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1 Running head: The floodplain food web mosaic

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3 **The floodplain food web mosaic: a study of its importance to salmon and steelhead with**
4 **implications for their recovery**

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46**Abstract**

Although numerous studies have attempted to place species of interest within the context of food webs, such efforts have generally occurred at small scales or disregard potentially important spatial heterogeneity. If food web approaches are to be employed to manage species, studies are needed that evaluate the multiple habitats and associated webs of interactions in which these species participate. Here, we quantify the food webs that sustain rearing salmon and steelhead within a floodplain landscape of the Methow River, Washington, USA, a location where restoration has been proposed to restore side channels in an attempt to recover anadromous fishes. We combined year-long measures of production, food demand, and diet composition for the fish assemblage with estimates of invertebrate prey productivity, to quantify food webs within the main channel and five different, intact side channels; ranging from channels that remained connected to the main channel at low flow to those reduced to floodplain ponds. Although we found that habitats within the floodplain had similar invertebrate prey production, these habitats hosted different local food webs. In the main channel, 95% of total prey consumption flowed to fishes that are not the target of proposed restoration. These fishes consumed 64% and 47% of the prey resources that were found to be important to fueling Chinook and steelhead production in the main channel, respectively. Conversely, in side channels, a greater proportion of prey was consumed by anadromous salmonids. As a result, carrying capacity estimates based on food were 251% higher, on average, for anadromous salmonids in side channels than the main channel. However, salmon and steelhead production was generally well below estimated capacity in both the main and side channels, suggesting these habitats are under-seeded with respect to food, and that much larger populations could be supported. Overall, this study demonstrates that floodplain heterogeneity is associated with the

47 occurrence of a mosaic of food webs, all of which were utilized by anadromous salmonids, and
48 all of which may be important to their recovery and persistence. In the long-term, these and
49 other fishes would likely benefit from restoring the processes that maintain floodplain
50 complexity.

51 **KEY WORDS:** floodplains, side channels, food webs, salmon, steelhead, ecosystem ecology,
52 secondary production

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Introduction

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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). However, most of these studies have been conducted at small scales, and do not investigate the spatial heterogeneity of landscapes within which species are embedded (Woodward and Hildrew 2002). The sub-discipline of 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 describing food webs for single habitats, or aggregating food web information over heterogeneous landscapes, it may be important to bridge the gap between food web and landscape ecology (Polis et al. 2004) by studying food webs across the variety of different habitats used by species of interest.

70 River floodplains are considered among the most biophysically complex and diverse
71 landscapes on earth (Bayley 1995, Tockner and Stanford 2002). Flood-pulses that redistribute
72 sediment and organic matter create a dynamic mosaic of aquatic and terrestrial habitat in
73 floodplains (Junk et al. 1989, Stanford et al. 2005). In the context of natural resource
74 management, the structure of food webs in these different habitats may be important to
75 sustaining species of interest (Winemiller 2004). Unfortunately, many river-floodplain systems
76 have been severely altered by human disturbance (Tockner and Stanford 2002), which has
77 constrained the physical processes that create and maintain habitat heterogeneity in floodplains.
78 (Tockner and Stanford 2002). This degradation, coupled with the desire to recover and preserve
79 species of concern, has resulted in increasing numbers of habitat restoration projects aimed at
80 floodplain reconnection (Bernhardt et al. 2005). Although pre-restoration assessments are now
81 commonly conducted to evaluate the potential for these efforts to succeed (e.g., Beechie et al.
82 2008), such studies are generally focused exclusively on physical habitat conditions (Wipfli and
83 Baxter 2010; NPCC 2011). The application of food web approaches in pre-restoration studies is
84 often over-looked, except in instances where food webs are being directly manipulated (e.g.,
85 nutrient additions, Kohler et al. 2012; predator removal/addition, Carpenter et al. 1985; etc.). In
86 the case of physical habitat restoration (e.g., floodplain reconnection), studies are needed which
87 not only evaluate how restoration will impact the quantity, quality and diversity of physical
88 habitats, but also how these changes will influence the flows of energy that sustain the species
89 restoration is often aimed at recovering.

90 In the Pacific Northwest of North America, floodplain restoration is often aimed at the
91 recovery of threatened and endangered Pacific salmon and steelhead (*Oncorhynchus spp.*) (Roni
92 et al. 2002). Although anadromous salmonids typically utilize many environments during their

93 complex life-cycle (ocean, estuary, large rivers, and headwaters), floodplains are targeted
94 because they are thought to contain important spawning and rearing habitats for these fish. For
95 example, floodplains have been shown to have more microhabitats (substrate, flow, depth and
96 temperature combinations) suitable for spawning and egg deposition (Montgomery et al. 1999,
97 Isaak et al. 2006). Furthermore, floodplain side channels are thought to be excellent nurseries for
98 juvenile fish, providing conditions favorable for growth, such as lower water velocity, moderated
99 water temperature, and enhanced food availability (Beechie et al. 1994, Sommer et al. 2001,
100 Ebersole et al. 2003, Jeffres et al. 2008). In fact, numerous floodplain restoration projects are
101 specifically targeted at reconnecting and/or recreating side channels to increase rearing capacity
102 for juvenile fishes (e.g., Richards et al. 1992, Bellmore et al. 2012). That said, floodplain
103 habitats are very diverse (e.g., ranging from large, highly connected channels to small, more
104 isolated channels), and are likely to contain food webs that are distinct from one another
105 (Winemiller 2004). Understanding how food webs vary across the floodplain habitat mosaic is
106 important, not only for evaluating the value of individual habitats to salmon and steelhead, but
107 also for assessing how overall landscape heterogeneity influences their populations.

108 In this study we apply food web and ecosystem approaches to investigate the mosaic of
109 floodplain habitats utilized by rearing salmon and steelhead in the Methow River, Washington
110 (USA; Figure 1). As in the case of many rivers throughout the Pacific Northwest, floodplain
111 reconnection has been identified as a priority for recovery of anadromous fishes in the Methow,
112 and pre-restoration assessments are needed to evaluate the potential for proposed restoration to
113 positively affect target species. We combined year-long measures of production, food demand,
114 and diet composition for the entire fish assemblage with estimates of invertebrate prey
115 productivity, to quantify food webs within the main channel and five different, intact side

116 channels; ranging from channels that remained connected to the main channel at low flow to
117 those reduced to isolated floodplain ponds. Together, this combination of food web and
118 ecosystem production-budget measurements allowed us to (a) elucidate dominant pathways of
119 material flow in different floodplain habitats, (b) assess the potential for food limitation of
120 populations of rearing Chinook salmon and steelhead, (c) evaluate the potential for exploitative
121 competition for food between target and non-target fishes, and (d) quantify the relative
122 importance of different habitats to sustaining juvenile salmon and steelhead production. Overall,
123 the results of this study highlight the importance of utilizing more holistic food web approaches
124 to understand the role of landscape heterogeneity in the ecology of species of conservation and
125 management concern.

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Methods

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Study Site and Design

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The Methow River is a fifth order tributary (4,662 km²) of the Columbia River, located in north-central Washington, USA (Figure 1). 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 River is typical of snow-melt dominated systems, with peak flows occurring in May and June, and peak discharges often exceeding 300 m³/s at the river mouth. Mean annual discharge for the period of record (1959 – present) is 43 m³/s, with a base flow of 5 m³/s (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

138 than 1,200 meters. Floodplain valley bottoms in the lower river are dominated by black
139 cottonwood (*Populus trichocarpa*) and aspen (*P. tremuloides*).

140 Prior to European settlement, the Methow River supported large runs of Chinook salmon
141 (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*) (Mullan et al.
142 1992). Today, runs of anadromous fish have been significantly depressed by a history of dams
143 and impoundments, water diversions, overfishing, exotic species and habitat degradation.
144 Currently, spring Chinook salmon are listed as endangered and summer steelhead as threatened
145 under the Endangered Species Act (ESA). Coho salmon, which were extirpated in the 1920s,
146 have recently been reintroduced, and small numbers have begun to spawn naturally in the
147 Methow. The resident (non-anadromous) fish assemblage of the Methow includes: westslope
148 cutthroat trout (*O. clarkia lewisi*; hereafter referred to as ‘cutthroat’), bull trout (*Salvelinus*
149 *confluentus*), rainbow trout (*O. mykiss*), mountain whitefish (*Prosopium williamsoni*; hereafter
150 referred to as ‘whitefish’), longnose dace (*Rhinichthys cataractae*; hereafter referred to as
151 ‘dace’), bridgelip sucker (*Catostomus columbianus*; hereafter referred to as ‘sucker’) and several
152 species of sculpin (*Cottus bairdi*, *C. confusus*, and *C. rhotheus*; hereafter referred to as
153 ‘sculpin’). Other fish species present in the Methow are native Pacific lamprey (*Lampetra*
154 *tridentata*), and non-native brook trout (*S. fontinalis*), brown bullhead (*Ameiurus nebulosus*), and
155 smallmouth bass (*Micropterus dolomieu*). However, these species were rare at the time and
156 place of our study, and were not included in our analyses. In addition, because we could not
157 distinguish between anadromous and resident rainbow trout, hereafter we refer to all rainbow
158 trout as ‘steelhead.’

159 The floodplain segment that has been targeted for restoration in the Methow is located
160 between the confluences with the Twisp and Chewuch Rivers (Figure 1). This 13.5 km long

161 segment has been developed for agricultural and residential use, and sections have been diked
162 (i.e., rip-rapped banks) to protect private property, leading to the disconnection of the river from
163 the floodplain. Despite of this degradation, large portions of the river and associated floodplain
164 remain relatively intact, and numerous side channel complexes still exist.

165 To evaluate the importance of different floodplain habitats to juvenile Chinook salmon
166 and steelhead, we quantified fish and invertebrate prey production, and constructed quantitative
167 flow food webs in six different floodplain aquatic habitats. These six habitats included the main
168 channel of the restoration segment, and five intact side channels, which varied naturally in their
169 level of hydrologic connectivity to the main channel. Three of the five side channels were
170 located within the restoration segment and two were located upstream (Figure 1). During spring
171 run-off (April-June), all side channels had both an upstream and downstream surface water
172 connection to the main channel, allowing aquatic organisms, including juvenile salmon and
173 steelhead, to move between side channels and the main channel. As flows receded, three of the
174 side channels became disconnected from the main channel and were eventually reduced to one or
175 more isolated pools, whereas two side channels retained some level of surface water connection
176 to the main channel year-round (see Appendix A for habitat photographs). For convenience, we
177 refer to the five side channels according to their level of hydrologic connectivity with the main
178 channel under low flow conditions during the period of our study (2009-10): ‘*con updwn*’ refers
179 to the side channel that retained both up and downstream surface water connections; ‘*con dwn*’ is
180 the side channel with only a downstream surface water connection; ‘*discon lrg*’ is disconnected
181 from the main channel but retained one relatively large pool; ‘*discon sml*’ is disconnected and
182 mainly represented by one small pool; and ‘*discon noscr*’ is disconnected with large pools, but in
183 contrast to the other side channels, its bed was not scoured by high flows during the study period.

184 Together, these five side channels, along with the main channel, represented a range of
185 hydrologic conditions (i.e., connectivity and disturbance history), physical character (e.g.,
186 temperature) and habitat dimensions (Table 1).

187

188 *Habitat Measurements*

189 Habitat surveys of each side channel were conducted approximately monthly during 2009
190 and 2010. Surveys measured the area (lengths and widths), average and maximum depth, and
191 proportion of different channel units (e.g., pools, riffles, glides, etc.) present. The area and
192 proportion of different channel units present in the main channel were determined from a single
193 survey completed in summer 2009. Water temperatures were recorded for the main channel and
194 each side channel during summer, fall and winter (except in a few cases; see Table 1) using
195 Onset HOBO[®] data loggers. Water temperature was not monitored during the spring due to high
196 flows.

