Competition between non-native brook trout and coho salmon in the Elwha River, WA during dam removal

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Abstract

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The removal of two dams on the Elwha River, WA is the largest dam removal project in US history. A major goal of this project is to restore historically abundant populations of Pacific salmon to the river, so it is important to know if competition between resident and anadromous species could inhibit salmon recolonization. We investigated competitive interactions in laboratory streams to determine how species, size, and group size affected competitive dominance and determined the level of habitat and prey resource use overlap to indicate the potential for competition in reaches of the Elwha River. Coho salmon were competitively dominant over brook trout regardless of size difference or group size, and will likely outcompete brook trout in the wild if resources become limited. Prey resource use overlap indicated potential for competition in sympatric areas, but density and distribution patterns did not suggest that competition was occurring at the reach scale.

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Overview

Competition for resources can influence the abundance and distribution of individuals and populations in nature. Competitive interactions are energetically expensive, so rather than compete for access to optimal territory or food resources, many organisms conserve energy by moving to suboptimal habitats in locations where competition is not as strong.

Competition in stream-dwelling salmonid fishes has been well studied because multiple native species can often be found within river systems, and many species share common habitat and prey resource preferences. Individuals establish foraging territories and readily engage in agonistic behaviors to protect territories and access to food.

Salmonid fishes are a popular target among recreational anglers and as a result many species have been widely introduced beyond their native ranges. These introductions sometimes occur in watersheds with closely-related native salmonid species and competition between the natives and non-natives can have negative outcomes, often for the native fish.

We took advantage of a unique restoration project on the Elwha River, WA to investigate competitive interactions between native and non-native salmonids. Two large dams on the Elwha River were removed between 2011 and 2014, allowing ongoing recolonization of the watershed by native anadromous Pacific salmonids (*Oncorhynchus* spp.). As recolonization occurs, anadromous species will interact with resident salmonids, including self-sustaining populations of non-native brook trout (*Salvelinus fontinalis*). Brook trout and juvenile coho salmon (*O. kisutch*) share habitat and prey resource preferences, so there is potential for competition between these species if resources are limited. A major goal of the Elwha River restoration is to

restore populations of Pacific salmon to the river, so it is important to understand how interactions between brook trout and coho salmon could affect recolonization.

To understand the nature of interactions between brook trout and juvenile coho salmon in the Elwha River, we used three approaches:

- Chapter 1: We conducted laboratory trials with pairs and groups of brook trout and coho salmon to determine how species, size, and group size affect the outcomes of competition for food, and

- Chapter 2: We investigated potential sources of competition by examining fish density and spatial overlap in newly available reaches of the Elwha River, and trophic overlap between the species using stomach contents and stable isotope analysis.

Chapter 1

Influence of species, size, and relative abundance on the outcomes of competitive interactions between brook trout and juvenile coho salmon

Abstract

Resource competition between animals is influenced by a number of factors including species, size, and the relative abundance of competing individuals. Stream-dwelling animals often experience variably available food resources and some employ territorial behaviors to increase their access to food. We investigated the factors that affect dominance between resident, non-native brook trout and recolonizing juvenile coho salmon in the Elwha River, WA, USA to see if brook trout are likely to disrupt coho salmon recolonization via interference competition. During dyadic laboratory feeding trials, we hypothesized that fish size, not species, would determine which individuals consumed the most food items, and that species would have no effect. We found that species, not size, played a significant role in dominance; coho salmon won 95% of trials, even when 52% the length of their brook trout competitors. As the pairs of competing fish spent more time together during a trial sequence, coho salmon began to win more food, and brook trout began to lose more, suggesting that the results of early trials influenced fish performance later. In group trials, we hypothesized that group composition and species would not influence fish foraging success. In single species groups, coho salmon consumed more than brook trout, but the ranges overlapped. Brook trout consumption remained constant through all treatments, but coho salmon consumed more food in treatments with fewer coho salmon, suggesting that coho salmon experience more intra- than inter-specific competition and that brook trout do not pose a substantial challenge. Based on our results, we think it is unlikely that competition from brook trout will disrupt Elwha River recolonization by coho salmon.

Introduction

In environments where food or other resources are limited, it is common for organisms to experience competition. This competition may be "exploitative" if resources are not readily defensible (e.g., fishes feeding on zooplankton in lakes) or "interference" if the behavior of individuals inhibits access to resources by conspecifics or heterospecifics (Schoener 1983; Krebs & Davies 1993). Under competitive pressure, organisms may establish and defend territories to secure continued access to necessary resources. Territorial behavior has been observed in numerous vertebrate taxa for food, space, and breeding habitat but many studies have investigated the maintenance of foraging territories because food-related variables strongly influence vertebrate spatial distributions (Maher & Lott 2000).

Freshwater ecosystems, and streams in particular, provide an excellent system in which to study territoriality and foraging behavior. Heterogeneity in physical conditions (e.g., water depth, velocity, substrate, shade) results in variation in food production, delivery, and capture efficiency by predators among resource patches (Fausch 2014, and references therein). Predators able to obtain and hold territories in locations that minimize energy expenditure and maximize foraging opportunities can grow faster than individuals in poorer-quality habitat, including non-territorial individuals (Fausch & White 1981; Fausch 1984; Nielsen 1992).

Territoriality in streams has been extensively studied in stream-dwelling salmonid fishes. In small streams, salmonids primarily feed on in-stream drift consisting of aquatic macroinvertebrates and small terrestrial organisms drifting in the water column or dropping onto the surface of the stream (Chapman 1966; Quinn 2005). Fish that acquire more or higher quality food resources grow more rapidly (Nielsen 1992), and size can be positively correlated with

survival, so the outcomes of territorial competitions have important consequences (Quinn & Peterson 1996; Roni et al. 2012).

Competitive interactions within and between salmonid species are influenced by a number of physiological, experiential, and environmental factors. Interference competition between salmonids commonly includes one or several territorial behaviors and the basic patterns (i.e., displays involving the fins and body position, and agonistic behaviors such as charging, nipping, and chasing) are generally similar among species (Abbott et al. 1985; Keeley & Grant 1995; Sabo & Pauley 1997). Many studies have investigated the factors controlling the outcomes of such competitions, and evidence indicates that size is very important; larger fish generally hold larger territories and exhibit dominance over smaller individuals (Keeley & Grant 1995; Imre et al. 2004). Aggression and dominance are also influenced by prior possession of the territory, metabolic rate, recent experience of winning or losing competition, and relative abundance of conspecifics (Rhodes & Quinn 1998; Grand & Dill 1999; Warnock & Rasmussen 2014). Further, certain species and populations seem to be inherently more or less aggressive than others (Rosenau & McPhail 1987; Hutchison & Iwata 1997; Macneale et al. 2010). As a result, outcomes of competitive interactions are highly context-dependent and results of contests between individuals from a given population in a particular region may not be representative of the outcomes of similar contests elsewhere.

Salmonids have been widely translocated throughout the world and non-native introductions have resulted in new sources of interspecific competition for native aquatic species (MacCrimmon & Campbell 1969; MacCrimmon et al. 1970; Crawford & Muir 2008; Cucherousset & Olden 2011). In most cases, the native fish are established and the non-native fish are invasive, and the outcomes of these interactions are complex. The native species may be

competitively superior to the invasive species but in other cases they are not. For example, brook trout, *Salvelinus fontinalis,* are generally dominated in their native range by non-native rainbow trout, *Oncorhynchus mykiss*, but outside their native range brook trout often dominate cutthroat trout, *O. clarki* (Dunham et al. 2002; Fausch 2008). Further, non-native brown trout, *Salmo trutta*, replace native brook trout in eastern North America, but are replaced by introduced brook trout in their native range in northern Europe (Korsu et al. 2007).

In this study we investigated an unusual situation where the non-native species is established and the native species is encountering them as they recolonize habitat from which they were extirpated. The demolition of the Elwha River dams in Washington State (2011-2014) is the largest dam removal project in United States history (Duda et al. 2008). The two dams were built without fish passage, extirpating migratory fish from the upper segments of the river for nearly a century (Wunderlich et al. 1994; Duda et al. 2008). Non-native brook trout were introduced to the watershed after dam construction, and they persist as a self-sustaining population between the two former dam sites (Brenkman et al. 2008). The dams were removed in 2012 and 2014 and Pacific salmon have begun to recolonize their historical territory in the Elwha River watershed, where they are interacting with the resident native and non-native species. The return of historically abundant salmon populations is a major goal of the Elwha River restoration project, so it is important to know whether interspecific competition with non-native brook trout is likely to hinder successful salmon recolonization (Wunderlich et al. 1994). More broadly, the removal of the Elwha River dams offers an opportunity to improve our understanding of how non-native species can influence the success of ecosystem restoration efforts. River systems undergoing restoration are often impacted by more than one anthropogenic influence, and proper

management practices hinge on understanding how these influences may interact and affect restoration efforts.

The goal of this study was to determine how fish species, size, and relative abundance influence dominance in competitive interactions between brook trout and juvenile coho salmon in laboratory stream channels. We first conducted snorkel observations in streams to determine the positions of the species in the water column (to help design subsequent study arenas) and to ascertain the extent of overlap in habitat use. We then conducted competition trials and recorded the number of food items acquired by individuals or species groups under different fish size and group size combinations. The null hypothesis was that there would be no effect of species on the number of food items consumed in competition trials. Fish size was hypothesized to influence foraging success, with larger fish being more successful than smaller fish. To the extent that this was the case, we sought to determine the size at which any species-specific disparity in competitive ability was overcome. We also hypothesized that in groups of size-matched fish, neither species nor group composition would affect individual foraging success. Our results intend to demonstrate the extent to which a non-native species has the capacity to inhibit native salmonid recolonization and will provide insight into how non-native species can affect restoration efforts.

Methods

Study populations

Adult coho salmon (*O. kisutch*) and brook trout spawn in the fall and the fry of both species emerge in the spring (Karas 1997; Behnke 2002). Coho salmon are typically larger as newly emerged fry and hatch earlier in the spring than brook trout (Fausch & White 1986).

However, the brook trout remain in the stream for their whole lives whereas Elwha River coho salmon migrate to sea in their first fall or their second spring of life (Quinn et al. 2013), so some brook trout are larger than any juvenile coho salmon. The two species share habitat and food preferences, which may cause competition if resources are limiting (Gibson 1981; Fausch & White 1986).

Field observations

In summer 2013, a single snorkeler (EJT) surveyed nine pool habitat units in Elwha River tributaries and floodplain side channels between the former dam sites. The snorkeler identified and counted fish in each pool and the position of each fish in the water column (split into upper, middle, lower thirds). We used a contingency table and Chi-square analysis to determine if brook trout and coho salmon were utilizing the same water column positions. Fish occupancy of similar positions was used to justify the experimental design, as it indicated that both species would be equally well-suited to the experimental arenas (see below).

