

AN ABSTRACT OF THE THESIS OF

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Title: Experimental Analysis of Intra- and Interspecific Competitive Interactions
Between Cutthroat Trout and Sculpins in Small Streams

Abstract approved:

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In the Pacific Northwest ecoregion of North America, sculpins represent a major constituent of freshwater assemblages in coastal rivers. Based on their prevalence and abundance, sculpins are likely important ecologically, yet little is known of their interactions with co-occurring species, such as widely studied salmon and trout (salmonines). In this study, I evaluated inter- and intraspecific interactions involving cottids (*Cottus sp.*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). I used a response surface experimental design to independently evaluate effects of cutthroat trout and sculpin biomass on growth and behavior.

There was evidence of both intra- and interspecific interactions between cutthroat trout and sculpins, but the interactions were asymmetrical with biomass of cutthroat trout driving both intra- and interspecific interactions, whereas sculpins had

little influence overall. Cutthroat trout biomass was positively related to conspecific aggressive interactions and negatively related to growth. Sculpin exhibited increased use of cover during the day in response to greater biomass of cutthroat trout, but not sculpin biomass. Nocturnal use of cover by sculpins was unaffected by biomass of either species.

This experiment provides insights into the species interactions and the mechanisms that may allow sculpins and salmonines to coexist in nature. As cutthroat trout appear to be superior competitors, coexistence between sculpins and cutthroat trout may depend on some form of refuge, either in the form of in-stream cover or crypsis coupled with diel resource segregation. Cutthroat trout are usually active during the day, indicating that nocturnal foraging by sculpins may in part represent a behavior that minimizes interspecific competition with cutthroat trout.

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Experimental Analysis of Intra- and Interspecific Competitive Interactions Between
Cutthroat Trout and Sculpins in Small Streams

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Ben S. Ramirez, Author

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CONTRIBUTION OF AUTHORS

Dr. Jason B. Dunham was involved in the study design, data analysis and editing of all sections of this manuscript.

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Introduction

Sculpins (Pisces: Cottidae) are widely prevalent in freshwater ecosystems of the northern hemisphere, including over 60 species within the genus *Cottus* (Adams and Schmetterling 2007, Kinziger et. al. 2005). In the Pacific Northwest region of North America, sculpins represent a major constituent of freshwater fish assemblages in coastal rivers (Bond 1963, Finger 1979, Reeves 1998), often dominating in terms of numbers and biomass in headwater streams (Carter et. al. 2004, Cyterski and Barber 2006). Furthermore, reported biomasses are likely underestimates as common methods of sampling can greatly underestimate the abundance of sculpins in nature (Bond 1963, Finger 1979, Reid et. al. 2009). Based on their prevalence and abundance, sculpins are likely important in freshwater ecosystems, yet little is known of their trophic ecology (Raggon 2010) or interactions with co-occurring species, such as widely studied salmon and trout (salmonines; Bond 1963).

Generally, sculpins are opportunistic, benthic feeders that can operate at multiple trophic levels, representing a potential predator or prey item for salmonine fishes that they commonly co-occur with (Bond 1963, Raggon 2010, Moyle 1977). Although the potential for ecological interaction between sculpins and salmonines seems great, they are poorly understood. In the confined habitats of headwater streams, sculpins have the potential to interact with conspecific or heterospecific

individuals in three important ways. These include exploitation and interference competition and intraguild predation (Figure 1). In the case of exploitative competition, consumers may rarely meet, but instead, compete through consumption of a shared and limited resource (Wootton 1992), as would be evidenced by influences of conspecific or heterospecific density on feeding or growth with no corresponding effect on measures of behaviors associated with interference. Conversely, in the case of interference competition, a consumer interferes directly with the activities of another fish, altering the behavior of both competitors (Wootton 1992), as would be evidenced by changes in behavior (aggressive interactions, cover use, etc.) in relation to densities of intra- or interspecific competitors. Competition can also be linked to predation within a guild. In the case of intraguild predation, predators prey on members of the same guild (Polis and Holt 1992), potentially influencing the outcome of competitive interactions by altering behaviors or reducing numbers of competitors (Figure 1).

In this study, I evaluated inter- and intraspecific interactions involving cottids (*Cottus sp.*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), which dominate fish assemblages in headwater streams of the Pacific coastal ecoregion of North America (Reeves et. al. 1998). Observational studies in these systems suggest these species frequently co-occur and can share common resources that can be limited in supply (Bond 1963, Finger 1979, Raggon 2010). However, there is, as of yet, no direct

evidence for competition between these species, as evidenced by changes in the behavior, growth, or population dynamics of one species in the absence of the other (Connell 1983, Fausch 1988, Forrester et. al. 2006). Here, I examined the potential for competition within and between these species by employing a response surface experimental design (Inouye 2001). A response surface experimental design provides the opportunity to independently examine the effects of changing composition and densities of intra- and interspecific competitors. More commonly used additive and substitutive designs lead to confounding of density and changing species composition: problems that can be avoided with a response surface design (Cousens 1991).