197

198 *Invertebrate Food Base Productivity*

199 We sampled benthic substrates for invertebrates in the main channel and each side
200 channel in June, August and October of 2009 and March 2010. June sampling occurred while all
201 side channels were still connected to the main channel. On each date, we collected at least three
202 replicate samples from each habitat, and in August we collected five samples. We collected all
203 benthic samples using a modified Surber sampler (250 μm mesh) that was attached to a shovel
204 handle, and which had a sample quadrat larger than traditionally sized Surber samplers (0.26 m^2
205 compared to 0.096 m^2). One person held the sampler in place, while another disturbed substrate
206 to a depth of ~ 10 cm. Each of our replicate samples represented a composite of several sub-

207 samples ($n = 3-11$), which we collected in proportion to the different channel unit types present
208 (e.g., riffles, pools, etc.) within each habitat. When sub-samples were combined, each replicate
209 sample incorporated the perceived variation within each habitat, for each sampling date. As a
210 result of this sub-sampling scheme, and the larger size of our Surber sampler, each replicate
211 sample in this study represented 0.8 to 2.9 m² of benthic area, which is at least 8X greater than
212 the benthic area sampled from a single sample using a traditional Surber sampler. Although we
213 sacrificed the ability to quantify variation within each habitat (i.e., between channel unit types)
214 using this approach, it allowed us to better represent the habitat as a whole, without significantly
215 inflating the total number of samples to be processed. Although we acknowledge that it would
216 have been ideal to have a larger sample size, we were limited by the amount of time necessary to
217 process each sample in the lab. We elutriated all samples through a 250 μm sieve and removed
218 as much of the inorganic material as possible. The remaining sample was preserved in 95%
219 ethanol. In the lab, a two-phased sorting approach was utilized (after Vinson and Hawkins
220 1996). In the first phase, all large invertebrates (≥ 10 mm) were removed from the sample. In
221 the second phase, successive subsamples were removed and sorted at 10X magnification until at
222 least 500 individuals were picked. We identified all invertebrates to genus or species, except for
223 Chironomidae, which we split into Tanypodinae and non-Tanypodinae. All invertebrates were
224 then dried at 60°C for 24 hrs and weighed. We used these seasonal data to calculate the mean
225 annual biomass of each taxon for each habitat. We calculated 95% confidence intervals for mean
226 biomass estimates via bootstrapping (see Benke and Huryn 2006), whereby the biomass of each
227 taxon for each habitat on each date was resampled with replacement 10,000 times to generate
228 10,000 separate estimates of mean annual biomass.

229 In order to estimate invertebrate secondary production, we collected a single composite
230 sample from the main channel and one side channel (*discon noscr*) at approximately monthly
231 intervals (June 2009 to June 2010). We processed these samples following the same methods
232 described above, except that we measured the lengths of all individual invertebrates to the
233 nearest 0.5 mm. The biomass of each taxon was then calculated using literature-based length-
234 weight relationships (Benke et al. 1999). We then estimated secondary production for all
235 common taxa using the size-frequency method (Benke and Huryn 2006), corrected for our best
236 estimate of cohort production interval from size-frequency data (see Benke and Huryn 2006).
237 Two additional estimates of non-Tanypodinae chironomid production were calculated using the
238 instantaneous growth method, based on the size- and temperature-specific equations of Huryn
239 (1990) and Walther et al. (2006). The three separate estimates of non-Tanypodinae chironomid
240 production were averaged for use in this study. We calculated production to biomass ($P:B$)
241 ratios by dividing production in each of these habitats by the average taxon biomass for that
242 habitat. Production at all habitats was then calculated by multiplying $P:B$ estimates by mean
243 annual biomass of each taxon within each habitat. To account for potential differences in
244 invertebrate growth rates between connected and disconnected habitats, $P:B$ estimates from the
245 *discon noscr* habitat were applied to all disconnected side channels (*discon lrg*, *discon sml*,
246 *discon noscr*), whereas $P:B$ values from the main channel were applied to connected side
247 channels (*Con updown*, *Con down*) and the main channel. Of course, $P:B$ values for similar taxa
248 could differ across all habitat types. However, in terms of estimating total invertebrate
249 secondary production, we assumed that uncertainty associated with taxon specific $P:B$ values
250 would be relatively minor compared to measured differences (and associated uncertainty) in the
251 composition and biomass of invertebrates across habitats. For rare taxa, we estimated secondary

252 production using published annual *P:B* ratios. When available, we used *P:B* ratios from nearby
253 production studies (Gaines et al. 1992, Robinson and Minshall 1998). Total annual benthic
254 invertebrate production was calculated as the sum of taxon specific production.

255 We measured terrestrial invertebrate flux to the main channel and each side channel
256 monthly (July, August, September) during summer 2009. We placed 10-12 pan traps (0.21 m²)
257 at the wetted edge of the stream at each habitat. Pans were distributed in proportion to the
258 presence of different riparian vegetation types (e.g., willow, cottonwood, conifer), because
259 invertebrate inputs are known to vary with riparian vegetation (Baxter et al. 2005). Traps were
260 filled with approximately 5 cm of water and a few drops of biodegradable soap to reduce water
261 surface tension. After collecting for three days, invertebrates were removed with dip nets (500
262 μm mesh). In the lab, we sorted samples under a dissecting scope to remove aquatic taxa. The
263 remaining terrestrial taxa were identified to order, dried at 60°C for 24 hrs and weighed. We
264 calculated total inputs by multiplying average daily fluxes by the number of days in each month.

265

266 *Fish Abundance, Biomass and Production*

267 We estimated the abundance of all but the rarest members of the fish assemblage using a
268 combination of snorkeling and electro-fishing. In side channels, the abundance of all salmonids
269 was calculated seasonally (June, August, and October 2009; and March 2010), using the
270 removal-depletion method (White et al. 1982). Block nets were placed at the upstream and
271 downstream of individual channel units (riffles, pools, glides, etc.) within each side channel, and
272 multiple electro-fishing passes were completed until an adequate depletion was achieved
273 (following Connolly 1996). Mark-recapture electro-fishing was utilized in channel units that
274 were too wide and/or deep to allow for adequate depletions. In channel units that were too deep

275 for electro-fishing, fish abundance was estimated with snorkeling. Captured fish were measured
276 for length and weight, and implanted with a passive integrated transponder (PIT) tag, to allow for
277 later detection of previously captured fish. Although these surveys were targeted at salmonids,
278 the numbers of non-salmonids (dace, sculpin, and sucker) were also recorded, and several
279 individuals of each species were captured to obtain lengths and weights. To estimate the
280 abundance of non-salmonids, we first calculated the capture efficiency for the first pass of
281 fishing surveys, obtained by dividing the number of salmonids captured on the first pass by the
282 total salmonid population estimate for that channel unit, which was approximately 0.5 for pools,
283 0.6 for riffles and 0.9 for glides/runs. We then multiplied these capture efficiencies by the
284 number of individuals of each non-salmonid species observed in different channel unit types.
285 Error for these estimates was calculated by propagating the standard error associated with the
286 salmonid electro-fishing depletions with the variance in capture efficiency for different channel
287 unit types (i.e., variance in capture efficiencies for riffles, runs, etc.), following standard
288 equations for error propagation (see Taylor 1997).

289 In the main channel, snorkel surveys were conducted approximately monthly to estimate
290 the abundance of larger fish (>150 mm) during 2009 and 2010. Surveys were not conducted
291 during mid-winter (December to February) and during high spring flows (April to June). Briefly,
292 four snorkelers would float downstream over an 8 km section of the main channel and enumerate
293 fish by species and size class (size classes: 150-300 mm, 300-500 mm, and >500 mm). Error of
294 snorkel estimates was determined by conducting three consecutive downstream surveys over a
295 three day period. To account for observation efficiency, we divided snorkel abundance estimates
296 by 0.40; a value that was determined by tagging a small sample of whitefish (n=30) with visible
297 tags, and counting how many tagged fish were observed the following day. To estimate the

298 abundance of juvenile salmonids (< 150 mm), the stream margin of three 400 to 800 m main
299 channel segments were single-pass electro-fished once in July 09, October 09, and March 10.
300 We estimated sculpin abundance in the main channel by sampling three randomly selected riffles
301 and three runs, within which we collected three quantitative sub-samples by electro-fishing
302 within the metal quadrat of the Surber sampler (0.26 m²). Because none of these methods were
303 appropriate for estimating the abundance of dace, we assumed dace abundance was similar to
304 that observed in the side channels where dace were present. We converted all fish abundance
305 estimates to areal biomass (g/m²), by multiplying by the average weight (g) of each species
306 within each habitat and then dividing by habitat area (m²). We converted wet biomass to dry
307 mass (DM) by assuming 80% water content for juvenile fish and 75% water content for adult
308 fish and sculpin (see Warren and Davis 1967, Elliot 1976, Berg and Bremset 1998).

309 We estimated annual secondary production of each fish species using the instantaneous
310 growth rate method (Hayes et al. 2007), whereby we multiplied the average annual biomass of
311 each species and age class, by size- and habitat-specific annual growth rates (or annual $P:B$
312 ratios). For all salmonids and suckers, growth rates were determined from recapture of marked
313 individuals. For whitefish, we calculated size-specific growth rates from length-at-age data,
314 which were determined by analyzing scales from approximately 80 fish (range: 190 – 500 mm
315 fork length). For sculpin, we conducted multi-pass electro-fishing depletions within one run and
316 one riffle in the *con updown* and *con down* habitats, which allowed us to calculate production for
317 these locations using the size-frequency method (Hayes et al. 2007). Sculpin production
318 estimates were subsequently divided by sculpin biomass in these habitats to estimate annual $P:B$
319 ratios. Sculpin production in all habitat types was then calculated by multiplying $P:B$ ratios by
320 average annual sculpin biomass. We estimated dace production by applying a $P:B$ ratio derived

321 from the literature (Neves and Pardue 1983). Error in production estimates was calculated by
322 propagating the standard errors associated with fish biomass and growth rate (Taylor 1997).

323

324 *Gut Content Analysis*

325 We collected gut content samples from all but the rarest members of the fish assemblage
326 seasonally in the main channel and each side channel (total $n = 375$). Diet samples for side
327 channels were collected during electro-fishing surveys. In the main channel, fish were captured
328 for diets using a combination of techniques, including trammel and gill netting, electro-fishing,
329 and angling. At each habitat on each date, we attempted to collect at least five diet samples from
330 all salmonid species, four from sculpin and three from dace and juvenile suckers. We stratified
331 steelhead sampling by age 0 and 1+. For salmonids > 75 mm and for all sculpin, we collected
332 gut contents via gastric lavage and preserved them in 70% ethanol. For dace and suckers,
333 individuals were sacrificed, preserved in 95% ethanol, and gut contents were later extracted by
334 removing the first 10% of the digestive tract. In the laboratory, we identified and measured the
335 length and head width of all prey items in fish diets. Invertebrate prey items were identified to
336 the family level and fish found in diets were identified to species. Invertebrate lengths and head
337 widths were converted to biomass using published regressions (Benke et al. 1999). The lengths
338 of fish found in diets were converted to biomass using length-weight regressions developed
339 using electro-fishing data. Dietary proportions were based on the proportion that each food item
340 contributed to total weight of gut contents. Diet proportions were averaged across all individuals
341 of each species at each habitat on an annual basis.

