthroat, MWF = mountain whitefish, SCP = sculpin.

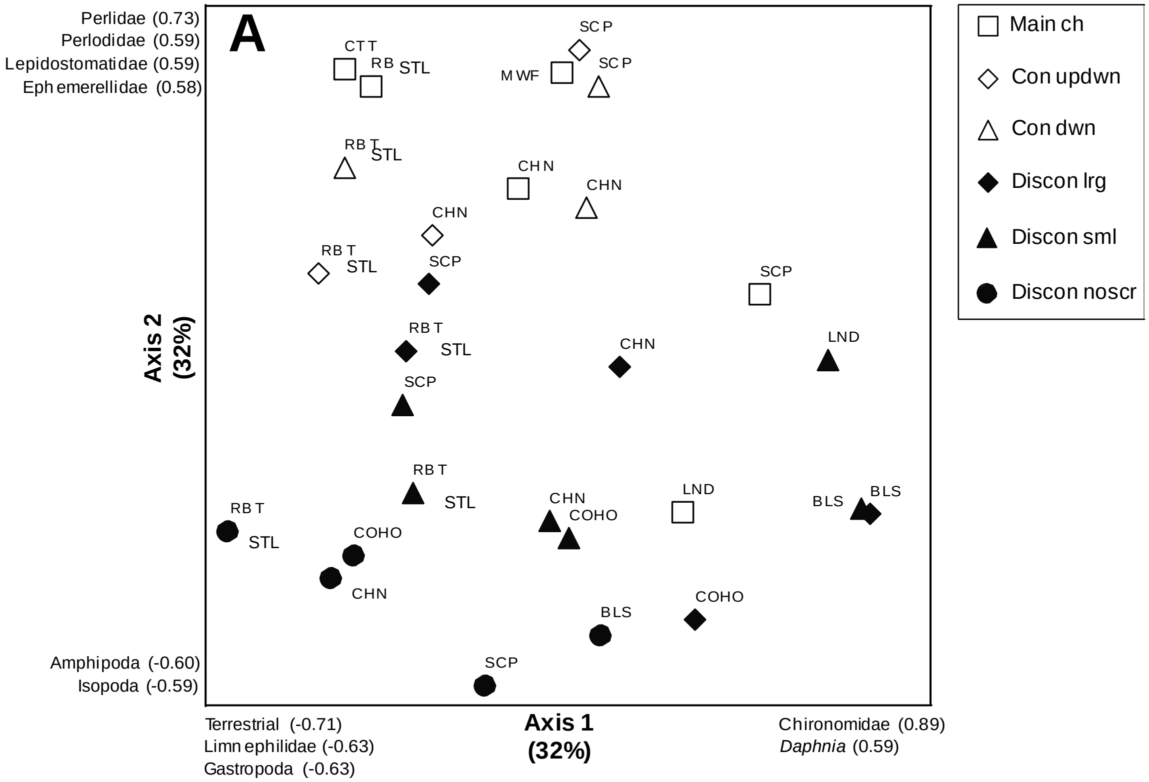


Figure 6. Nonmetric multidimensional scaling (NMDS) ordination plots of trophic basis of production for each fish species within each site. Numbers in parentheses below axis titles represent % of variation explained by each axis. Numbers in parentheses next to taxon names are Pearson’s correlation coefficients between the taxon and the axis. BLT = bull trout, CHN = Chinook, LND = longnose dace, BLS = bridge lip sucker, STL = steelhead, CTT = cutthroat, MWF = mountain whitefish, SCP = sculpin.

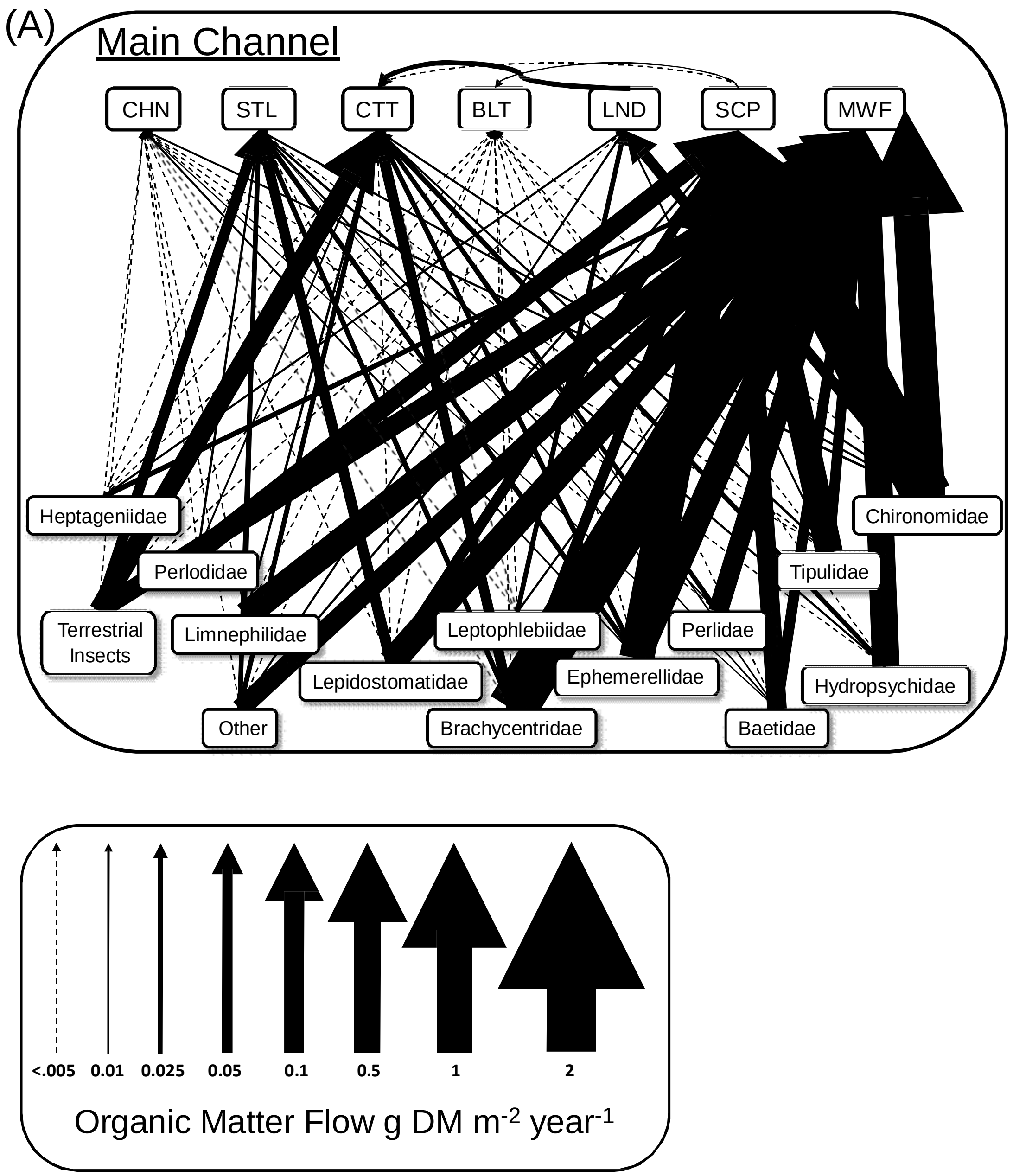


Figure 7. Annual organic matter flows to fish consumers (i.e., consumption in g DM m^{-2} y^{-1}) in the main channel Methow (A) and side channel sites (B-F) for 2009-2010. Arrow widths represent the magnitude of flows from prey to fish consumers (see key inset). BLT = bull trout, CHN = Chinook, LND = longnose dace, BLS = bridge lip sucker, STL = steelhead, CTT = cutthroat, MWF = mountain whitefish, SCP = sculpin.