Fish collection and holding

Brook trout (mean fork length (FL) ± SE; 74.1 mm ± 3.4) were collected via single pass backpack electrofishing on 13 August and 10 September 2013 from Campground Creek, a tributary to the Elwha River in Olympic National Park, approximately 14 km southwest of the city of Port Angeles in Washington State. Juvenile coho salmon (58.8 mm ± 1.2) were collected on the same dates from Salt Creek, the nearest stream approximately 9 km west of the Elwha River, because removing native Elwha River fish was inconsistent with the conservation goal of allowing full recolonization of the river. Fish were separated by size (to avoid predation) and transported to the U.S. Geological Survey's Western Fisheries Research Center (WFRC), Seattle, WA, in insulated, oxygenated coolers. At WFRC, fish were separated by species and placed in

0.61 m diameter aerated holding tanks at ambient Lake Washington water temperature (range: 7.5 °C–10.5 °C). Fish were fed a maintenance ration of frozen *Mysis* shrimp and bloodworms twice daily through a vinyl subsurface feeding tube to simulate drift. Fish were allowed to acclimate to the holding environment for at least 24 h prior to feeding trials.

Experimental setup

We conducted feeding trials in a semi-enclosed shed under ambient photoperiod at WFRC in three fiberglass stream channels 10.2 m long and 1.5 m wide (Kuehne et al. 2012). Each stream channel contained a natural gravel/cobble substrate and was subdivided into five 2.55 m^2 arenas by plastic mesh and PVC screens (Fig. 1). Regularly spaced 25 cm x 22 cm acrylic windows allowed the fish to be observed from at least one side of each arena (Kuehne et al. 2012). Water current was generated by a recirculating pump for a maximum water velocity of 0.1 $m \cdot s^{-1}$. Water depth was approximately 60 cm throughout the arenas and temperature during trials varied between 13.5 °C and 16 °C, representative of temperatures in habitats where these fishes were found in the Elwha River system (EJT, unpublished data). A vinyl feeding tube was attached to the center of the upstream screen of each arena and extended below the surface to simulate drift.

Competition trials

Experiment I: Dyadic trials

One fish of each species was selected from the holding tanks, weighed, and measured (FL). Fish pairs were selected to produce a range of size differences as well as size-matched pairs. Pairs were placed into arenas simultaneously to eliminate effects of prior residence (Tatara & Berejikian 2012). About 15 min after a pair of fish was placed in each of the arenas, approximately 15 food items were injected through each arena's feeding tube. This initial

feeding allowed fish to experience the food delivery site. Fish were then left 14-15 h to acclimate in the arenas overnight.

Feeding trials began at 08:00 h the following day and were conducted every 3 h until 17:00 h, resulting in four trials per day for each pair of fish. During each trial, five food items were inserted into the arena through the feeding tube, one at a time, at one min intervals. The first fish to get the food item in its mouth "won" and the other fish "lost" that item (see Rhodes & Quinn 1998). Food items were either consumed, resulting in a point for the fish that won that item, or went to the bottom or back of the arena, in which case neither fish won. If fish were tied after five food items, additional food items were added until the tie was broken. Trials began at the downstream-most arena (#5; Figure 1) and sequentially moved upstream to pairs in arenas #4, #3, #2, and #1. We worked in an upstream manner to ensure that uneaten food items from upstream did not influence downstream fish foraging. After the fourth trial of the day, fish were left in the arenas overnight and removed the following morning. They were then euthanized by overdose of MS-222 buffered to pH consistent with the environment, weighed, measured, and frozen. Twenty pairs of fish were tested in experiment I.

Our initial analysis pooled all data collected from a pair of fish throughout the four trials. For each pair of fish, data were converted to win proportions (i.e., number of food items won by coho/total food items won) for both species, and paired proportions were compared using the Wilcoxon signed-rank test to determine if the two species differed in level of foraging success. We then used generalized linear models to determine whether fish FL, absolute length difference (coho salmon FL - brook trout FL), and proportional size difference (coho salmon FL / brook trout FL) explained differences in the proportion of food items won by coho salmon.

To determine how foraging success changed over the course of the four trials, we used a nonparametric, repeated measures Friedman test (with each trial as a repeated measure) to compare the number of food items consumed by each species in each trial. Post-hoc Wilcoxon signed-rank tests with Bonferroni p-value adjustments were used for multiple comparisons.

Experiment II: Group trials

Four similarly-sized fish (within 10 mm FL) were selected for each group trial. Groups consisted of one of the following combinations of fish: four coho salmon, three coho salmon and one brook trout, two coho salmon and two brook trout, one coho salmon and three brook trout, or four brook trout. All trials were carried out at constant fish density (1.57 fish$\cdot m^{-2}$), and all individuals were added to the arena simultaneously to eliminate effects of prior residency.

Methods for group trials were the same as those described for one-on-one trials. Five food items were dropped into each arena every 3 h from 9:00 to 15:00, resulting in three trials per day, and wins were recorded for each species. After the final trial, fish were left in arenas overnight. The following morning they were euthanized, weighed, measured, and frozen. Seventeen groups of four fish participated in experiment II.

Wins were converted to per-capita consumption data for each group of four fish and normalized via a square root transformation for both species. To test for stream channel and arena effects, we conducted individual analysis of variance (ANOVA) tests for each treatment of sufficient sample size to determine if the response varied by channel or arena. When no channel or arena effects were found, we conducted separate ANOVAs for each species to determine if individual foraging success varied by treatment group. Post-hoc Tukey's HSD test was used to determine which treatments were significantly different from one another.

Results

Snorkel observations indicated that brook trout and coho salmon were only found in the middle and lower thirds of the water column (i.e., neither foraged at the surface). Both species were primarily distributed in the bottom third of the water column but brook trout were more so than coho salmon (40 of 41 brook trout *vs.* 71 of 86 coho salmon, $X^2 = 4.40$, df = 1, $p = 0.04$). Both species were found in pools and in most pools they were the most abundant salmonids but the two species were not found together in any of the 9 pools that were surveyed. That is, pools had coho salmon (n = 6, mean = 0.78 fish per m^2) or brook trout (n = 3, mean = 0.52 fish per m^2) but not both. Rainbow trout (*O. mykiss*), Chinook salmon (*O. tshawytscha*) and sculpins (*Cottus* spp.) were also present in some pools.

Experiment I

In the dyadic trials, coho salmon won a significantly larger proportion of food items than did brook trout ($T_{min} = 14$, approximate $p < 0.001$; Fig. 2). Coho salmon FL ranged from 53 to 84 mm, brook trout FL ranged from 54 to 140 mm, and paired absolute size differences ranged from -60 mm to 15 mm. Variation in the proportion of food items won by coho salmon was not affected by coho salmon FL ($p = 0.59$), brook trout FL ($p = 0.13$), absolute size difference ($p = 0.19$), or proportional size difference ($p = 0.19$). Thus over the size range tested, coho salmon were almost invariably successful in obtaining the majority of the food items, despite a considerable size deficit. We also found that coho salmon consumption of food items increased from earlier to later trials within pairs of fish tested during the day ($X^2 = 25.85$, df = 3 , $p < 0.001$, Fig. 3) whereas brook trout consumption did not change throughout the day ($X^2 = 4.81$, df = 3, $p = 0.19$, Fig. 3).

Experiment II

There were no channel or arena effects on square root per capita consumption by coho salmon or brook trout (all $p > 0.05$). Coho salmon foraging success (per capita) increased as relative abundance of brook trout increased and relative abundance of coho salmon decreased ($F_{3,10} = 4.81$, $p = 0.03$). Coho salmon foraging success in the different treatments was classified into overlapping categories (a and b; Fig. 4). Brook trout foraging success was similarly low in all treatments ($F_{3,9} = 1.51$, $p = 0.28$; Fig. 4). In mixed-species treatments, coho salmon consumption was always greater than brook trout consumption (Fig. 4). In single-species treatments, the ranges of square root number of food items consumed by each species overlapped (Fig. 4).

Discussion

Salmonid fishes are important components of native fish communities in many north-temperate and boreal systems, and are now equally important components of many systems in the southern hemisphere as a consequence of transplanted populations (McDowall 2006). Moreover, interactions with non-native salmonids, primarily in streams, affect the health of many native populations (Dunham et al. 2002; Fausch 2008). Therefore, a better understanding of the factors controlling the outcomes of interspecific competition is important for fish conservation. Typically, the established species is the native but in our case the non-native brook trout are established and the native coho salmon are recolonizing their former habitat after a century of extirpation. In a report predicting recolonization patterns of Elwha River salmonids, Brenkman et al. (2008) anticipated competitive interactions between resident and recolonizing salmonids, including those between juvenile coho salmon and resident, non-native brook trout.

Our results indicated that recolonizing coho salmon will have a competitive advantage over resident non-native brook trout because we found a consistent advantage for coho salmon under all experimental scenarios.

Contrary to our first null hypothesis, fish species played a significant role in the outcomes of one-on-one feeding contests, while no measure of fish size or size difference between species influenced the results. However, fish size within a species such as coho salmon can have a strong influence on the outcomes of competitive interactions (Chapman 1962, Maynard 1987). We found no threshold size disparity after which brook trout became dominant, although to avoid predation we did not test fish pairs where one individual was less than half the length of its opponent. It is possible that at greater size disparities brook trout might start winning contests, or might consume small coho salmon.

Coho salmon food consumption increased over the trials during the day whereas brook trout consumption did not change as trials progressed, so the outcomes of the early trials may have influenced the outcomes of later ones. In salmonids, prior experience influences the outcomes of subsequent interactions, both with novel and familiar opponents (Johnsson 1997; Rhodes & Quinn 1998). Fish that have won contests are more likely to win in the near future, and fish that have lost are more likely to lose (Rhodes & Quinn 1998). In our study, coho salmon often won more food items than brook trout in the first one-on-one trial. The coho salmon continued to win subsequent trials, and the brook trout continued to lose. In the later trials of our study, brook trout appeared to be more passive than in earlier trials, as though they did not engage in repetitive contests that they were likely to lose.

Our second null hypothesis was that species and group composition would not affect individual foraging success in size-matched groups. In group trials with constant fish density but

different proportions of the two species, fish species influenced individual foraging success, as coho salmon were more successful than brook trout in all sympatric treatments. Coho salmon were superior foragers and competition was highest and salmon per capita consumption was lowest in treatments with more coho salmon. These findings are supported by Grand and Dill (1999), who found that coho salmon foraged more aggressively in larger groups. As the number of coho salmon in a treatment decreased, coho per capita consumption increased significantly because fish were released from intraspecific competition and brook trout posed little challenge. Similarly, Fausch and White (1986) found that in group trials the coho salmon occupied more profitable stream positions than brook trout, indicating that they were competitively dominant.

Snorkel surveys in the Elwha River system did not reveal these species in sympatry on fine spatial scales, thus the majority of their potential interactions were with conspecifics or other native salmonids. Other work investigating brook trout – native salmonid competition also found that the majority of encounters occurred between conspecifics, perhaps based on some degree of habitat segregation (Macneale et al. 2010). This means that the single-species group treatments from our experiment were the most representative of what is currently occurring in the river, and that coho salmon are more likely to experience intraspecific rather than interspecific competition during the early phases of recolonization during and following dam removal. As recolonization continues and coho salmon establish themselves in all suitable habitats, the encounter rate between the two species might change.

We do not believe that the channel setup gave either species an unnatural competitive advantage. Experimental arenas were designed to simulate pool habitat units, an environment in which both species are commonly found. Further, both species were seen eating during the initial

feeding the evening before trials began, so they both rapidly acclimated to the extent that they fed in the novel environment.