342

343 *Trophic Basis of Production and Flow Food Webs*

344 We quantified organic matter flows to all fish using the trophic basis of production (TBP)
 345 method, which estimates (a) contributions of different prey to fish production, and (b) rates of
 346 resource consumption that support measured rates of fish production (Benke and Wallace 1980,
 347 Cross et al. 2011). The relative fraction of annual fish attributed to each prey type (F_i) was
 348 calculated as:

$$349 \quad F_i = G_i \times AE_i \times NPE$$

350 where G_i = proportion of prey type i in fish diet, AE_i = assimilation efficiency of prey type i , and
 351 NPE = net production efficiency. For each fish species j , the proportion of fish production
 352 attributed to each prey type (PF_{ij}) was then calculated from the relative fractions (F_i) as:

$$353 \quad PF_{ij} = \frac{F_i}{\sum_{i=1}^n F_i}$$

354 Lastly, annual flows from each prey type i to fish consumer j (FC_{ij} measured in $\text{g DM} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$)
 355 were calculated as:

$$356 \quad FC_{ij} = \frac{PF_{ij} \times P_j}{AE_i \times NPE}$$

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

358 We used the following assimilation efficiencies for all salmonid species: 0.75 for aquatic
 359 invertebrates, 0.70 for terrestrial invertebrates, and 0.95 for fish tissue (see Warren 1971,
 360 Brocksen and Bugge 1974, Elliot 1976, Warren and Davis 1976). Diets of non-salmonids
 361 consisted almost entirely of aquatic invertebrates and assimilation efficiencies were set at: 0.90
 362 for dace, 0.85 for sucker, and 0.82 for sculpin (see Davis and Warren 1965, Atmar and Stewart
 363 1972, Eiriksdottir 1974). Net production efficiency values were set at 0.125 for adult fish (bull
 364 and cutthroat trout, steelhead and whitefish), whereas a production efficiency of 0.250 was used

365 for juvenile salmonids (< 150 mm) and all non-salmonid species (Donner 2011, Cross et al.
366 2011). We applied different net production efficiencies for juvenile and adult fish to account for
367 the allometric relationship between fish consumption and growth with fish size (i.e., larger, older
368 fish spend proportionately more energy on maintenance than on growth). A previous study on
369 rainbow trout (Donner 2011) found that this coarse adjustment in production efficiency was
370 adequate to generate estimates that were comparable to a more highly parameterized Wisconsin
371 type (Hanson 1997) bioenergetics model. Although assimilation and production efficiencies
372 might also vary with temperature, we assumed that differences in fish production across habitat
373 types, and the uncertainty associated with these estimates, would outweigh any relatively small
374 differences in assimilation and production efficiencies.

375

376 *Interaction Strength, Interspecific Competition, and Carrying Capacity*

377 The potential strengths of interactions between fish predators and each invertebrate prey i
378 were calculated as (Woodward et al. 2005; Benke 2011):

379
$$I_i = \frac{FC_i}{PP_i}$$

380 where FC_i = total annual consumption of prey type i (g DM·m⁻²·y⁻¹) by the fish assemblage, and
381 PP is the annual production of prey type i . This metric, hereafter termed ‘interaction strength,’ is
382 a unit-less value, ranging from 0 to 1, which represents the proportion of annual prey-specific
383 production consumed by the fish assemblage. Values greater than 1 (i.e., the fish assemblage is
384 consuming more than is being produced) are energetically impossible, and indicate potential
385 errors in our estimates of invertebrate production, fish production, and/or fish dietary
386 proportions. In our results, however, values >1 were simply reported as 1 (i.e., prey production
387 = consumption). In a few cases, it appeared that discrepancies between production and demand

388 were the result of dietary proportions skewed by individual fish that may have been feeding
 389 outside of our study habitats. These individuals were identified by diet compositions dominated
 390 by prey taxa that appeared to be rare or absent at the location where they were sampled. In total,
 391 we identified only three of these individuals, which we removed from the analysis. Although
 392 individual fish may accrue production outside of the habitats where they were sampled, we
 393 assumed that this was balanced by fish movement and foraging both inside and outside of each
 394 habitat.

395 To evaluate potential for exploitative competition for prey between each fish species j
 396 and the rest of the fish assemblage h , we calculated ‘competition coefficients’ (CC) as:

$$397 \quad CC_j = \sum_{i=1}^n \frac{FC_{ih}}{PP_i} \times PF_{ij}$$

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

405 Finally, we estimated the potential level of juvenile Chinook and steelhead production (g
 406 $\text{DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) that could be sustained ($PotenP$) per area within each habitat, which we considered
 407 an estimate of carrying capacity with respect to food resources. This was calculated as:

$$408 \quad PotenP_j = \sum_{i=1}^n ((PP_i - FC_{ih}) \times AE_{ij} \times NPE_j \times PF_{ij})$$

409 where AE_{ij} and NPE_j are assimilation and net production efficiencies for prey type i by fish j (i.e.,
410 juvenile Chinook or steelhead). This metric assumes: (1) that production by all other members
411 of the fish assemblage does not change, (2) that the dietary proportions of all members of fish
412 assemblage (including Chinook and steelhead) remain static, and (3) that Chinook and steelhead
413 are able to perfectly track the production of their prey. Although these assumptions may not be
414 realistic in all cases, these assumptions were imperative for deriving relative per meter squared
415 estimates of carrying capacity for juvenile Chinook and steelhead in terms of food. Assessing
416 carrying capacity estimates for the entire river segment would simply require scaling these per
417 meter squared estimates by the area of different aquatic habitat types within the floodplain.
418 However, at the time of this study, the habitat information necessary to conduct this additional
419 analysis was not available.

420

421 *Statistical Analyses*

422 To evaluate differences in prey production versus fish demand, we visually compared
423 percentile 95% confidence intervals (Huryn 1996, 1998; Cross 2011). Means with non-
424 overlapping confidence intervals were interpreted as significantly different. We analyzed trophic
425 basis of production data via nonmetric multidimensional scaling (NMDS), followed by
426 multiresponse permutation procedures (MRPP) to test for differences in TBP among different
427 habitats and species (Mielke and Berry 2001). In addition, we utilized permutation-based
428 nonparametric MANOVAs to evaluate the amount of variation in TBP explained by both habitat
429 type and species (Anderson 2001). Simple linear regression was conducted to explore potential
430 relationships between water temperature, and the production, biomass and growth of key
431 invertebrate and fish taxa. However, we could only conduct this analysis using summer water

432 temperature data, because we lacked temperature data for all habitats during the fall, winter and
433 spring (see Table 1).

434

435 **Results**

436 *Fish Production, Prey Production and Total Consumption by Fishes*

437 Total estimated fish assemblage production in the main channel was $1.38 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$,
438 and was consistently greater than fish production on a per area basis in side channels, which
439 ranged from 0.11 to $0.63 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Figure 2a). Approximately 95% of the production in the
440 main channel was by sculpin and whitefish. The composition of fish production varied greatly
441 among side channels that differed in connectivity with the main channel. In the three side
442 channels that were disconnected from the main channel at low flow, a larger number of species
443 contributed more evenly to total fish production, with 52% to 70% being comprised of
444 salmonids, principally juvenile steelhead, along with juvenile coho and Chinook salmon. On the
445 other hand, production in the two side channels that remained connected to the main channel was
446 dominated by sculpin. Absolute production per area by Chinook and steelhead was generally
447 highest in disconnected side channel habitats (Figure 2a). Whitefish, cutthroat and bull trout
448 were rarely encountered in side channels (see Appendix B for fish abundance, biomass and
449 production estimates). Water temperature was not found to be significantly related to fish
450 production, biomass or growth, except for Juvenile Chinook salmon growth rate, which had a
451 significant positive relationship with average summer water temperature (R -squared = 0.73, P =
452 0.03).

453 Total aquatic invertebrate production was higher in the main channel ($14.1 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$)
454 than most side channels (4.7 to $18.8 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$; Figure 2b) (see Appendix C for taxon-specific

455 estimates of biomass, production, and $P:B$. In contrast, the input of terrestrial invertebrates was
456 generally higher in side channels (2.9 to 20.8 g DM·m⁻²·y⁻¹) than in the main channel (4.7 g
457 DM·m⁻²·y⁻¹), but was highly variable among habitats (Figure 2b). When terrestrial inputs were
458 added to benthic invertebrate production, total invertebrate prey production did not significantly
459 differ between habitats, except for in *discon noscr*, which had higher prey production than the
460 two other disconnected side channels (Figure 2c). Water temperature was not found to be
461 significantly related to invertebrate production, biomass or $P:B$.

462 Demand for invertebrate prey by the fish assemblage (i.e., consumption) in the main
463 channel was not significantly different (non-overlapping 95% CIs) than invertebrate production
464 (Figure 2c). In contrast, invertebrate production in side channels was consistently higher (on
465 average 20X higher) than demand by the fish assemblage. In particular, the two connected side
466 channels had over 25X more prey production than estimated fish demand.

467 *Trophic basis of production*

468 In the main channel, nearly 80% of the production by the entire fish assemblage was
469 fueled by only four prey taxa: Chironomidae, Brachycentridae, Ephemerellidae, and Tipulidae
470 (Figure 3). In contrast, across all side channels, a comparable proportion of total fish assemblage
471 production was fueled by at least 6 and up to 13 prey taxa (Figure 3). The contribution of more
472 lentic taxa (e.g., *Daphnia*, Amphipoda, Isopoda, Leptophlebiidae) was highest in the less
473 connected side channels (*discon lrg*, *discon sml*, and *discon noscr*), sustaining between 16% and
474 71% of total fish production (see Appendix D for detailed information on prey contributions to
475 fish diet). Total fish assemblage production in the two side channels that were more connected
476 (*con dwn* and *con updwn*) was derived from more lotic taxa, though the contributions were more

478 evenly distributed among prey than was the case in the main channel. Total fish production
479 derived from terrestrial invertebrates in side channels ranged from 3.2% to 10% and was always
480 at least double that of the main channel (1.4%). Within each habitat, the production of different
481 fish species was largely derived from similar prey taxa (see Appendix E for TBP figures for each
482 fish species). In the main channel, Chinook and steelhead had the most similar TBP. However,
483 at least 45% of production for all fish species in the main channel, except for cutthroat and bull
484 trout, was sustained by the same five taxa: Chironomidae, Brachycentridae, Ephemerellidae,
485 Tipulidae, and Lepidostomatidae. In contrast, cutthroat and bull trout production was derived
486 from much higher proportions of terrestrial insects (32%) and fish (>99%), respectively.

487 In the two most connected side channels, Chinook, steelhead and sculpin all had similar
488 TBP (see Appendix E for TBP figures for each species), although sculpin production generally
489 lacked contributions from terrestrial invertebrates. Over 40% (and up to 67%) of production by
490 Chinook, steelhead and sculpin within these habitats was attributable to the same six taxa:
491 Chironomidae, Ephemerellidae, Lepidostomatidae, Limnephilidae, Baetidae, and Heptageniidae.
492 In the disconnected side channels that had scoured during high flows (*discon lrg* and *discon sml*),
493 the proportion of fish production sustained by each prey item was highly variable between
494 species. However, between 30% and up to 100% of production for each fish species was
495 attributed to the same six prey taxa: Chironomidae, Leptophlebiidae, *Daphnia*, Baetidae,
496 Limnephilidae, and Heptageniidae. In both habitats, suckers derived all of their production from
497 only two prey taxa—Chironomidae and *Daphnia*. In the side channel that did not scour during
498 high flows (*discon noscr*), all five fish species had very similar TBP, with at least 50% of
499 production by each species sustained by only four prey items: Chironomidae, Amphipoda,
500 Isopoda and Limnephilidae.

501 Variation in the composition of fish TBP among habitats reflected differences in the level
502 of hydrologic connectivity with the main channel (Figure 4). The NMDS ordination for each
503 species-habitat combination, which explained 64% of the variation in TBP, showed almost
504 complete separation between side channels connected to the main channel versus those that were
505 disconnected at low flow (MRPP, $A = 0.145$, $P < 0.001$). Connected side channels and the main
506 channel were separated in the ordination from disconnected side channels along axis 2, which
507 explained 32% of the variation in TBP. Although both species and habitat type were significant
508 factors in explaining total variation in the TBP data (perMANOVA, $P < 0.05$), habitat explained
509 2.5X more variation than species (35% versus 14%).

510

511 *Flow Food Webs*

512 The direction and magnitude of organic matter flowing between fish and their prey
513 differed between the main channel and side channels, and also among side channels (Figure 5).
514 The overall magnitude of organic matter flow to the entire fish assemblage (i.e., consumption)
515 was highest in the main channel ($9.82 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) and lowest in the connected side channels
516 ($con\ updown = 0.66$ and $con\ down = 0.57$) reflecting differences in fish production (Figure 2a). In
517 the main channel, 94% of all invertebrate flows were to whitefish and sculpin (Figure 5a). The
518 highest magnitude flows in the main channel were from Brachycentridae to whitefish (2.6 g
519 $\text{DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), Chironomidae to sculpin (2.0) and whitefish (0.8), Ephemerellidae to sculpin (0.9),
520 and Tipulidae to sculpin (0.62). In the two connected side channels, $con\ updown$ and $con\ down$,
521 approximately 62% and 53% of invertebrate flows were to sculpin, respectively (Figure 5b and
522 c). At the $con\ updown$ side channel, the five highest magnitude flows were all to sculpin,
523 including: Limnephilidae ($0.8 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), Chironomidae (0.7), Baetidae (0.05), Perlidae

524 (0.05), and Perlodidae (0.05). At the *con dwn* side channel the largest flows were from
525 Ephemerellidae to sculpin ($0.07 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), Chironomidae to sculpin (0.06), Heptageniidae to
526 sculpin (0.04), Lepidostomatidae to juvenile steelhead (0.04), and Perlidae to sculpin (0.03).