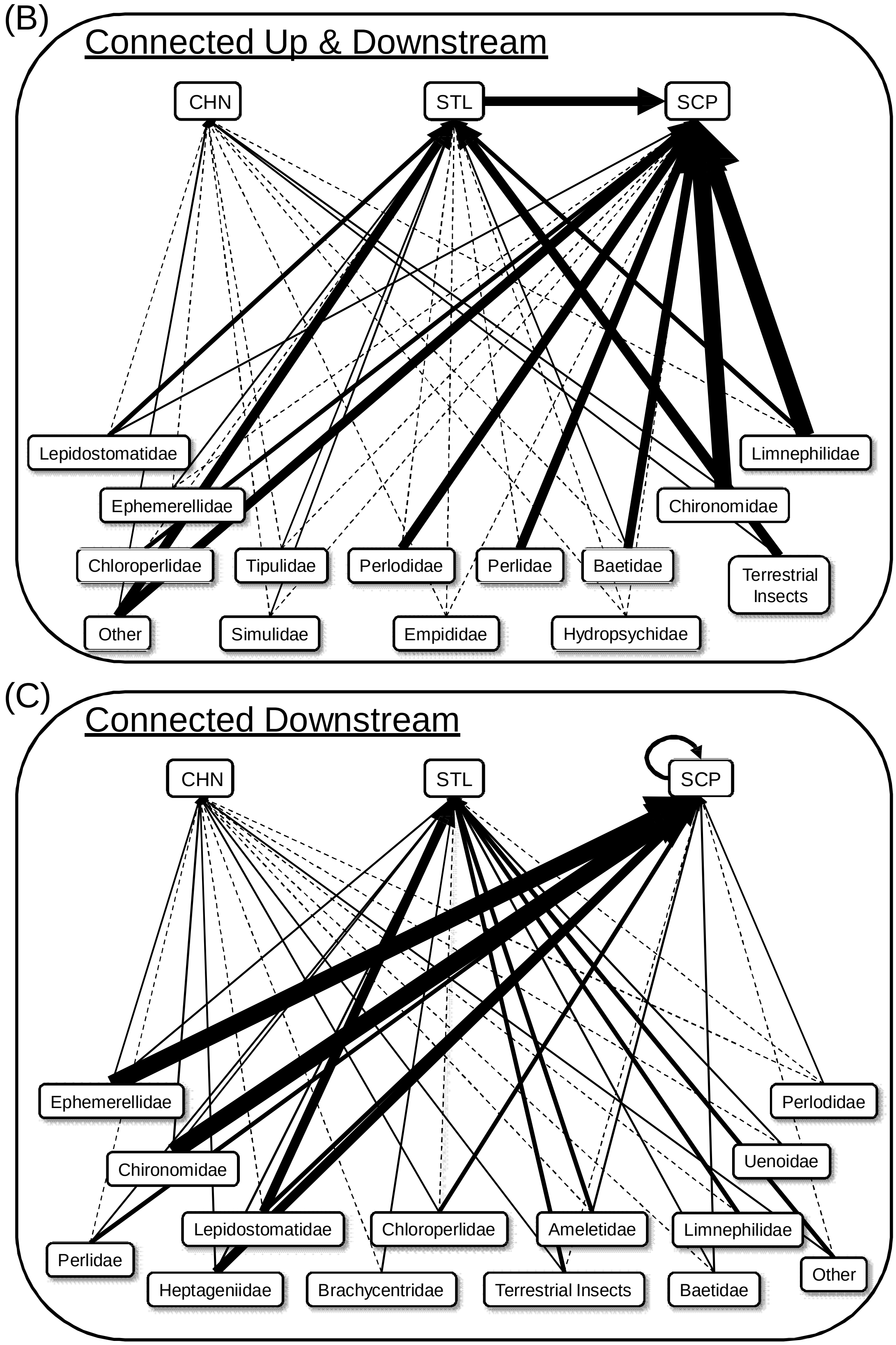
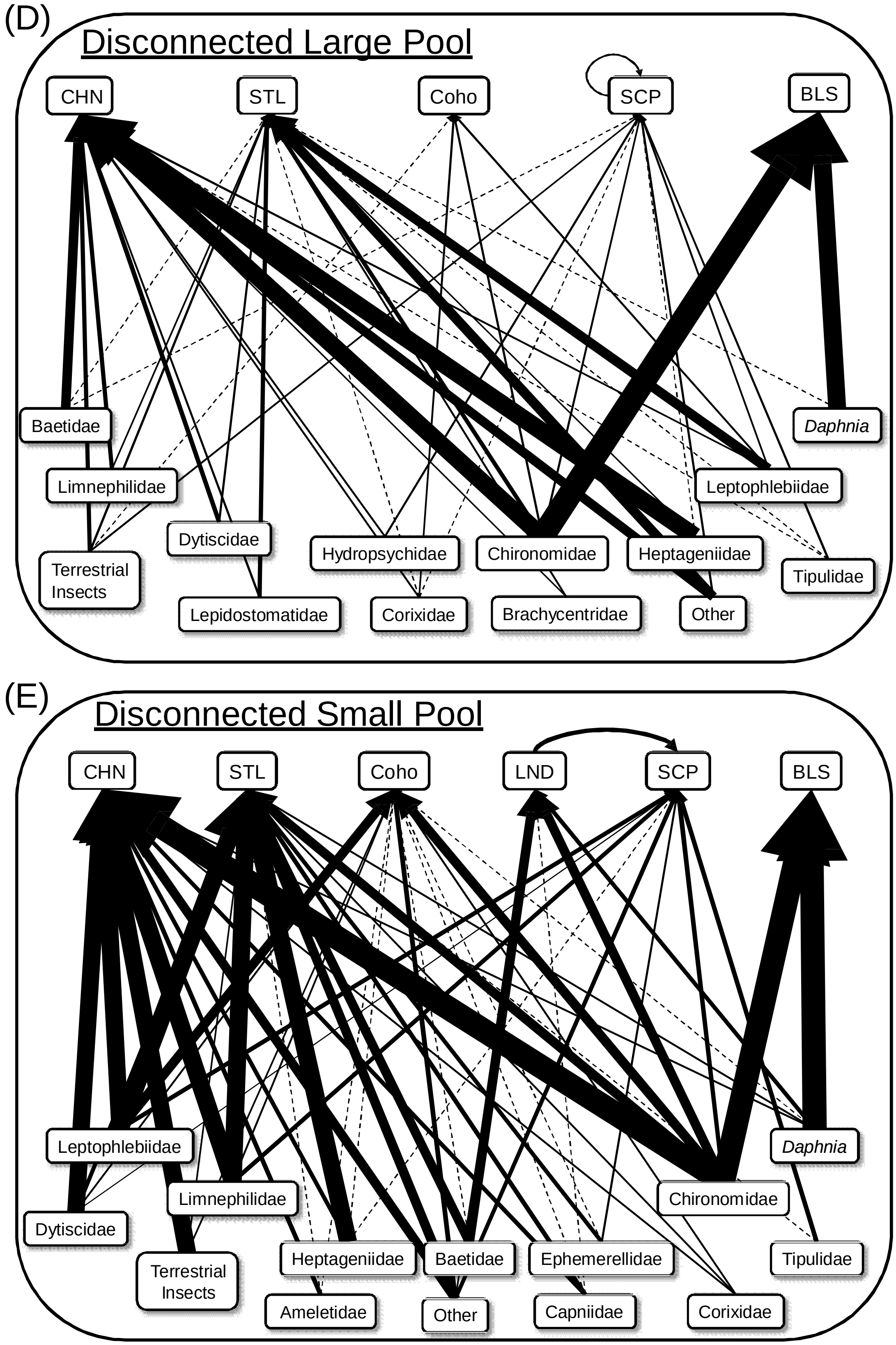


Figure 7. Continued.



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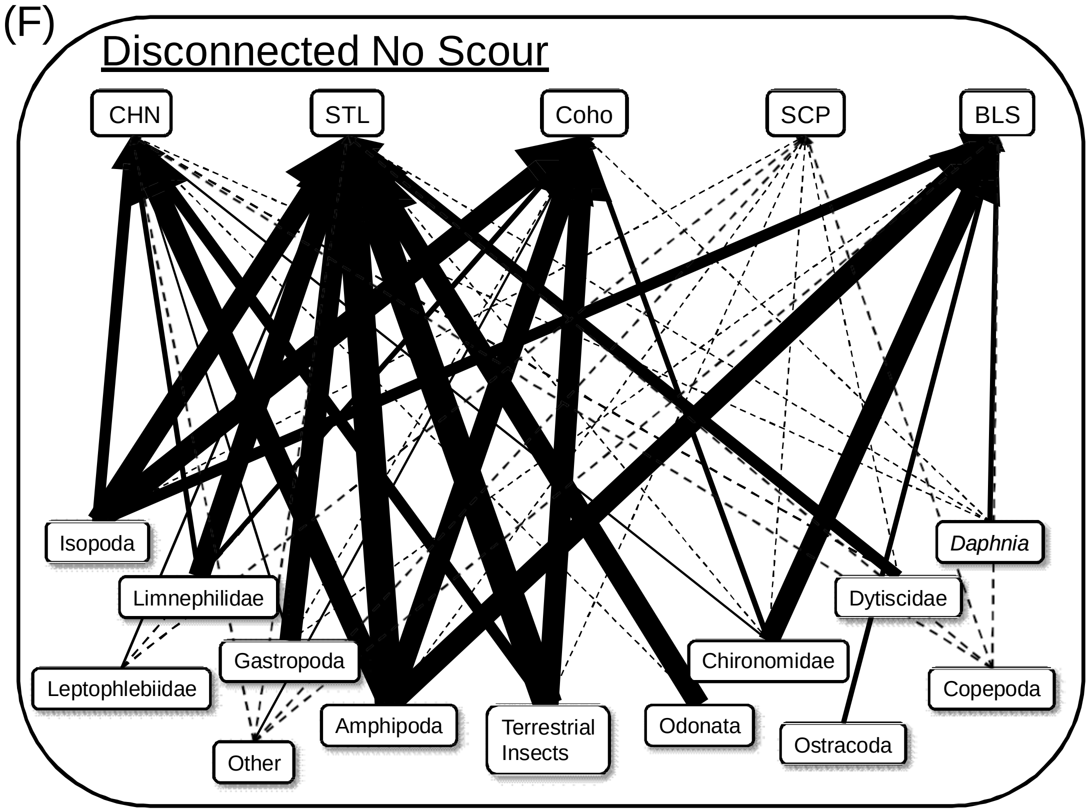