Species-specific life histories likely influenced the outcomes of our competitive experiments. Young coho salmon in the Elwha River enter the marine environment in the fall of their first year of life or (more often) after a year, as is typical of the species in this region (Quinn et al. 2013). In each year the larger individuals are more likely to survive at sea than the smaller ones (Holtby et al. 1990; Irvine et al. 2013). Therefore, juveniles with high metabolic rates that forage aggressively and grow rapidly are more likely to survive than more timid, and consequently smaller, conspecifics, even if aggressive foraging makes them more visible to predators. Conversely, Elwha River brook trout are lifetime stream residents and the species commonly matures at a small body size (Hutchings & Morris 1985), so they may not experience strong selective pressure for more aggressive feeding behavior or high growth rate. Our observations indicated that both species occupied the middle and lower parts of the water column but the brook trout were significantly more often near the bottom, consistent with experimental observations by Gibson (1981) and a more risk-averse life history strategy. Gibson (1981) also concluded that coho salmon were dominant over brook trout but Hutchison and Iwata (1997) found that brook trout were the most aggressive of the 11 salmonid species tested in a laboratory study, including coho salmon. The simplified, controlled nature of our stream channels relative to natural streams may have affected the outcome of competitive tests, and extension of such experiments to field situations should always be done cautiously. Temperature, water depth, and other variables can all affect experimental outcomes (Gibson 1981). Finally, population-specific variation in aggression (Rosenau & McPhail 1987) or movement (Andrews et al. 2013) might affect the results of experiments, depending on the attributes of the population used.

A major goal of the Elwha River dam removal project is to restore historically abundant populations of Pacific salmon to the river (Wunderlich et al. 1994). One important consideration for this project is how recolonizing salmon might interact with resident fish in the river, and whether competition between the two groups could possibly slow or thwart recolonization efforts (Brenkman et al. 2008). Our laboratory study was the first step in understanding how two species, recolonizing coho salmon and resident, non-native brook trout, might interact during recolonization. Based on our results, it seems very unlikely that brook trout will pose a threat to juvenile coho salmon via competition for food resources. It is possible that brook trout larger than those tested in this study might outcompete or prey upon juvenile salmon, though such large fish seem to be scarce. Monitoring efforts in 2012 and 2013 indicate that species distributions overlap at broad (sub-watershed and reach) spatial scales, but not at fine (habitat unit) ones, as indicated by the snorkel surveys. It is possible that the species, which utilize similar habitats, have segregated as a result of strong competition – more specifically, that brook trout have been forced from habitats that coho salmon have recolonized into inferior habitats. The results of this study highlight the importance of understanding the nature of native-non-native interactions in river systems undergoing restoration, as they are highly context-dependent and may have important implications for the success of ecosystem restoration.

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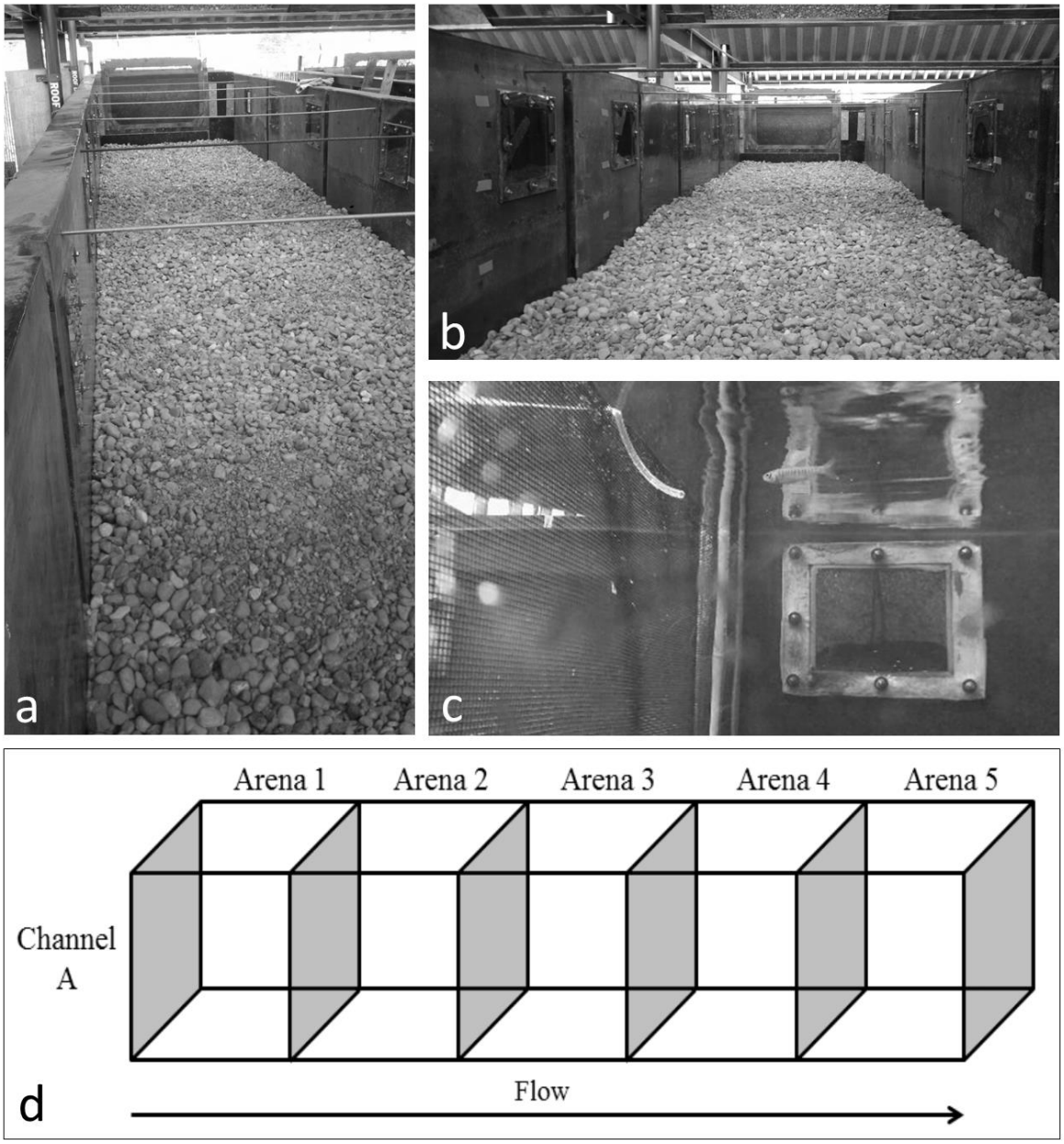

Figure 1: Stream channel setup; a, b) Longitudinal views of stream channel from above (a) and within (b) prior to filling and installation of PVC screens; c) View of feeding station, PVC screen, and acrylic window; d) Diagram of stream channel and arenas. All channels were identical and were divided into 5 equal-sized arenas. Gray panels represent plastic mesh and PVC screens separating arenas. Experiment I took place in all arenas, whereas experiment II took place in arenas 1, 3, and 5 only.

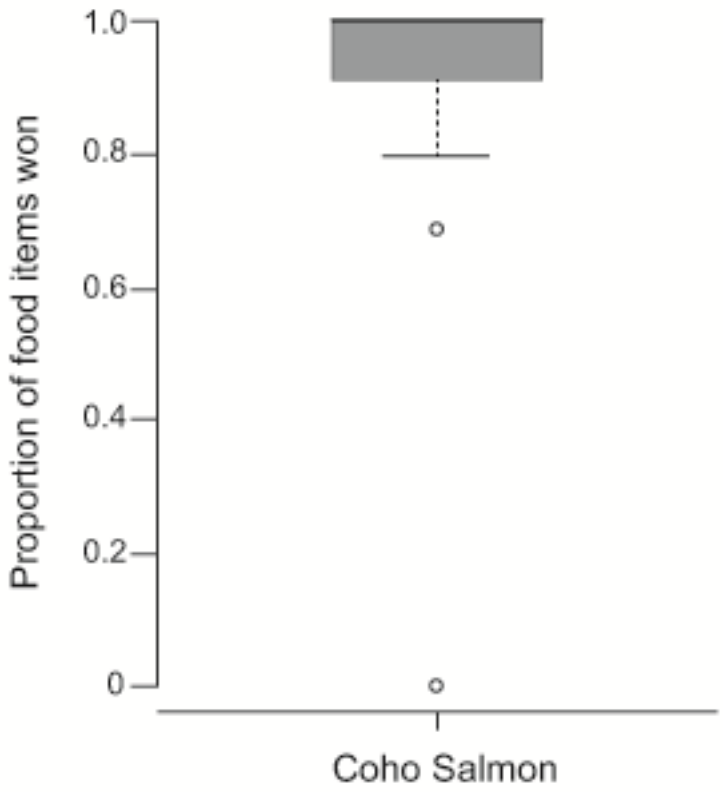

Figure 2: Proportion of food items won by juvenile coho salmon during one-on-one trials (pooled).

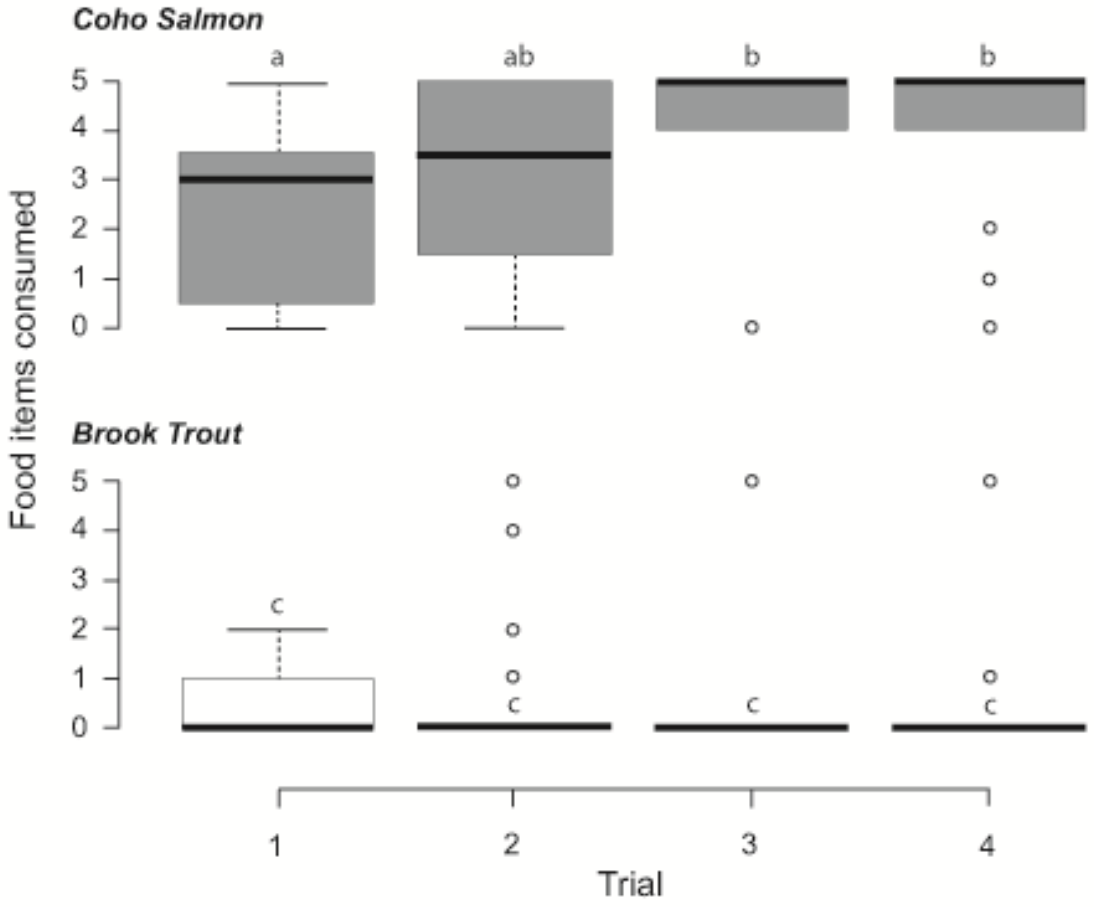

Figure 3: Number of food items consumed by coho salmon (gray; top row) and brook trout (white; bottom row) in each trial of the one-on-one experiment. Boxes are in chronological order with the earliest trial on the left and the latest trial on the right. Bars with the same letter represent statistically similar treatments based on post hoc multiple comparisons tests.