527 Invertebrate flows in the disconnected side channels were more evenly distributed among
528 fish species (Figure 5d – f). In particular, flows of invertebrates to Chinook were on average
529 19X greater, whereas flows to sculpins were 95% lower than in connected side channels and the
530 main channel. At the *discon lrg* side channel, 38% of invertebrate flow was to Chinook, 37% to
531 suckers, and 17% to steelhead (Figure 5d). The largest magnitude flows were: Chironomidae to
532 suckers ($0.43 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) and Chinook (0.19), Heptageniidae to Chinook (0.10), *Daphnia* to
533 suckers (0.08), and Baetidae to Chinook (0.05). Similar to the *discon lrg* side channel, 40% of
534 invertebrate flows at the *discon sml* side channel were to Chinook, 30% to suckers and 18% to
535 steelhead (Figure 5e). The five largest magnitude flows were from *Daphnia* to suckers (0.54 g
536 $\text{DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), Chironomidae to suckers (0.44) and Chinook (0.49), Leptophlebiidae to Chinook
537 (0.30), and terrestrial invertebrates to Chinook (0.16). At the *discon noscr* side channel, 46% of
538 all invertebrate flows were to coho, 28% to suckers and 18% to Chinook. The largest magnitude
539 flows were from amphipods to coho ($0.20 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) and suckers (0.12), isopods to coho
540 (0.20), terrestrial invertebrates to coho (0.11), and chironomidae to suckers (0.11) (Figure 5f).

541 A small portion of organic matter flow, generally less than 5% within each habitat,
542 occurred along piscivorous pathways (Figure 5). The largest magnitude piscivorous fluxes were
543 consumption of steelhead by sculpin at *con updown*, the consumption of sculpin by other sculpin
544 at *con dwn*, and consumption of dace by cutthroat in the main channel. Although bull trout in
545 the main channel consumed nearly 100% fish (see Appendix B for TBP figures for each species),

546 their production and associated food demand was small (Figure 2a), and as a result, the total
547 piscivorous flux to bull trout was low (Figure 5a).

548

549 *Interaction Strength, Competition Coefficients and Carrying Capacity*

550 Estimates of the proportion of taxa-specific prey production consumed by the entire fish
551 assemblage revealed that fish interacted more strongly with their prey in the main channel than
552 in any of the side channels (Figure 6, left panel). Of the top 15 prey taxa consumed by fish in the
553 main channel, 9 had interaction strengths ≥ 0.9 , indicating that the fish assemblage consumed a
554 majority of production of those prey (Figure 6a) (see Appendix C for taxon-specific estimates of
555 invertebrate production). In contrast, the two connected side channels combined had only one
556 interaction strength that was ≥ 0.9 (Figure 6b, c). The number of interactions > 0.9 in the three
557 disconnected side channels ranged from a high of 6 in *discon sml* to 0 in *discon noscr* (Figure 6d,
558 e, f).

559 Competition coefficients, which represented the proportion of prey important to the TBP
560 of a selected fish species that was consumed by other members of the fish assemblage, reflected
561 general differences in interaction strengths among habitats (Figure 6, right panel). In general,
562 fish in the main channel had the highest competition coefficients, ranging from 0.21 for whitefish
563 to 0.60 for dace (Figure 6a). Connected side channels had the lowest values, ranging from: 0.05
564 for sculpin to 0.09 for steelhead in *con updown*, and 0.07 for sculpin to 0.12 for Chinook in *con*
565 *dwn* (Figure 6b, c). Disconnected side channels had values intermediate to those in the main
566 channel and connected side channels, ranging from: 0.08 for sucker to 0.20 for steelhead and
567 coho in *discon lrg*; 0.7 for sucker to 0.55 for steelhead in *discon sml*; and 0.05 for suckers to 0.15
568 for sculpin in *discon noscr* (Figure 6d, e, f).

569 Based on our estimates of existing food resources, the potential amount of Chinook and
570 steelhead production that could be supported on a per area basis in each habitat was on average
571 25X higher than measured production levels for Chinook and 15X greater for steelhead (Figure
572 7). However, within the *Discon lrg* and *Discon sml* side channels, both juvenile Chinook and
573 steelhead appeared to be at or approaching estimated carrying capacity. In the *Discon sml* side
574 channel, measured steelhead production was actually slightly above estimated carrying capacity,
575 which is energetically impossible. This finding likely reflects error in our estimates of both
576 measured fish production and modeled carrying capacity. We estimated that the highest levels of
577 fish production could be supported in *Discon noscr* for steelhead ($0.94 \text{ g DM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) and
578 Chinook (0.98), followed by the *Con updown* side channel (Figure 7). The lowest carrying
579 capacities values were found in the main channel for Chinook (0.16), and the *Discon sml* side
580 channel for steelhead (0.06).

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Discussion

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Consistent with the paradigm that floodplains are hotspots of biophysical complexity
(Junk et al. 1989, Bayley 1995, Stanford et al. 2005), our findings show that floodplains can also
be hotspots of food web complexity. Food web variability in the Methow River floodplain
paralleled the diversity of different habitats 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. 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 habitats. This flexibility may be particularly
important in the Methow River, as fish species that are not the focus of restoration (i.e., mountain

592 whitefish and sculpin) dominated prey consumption in the main channel, resulting in potentially
593 strong competition for food. However, carrying capacity estimates for both the main channel
594 and side channels suggest that Chinook salmon and steelhead are currently under-seeded with
595 respect to the available prey base. If true, this finding would indicate that the floodplain segment
596 of the Methow River studied here could potentially support much greater anadromous salmonid
597 populations. Overall, these findings illustrate that habitat complexity, such as that found in
598 floodplain landscapes, may be important to sustaining salmon and steelhead populations, and that
599 restoration aimed at preserving and restoring the processes (i.e., large wood recruitment, cut and
600 fill alluviation, etc.) that create and maintain this complexity may be appropriate in the Methow
601 River.

602 By applying this approach across multiple habitats within a complex floodplain
603 landscape, we observed substantial variation in food web structure (i.e., the organic matter
604 flows). Differences in food web structure (i.e., the direction and magnitude of organic matter
605 flows) among floodplain habitats were primarily driven by differences in fish assemblage
606 composition and production. For example, habitats with the highest magnitude organic matter
607 flows (i.e., consumption) also had the highest levels of total fish production. In particular, the
608 distribution and abundance of whitefish and sculpin strongly controlled organic matter flow.
609 Sculpin were the most productive fish species in both the main channel and connected side
610 channels and dominated organic matter flows in these habitats. In contrast, sculpin were much
611 less productive in disconnected habitats, and hence their consumption represented only a small
612 proportion of total organic matter flows. Similar to sculpin, whitefish were also very abundant in
613 main channel habitats but were virtually absent from side channels, which is not surprising given
614 their propensity for larger streams and rivers (Northcote and Ennis 1994). The Methow is not

615 unique with respect to high production of sculpin and whitefish. In fact, these and other non-
616 salmonid species are common, and often highly abundant, throughout much of the range
617 occupied by salmon and steelhead (Wydoski and Whitney 2003, Lance and Baxter 2011).
618 However, relatively little work has been conducted on their trophic ecology or their potential
619 interactions within riverine food webs.

620 The degree of potential exploitative competition between target and non-target fishes for
621 food was dependent on the demand for shared prey items and the productivity of those prey
622 items in the environment. For instance, even though sculpin dominated organic matter flows in
623 the two connected side channels, their estimated impact on anadromous salmonids via
624 exploitative competition was low because production for shared prey items was generally well
625 above consumption. As a result, potential competition for food (i.e., competition coefficients),
626 or the proportion of prey items important to Chinook or steelhead consumed by other species,
627 was low. In the main channel, however, sculpin and whitefish consumed a majority of the prey
628 base, resulting in much higher levels of potential exploitative competition with Chinook and
629 steelhead. In disconnected side channels, non-target fish production was low and competition
630 for food was generally intermediate between the main channel and connected side channels, and
631 was largely attributable to competition between Chinook and steelhead. These findings highlight
632 the need for improved estimates of production by species like whitefish and sculpin. However,
633 given the magnitude of these species role and the estimated differences between main versus side
634 channels, we expect our basic findings would be robust to the addition of such information.

635 Although numerous competition coefficients have been developed over the last several
636 decades (e.g., MacArthur and Levins 1964, Schoener 1974), to our knowledge, this is the first
637 time that potential for interspecific competition has been calculated in terms of the proportion (0

638 to 1) of prey production important to a species of interest that is consumed by another species, or
639 in this case, all other members of the fish assemblage. Given the simplicity of the calculation
640 (see *Interaction Strength, Interspecific Competition, and Carrying Capacity* in Methods section),
641 it may be that competition has not been calculated in this way before because it requires
642 estimates of both predator and prey production, which are rarely available. Whatever the case
643 may be, this technique could be useful for estimating potential exploitative competition among
644 numerous types of organisms in both aquatic and terrestrial environments. Reciprocally, this
645 approach also allowed us to determine the amount of prey production important to a species of
646 interest that was not consumed by other species, information which we used to calculate
647 energetic carrying capacities (*‘Potential Production’*) for Chinook and steelhead habitats.

648 Our estimates of the carrying capacity of different floodplain habitats to sustain juvenile
649 Chinook salmon and steelhead production varied over one order of magnitude. In the main
650 channel, where production and food consumption by sculpin and whitefish was high, fewer
651 resources were available to support Chinook salmon and steelhead, and as a result, carrying
652 capacity values per unit area of aquatic habitat were generally lower than that found in side
653 channels. In contrast, non-target fish production was much lower in side channels, and as a
654 result, we estimated that side channels generally have higher per unit area carrying capacities
655 than the main channel. Overall, however, our findings indicate that juvenile anadromous fishes
656 were generally under-seeded with respect to these energetic carrying capacities, in both the main
657 channel and side channels. In a separate study, similar results were observed within other
658 salmon bearing tributaries of the Columbia Basin (Bellmore et al. 2012). These findings could
659 mean that much higher Chinook and steelhead production could be supported with minimal
660 density-dependent affects (i.e., growth, condition, and survival) on individuals.

661 In contrast to observed differences in carrying capacity, gross prey production was
662 relatively consistent among side channels and also between side channels and the main channel.
663 This finding contrasts to empirical reports (e.g., Bayley 1988, Lewis et al. 2001) and conceptual
664 models (e.g., Junk et al. 1989) of floodplain systems, which have frequently emphasized the
665 disproportionate importance of side channel to overall floodplain productivity. One explanation
666 for this inconsistency may be that the Methow River is much smaller and has different
667 hydrologic characteristics compared to the larger tropical (e.g., Amazon and Orinoco Rivers) and
668 temperate (e.g., Mississippi River) rivers where much floodplain research has been conducted.
669 Nevertheless, in large part due to this body of research, it is often assumed that side channels
670 utilized by salmonids have enhanced food base productivity and therefore are more favorable
671 rearing habitats for these fish. However, this assumption has never been adequately tested in
672 salmon bearing streams. Although a few studies have calculated the density or standing crop
673 biomass of the food base in these side channels (e.g., Morely et al. 2005), this is the first study to
674 undertake the additional efforts necessary to calculate annual food base productivity (i.e.,
675 secondary invertebrate production and terrestrial invertebrate fluxes), which are a necessary
676 component of ecosystem-based energetic approaches (Odum and Barrett 2005). In fact, utilizing
677 biomass or standing crops estimates in energetic analyses can produce paradoxical results (i.e.,
678 Allen's Paradox; Hynes 1970, Water 1988), whereby the amount of production at one trophic
679 level is insufficient to support observed consumption at higher trophic levels (Allen 1951). That
680 said, this study did not include estimates of invertebrate production available in the drift. Given
681 that salmonids, such as juvenile Chinook and steelhead, are considered to be primarily drift
682 feeders (Zaroban et al. 1999), understanding how benthic production and invertebrate drift are
683 correlated would be useful in some contexts. In our study, however, drift measurements were

684 impractical because three of the side channels had no measureable water velocity for a majority
685 of the year. Moreover, invertebrate drift is notoriously variable (Brittain and Eikeland 1988),
686 such that the approaches taken (e.g., infrequent measures in space and time which are then
687 broadly extrapolated) can result in estimates that are likely to be unreliable as absolute (versus
688 relative) measures of food availability.