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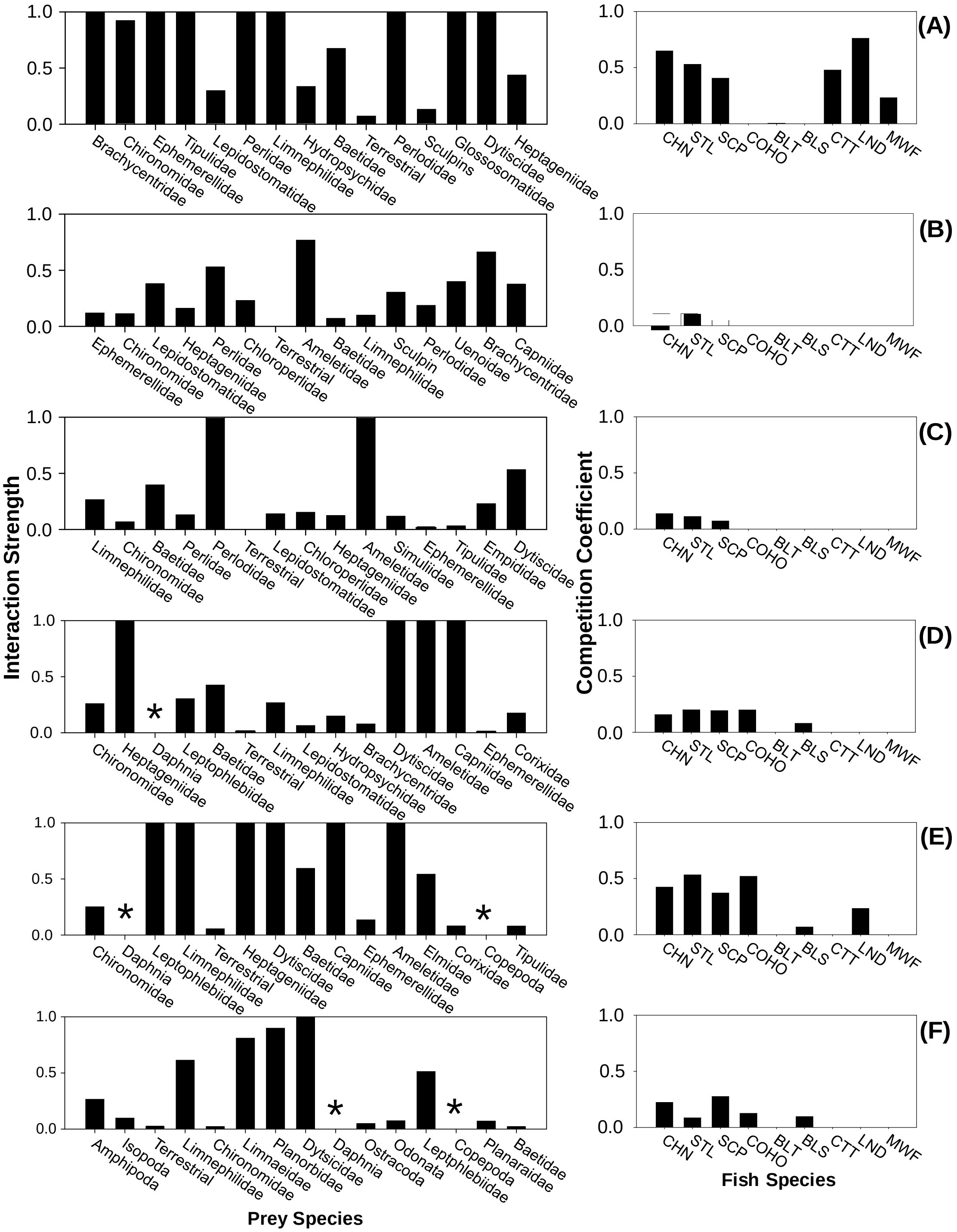

Figure 8. Interactions strengths for the top 15 prey items consumed by fish (left column) and competition coefficients for fish species (right column) in 2009-10 for the main channel Methow River and each side channel: (B) *con updnw*, (C) *con dwn*, (D) *discon*

lrg, (E) *discon sml* and (E) *discon noscr*. See text for further description of interaction strengths and competition coefficients. BLT = bull trout, CHN = Chinook, LND = longnose dace, BLS = bridge lip sucker, STL = steelhead, CTT = cutthroat, MWF = mountain whitefish, SCP = sculpin.