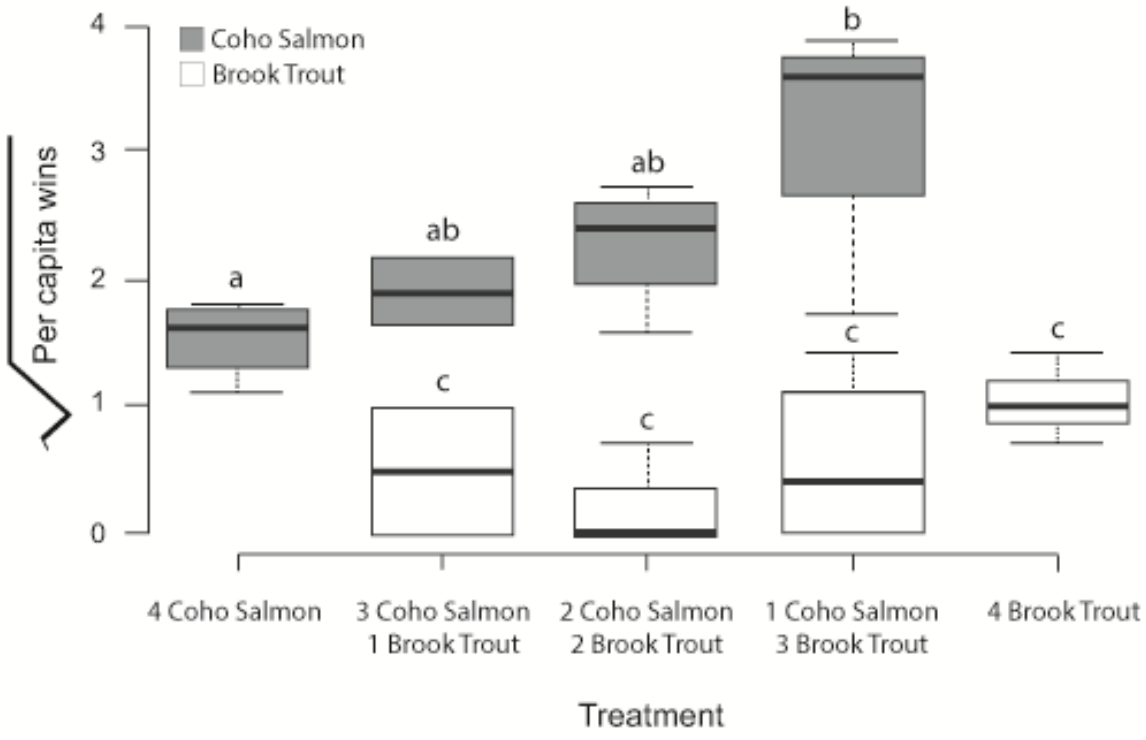

Figure 4: Square root per capita consumption for juvenile coho salmon (gray) and brook trout (white) in each treatment composed of different numbers of coho salmon and brook trout for a total of four fish in each treatment. Bars with the same letter represent statistically similar treatments based on post hoc multiple comparisons tests.

Chapter 2

Common resource utilization as an indicator of competition between brook trout and juvenile coho salmon in the Elwha River, WA during dam removal

Abstract

Dam removal is an increasingly common method of river restoration, and reestablishment of native migratory fish populations is often a goal of restoration efforts. Removal of a barrier does not necessarily guarantee successful recolonization by migratory species. If stream-dwelling resident fishes occurring in the river compete successfully with recolonizing species for food or space, migratory fish may be unable to establish populations in newly available habitat. Here we examine the extent of overlap in habitat and prey resource use as an indicator of potential competition between non-native brook trout and juvenile coho salmon in the Elwha River, WA during dam removal (2012-2014). Our data were collected from 100 m reaches within the middle Elwha River, i.e. the section of river between the former dam sites where the first interactions between recolonizing and resident salmonids occurred. We found that both species were present in 25% to 67% of reaches over the study period. Average coho salmon density varied but showed no trend over time. Average brook trout density decreased from 2012 to 2014 but the distribution of brook trout was not affected by the presence of coho salmon (and vice versa). Our density and distribution results suggested no competition between the species at the 100 m reach scale. Stomach content analysis indicated moderate, and in some cases significant, overlap between prey resource use, but stable isotope analysis, which was more sensitive to species- and site-specific differences in prey resources, indicated almost no overlap. Prey resources may not have been limiting in our reaches at the time of this study, but

competition at smaller spatial scales than the reaches we studied would not have been detected in this study.

Introduction

Dam removals are increasingly being implemented in the United States as a means of restoring rivers and the fish populations that they support (Service 2011; O'Connor 2015). Most of the dams removed to date have been small, and located in the northeastern part of the country (Service 2011). However, several large dams in the western United States have recently been removed, altered to allow fish passage, or removal is planned (e.g., Marmot Dam in Oregon, Condit Dam in Washington, and Klamath River Dams in California and Oregon; O'Connor et al. 2015; Quiñones et al. 2015). One positive ecological effect of dam removal can be rapid recolonization by native migratory fishes (Hogg et al. 2013; Pess et al. 2014; Raabe and Hightower 2014). In systems where the restoration of migratory fish populations is a goal of dam removal, it is important to monitor the recolonizing species to ensure that self-sustaining populations become established (Anderson et al. 2015). If recolonization is not successful, the monitoring information can be used to help determine the reasons for failure, and the efficacy of human intervention to assist in recolonization.

Success of recolonization can depend on numerous physical and biological factors, including suitability of the habitat for the target species and ecological interactions with previously established resident species. Salmonids are an excellent model through which to examine such interactions because their basic ecology is well-studied in a wide range of habitats (Fausch 1988; Quinn 2005; Jonsson and Jonsson 2011). Moreover, they are native to the northeastern and northwestern United States, where many dams are being removed (Service 2011; O'Connor et al. 2015), and restoration of anadromous salmonid populations is often an explicit goal (Wunderlich 1994; Pess et al. 2014). Further, in many rivers, multiple salmonid species are sympatric, so there is potential for the diverse ecological interactions between species

documented in salmonids, including competition for breeding habitat (Hayes 1987; Essington et al. 1998) and predation (Ruggerone and Rogers 1992). However, it has long been recognized that competition for food and space by juveniles strongly influences the populations of stream-rearing salmonids (Chapman 1966). These competitive interactions can occur within the river at different spatial scales as a result of heterogeneity in the densities and distributions of the species.

Competition between salmonids, including native and non-native species (Fausch 1988, 2007, 2008) often occurs because many salmonids consume similar prey using similar foraging tactics. Stream salmonids consume aquatic and terrestrial invertebrates, and they may forage on benthos or from the water's surface, but drift foraging is most efficient (Newman and Waters 1984; Wilzbach and Hall 1985; Fausch 2014). Salmonids are opportunistic feeders and may actively search for prey or hunt from foraging stations (Fausch 1984; Stradmeyer and Thorpe 1987; Nielsen 1992; Tunney and Steingrímsson 2012). Frequently, stream-dwelling salmonids establish dominance hierarchies and defend territories for access to drifting food resources (Chapman 1962; Keenleyside and Yamamoto 1962). These foraging patterns have been extensively studied in salmonid fishes because of the links to intra-specific competition but diet or spatial segregation commonly occur between species (Bisson et al. 1988, Nakano et al. 1999), and competitively inferior species may move to sub-optimal habitats in the presence of the superior competitor (Sabo and Pauley 1997). Energy spent in competitive interactions cannot be allocated to fish growth or body condition, so competitive interactions may have consequences for fish (Keeley 2001).

Despite having the apparent advantage of local adaptation through evolutionary processes, native species sometimes fare poorly in competition with non-native species, even

when those non-native species are themselves outcompeted in their native habitat (Dunham 2002; Fausch 2008). One conspicuous example is the brook trout, *Salvelinus fontinalis* Mitchill. In its native range (eastern North America), it is typically displaced by non-native rainbow trout, *Oncorhynchus mykiss* Walbaum, from western North America, and brown trout, *Salmo trutta* Linnaeus, from Europe. However, when transplanted to western North America, brook trout compete successfully with native cutthroat trout, *O. clarkii* Richardson, and have been implicated in declines of Pacific salmon (Levin et al. 2002; Fausch 2008).

This study examines the recolonization of Pacific salmonids in the Elwha River, WA, a system recovering from a century of fragmentation by dams. By October 2014, both dams on the river had been completely removed, and native Pacific salmon were returning to their historic home range in the river reaches between and beyond the former dam sites (O'Connor 2015). As they recolonize, Pacific salmon are interacting with salmonids that already occupy the river, including non-native brook trout (Brenkman et al. 2008).

Our goal was to determine the extent of competition for habitat and food between recolonizing coho salmon *O. kisutch* Walbaum and brook trout within the middle Elwha River (between the former dam sites) during dam removal (2012-2014). These species were selected as the focus because 1) coho salmon have been excluded from this part of the river by one of the dams for nearly a century (Pess et al. 2008), 2) laboratory experiments found that brook trout were especially competitive and aggressive as juveniles (Hutchison and Iwata 1997; but see Fausch and White 1986 for evidence to the contrary), 3) brook trout are non-native and have been successful in competition with other salmonids outside their native range (Dunham et al. 2002), and 4) shared habitat preferences and foraging habits could result in competition for mutually preferred resources. Specifically, we determined: 1) the density and spatial distribution

of resident brook trout and recolonizing juvenile coho salmon in three immediate post-dam removal years (2012 – 2014), 2) the extent of coarse-scale overlap or segregation between these species, 3) the trophic positions of brook trout and coho salmon using stomach content and stable isotope analysis, and 4) the extent of diet overlap between the species.