689 Although we observed similar production of invertebrate prey among habitats, the
690 composition of invertebrates that fueled the TBP (trophic basis of production) of the fish
691 assemblage was highly variable among habitats and appeared to be associated with differences in
692 hydrologic connectivity. In fact, differences in TBP were much greater between different
693 habitats, than between different fish species. In particular, as side channels became more
694 disconnected from the main channel, fish TBP was comprised of more lentic type invertebrate
695 taxa. This finding parallels results of many studies that have shown significant variation in
696 aquatic invertebrate assemblages across floodplain landscapes (e.g., Arscott et al. 2005). In
697 addition, this result indicates that fish species in the Methow River, especially juvenile Chinook
698 salmon and steelhead, are flexible enough to exploit different types of prey resources across a
699 variety of habitat types.

700 Our research shows that the importance of side channels to juvenile Chinook salmon and
701 steelhead in the Methow is not necessarily a function of enhanced food base productivity within
702 those habitats. Instead, our findings indicate that side channels offer reduced competition for
703 available prey. Moreover, these habitats appear to provide refugia from larger, more piscivorous
704 species like bull trout and cutthroat trout, which were generally absent from side channels. That
705 said, this study was not aimed at quantifying organic matter flows along piscivorous pathways;
706 larger sample sizes would be needed to evaluate these temporally discrete but potentially

707 important events. Even if piscivory is lower in side channels relative to the main channel,
708 predation along alternative pathways may be greater. Research suggests that as flows recede and
709 habitats become shallow and isolated, the risk of predation by terrestrial predators, such as birds
710 (e.g., herons, king fishers, etc.) and mammals, is likely to increase (Power 1987, Schlosser
711 1991). In contrast, the lower water velocities generally associated with isolation from the main
712 channel might reduce energetic costs associated with swimming (Fausch 1984), and depending
713 on the availability of food, may be beneficial to rearing salmon and trout (Rosenfeld et al. 2005).
714 Although we were unable to detect a clear relationship between water temperature and
715 fish/invertebrate production in this study, temperature is also likely to play a key role in the
716 relative success of fish in different habitats. Channels with extensive hyporheic connections
717 generally have less variable temperatures during the winter and summer (Torgersen et al. 1999,
718 Baxter and Hauer 2000, Ebersole et al. 2003), which may be more energetically favorable for
719 growth. Side channels with limited surface or groundwater connectivity may result in water
720 freezing during the winter and/or exceeding critical temperatures during the summer. In
721 addition, many side channel habitats completely disappear during low flow periods, stranding
722 fish on the floodplain surface. Overall, this heterogeneity in food web structure and physical
723 conditions creates a mosaic of different habitats across the floodplain landscape. Consequently,
724 choosing the best or most energetically favorable habitat would require fish being able to
725 respond to differences and trade-offs among numerous physical and biotic variables.

726 Although particular habitats may be identified as favorable at any single point in time, the
727 mosaic of different aquatic habitats and associated food web structures within floodplain systems
728 is likely to be more important to sustaining resilient and productive populations, and the overall
729 stability of the biotic community over longer temporal scales (Groot and Margolis 1991,

730 McCann 2000, Hilborn et al. 2003, Bisson et al. 2009). As climate and hydrology change over
731 shorter (e.g., El Niño/Southern Oscillation and Pacific Decadal Oscillation) and longer (e.g.,
732 climate change) time scales, the potential for different habitats across the landscape to sustain
733 fish productivity is likely to shift. Moreover, maintaining a mosaic of habitats that encompasses
734 distinct physical and biotic conditions may help sustain multiple salmonid life-history strategies
735 (Groot and Margolis 1991, Reeves et al. 1995). Consequently, conserving a diverse portfolio of
736 habitats across the floodplain landscape increases the chance that at least one habitat or life-
737 history strategy will be favored as environmental conditions change. For example, Hilborn and
738 others (2003) found that biophysical complexity in the Bristol Bay region of Alaska supported a
739 wide array of sockeye salmon life-histories, which helped maintain the productivity of the
740 population, despite major changes in climate conditions. At a smaller spatial scale, the
741 biophysical mosaic found in floodplains could serve as ‘nodes of resilience’ for endangered
742 species like Chinook salmon and steelhead.

743

744 *Implications for Habitat Restoration in the Methow River*

745 Our findings show that side channels are important habitats for juvenile rearing Chinook
746 salmon and steelhead in the Methow River. In particular, Chinook and steelhead rearing in side
747 channels had lower potential exploitative competition for food with other non-target fishes (e.g.,
748 sculpin and whitefish), and as a result, side channels appeared to have a greater capacity to
749 sustain juvenile Chinook and steelhead production relative to the main channel. Although
750 floodplain reconnection efforts often assume that creating side channels that remain fully
751 connected to the main channel year-round would create the largest benefit for salmonids, our
752 findings did not reveal any correlation between hydrologic connectivity and productivity.

753 Instead, these findings suggest that habitat restoration efforts should focus on maintaining
754 current floodplain complexity, and when and where necessary, restoring the ability of the river to
755 create and maintain this complexity (e.g., removing dikes, restoring large woody debris
756 dynamics, etc.) (*sensu* Reeves et al. 1995, Ebersole et al. 2003, Stanford et al. 2005). That said,
757 we also present some evidence that existing floodplain habitats may be substantially under-
758 seeded with juvenile Chinook salmon and steelhead, which might indicate that insufficient
759 numbers of spawning adults are returning to fully utilize available food production.

760 This study presents an example of how quantitative ecosystem and food web approaches
761 can be combined to address problems of direct relevance to natural resource management. This
762 combined approach allowed us to quantify: (1) primary organic matter flow pathways that
763 sustain fish production, (2) prey-specific food limitation, and (3) potential competition for food.
764 Our findings demonstrate that the pathways of organic matter flow that sustain Chinook salmon
765 and steelhead are widely variable among habitats, and that fish species that are not the target of
766 restoration can have an overwhelming influence on organic matter flows; a finding which calls
767 into question the validity of assessments focused on single species alone. Overall, this study
768 demonstrates that landscape heterogeneity is associated with the occurrence of a mosaic of food
769 webs in river floodplain systems, all of which are utilized by salmon and steelhead, and all of
770 which maybe important to their recovery and long-term persistence. Future investigations are
771 needed to quantify the basal organic matter sources (i.e., primary producers) that are the primary
772 food for invertebrate prey, and organic matter flows along piscivorous pathways. Together, this
773 information would provide the basis for conducting food web modeling that could be used to
774 evaluate the implications of alternative management scenarios (e.g., habitat restoration, nutrient

775 additions, etc.), species introductions, and environmental changes (e.g., climate change) on
776 salmon and steelhead populations in this and other similar river systems.

777

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785

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1007

1008 **Ecological Archives Material**

1009 **Appendix A.** Photographs of a rip-rapped bank along main channel Methow River, Washington,
1010 USA, and the five side channels included in this study.

1011 **Appendix B.** Fish abundance, biomass, and production estimates within different floodplain
1012 aquatic habitats.

1013 **Appendix C.** Biomass, Production, and *P:B* estimates of aquatic invertebrates within different
1014 floodplain aquatic habitats.

1015 **Appendix D.** Percentage of prey found in the gut contents of fish sampled within different
1016 floodplain aquatic habitats.

1017 **Appendix E.** The proportion of production by fish species derived from different prey items
1018 (i.e., trophic basis of production) within different floodplain aquatic habitats.

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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, and N = No.

Habitat type	Habitat name	Surface water connection?		Bed scour?	Habitat area (m ²)			Temperature (C)		
		Downstream	Upstream		High flow	Base flow	Length (m)	Summer	Fall	Winter
Main channel	<i>Main ch</i>	Y	Y	Y	-	760000	17000	15.2	-	4.2
Side channel	<i>Con updown</i>	Y	Y	Y	3550	2875	310	13.6	6.9	5.4
Side channel	<i>Con down</i>	Y	N	Y	13975	6325	690	11.4	6.7	5.1
Side channel	<i>Discon lrg</i>	N	N	Y	6425	2200	490	14.9	7.4	5.4
Side channel	<i>Discon sml</i>	N	N	Y	7500	1100	605	16.1	4.7	-
Side channel	<i>Discon noscr</i>	N	N	N	6150	3400	582	13.2	4.9	1.4

Figure Legends

Figure 1. Map of the Methow River showing the location of side channel habitats and the proposed habitat restoration segment. Inset shows the location of the Methow River in Washington State.

Figure 2. Per area estimates of fish production by species \pm 1 standard error (A), aquatic invertebrate production and terrestrial insect flux to aquatic habitats with 95% confidence intervals (B); and comparisons of total invertebrate prey production (aquatic + terrestrial contributions) to invertebrate prey demand by the entire fish assemblage with 95% confidence intervals (C) for the main channel and each side channel in 2009-10.

Figure 3. Trophic basis of production figure that shows the proportion of total fish production in each habitat derived from different prey items during 2009-10.

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination plots of trophic basis of production for each fish species within each habitat. 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 = dace, BLS = bridgelip sucker, STL = steelhead, CTT = cutthroat, MWF = whitefish, SCP = sculpin.

Figure 5. 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 channels (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 = dace, BLS = bridgelip sucker, STL = steelhead, CTT = cutthroat, MWF = whitefish, SCP = sculpin.

Figure 6. 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) Connected 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 = dace, BLS = bridgelip sucker, STL = steelhead, CTT = cutthroat, MWF = whitefish, SCP = sculpin. Asterisks demark interaction strengths that we were able to calculate due to unknown prey taxa production.

Figure 7. 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.

Figures

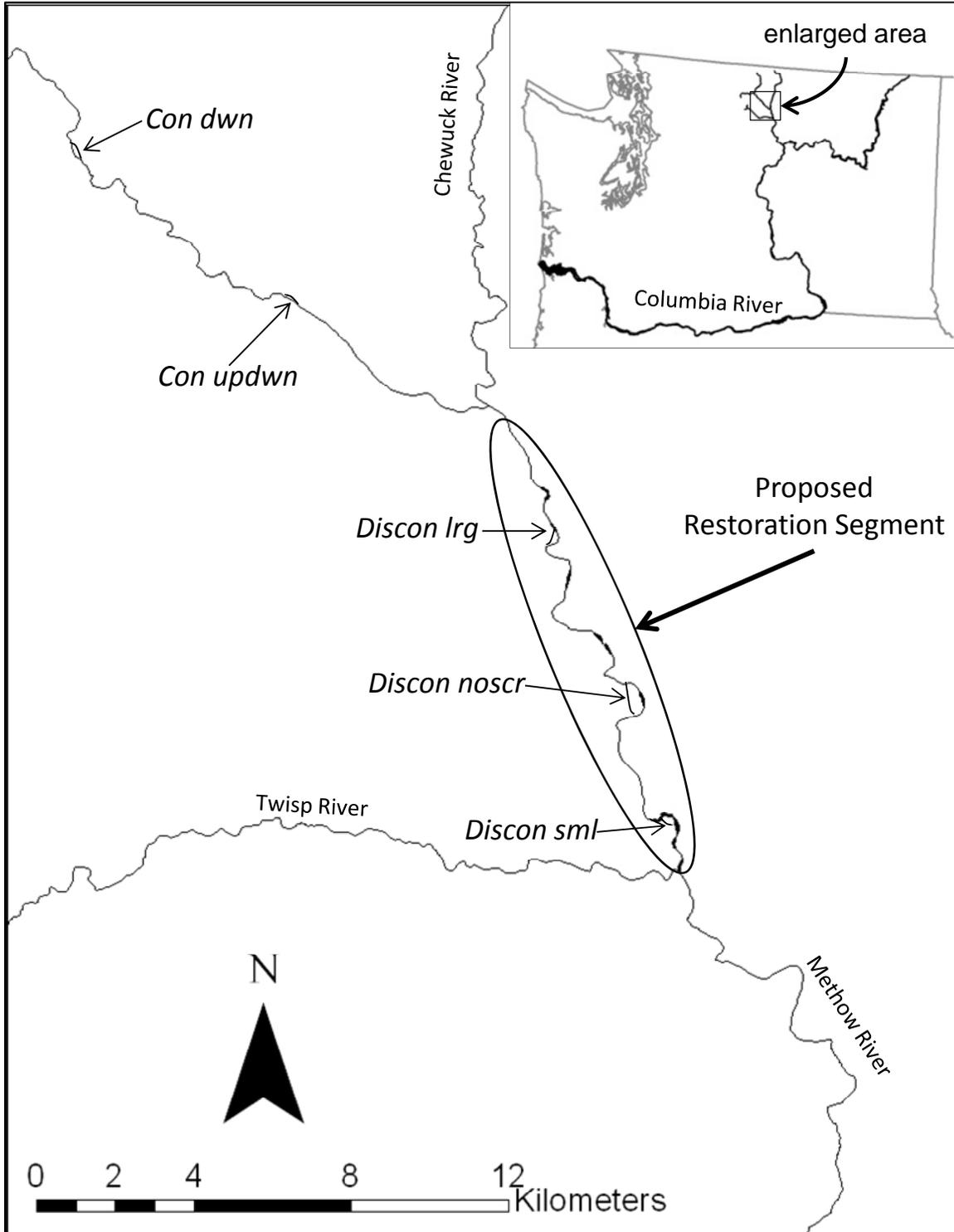


Figure 1.