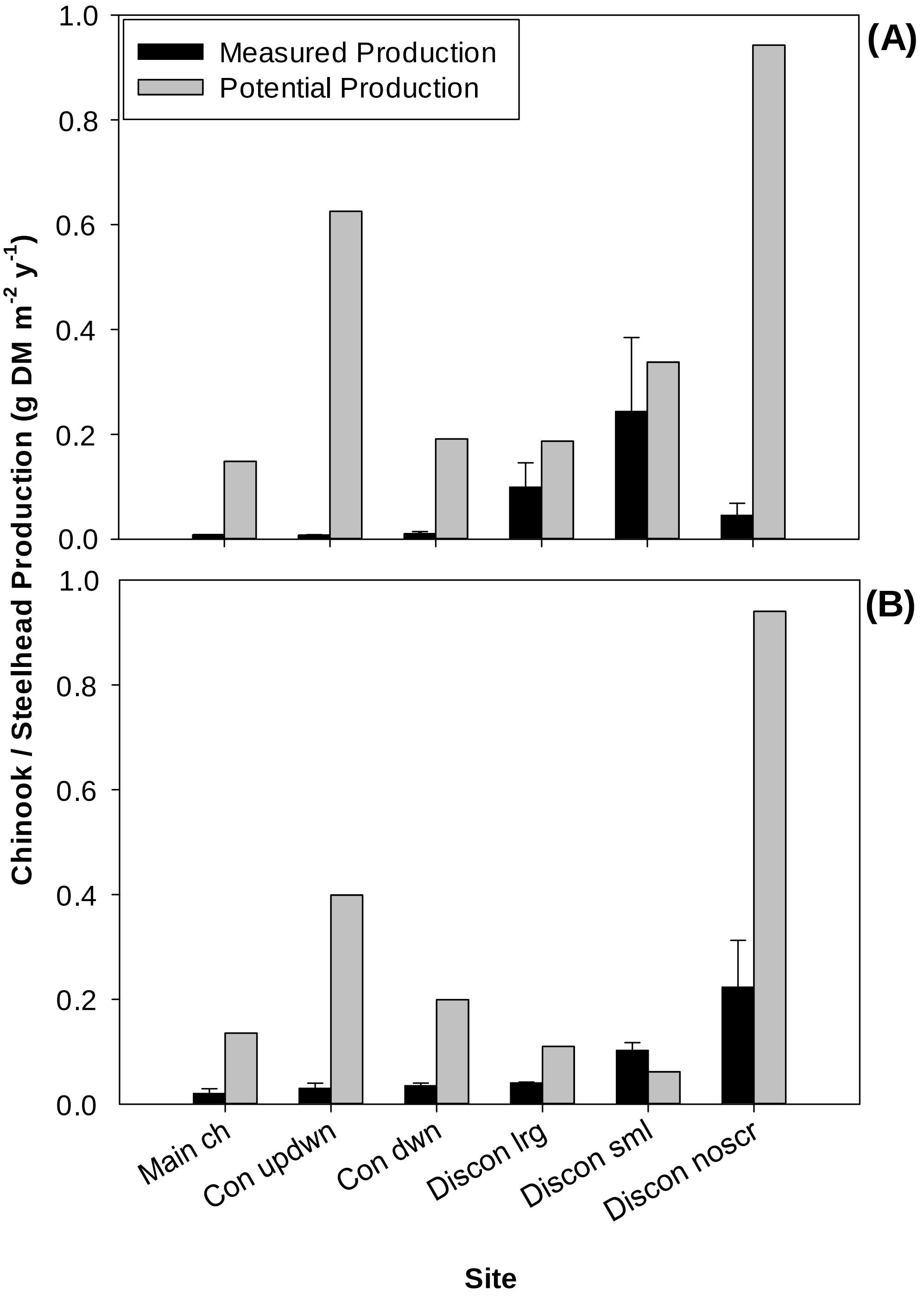

Figure 9. Measured annual production and potential annual production for juvenile Chinook salmon (A) and juvenile steelhead (B) for the main channel and each side channel in 2009-10, based on available food resources. Error bars represent 95% confidence intervals.

Chapter Four

Diversity, food web complexity, and predator-prey interaction strengths in a spatially heterogeneous floodplain landscape

Abstract

Mathematical simulations of biotic communities emphasize the importance of the strengths of trophic interactions between consumers and resources. However, parameterizing these models has been restricted by lack of empirical food web data. In addition, both empirical studies and mathematical models of food webs have yet to fully incorporate the spatial landscape heterogeneity that exists in nature. In this study I empirically evaluated aquatic food webs and the strength of interactions between fish predators and invertebrate prey within six habitat patches in a complex floodplain landscape. I found that increasing landscape complexity by sequentially aggregating food webs from individual patches increased the complexity of the meta-food web, resulting in a lower proportion of strong trophic interactions and a higher proportion of weak interactions. In addition, this complexity increased heterogeneity in predator-prey interaction strengths across the landscape. If hypotheses regarding the distribution of interaction strengths in food webs are correct (i.e., weak interactions promote stability), then these findings have important implications for the influence of landscape heterogeneity on community stability, and highlight the importance of studying food webs in a landscape context.

Introduction

The idea that diverse communities are more stable (the Diversity—Stability Hypothesis) has been conceptually appealing to ecologists for decades (MacArthur 1955; Elton 1958). Although empirical evidence has suggested that diverse communities are indeed more stable (e.g., McNaughton 1985; Tilman and Downing 1994), early mathematical analyses of model communities indicated that diversity might actually be destabilizing (May 1973). As a result, the mechanism by which diversity enhances stability has remained elusive. Today there is increasing evidence that greater complexity does enhance community stability, but only if the food webs are dominated by many weak consumer-resource interactions (McCann et al. 1998, McCann 2000). In food web models (e.g., McCann et al. 1998), weak consumer-resource interactions dampen the destabilizing oscillations often associated with strong trophic interactions (see Hastings and Powell 1996). Although empirical food web studies are now common and there is mounting evidence that weak trophic interactions are prevalent in nature (e.g., Ruiter et al. 1995, Sala and Graham 2002), there have been relatively few studies that evaluate interaction strengths and the distribution of these interactions within complex natural food webs. An understanding of interaction strengths within natural communities is absolutely necessary for the parameterization, simulation and validation of food web models.

In addition to a lack of empirical food web data by which to evaluate consumer-resource interaction strengths, another major weakness associated with the diversity-stability debate is that it has often been addressed as a problem with no spatial element. However, most communities exist in landscape mosaics, and this spatial heterogeneity itself has long been recognized as important to sustaining populations (Hanski 1982), predator-prey systems (Huffaker 1958), and communities (Holyoak et al. 2005). Although several food web stability models have attempted to incorporate landscape heterogeneity and so-called “metacommunity” dynamics (Guichard 2005; McCann et al. 2005; Gravel et al. 2011), empirical studies of food webs have yet to catch up. To date, most food web studies have been conducted either at small spatial scales, or have disregarded potentially important spatial heterogeneity, and therefore may be inadequate characterizations of the complex landscape mosaics within which communities are embedded (Woodward 2002; Massol et al. 2011). In order to understand how the stability of communities is related to the spatial heterogeneity found in nature, empirical studies are needed that evaluate the impact of landscape mosaics on biodiversity, food web complexity, and predator-prey interactions.

River-floodplain systems are considered to be among the most biophysically complex and diverse landscapes on earth (Bayley 1995, Figure 1). Flood-pulses that redistribute sediment and organic matter create a dynamic mosaic of physical habitat features within floodplain landscapes, which support diverse and productive biotic communities (Junk et al. 1998, Stanford et al. 2005). In this study, I utilized the natural complexity and diversity of a floodplain ecosystem to investigate aquatic food webs in the context of a heterogeneous landscape mosaic. My aims were to (1) calculate interaction strengths between fish predators and their invertebrate prey for different patches of the floodplain mosaic, (2) evaluate how biodiversity, food web complexity and predator-prey interaction strengths vary between these patches, and (3) evaluate the influence of landscape heterogeneity (via the aggregation of patch-scale food webs into floodplain meta-food webs) on biodiversity, the complexity of food webs and the distribution of predator-prey interaction strengths. This study provides two things that are currently rare or absent from food web literature, but are much needed to more rigorously address the stability-diversity question: (1) multiple predator-prey interaction strength distributions for real food webs, and (2) a quantitative evaluation of how interaction strength distributions change with increasing habitat complexity.

Methods

Study Site

The site for this study is the Methow River, a fifth order tributary (4662 km^2) of the Columbia River, located in north-central Washington, USA. The headwaters drain east and south from an elevation of 1,700 m in the Cascade Mountains, to 240 m at the confluence with the Columbia River. A majority of the precipitation falls in the winter in the form of snow. The hydrograph of the Methow is typical of snow-melt dominated systems, with peak flows occurring in May and June, and peak discharges often exceeding 300 m^3/sec at the river mouth. Mean annual discharge is 43 m^3/sec, with an average base flow of 5 m^3/sec. The geomorphic character of the Methow basin is strongly influenced by Pleistocene glaciation, which carved several broad U-shaped valleys that are now filled with unconsolidated sediments of glaciofluvial origin (BOR 2010). A legacy of cut and fill alluviation in these floodplain valley segments has created a complex landscape mosaic that includes numerous aquatic habitat patches of different sizes with different degrees of hydrologic connectivity to the main channel.

The focus of my study was a 13 km long floodplain segment located along the mainstem Methow River between the junctions of two large tributaries (the Twisp and Chewuch Rivers). Within this segment, I quantified food webs for the main channel (‘*main_ch*’) and five side channel habitat patches that varied in their degree of hydrologic connectivity to the main channel. For convenience, I have labeled these five patches according to hydrologic connectivity and habitat size during low flow conditions: '*con_updwn*' refers to the side channel that retains both up and downstream surface water connections; '*con_dwn*' is the side channel with only a downstream surface water connection; '*discon_lrg*' is disconnected from the main channel but retains one relatively large pool; '*discon_sml*' is disconnected and mainly represented by one small pool; and '*discon_noscr*' is disconnected with large pools, but in contrast to the other side channels, its bed did not scour during high flows (see Table 1, Chapter 3). During peak flows (April to June), all habitat patches had both an upstream and downstream surface water connection to the main channel, allowing aquatic organisms to move between habitat patches. Fish taxa present in the Methow River that were included in my food web analyses included Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), rainbow trout/steelhead (*O. mykiss*), cutthroat trout (*O. clarkii*), bull trout (*Salvelinus confluentus*), mountain whitefish (*Prosopium williamsoni*), longnose dace (*Rhinichthys cataractae*), bridge lip sucker (*Catostomus columbianus*) and sculpin (*Cottus spp.*).