Methods

Study System

The Elwha River flows north from Olympic National Park on Washington State's Olympic Peninsula and into the Strait of Juan de Fuca. Early in the 20th century, two dams were built on the Elwha River without means of fish passage, and migratory species (e.g., anadromous Pacific salmon, *Oncorhynchus* spp.) were prevented from accessing the river above the dams (Duda et al. 2008). Brook trout were stocked in the river from 1935 until 1976, and established a naturalized population in the middle section of the river between the two dams (Samuel Brenkman, National Park Service, personal communication; Brenkman et al. 2008). The Elwha Dam, closest to the mouth of the river, was removed in spring 2012, and the upper Glines Canyon Dam was fully demolished by late summer 2014. The middle river was open to fish recolonization before the remainder of the watershed, so it was the main theater for interactions between recolonizers and residents during dam removal.

To facilitate recolonization, 600, 307, and 1052 adult coho salmon were transported above the Elwha Dam dam site in fall 2011, 2012, and 2013, respectively (McMillan and Moses 2011, 2012; McMillan et al. 2013). These transplants also helped recolonizing coho salmon avoid some of the negative effects of high sediment loads in the river (McMillan and Moses 2012). During dam removal, the main stem and side channels of the Elwha River were impacted

by high turbidity and siltation from loosened sediment stored behind the former dams (Warrick et al. 2015) but tributaries were largely unaffected by sediment until after our study.

There are two major tributaries to the middle Elwha River: the Little River flows in from the east just upstream of the former Elwha Dam reservoir, and Indian Creek flows in from the west at approximately the same location. There are also several smaller tributaries (Campground Creek, Madison Creek, among others) and floodplain side channels. Our sampling occurred in both large and small tributaries, side channels, and the main stem of the river (Figure 5).

Spatial Distribution and Density Sampling

We used a stratified Generalized Tessellation Stratified (S-GRTS) design to select 15 reaches in the middle Elwha River that incorporated 5% of the total area available to recolonizing salmonids (Pess et al., in prep.). We selected reaches within the middle section of the Elwha River because brook trout occupied this section for several decades prior to dam removal and presumably had stabilized in their abundance and distribution, and because this section of the river falls within the area where interspecific interactions with recolonizing salmon were predicted to be most common (Brenkman et al. 2008). We selected sites in tributary and floodplain channel habitats, and those characterized by a range of gradients, levels of confinement (ratio of valley width to channel width), and distance from the former Elwha Dam site (Pess et al. in prep.). We used three-pass backpack electrofishing with downstream and upstream blocking seines and sampled upstream from the downstream end of each reach. All fish captured were identified to species (except rainbow and cutthroat trout < 60 mm, which were classified as "trout fry"), measured to fork length, and released after the third pass (Pess et al. in prep.). We recorded the length of each reach and measured the width and depth at the upper, middle, and lower section of each reach. Fish sampling took place in late summer (August-

September) in 2012, 2013 and 2014. For this study, we selected 11 of the 15 reaches because they had been surveyed in late summer in each of the three years.

Fish abundance was calculated in each reach and year from our three-pass fish catches according to Carle and Strub (1978; R package {FSA}, Ogle 2015). Reach area was calculated by taking the average of three width measurements and multiplying by the length of the reach (about 100 m). Fish density for each species was calculated by dividing the estimated abundance of fish caught in each reach in each year by the reach area for that year. We calculated the average densities of coho salmon and brook trout over all reaches within each year, and in all years pooled for each reach. We also calculated frequency of occurrence for each species in each reach and the percent of reaches in which coho salmon were sympatric with brook trout in each year. We used contingency tables and the Fisher-Irwin test to determine whether brook trout were equally likely to be present in reaches with and without coho salmon in each year (Fisher 1935; Irwin 1935).

Sample Collection and Analysis of Diet Samples

In July - September 2013, salmonids were collected by backpack electrofishing in the Elwha River, the Little River, and in other smaller tributaries and side channels in the Elwha River's middle section, between the locations of the former dams. Stomach contents of coho salmon were collected via gastric lavage, washed through a 53 µ sieve, and preserved in 95% ethanol for later analysis. We recorded fish fork length (FL) and mass, and collected a small piece of tissue from the upper lobe of the caudal fin of each fish, which was air dried for later analysis. Brook trout were lethally sampled, frozen or preserved in 95% ethanol, and were dissected in the laboratory. We recorded FL and mass for all dissected fish and removed a caudal fin clip from frozen fish only. The top lobe of the caudal fin was removed in fish larger than 50

mm FL, and the entire caudal fin was removed in fish smaller than 50 mm. Digestive tracts were removed from the fish and stomach contents anterior to the pyloric caeca were washed through a 53 µ sieve and preserved in 95% ethanol.

Brook trout and coho salmon in the middle Elwha River (between the two former dams) were spatially segregated at the time and locations of diet sampling, so fish samples came from reaches dominated by one species with very few (1 or 2 individuals) or none of the other species (Thornton, unpublished data; Heidi Hugunin, National Park Service, personal communication). Snorkel observations in pool habitat units (n = 9) showed that the two species were always allopatric at that spatial scale (Thornton MS Thesis). As a result, the diet information that we collected indicated what these species consumed in near or complete allopatry in 100 m reaches, even though they were found in the same region of the river system and thus sympatric at a more coarse spatial scale.

Preserved stomach contents were examined under a dissecting microscope and diet items were identified conservatively and to the lowest practical taxon, usually order (see Vinson and Budy 2011). We recorded counts for each taxon and identified a total of 21 prey taxa from 27 brook trout and 35 coho salmon stomachs. We calculated the mean proportion of diet by number for each prey taxon for each predator species. These metrics provide complementary information on how important different prey items were to each species. We also calculated the range of the number of items consumed for each prey taxon for each predator species. Stomachs without identifiable prey were removed from analysis. We used Spearman's rank-order correlation between mean diet proportions and percent frequency for each species to help determine diet similarity between them.

To assign a value to the degree of diet overlap between brook trout and juvenile coho salmon, we used Schoener's overlap index (Schoener 1970):

$$overlap = 1 - 0.5 * (\Sigma \left| p_{coho\ salmon,i} - p_{brook\ trout,i} \right|)$$

where $p_{coho\ salmon,i}$ is the mean proportion of prey item i in coho salmon stomachs, and $p_{brook\ trout,i}$ is the mean proportion of prey item i in brook trout stomachs. An overlap value of 0.6 or greater indicates significant diet overlap (Vinson and Budy 2011; Tagliaferro et al. 2015).

We used non-metric multidimensional scaling (NMDS) on Bray-Curtis dissimilarity to summarize dominant gradients of variation in diet composition and compare diets between brook trout and coho salmon (Kruskal and Wish 1978). NMDS is an ordination method that preserves the rank-ordered distances between sample points in ordination space. We then used ANOSIM, a nonparametric multivariate procedure analogous to analysis of variance, to test for differences in diet composition between brook trout and coho salmon. Prey taxa present in less than 5% of stomachs, as well as those that were judged to be incidental catches, were removed from NMDS and ANOSIM computations to eliminate their unduly influence on the multivariate analyses.

Isotope Sample Preparation and Analysis

Fin clips collected in the field were air dried, those collected in the lab were frozen, and all samples were freeze dried for 24 h. Samples were then homogenized using a mortar and pestle or small scissors. Aliquots of each tissue sample (0.4-0.6 mg) were weighed into tin capsules and sent to the University of Washington Isolab for $\delta^{13}C$-$\delta^{15}N$ isotope analysis using mass spectrometry. All values for $\delta^{13}C$ were lipid corrected according to Post et al. (2007). Thirty-eight brook trout and 15 coho salmon fin samples were included in analysis. Coho salmon were all young-of-the-year and ranged from 52 to 68 mm FL. Brook trout were not aged, but were likely from young-of-the-year to several years old, as they ranged from 34 to 148 mm FL.

We compared the $\delta^{13}C$ and $\delta^{15}N$ of the two species using two-sample t-tests. We used convex hull total area (after Cornwell et al. 2006; Layman et al. 2007; R package {siar}, Parnell and Jackson 2013) to determine the extent of overlap between brook trout and coho salmon trophic niches (Villéger et al. 2011). We also examined isotope signature as a function of fish length for both isotopes and both species using linear regression.

Results

Density and Distribution

The 11 reaches within the middle Elwha River yielded six species of salmonids at varying densities (Pess et al. in prep.). Coho salmon mean density over the years was 0.060 fish · m^{-2} and brook trout mean density was 0.023 fish · m^{-2} (Table 1). Coho salmon were found in 82% of sites in 2012 and 73% of sites in 2013 and 2014 (Table 2). Brook trout were found in 64% of sites in 2012, 45% of sites in 2013, and 55% of sites in 2014. They were relatively abundant in a few reaches, but absent or in low densities in most reaches. Brook trout were sympatric with coho salmon in 66.7% of reaches in 2012, 25% of reaches in 2013, and 50% of reaches in 2014 (Table 2). Over the sampling period, juvenile coho salmon were most abundance in reaches of Little River (h1) and Madison Creek (h7). Brook trout were most abundant in Campground Creek (h8) and side channel 17gwone (h6; Table 3).

The densities of each species varied between years and between reaches in a single year (SD > mean; Table 1, Table 3). Brook trout density decreased over the three years, but we detected no directional changes in the average density of coho salmon over time (Table 1).

The presence of brook trout did not influence whether coho salmon were present or absent in a particular reach in any year ($p > 0.05$ in all cases). The computations of the Fisher-

Irwin test can result in inflated p-values, which increase the chance of type II error (failing to reject H_0 – the presence of brook trout has no effect on the presence of coho salmon – when it is false). Most of our p-values were sufficiently large that they were probably not significant in spite of inflation. However, the p-value for the contingency table between brook trout and coho salmon in 2013 was significant at α=0.10 ($p = 0.06$), so there may have been a small influence of one species on the other in that year only.

Stomach Contents

The main components of the diet were similar for both species. Diptera (0.30), Ephemeroptera (0.26), Coleoptera (0.13), and Cladocera (0.08) represented the highest mean proportions of coho salmon diets by prey count. Brook trout diets primarily consisted of Diptera (0.53), Coleoptera (0.09), Acari (0.07), and Ephemeroptera (0.07). Three of the four most heavily represented prey taxa were common to both fish species, though the proportions of these items differed (Table 4). Prey items from the same three orders (Diptera, Ephemeroptera, Coleoptera) also appeared most frequently in the diets of both fish species (Table 4). Despite these similarities, each species consumed several unique items. Only brook trout ate prey items in the following taxa: Annelida, Copepoda, Gastropoda, Hymenoptera, Megaloptera, Orthoptera, and Pseudoscorpionida. Only coho salmon consumed prey in the taxa Chilopoda, Collembola, Diplopoda, and Nematoda. However, none of the prey taxa unique to either predator species were very common in the species that did consume them (Table 4). Spearman's rank-order correlations revealed positive correlations between mean proportion (rho = 0.57, $p = 0.006$) and frequency of occurrence (rho = 0.67, $p = 0.001$) of prey items in brook trout and coho salmon stomachs. Schoener's overlap index for brook trout and coho salmon diet contents was 0.63, which represents 63% overlap in diet.