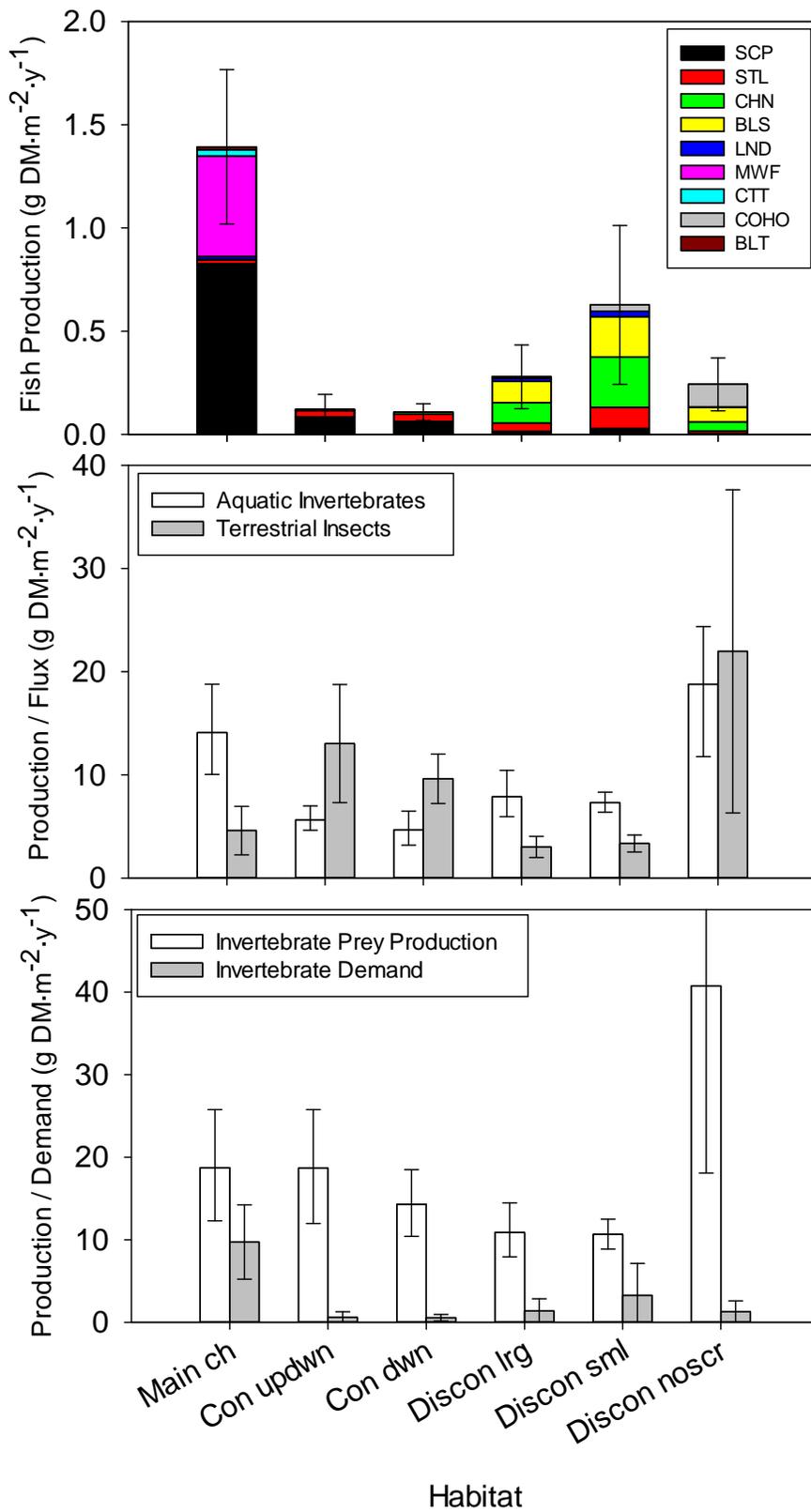


Figure 2.

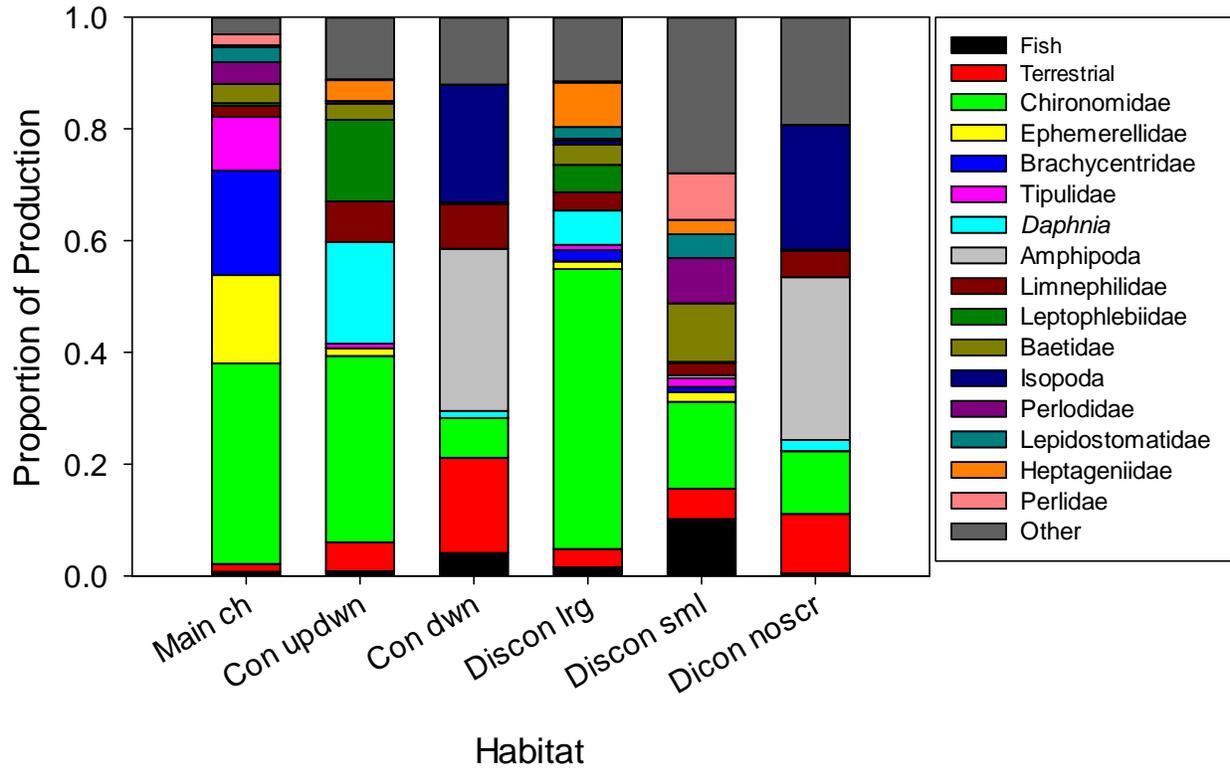


Figure 3.

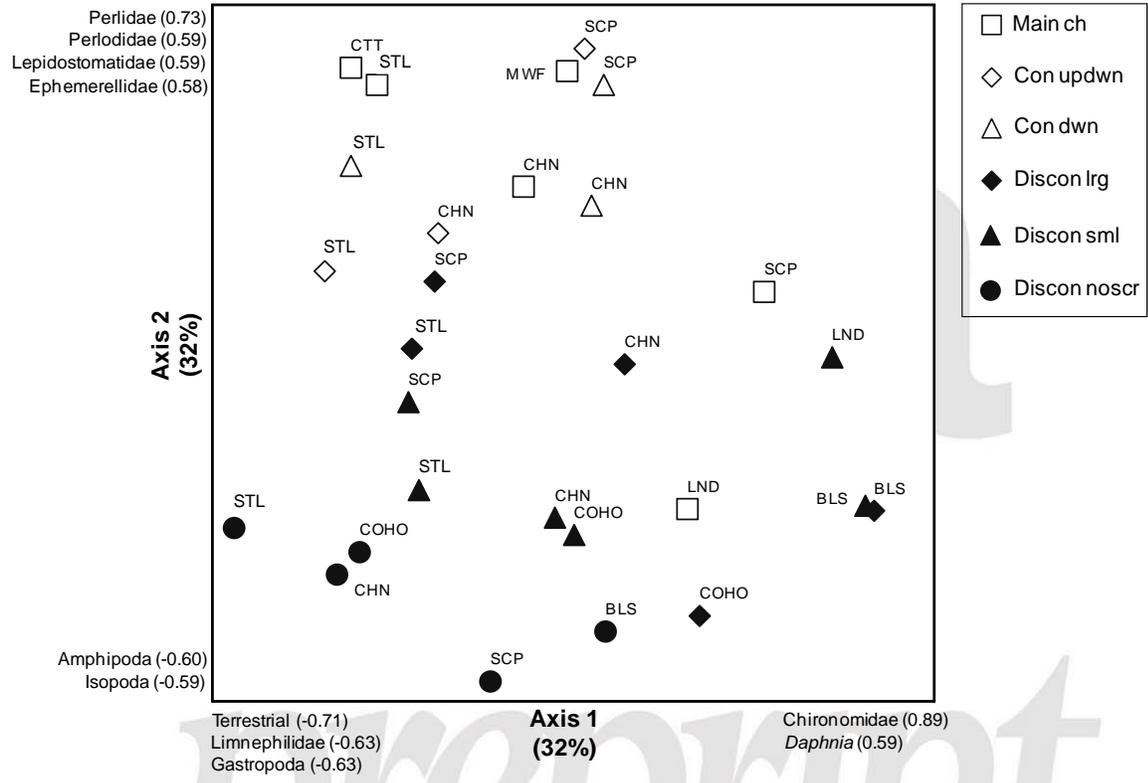


Figure 4.