Analysis

For each individual patch where food web measurements were collected, I calculated (1) total prey and predator taxa richness, (2) total number of fish predator—invertebrate prey food web links (a simple measure of food web complexity), and (3) population level interaction strengths for each predator-prey linkage. Interaction strengths (*IS*) were calculated as:

$$IS_{ij} = \frac{C_{ij}}{P_i}$$

where C_{ij} = total annual consumption of prey taxa i (g DM m^{-2} y^{-1}) by fish predator j, and PP is the annual production of prey taxa i. Outputs from this equation range from 0 to 1 and represent the proportion of prey i annual production consumed by fish predator j. The interaction strength of the entire predator assemblage on each prey taxa (*Total IS*) was calculated by combining the *IS* of each individual predator species n:

$$Total\ IS_{ij} = \sum_{j=1}^{n} IS_{ij}$$

The contribution of each individual habitat patch to patterns at the landscape-level was evaluated by consecutively adding habitat patches to the floodplain mosaic. I started with a simple system that contained only the main channel. From that starting point, I added one habitat patch at a time to the landscape. As each consecutive habitat patch was added values were recalculated for (1) prey taxa richness, (2) total number of unique predator-prey food web linkages, (3) number of repeated food web linkages (i.e., predator-prey interactions found in more than one habitat), and (4) predator-prey *IS*. For variables (1), (2) and (3) this simply required adding the number of new prey species (i.e., species not found in the landscape before the addition) and new food web links (and repeated links) associated with each addition habitat patch. To calculate *IS* of the meta-food web, I adjusted equation 1 so that the contribution of each habitat patch was weighted by the total area of that patch. This required extrapolating *IS* for individual patches by the total availability of each patch type within the floodplain landscape, as follows:

$$Landscape\ IS_{ij} = \frac{\left(\frac{C_{ij1}}{P_{i1}} \times A_1\right) + \left(\frac{C_{ij2}}{P_{i2}} \times A_2\right) + \ldots}{A_1 + A_2 + \ldots}$$

where C_{ij1} is the consumption of prey type i by consumer j in patch 1 (i.e., the main channel), and A_1 is the total area (m^2) of patch 1. I estimated the total area of each patch by utilizing digitized maps and associated metadata provided by the US Bureau of Reclamation (BOR 2010). Interaction strength data was summarized by (1) averaging interaction strengths within individual patches and across the landscape, and (2) graphically depicting the relative frequency of interaction strengths. Information on sampling design, field and laboratory methods, and estimates of annual prey production and predator consumption are detailed in Chapter 3.

Results

Prey taxa richnes was consistent among all habitat patches, ranging from 58 in the main channel to 79 in the *con_updwn* patch (Figure 2a). The richness of fish predators was highest in the main channel and *discon_sml* patches with six species and lowest in the two most connected patches with only three predator species (Figure 2a). The number of food web links was highest in the main channel within 142 different predator- prey links (Figure 2b), and lower, but relatively consistent among all side channel habitat patches (range = 84 – 64 links). The average predator-prey *IS* across all sites was consistently low (< 0.16), but was still variable, ranging from 0.088 in the *con_dwn* patch to 0.159 in *discon_sml* (Figure 2c). As food webs associated with each habitat patch were added to the landscape, total prey taxa richness, number of unique food web links, and number of repeated food web links increased in a linear fashion (Figure 2d & e). The total prey taxa richness increased from 58 when the landscape included only the main channel to 126 when all six patches were included (Figure 2e). The number of unique food web links increased from 142 to 238; the number of repeated links started at 0 but quickly increased to 269. In contrast, average *IS* decreased with the sequential aggregation of food webs from each patch, from 0.140 to 0.089, a total reduction of 36% (Figure 2f).

The relative frequency distribution of interaction strengths was similar among all habitat patches, with few stronger (*IS* > 0.3) predator-prey interactions and many weaker (*IS* < 0.2) interactions (Figure 3a). As food webs from each habitat patch were added to the meta-food web of the landscape mosaic, the frequency distribution appeared to change very little (Figure 3b). However, when comparing the proportion of relatively strong (*IS* > 0.5) versus very weak (*IS* < 0.0001) interactions (Figure 3c), the proportion of weak *IS* increased and, concomitantly, the proportion of strong *IS* decreased as each patch was added to the landscape. For those prey items that were consumed by predators in two or more habitat patches, the proportion of their annual production consumed by the entire predator assemblage (*total IS*) was highly variable (Figure 3d). As a result, when *total IS* on a particular prey item was very strong (>0.8) at one location, this was generally (15 out of 16 cases) balanced by much weaker interactions (<0.2) at another location (Figure 3d).

Discussion

The strength and distribution of trophic interactions in food webs has been hypothesized to have important consequences for community stability and the persistence of species (May 1973; McCann et al. 1998; McCann 2000). However, there have been very few studies that empirically evaluate such hypotheses via direct measures of interaction strengths in real communities. In this study, I present trophic interaction strengths between fish predators and their invertebrate prey for not only one habitat type, but six different habitat patches within a complex floodplain landscape. Consistent with findings from other studies (e.g., de Ruiter 1995; Sala and Graham 2002), I observed that the distribution of trophic interactions was highly skewed toward weak interactions within all habitat patches. In addition, I found that sequentially aggregating food webs from individual patches into an increasingly more complex landscape resulted in correspondent decreases in the average strength of interactions between predators and prey, owing to an increase in the proportion of very weak interactions and a decrease in the proportion of strong interactions in the meta-food web. If hypotheses regarding the distribution of interaction strengths in food webs are correct (i.e., weak interactions promote stability; McCann et al. 1998), then this finding has important implications for the stability-diversity debate, and highlights the importance of food web studies that encompass and directly investigate the consequences of spatial heterogeneity.

Although it is not a new idea that complex and heterogeneous landscapes enhance stability (Huffaker 1958; Hanski 1982; Holyoak et al. 2005), this is the first study to empirically identify pathways and mechanisms by which landscape complexity might influence stability in a real food web. I identify two potential mechanisms by which complex landscapes might stabilize ecosystems and reduce the likelihood of species extinctions (Figure 4). First, landscape complexity decreased the average strength of predator-prey interactions via a greater proportion of weak links, which are hypothesized to stabilize communities by reducing destructive predator-prey oscillations (McCann et al. 1998). Second, different habitat patches within complex landscapes created variation in interaction strengths for particular prey items, whereby a strong predator impact on a prey taxon in one habitat was coupled with weaker interactions for that same prey in other patches. In other words, although some individual invertebrate taxa were heavily preyed upon by fish in one patch type, other habitat patches existed in the landscape where these prey were released from strong predation. This spatial heterogeneity in predator-prey interaction strengths has been outlined numerous times in the literature (e.g., Menge 1994, Schauber et al. 2009), and is believed to have important implications for species persistence (Huffaker 1958; Schauber et al. 2009; Holyoak et al. 2005), but it has not before been quantified in the context of a natural food web in a spatially complex landscape. The pathways by which landscape complexity appears to influence these two mechanisms, however, are not identical.

Based on a synthesis of my findings, I have outlined a series of potential relationships that may link landscape complexity, community stability, and maintenance of biodiversity (Figure 4). Landscape complexity may increase the complexity of food webs (e.g., the total number of food web links) directly, by providing more distinct habitat patch types, and indirectly via increases in biodiversity or species richness. More complex food webs have a greater number of unique links (i.e., links found only once within the landscape), and repeated links (i.e., predator-prey interactions that occur in two or more habitat patches within the landscape). I hypothesize that a greater number of unique food web links, and to some extent repeated food web links, reduce average predator-prey interaction strengths as landscapes become more complex; whereas a greater number of repeated links create greater variation in the strength of predator-prey interactions across the landscape. Together, both of these mechanisms are likely to be important to maintaining biodiversity and community stability.

There are several limitations to my study and to the approach I applied that are worthy of discussion. First, I employed an observational approach to calculate predator-prey interaction strengths, which represent flows of energy, or the proportion of prey production consumed along food web links (*sensu* Wooton 1997, Hall et al. 2000). Although this approach might not be ideal for determining the strength of trophic interactions, as it does not experimentally evaluate the impact of predators on prey populations (Paine 1980), observational approaches of this kind provide information on interaction strengths without numerous experimental manipulations that are logistically difficult to conduct in complex natural food webs (Wootton and Emmerson 2005). Second, instead of presenting per capita estimates of predator-prey interactions, which are now widely advocated (Wooton and Emmerson 2005), my approach yielded estimates of interaction strength for entire predator and prey populations. That said, per capita estimates do not account for the abundance or rarity of different predators in the environment, making it difficult to determine the impact of particular species on prey populations. In addition, population-level estimates of interaction strength can easily be converted to per capita estimates by scaling them to consumer densities. Another caveat associated with this study is that I quantified only a subset of the actual floodplain food web (fish and aquatic invertebrates), and did not include interactions other than those of predator and prey (e.g., competition, mutualism). Although I am uncertain what impact that including these other interactions might have, I speculate that their inclusion would amplify the patterns I observed. Perhaps a more serious omission from this study was in my not explicitly accounting for the movement of organisms between patches in the floodplain landscape, which is likely to have implications for food webs and stability (Holyoak et al. 2005). Ongoing research is uncovering movement patterns of fishes in this river system (P. Connolly, USGS, Columbia River Research Laboratory), and in the near future, should provide information on how these movements influence the food web patterns presented here.