There were significant differences in the diet composition between species (ANOSIM R = 0.14, P = 0.001). The dispersion of rank dissimilarities for the two predators were similar, though brook trout were slightly less dispersed (Fig. 6). NMDS ordination demonstrated separation between the diets of brook trout and coho salmon in 2D ordination space, though some overlap in diet composition was evident (Fig. 7). Most of the separation between species occurred along NMDS1, with brook trout diets characterized by more Diptera and coho salmon diets characterized by more Ephemeroptera (vector loadings: -0.94 and 0.81, respectively; Table 5). Positive values on NMDS2 were characterized by more Collembola, Trichoptera, and Coleoptera, and negative values were characterized by more Plecoptera (vector loadings: 0.86, 1.00, 0.86, and -1.00, respectively; Table 5), though there was not as much separation between coho salmon and brook trout on this axis.

Isotopes

Brook trout and coho salmon had significantly different carbon (t = -6.73, df = 51, p < 0.001) and nitrogen signatures (t = 8.35, df = 51, p < 0.001), though there was some overlap between the values for both species (Fig. 8). Convex hull total area for the brook trout was 17.57 compared to 6.11 for coho salmon. The area of convex hull overlap was 0.01, resulting in a 0.06% overlap for brook trout and a 0.16% overlap for coho salmon (Fig. 8). Brook trout in the same size (FL) range as coho salmon had a total area of 3.47 and the area of overlap with coho salmon was 0.01 (0.05% overlap for size-matched brook trout and 0.15% overlap for coho salmon). The overlap between the species was caused by the isotope signatures of a single coho salmon. Without this individual, no overlap would have occurred. Brook trout length was positively correlated with $\delta^{13}C$ ($F_{1,36}$ = 17.23, multiple R^2 = 0.33, p < 0.001) and $\delta^{15}N$ ($F_{1,36}$ =

26.81, multiple $R^2 = 0.43$, $p < 0.001$; Fig. 9) but no relationship was detected in coho salmon for $\delta^{13}C$ ($F_{1,13} = 3.15$, $p = 0.10$) or $\delta^{15}N$ ($F_{1,13} = 1.12$, $p = 0.31$; Fig. 9).

Discussion

The goal of this study was to assess the potential for competition between brook trout and juvenile coho salmon in the Elwha River by examining overlap in habitat use and prey resources. Coho salmon and brook trout were sympatric in several reaches of the middle Elwha River between 2012-2014, so there was potential for interaction and competition at the 100 m reach scale. We found no consistent directional changes in coho salmon density over three years immediately following restoration of fish passage, but mean brook trout density decreased over the course of our study. There was no consistent relationship between the presence of brook trout and the absence of coho salmon (or vice versa) that would have indicated competition between them. Our diet analyses all indicated some small, and in some cases significant, overlap in diet, but stable isotope analyses indicated virtually no overlap in values between the species. Based on our distribution results, strong competition for food was likely not occurring at the reach scale. Another study found that coho salmon were not sympatric at the habitat unit scale, so competition for food may occur at finer spatial scales than we studied here, and may have caused the two species to segregate into separate pool habitats (Thornton MS Thesis).

In the years after habitat becomes available to migratory fish, we expect the densities and distributions of recolonizing species to increase until all suitable habitats are occupied and the carrying capacity is reached, and this process is occurring in the Cedar River, WA following recolonization by coho salmon (Anderson et al. 2013, 2015; Buehrens et al. 2014). Coho salmon densities in the middle Elwha River varied within and between reaches, but there was no

consistent change in density or distribution in the three years during dam removal. The average density of coho salmon in the Elwha River between 2012 and 2014 (0.06 fish · m^{-2}) was low compared to western Washington rivers in general (Quinn 2005), but was higher than densities of juvenile coho salmon in the Cedar River watershed in the years immediately following restoration of fish passage, and within the range of densities recorded in the Cedar River 2 to 6 years following restoration of fish passage (Anderson et al. 2008; Buehrens et al. 2014). The coho salmon distribution patterns that we found resulted from early dispersal and colonization by offspring of adults that spawned below the dam, or more likely, offspring of adults that were transplanted above the dam the previous year. Redd surveys from fall 2011, 2012, and 2013 showed that adult coho salmon mostly spawned in the Little River and Indian Creek (McMillan and Moses 2011, 2012; McMillan et al. 2013), where we found some of the highest densities of juveniles. Juvenile coho salmon can also be very mobile, moving up to 6.3 km from the site where they were spawned (Anderson et al. 2013). Therefore, the distribution of juvenile coho salmon in the Elwha River was the result of a combination of adult spawning locations and juvenile dispersal.

If recolonizing coho salmon were competing strongly with brook trout, one of the species might alter its spatial distribution to avoid competition and we would not find both in the same locations (Vehanen et al. 1999; Thibault and Dodson 2013). We found no evidence for interspecific competition at the reach scale. Brook trout experienced a decrease in mean density from 2012-2014, but coho salmon presence did not affect whether brook trout were present or absent in a particular reach, so decreases in density may have been due to factors other than competition. The strength of competition often increases as fish density increases (Hasegawa and Yamamoto 2009; Richard et al. 2015), so coho salmon density may have been too low to induce

competition with brook trout at the reach scale. It is also possible that recolonizing coho salmon compete more intensely with conspecifics than with resident salmonids, so their density will have less of an impact on other species than if interspecific competition was more intense. (Macneale et al. 2010, Pess et al. 2011).

Most of the important prey taxa by mean proportion of diet and frequency of occurrence were common to both coho salmon and brook trout, and mean prey proportion and prey frequency of occurrence for both fish species were moderately but significantly correlated. Schoener's overlap index revealed a significant 63% overlap between the diets of the salmonids, so in sympatric reaches with limited resources competition for prey could occur.

NMDS results were consistent with mean proportions and frequency of occurrence for prey taxa. There was some overlap between predator species, but brook trout stomach contents were characterized by Diptera (the largest mean proportion of their diet and the most frequently consumed taxon) to a greater extent than coho salmon, for which Ephemeroptera was the most frequently consumed taxon. Rank dissimilarities for mean prey proportions were significantly different between predator species. This result is likely driven by a combination of the stomach content data and a small degree of heterogeneity in multivariate dispersion between brook trout and coho salmon.

Brook trout had a much broader trophic niche than coho salmon based on the total area from convex hull analysis of isotope signatures. A broader trophic niche could also be the result of sampling brook trout over a wider spatial and temporal range than coho salmon, more generalist feeding by brook trout, or the greater size range of the brook trout we sampled compared to coho salmon. Coho salmon in the Elwha River usually emigrate to the marine environment after 1 year in freshwater or at the end of their first summer, so all individuals

caught for our diet analyses were young of the year (Quinn et al. 2013). Elwha River brook trout are lifetime stream residents (Brenkman et al. 2008) and the individuals sampled likely ranged from young of the year to several years of age. Like many salmonids, brook trout experience an ontogenetic shift in diet, consuming small prey items as gape-limited juveniles and increasing the size and type of their prey as they grow (Sempeski and Gaudin 1996; Keeley and Grant 1997).

Our isotope samples for brook trout represented diets from a spectrum of sizes, sites, and dates, whereas our coho samples represented a single cohort in fewer sites over a shorter time period. Therefore, it is not surprising that brook trout had a broader isotopic trophic niche than coho salmon. Brook trout had a narrower trophic niche than did coho salmon of the same size, so small brook trout were more specialist foragers than coho salmon and brook trout in general.

An ontogenetic shift in diet was apparent when we investigated the effect of brook trout length on isotope signatures. There was a positive relationship between nitrogen and carbon isotope signatures and length for brook trout, with larger fish having higher (or less negative) signatures for carbon and nitrogen. Increases in isotope signatures can be associated with prey switching. An increase in $\delta^{15}N$ could result from an elevation in trophic position after a diet shift to larger, predatory insects or small fishes (Vander Zanden et al. 1997). An increase in $\delta^{13}C$ could result from a switch to a prey subsidy from another habitat type or ecosystem (e.g., terrestrial; Findlay 2001). Coho salmon length had no influence on isotope signatures, probably because they had a limited length range.

The extent of isotopic and trophic niche overlap between brook trout and coho salmon was very small, even among fish of the same size. Stomach contents indicated considerable but not complete overlap, but were not sensitive to family-, genus-, or species-specific differences in prey items. Isotope analysis was sensitive to these differences, but also to site-specific

differences within species or other taxa (e.g., Duda et al. 2011), therefore potentially underestimating the level of prey taxon overlap, especially because fish used for these analyses were usually allopatric. Other work has found that in paired stomach content-isotope studies, isotope analyses tend to indicate less overlap than stomach contents (Vinson and Budy 2011, and papers therein), but both techniques yield valuable information. We believe that the true level of diet overlap between these species is likely low, but greater than that indicated by isotope analysis.

In the Elwha River during dam removal, site-specific differences in fish stomach contents and isotopes may have been particularly extreme as a result of active dam removal occurring during our sampling. Brook trout were collected from main stem, side channel, and tributary reaches, while coho salmon were only collected from tributary reaches. The macroinvertebrate communities in these different types of reaches were not the same prior to dam removal (Morley et al. 2008). Large volumes of suspended sediment released from the dam reservoirs during deconstruction have impacted main stem and side channel habitats, decreasing the density of macroinvertebrates overall and resulting in shifting communities (Warrick et al. 2015; S. Morley, NOAA, personal communication). These changes did not occur in tributary habitats during the course of this study. Though sedimentation should be taken into account when determining the cause of diet differences between different species in different sites, our results are still representative of what coho salmon and brook trout were consuming during the dam removal period.

It is widely recognized that ecological processes within rivers manifest themselves differently at varying spatial and temporal scales (Fausch et al. 2002; Thorp 2014). Recent studies of salmonids have taken this into account and have found that fish distribution and

processes such as competition and density-dependence play out differently at different scales because physical and biological factors that influence competition change over space and time (Brenkman et al. 2012; Marco-Rius et al. 2013; Teichert et al. 2013). All overlap indexes from this study suggest that brook trout and coho salmon could compete for food resources when they become limiting. It is possible that food was not limiting in the middle Elwha River at the time of our study, but it is also possible that competitive interactions occur primarily at a different spatial scale from the ones we sampled. Stream salmonid competition is often studied at the habitat unit scale, where many species establish and defend foraging territories (Keeley and Grant 1995). It is likely that competitive interactions occurred at this fine scale, where fish had more opportunity to come into contact with one another. A concurrent study on Elwha River brook trout and coho salmon found that both species occupied similar pool habitat units, but the two species were never found in the same pools together (Thornton MS Thesis). There may have been some undocumented physical or biological difference between the two types of pools, or spatial segregation resulted from previous competitive interactions at the habitat unit scale.

The Elwha River is in the early stages of recovery after the removal of two dams on its main stem. As part of this recovery process, anadromous Pacific salmonids are recolonizing the river and interacting with the resident salmonid species already there. Due to limited competition for resources, we believe that it is very unlikely that brook trout will prevent coho salmon from reestablishing a population in the Elwha River. Coho salmon density and distribution are likely to increase as they have in other newly available habitats (Pess et al. 2011), and the spatial overlap and scope for competition between coho salmon and brook trout may increase. If this occurs, it is likely that coho salmon will outcompete brook trout (Thornton MS Thesis) and limit their distribution to suboptimal habitats. We encourage continued monitoring of recolonization in

the middle Elwha River to focus on how rising coho salmon densities affect the distribution of brook trout in future years.