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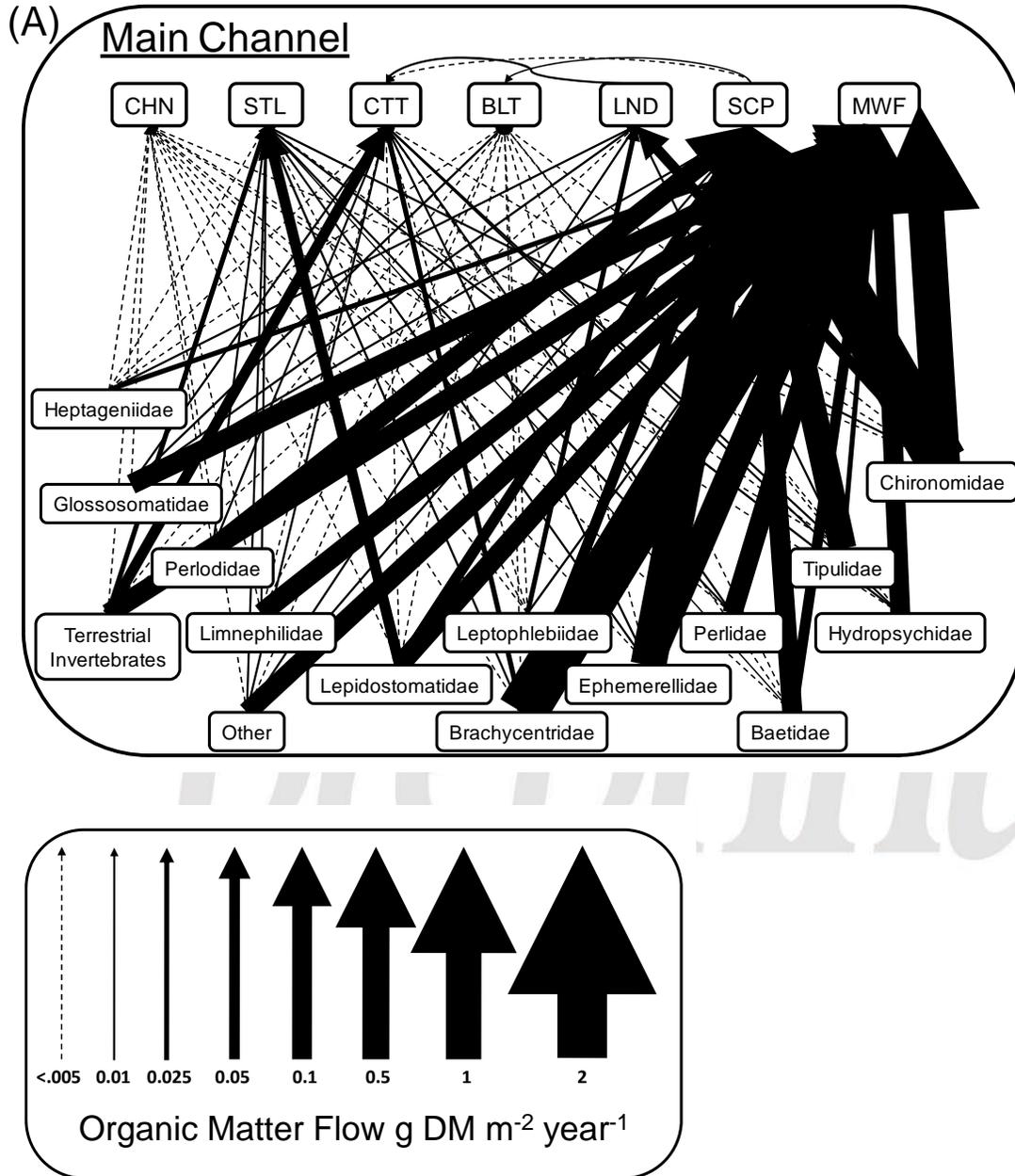


Figure 5.

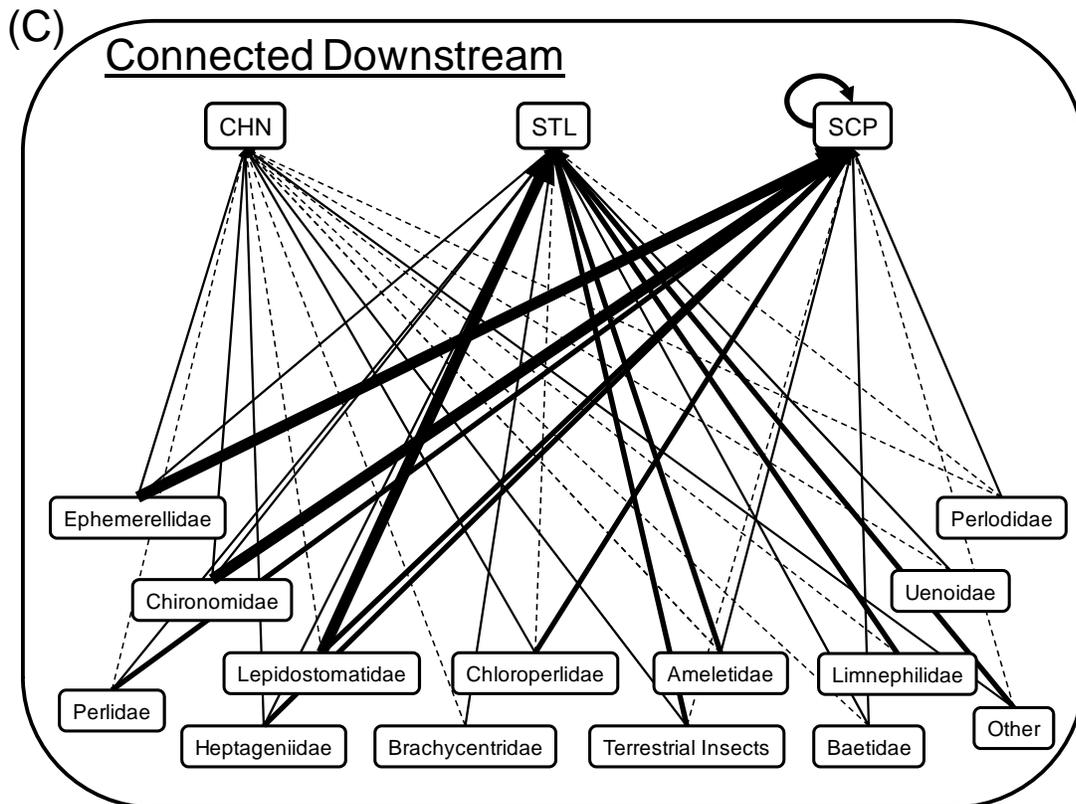
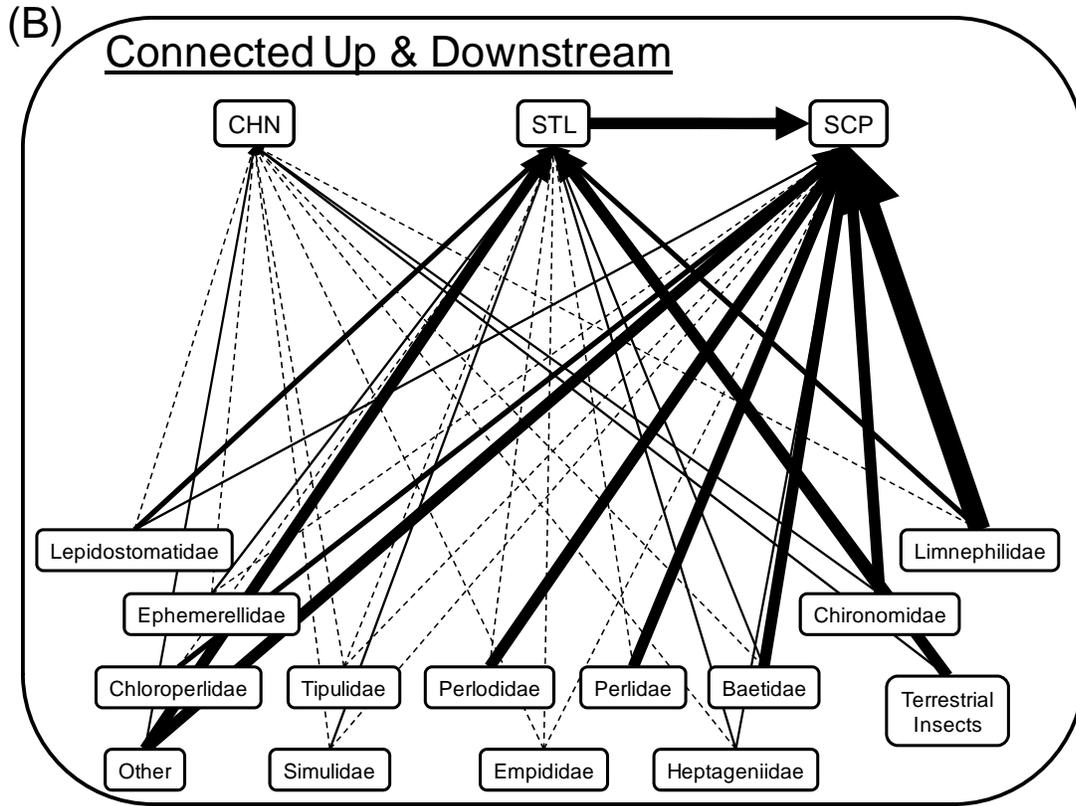


Figure 5. Continued.

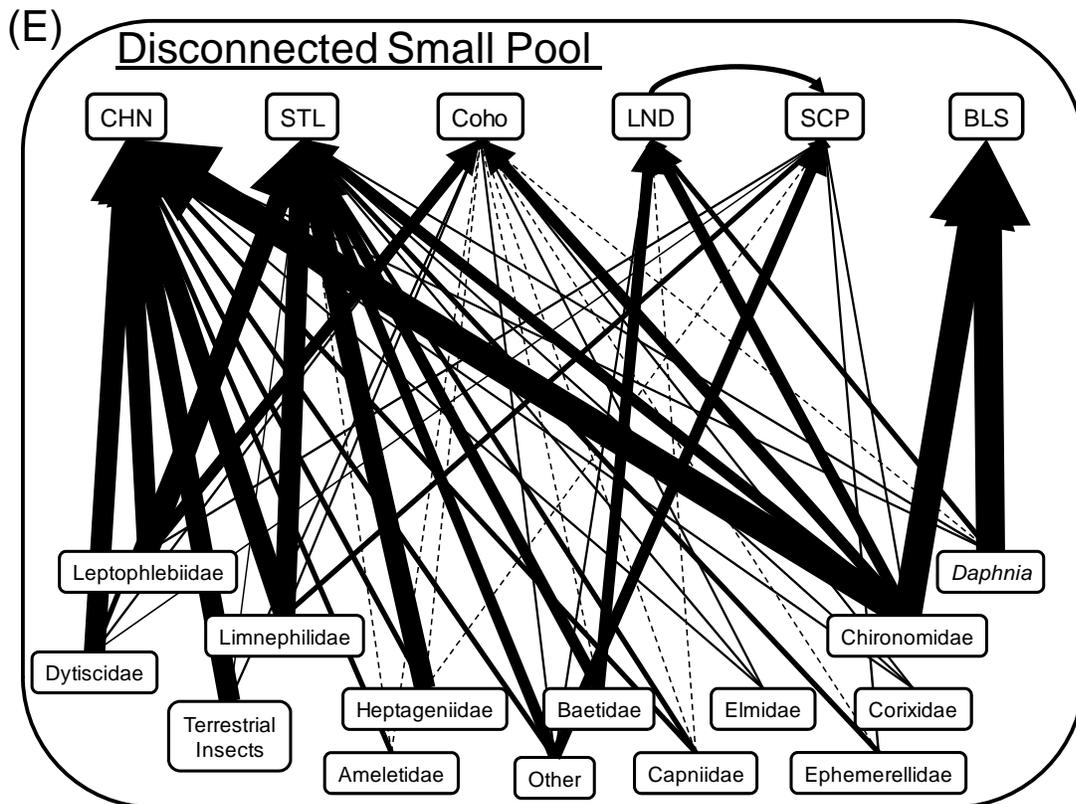
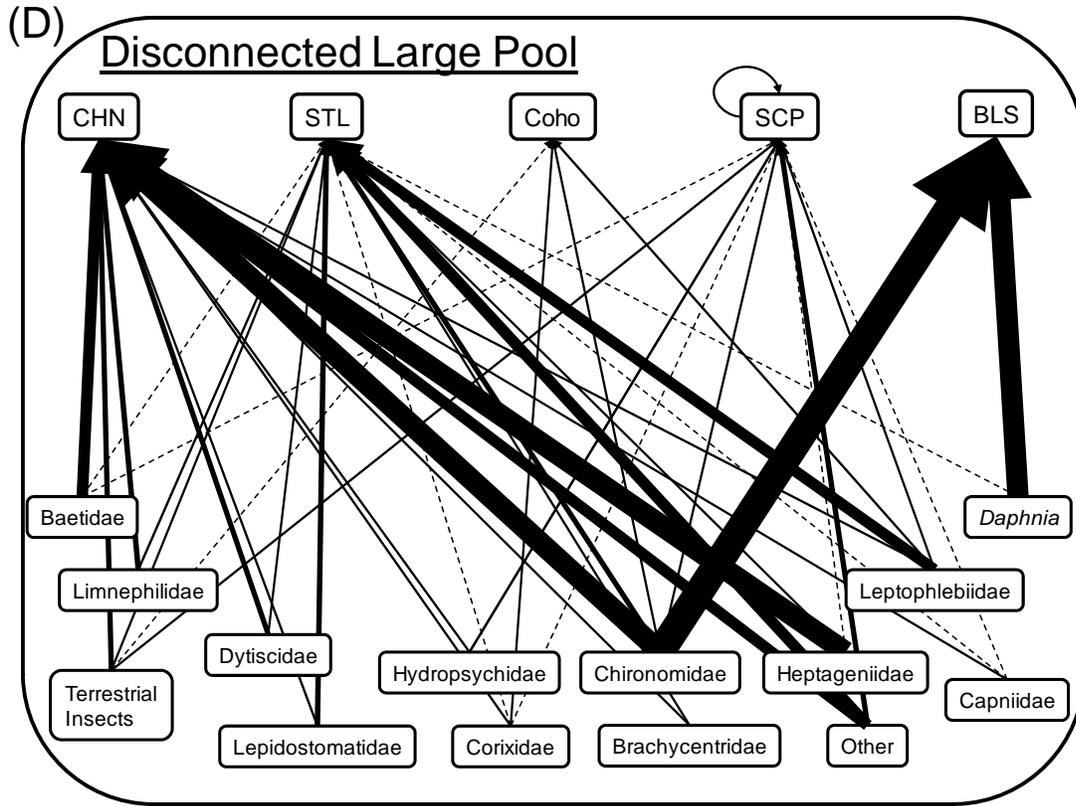


Figure 5. Continued.