The findings of this study emphasize that hypothesized relationships between diversity and stability are likely dependent on the complexity of the landscape mosaic; that is, biophysically diverse and heterogeneous landscapes may possess more stable communities than simple and homogeneous landscapes. If true, this could have important implications for how we think about landscape complexity, its degradation, and efforts aimed at its conservation or restoration. Not only are river floodplains are among of the most biophysical diverse and productive systems on Earth (Junk et al. 1989; Bayley 1995), my findings show that floodplain systems may also be 'hotspots' of community stability, and serve as 'nodes of resilience' for species that utilize floodplains, many of which are economically and culturally important to humans (e.g., Pacific salmon and steelhead). Unfortunately, river floodplains are also some of the most degraded ecosystems on Earth (Tockner and Stanford 2002), due particularly to channelization and flow regulation. As a result, millions of dollars are now being spent each year on efforts to restore the functionality and complexity of these systems (Bernhardt et al. 2005). Although these types of habitat restoration efforts often proceed with goals of enhancing or restoring ecosystem services and/or threatened and endangered species (Bernhardt et al. 2005; Benayas et al. 2009), restoration of floodplains might also restore the weak trophic interactions and spatial variation in predator-prey interaction strengths that I have reported here.

By quantifying trophic interaction strengths for multiple habitat patches in a heterogeneous floodplain, this study emphasizes the importance of landscape complexity for food webs, and outlines potential mechanisms and pathways by which complex landscapes influence community stability and species persistence. I show that meta-food webs in complex landscapes have a greater proportion of weak trophic interactions and also more spatial heterogeneity in predator-prey interaction strengths than the simpler food webs of individual patches, both of which are hypothesized to be stabilizing. Consequently, human disturbances that simplify and disconnect landscapes may have significant and destabilizing affects on ecological systems. Past empirical studies and mathematical models of food webs are generally either confined to small spatial scales and/or ignore important spatial heterogeneity. Future studies like this one are necessary to expand the scope of food web ecology and provide empirical data that better reflects the complexity found in nature. As this is done, models of food webs will become more realistic and will be better suited to uncover new patterns and provide answers to fundamental questions and long-standing riddles in ecology.

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Figures

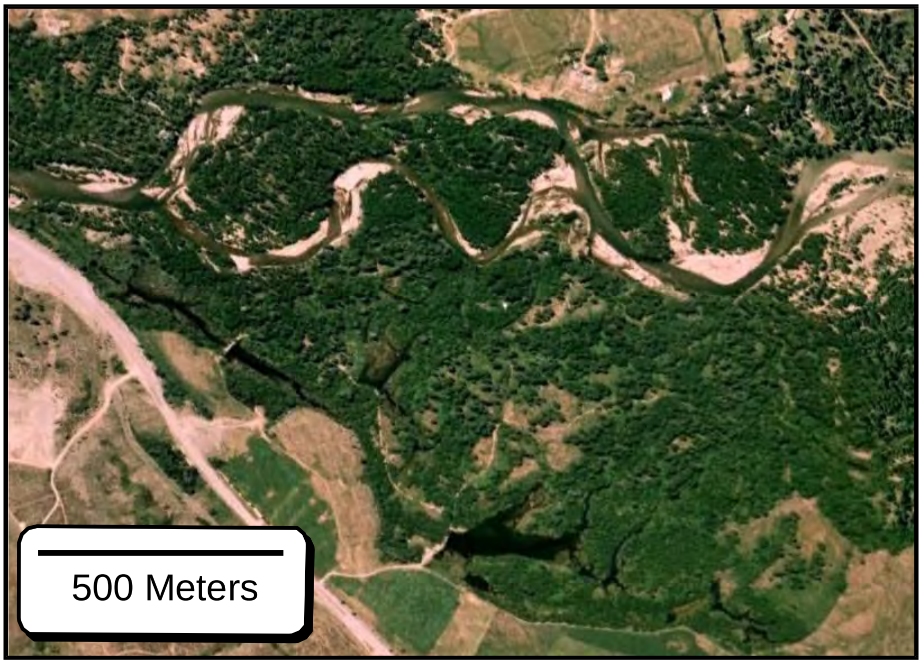

Figure 1. Floodplains are highly complex landscapes that contain a diversity of aquatic habitat patches, ranging from large and connected main channels, to small isolated side channels. Photo of a floodplain segment of the Methow River, Washington state, USA.

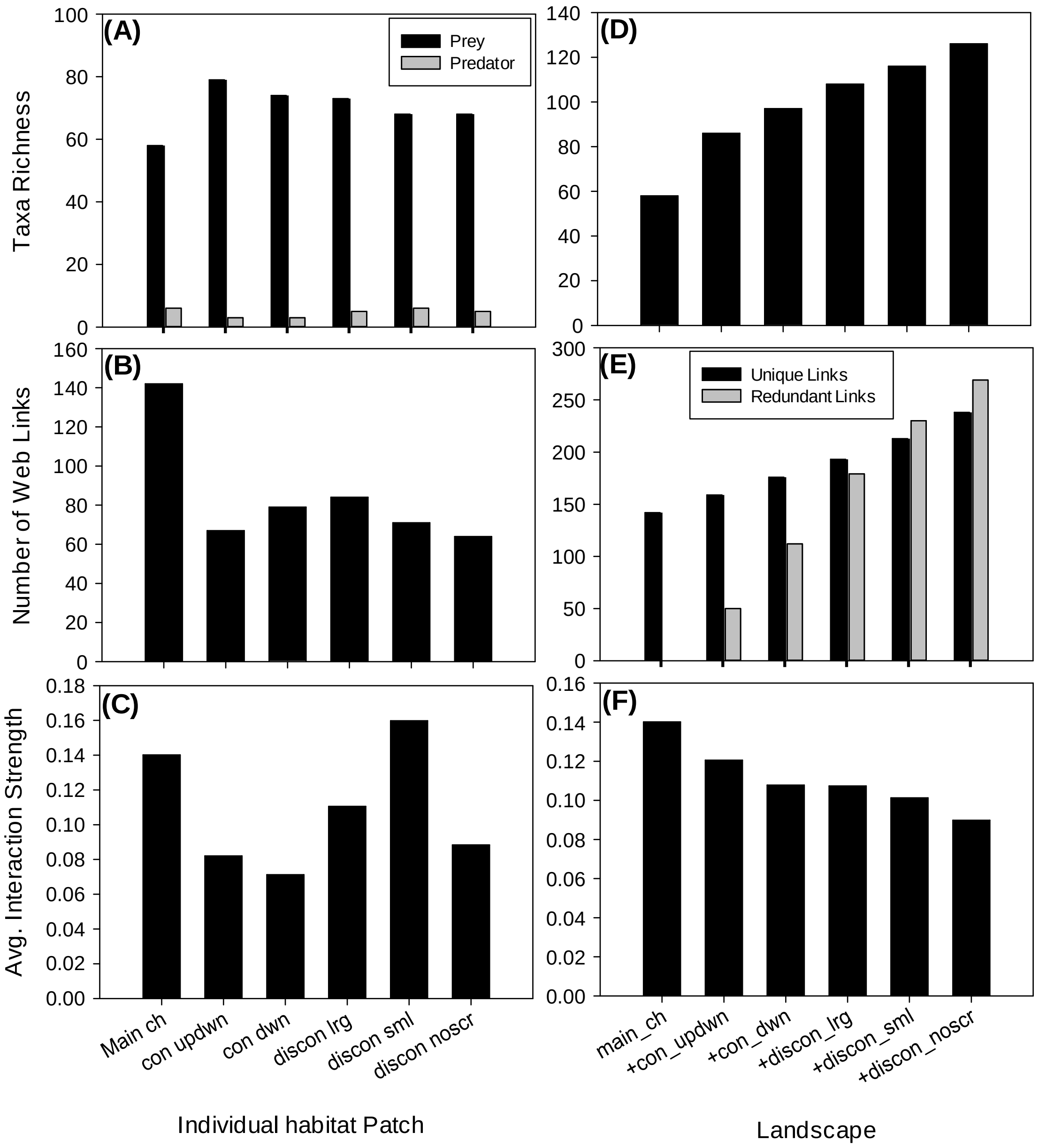

Figure 2. Number of prey taxa (A), number of food web links (B), and average predator-prey interaction strength (IS) (C), for each *individual* habitat patch. Cumulative number of prey taxa (D), cumulative food web links and repeated links (E), and cumulative average IS (F), for the floodplain *landscape*; calculated by sequentially adding patch types one by one to the floodplain landscape. Cumulative and repeated food web links

represent the number of unique predator-prey links and the number of repeated links across the landscape, respectively.