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Table 1. Mean densities (fish * m^{-2}) and (standard deviations) of coho salmon (*O. kisutch*) and brook trout (*S. fontinalis*) over all reaches in each year.

Species	2012		2013		2014		All Years	
coho salmon	0.078	(0.098)	0.028	(0.032)	0.073	(0.111)	0.060	(0.088)
brook trout	0.040	(0.069)	0.023	(0.041)	0.005	(0.012)	0.023	(0.048)

Table 2. Frequency of occurrence for coho salmon (*O. kisutch*) and brook trout (*S. fontinalis*) and percent sympatry with coho salmon in all years.

	Frequency of Occurrence			% Sympatry with Coho Salmon		
Species	2012	2013	2014	2012	2013	2014
coho salmon	0.82	0.73	0.73			
brook trout	0.64	0.45	0.55	66.7	25	50

Table 3. Mean densities (fish * m^{-2}) and (standard deviations) of coho salmon (*O. kisutch*) and brook trout (*S. fontinalis*) averaged over all years in each reach.

Site Name	Site Code	coho salmon		brook trout	
Little 2	h1	0.191	(0.141)	0.008	(0.012)
Little 11	h2	0.062	(0.007)	0	(0.001)
Little 14	h3	0.07	(0.042)	0	(0.001)
Little 21	h4	0.041	(0.050)	0	(0.001)
Indian 19	h5	0.039	(0.030)	0.001	(0.001)
17gwone	h6	0		0.115	(0.069)
Madison	h7	0.127	(0.201)	0.047	(0.039)
Campground	h8	0.053	(0.092)	0.075	(0.084)
16	h9	0.003	(0.005)	0.002	(0.002)
Indian 9	h10	0.069	(0.013)	0	
Indian 12	h11	0.002	(0.002)	0	

Table 4. Mean proportion of diet, range of items consumed, and frequency of occurrence of each prey taxon for each species. Values in bold represent the 4 most common taxa for each species and enumeration method.

Taxon	Mean Proportion of Diet		Count Range of Items Consumed				Frequency of Occurrence	
	Coho Salmon	Brook Trout	Coho Salmon		Brook Trout		Coho Salmon (of 34)	Brook Trout (of 26)
			Min*	Max	Min*	Max		
Acari	0.026	**0.074**	1	2	1	4	0.235	**0.346**
Annelida	0.000	0.001			1	1	0.000	0.038
Araneae	0.011	0.028	1	2	1	1	0.147	0.192
Chilopoda	0.001	0.000	1	1			0.029	0.000
Cladocera	**0.080**	0.006	1	1	1	1	0.176	0.077
Coleoptera	**0.134**	**0.086**	1	24	1	8	**0.588**	**0.423**
Collembola	0.019	0.000	1	2			0.088	0.000
Copepoda	0.000	0.014			3	3	0.000	0.038
Diptera	**0.302**	**0.526**	1	24	1	240	**0.794**	**0.923**
Diplopoda	0.017	0.000	1	1			0.118	0.000
Ephemeroptera	**0.261**	**0.066**	1	25	1	79	**0.824**	**0.423**
Gastropoda	0.000	0.026			1	4	0.000	0.154
Hemiptera	0.029	0.031	1	2	1	5	0.235	0.269
Hymenoptera	0.000	0.015			1	30	0.000	0.115
Lepidoptera	0.002	0.007	1	1	1	1	0.029	0.077
Megaloptera	0.000	0.000			1	1	0.000	0.038
Nematoda	0.005	0.000	1	1			0.029	0.000
Orthoptera	0.000	0.013			1	2	0.000	0.115
Plecoptera	0.054	0.056	1	3	1	9	**0.471**	0.308
Pseudoscorpionida	0.000	0.001			1	1	0.000	0.038
Trichoptera	0.059	0.048	1	16	1	3	0.353	0.269

*non-zero minimum

16 Table 5. NMDS vector loadings for each diet taxon. Asterisks (*) represent significant vectors (α
17 = 0.05).

Taxon	NMDS1	NMDS2	r2	Pr(>r)	
Araneae	-0.577	0.817	0.069	0.172	
Coleoptera	0.517	0.856	0.567	0.001	*
Collembola	-0.511	0.859	0.114	0.045	*
Diptera	-0.944	-0.331	0.777	0.001	*
Diplopoda	-0.723	0.691	0.044	0.299	
Ephemeroptera	0.805	-0.593	0.729	0.001	*
Gastropoda	-0.284	0.959	0.051	0.257	
Hemiptera	0.393	-0.920	0.106	0.051	
Hymenoptera	-0.222	-0.975	0.012	0.723	
Lepidoptera	0.941	-0.339	0.017	0.655	
Orthoptera	-0.247	0.969	0.086	0.121	
Plecoptera	-0.102	-0.995	0.144	0.015	*
Trichoptera	0.035	0.999	0.258	0.002	*

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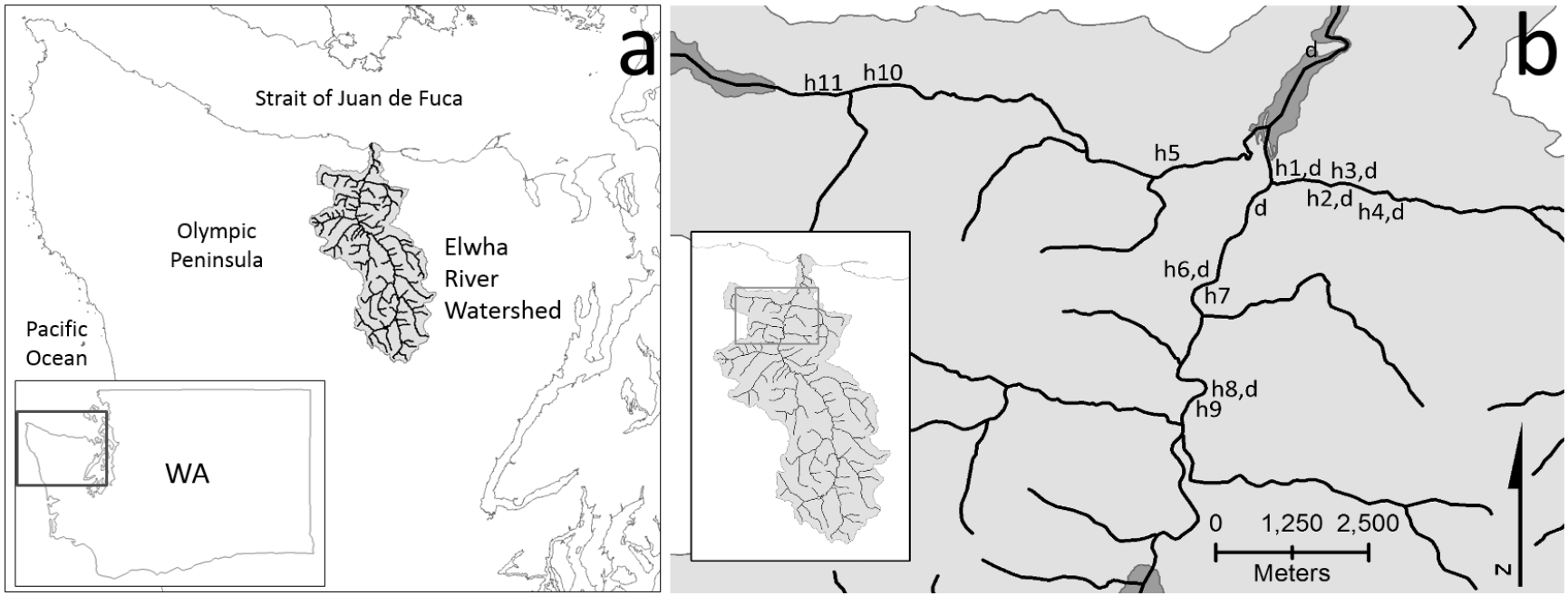

Figure 5. Study sites. a) Location of the Elwha River within Washington State, and b) the locations of our sampling sites within the middle Elwha River. Sites indicated by "h#" codes represent reaches where density and distribution data were collected, numbered by increasing distance from the Elwha Dam site. The letter "d" represents sites where diet information was collected. Dark gray shapes at the top and bottom of panel b represent former reservoirs, and the dark gray shape on the left edge of panel b is a natural lake.

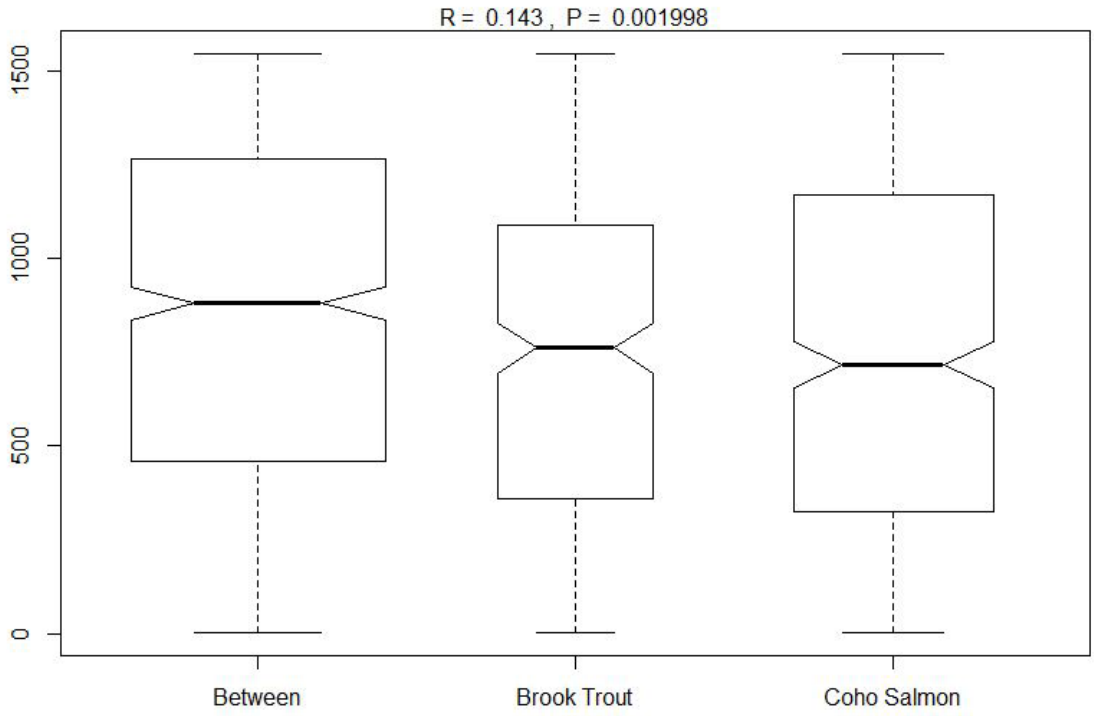

Figure 6. ANOSIM summary boxplot for mean proportion of diet. The width of each bar represents the variation or dispersion within each group (brook trout vs. coho salmon).