(F)

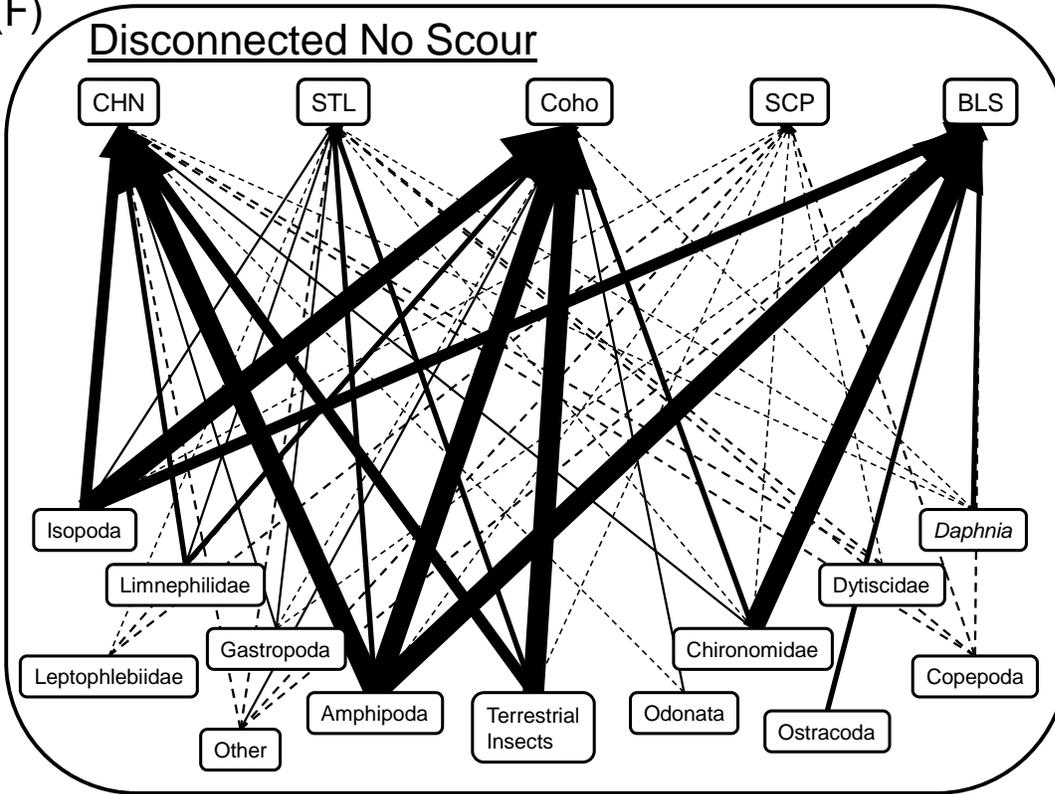


Figure 5. Continued.

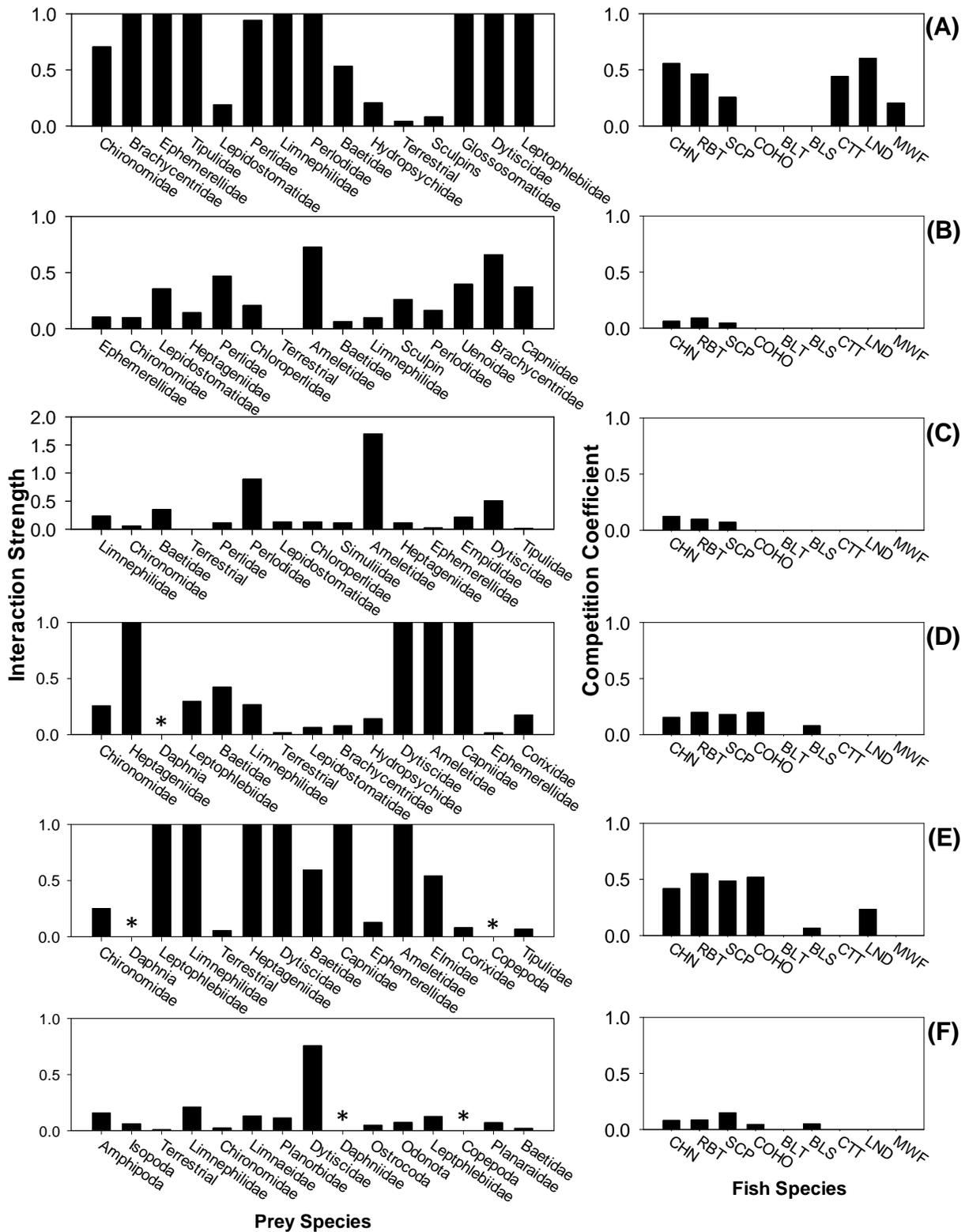


Figure 6.

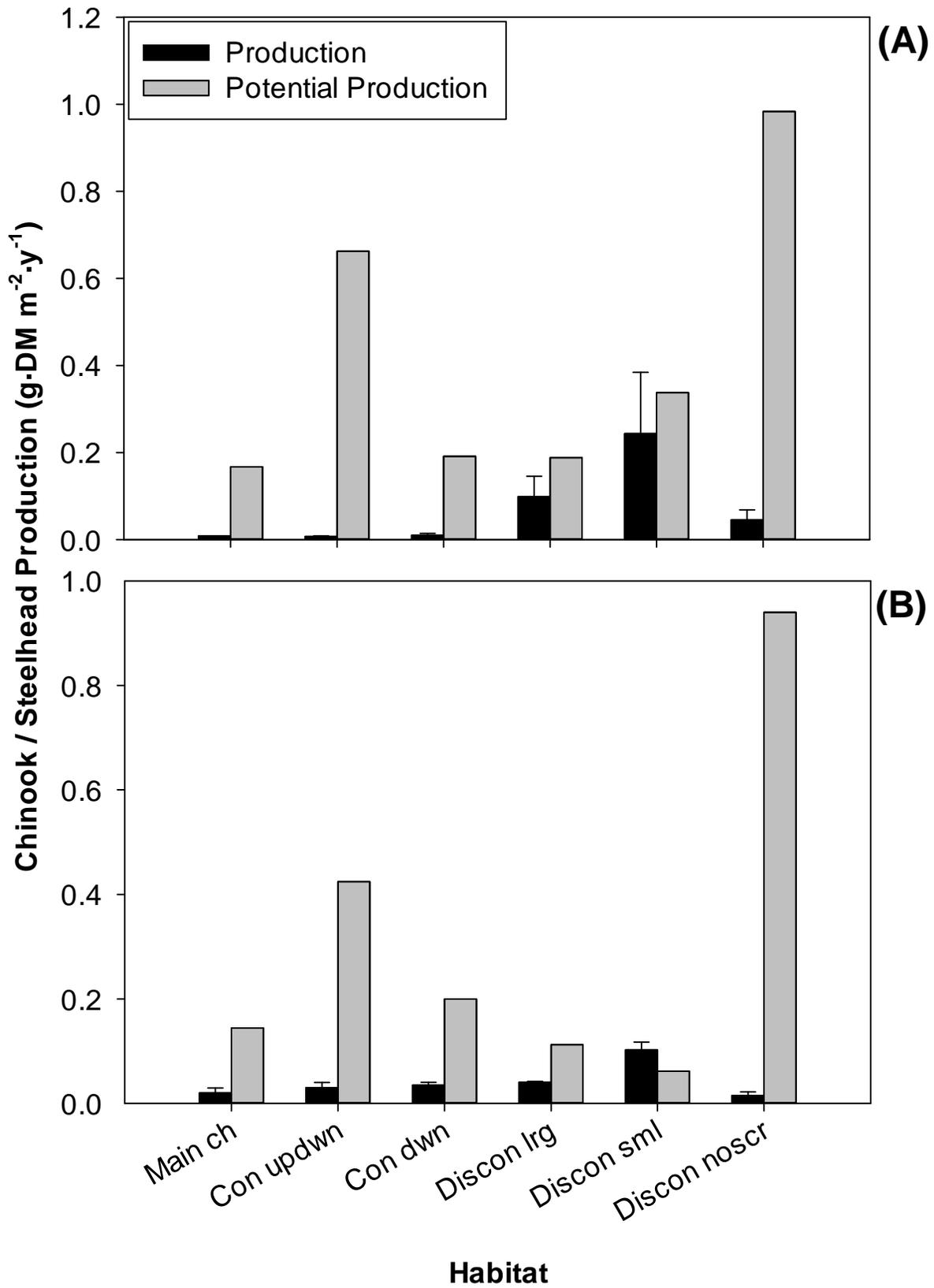


Figure 7.