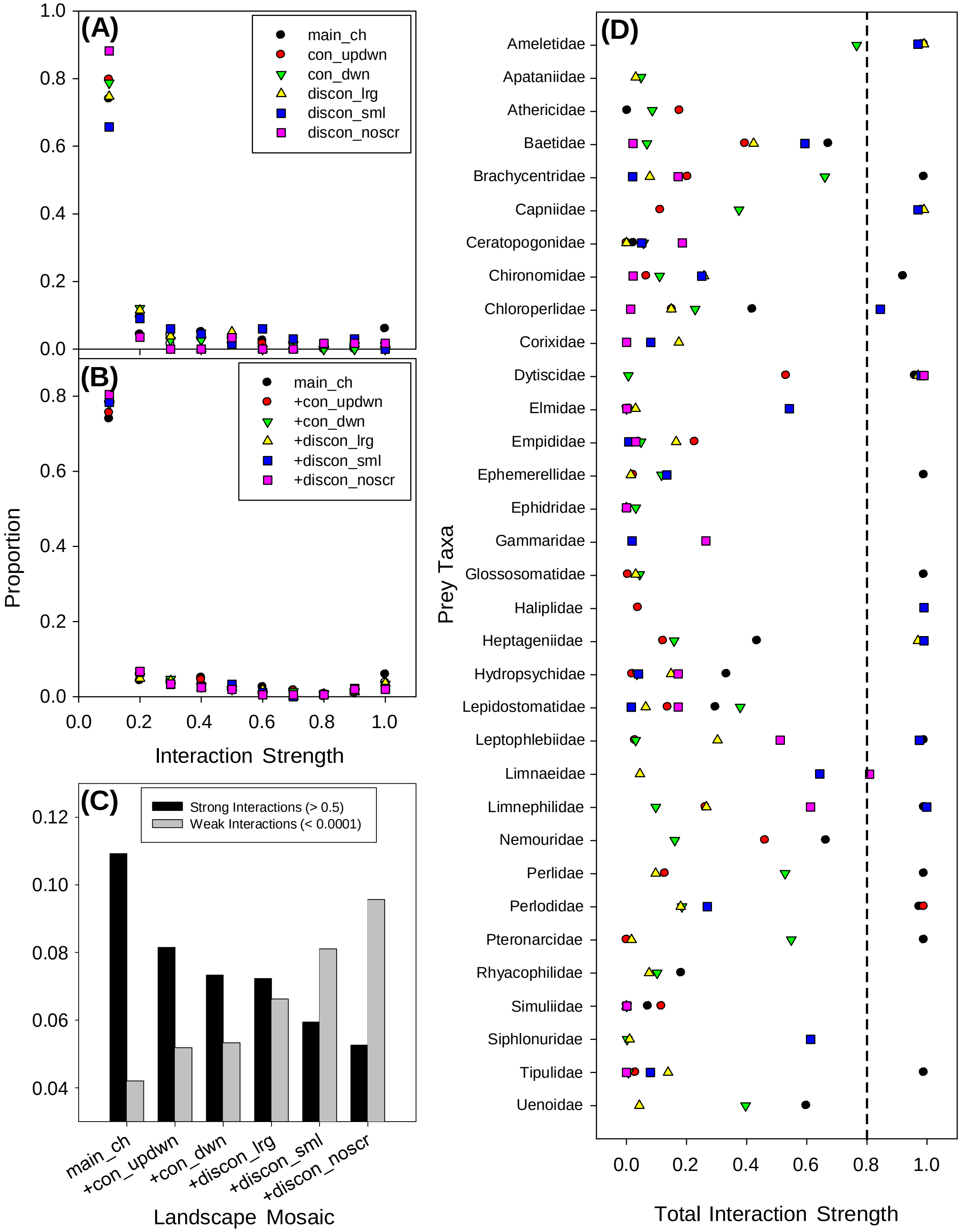

Figure 3. Frequency distribution of predator-prey interaction strengths (*IS*) for each *individual* habitat patch (A); normal and log-transformed cumulative *IS* distributions for

the *landscape* (B, C), illustrating how proportional *IS* distributions change as food webs associated with each habitat patch are added to the meta-food web of the floodplain landscape; and *total IS* for each prey taxa within each habitat patch (D), which represents the proportion of prey annual production consumed by the entire predator assemblage. The vertical dotted line is placed at 0.8 to indicate that patches with strong *total IS* for certain prey items, are balanced by other habitats in the landscape with weaker interactions.

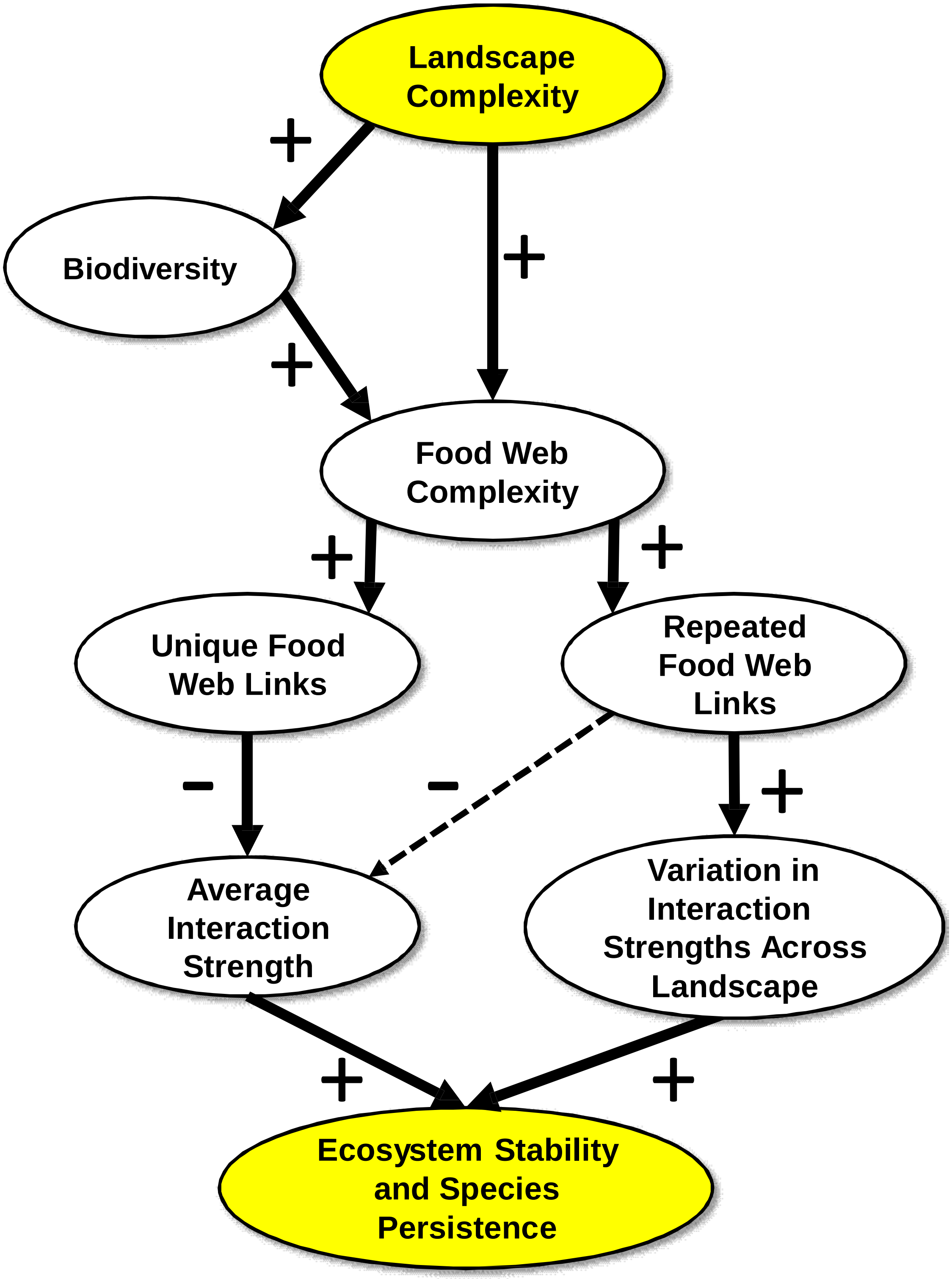

Figure 4. A conceptual diagram that illustrates the potential relationship between landscape complexity and the proportion of strong and weak predator-prey interaction strengths (*IS*) within the food web.