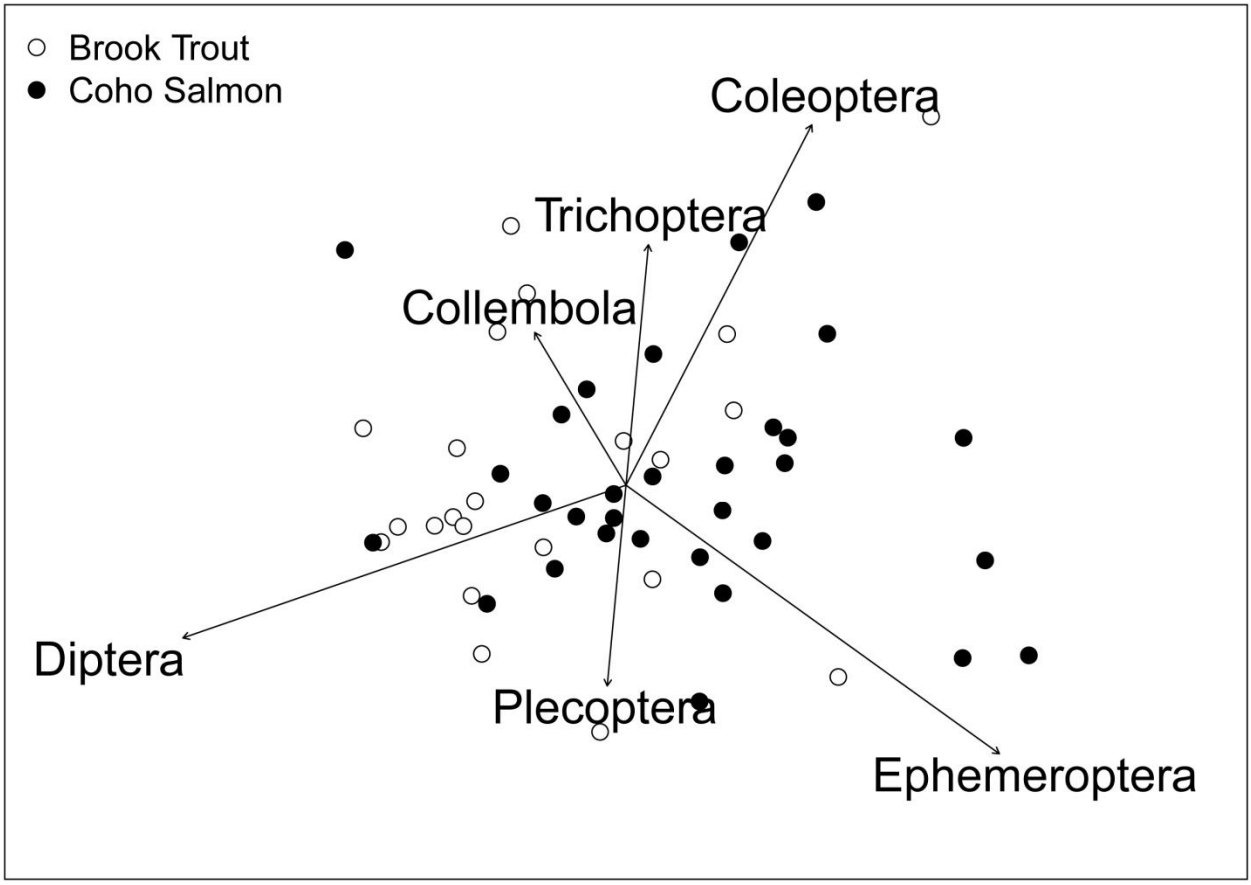

Figure 7. Two-dimensional NMDS ordination of brook trout and coho salmon mean proportional diet contents. Arrows represent significant loading vectors for common prey taxa (threshold value = 0.05). Stress = 0.15

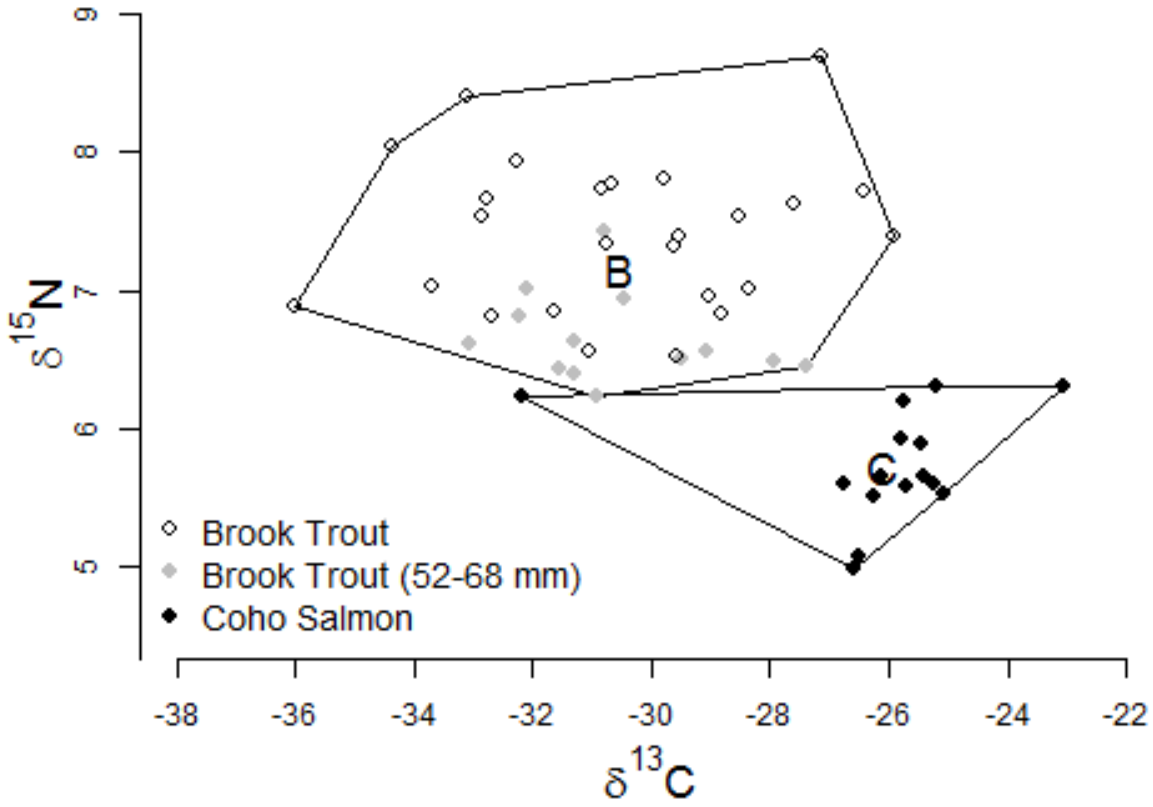

Figure 8. Convex hulls around carbon and nitrogen isotope signatures for brook trout and coho salmon. Each point represents one fish. Brook trout between 52 and 68 mm are the same size range as the coho salmon sampled. Letters within polygons represent convex hull centroids for brook trout (B) and coho salmon (C).

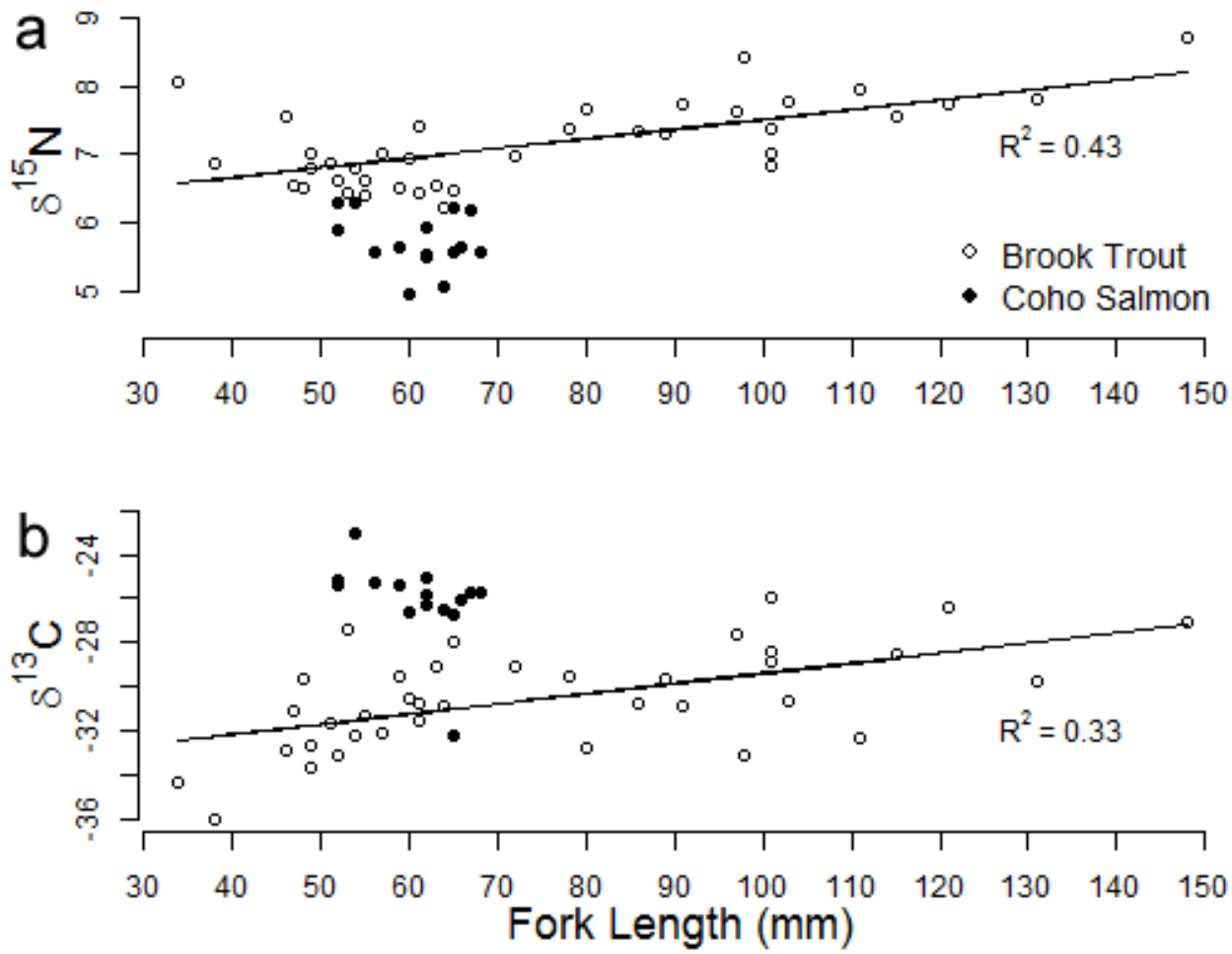

Figure 9. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) as a function of fish length. Multiple R^2 values are displayed for linear models for brook trout isotope signature as a function of length.

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R code for calculating overlap of convex hulls (after Villéger et al. 2011) is publicly available at http://villeger.sebastien.free.fr/R%20scripts/CHVintersect.r