Summary and Conclusions

River floodplain systems are among the most heterogeneous and dynamic landscapes on Earth, and are often considered to be “hotspots” of biological diversity and productivity (Bayley 1995). Unfortunately, floodplains are also some of the most degraded systems on Earth (Tockner and Stanford 2002). As a result, floodplains are a frequent target of habitat restoration aimed at restoring ecosystem structure and function (Bernhardt et al. 2005), and conserving or recovering species that utilize these landscapes. That being said, very few studies have evaluated the importance of floodplains in terms of ecosystem function, the impact of degradation on these functions, and the potential for restoration to restore floodplain functionality or recover species of interest to humans. I conducted four studies within two separate river systems in the Pacific Northwest of the United States, a region where floodplain restoration is common, and is often tied to ongoing salmon and steelhead recovery efforts. Together, these studies evaluated (1) the importance of floodplains in terms of biotic productivity and the flows of energy that sustain productivity, (2) the impact of degradation that disconnects floodplains, and (3) the potential for restoration to restore both floodplain function and salmon and steelhead populations.

Although there have been numerous empirical studies (e.g., Lewis et al. 2001) and conceptual models (e.g., Junk et al. 2001) that indicate that floodplains are highly productive, few studies have evaluated floodplain productivity across multiple trophic levels, nor compared floodplain segments to other river segment types in terms of ecosystem structure and function. In montane regions, for example, floodplain river segments are often juxtaposed between long canyon-confined segments. By pairing five confined river segments to five floodplain segments, I found that confined segments have greater allochthonous inputs than floodplains, but a lower capacity to retain those inputs, whereas floodplain segments have a high capacity to retain transported organic matter, and also a diverse assemblage of invertebrates and higher overall community respiration to "digest" this organic matter. On the other hand, I found little evidence that floodplain segments have higher aquatic primary production, nor invertebrate secondary production relative to confined segments. These findings suggest that confined segments are sources for organic matter within river networks, whereas floodplains act as filters, removing and processing organic matter transported from upstream confined segments. Thus, the function of floodplains in smaller montane systems may be different from that of larger temperate and tropical rivers where much productivity arises from longer and spatially extensive inundation of lateral floodplain surfaces (Junk et al. 1989; Lewis et al. 2001).

Consistent with floodplain theory (Winemiller 2004), however, my results do show that floodplains are hotspots of food web complexity. In the Methow River, food web diversity paralleled the diversity of habitat patches within the floodplain landscape. In particular, variation in hydrologic connectivity between the main channel and different side channels appeared to create distinct food web structures across the landscape. Endangered Chinook salmon and steelhead utilized all of these food webs, indicating that these species are flexible enough to exploit resources from a wide variety of habitat types within floodplains. This flexibility may be particularly important in the Methow River, where my results show that non-target fish species (i.e., mountain whitefish and sculpin) consume much of the prey base in main channel habitats. In contrast, side channels had a larger portion of energy flowing toward juvenile Chinook salmon and steelhead. In addition, side-channel habitats appeared to be under-seeded with respect to the invertebrate prey base, indicating that much more salmon and steelhead production could be sustained in these habitats. My research also showed that this mosaic of different food web types has important implications for overall landscape level biodiversity, food web complexity, and the strength of predator-prey interactions. By sequentially aggregating the food webs associated with individual habitat patches into a meta-food web for the floodplain landscape, I found that increasing landscape complexity was associated with increased biodiversity, greater food web complexity, and weaker average trophic interaction strengths. If hypotheses regarding the distribution of interaction strengths in food webs are correct (i.e., weak interactions promote stability; McCann 2000), then this finding has important implications for the diversity-stability debate, and indicates that floodplains may be nodes of stability for communities within river systems.

The impact of degradation that disconnects floodplains was evaluated by comparing a severely dredge-mined floodplain in the Yankee Fork Salmon River to five intact reference condition floodplains. Utilizing a simple ecosystem approach, I found that the dredged segment had comparable terrestrial leaf and invertebrate inputs, aquatic primary producer biomass, and production of aquatic invertebrates relative to five reference floodplains. Thus, the biotic productivity in the dredged segment did not necessarily appear impaired. Although this study has limited inference, it indicates that the consequences of habitat degradation on ecosystem function (i.e., biotic productivity) are not always straightforward, as has been demonstrated in other contexts (e.g., riparian logging can increase stream productivity, tailwaters below dams can be highly productive, etc.). Although I was unable to identify how the dredged segment was impaired, my results do show that previous habitat restoration in the dredged segment, which created several side channel habitat patches, significantly increased biotic productivity. This finding indicates that floodplain restoration efforts that reconnect and/or recreate side channel habitats may increase biotic productivity and the food base that fuels the production of target species, such as salmon and steelhead. Although not directly tested, results from my food web studies in the Methow River also indicate that restoration of these side channel habitats may increase biodiversity, food web complexity, and ecosystem stability.

The successful restoration of physical habitat or ecosystem function does not, however, guarantee that restoration will succeed at restoring the target species at which restoration may be aimed. In the Yankee Fork Salmon River (YFSR), for example, I found that the food base that fuels fish production was well above the demand for food by the fish assemblage, a result which indicates that fish populations may not be limited by food. Consequently, it is unclear whether or not further food production provided by habitat restoration would have any impact on the recovery of target salmon and steelhead. My findings demonstrate a simple lesson: while it is usually possible to identify a form (or forms) of “improvement” that might result from restoration, the true potential for a project to restore a target population cannot be assessed without evaluating whether or not restoration will address a factor that is limiting population recovery (Budy and Schaller 2007). Although my simple production/demand model is admittedly coarse, and may be inaccurate for a number of reasons, the outcome of this heuristic exercise emphasizes the need to more rigorously evaluate the role food may play in limiting fish populations. In many river systems alternative management and restoration strategies are applied founded on assumptions, often implicit, about food limitation. This is particularly evident in the Pacific Northwest, where multiple strategies, often with contradictory assumptions about food limitation, are utilized in the name of recovering anadromous salmonids (Williams and others 1999, ISAB 2011). For example, habitat restoration is implemented based on the assumption that food and/or habitat limit freshwater production of anadromous fish. Similarly, nutrient and salmon carcass analog additions are proposed under the same assumption. In contrast, hatchery supplementation is used as a tool in recovery, based on the assumption that ample resources (including food) exist to sustain supplemented fish. Without some measure of the degree to which food limits these populations, a key piece of the ecological rationale is missing for prioritizing alternative recovery actions for anadromous fishes.

In contrast to the YFSR, I found some evidence that food might limit fishes in the Methow River. In the main channel of the Methow River much of the invertebrate food base was consumed by non-target fish species, leaving little room for additional salmon and steelhead production. In contrast, side channels in the Methow River appeared to have ample food resources, which could likely support many more fishes. This result indicates that side channels are likely important to supporting anadromous fishes in the Methow, and that the reconnection/recreation of these habitats could potentially assist in population level recovery. That being said, my findings also indicate that currently existing side channels may be largely under-seeded with respect to food. Consequently, similar to the case of the YFSR, an alternative hypothesis is that not enough adult spawners are currently returning to the Methow River to fully seed these habitats. If true, this would indicate that factors outside of the Methow are limiting fish production (e.g., hydropower system, estuary habitat, ocean conditions).

River floodplain systems are a remarkable example of the heterogeneity and complexity found in nature. My research indicates that this heterogeneity has important consequences for ecosystem function and structure. However, my findings also illustrate that the impact of floodplain degradation on system function may not always be straightforward. Consequently, prior to spending significant monetary resources restoring perceived degradation, restoration efforts should be preceded by studies that evaluate if and how systems are impaired, and whether restoration is appropriate to alleviate impairment. When restoration is targeted at recovering single species of interest, pre-restoration studies should also be conducted to evaluate what, if any, factors limit these species, and whether restoration will alleviate these limitations. Future studies may benefit from the ecosystem and food web approaches utilized here, which elucidate the energetic pathways that sustain target species, and highlight the complex food webs within which these species are embedded.

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