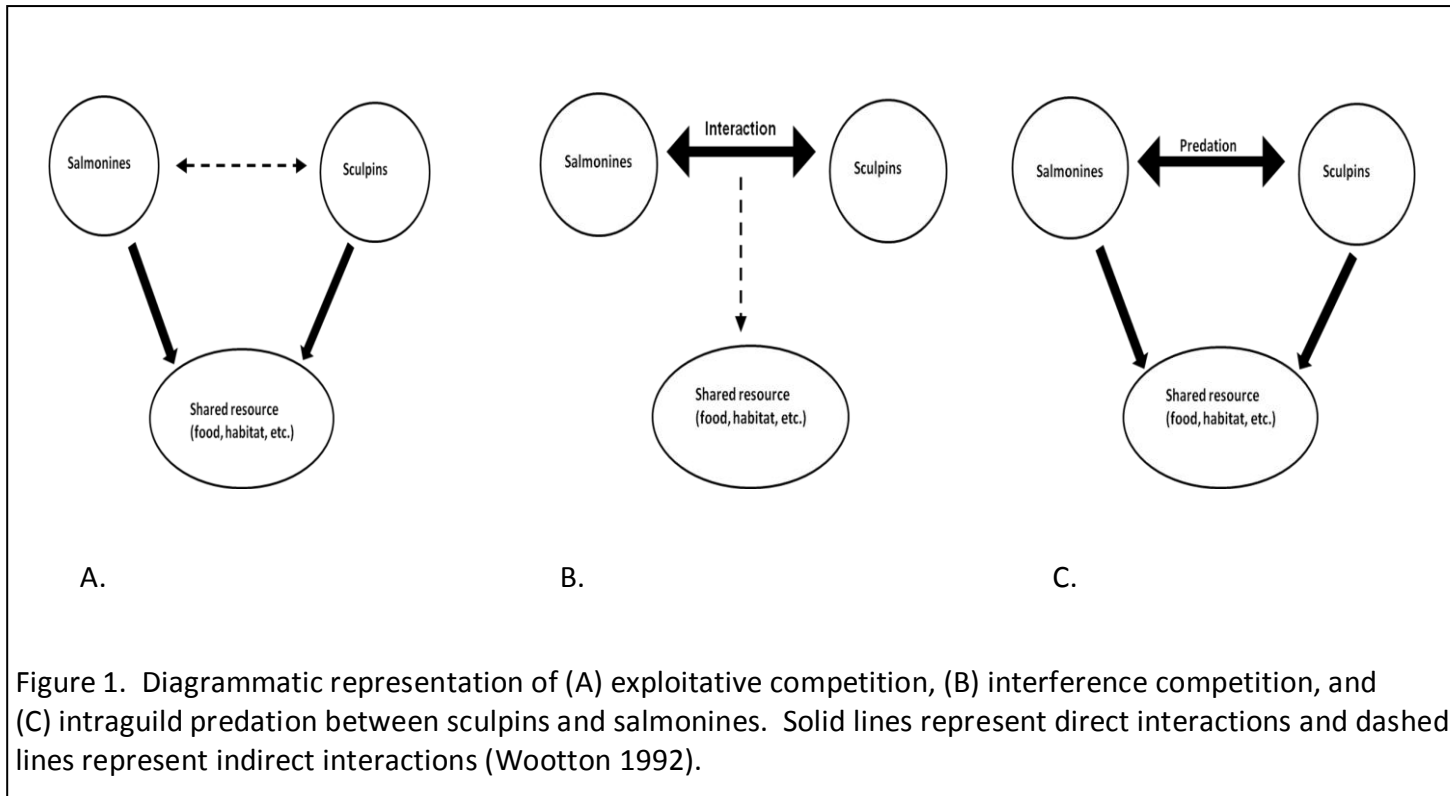
I experimentally manipulated densities of sculpins and cutthroat trout in semi-natural artificial stream channels, with treatments ranging from each species in isolation at low densities to species in combination at high densities. To evaluate evidence for intra- or interspecific exploitative competition I quantified sculpin behavior (cover use) and growth rates for each species in relation to densities of each species (Table 1). I assessed the evidence for intra- or interspecific interference competition by again quantifying behavior of sculpins (cover use) and growth rates of each species, but cutthroat trout behavior (aggressive interactions) was also quantified to assess interference competition linked to territoriality in cutthroat trout (Table 1). To assess the evidence for the potential importance of intraguild predation, I tracked

occurrence of piscivory throughout the experiment (Table 1). Piscivory is a necessary pre-requisite for this process to play a role in affecting the outcome of intra- or interspecific competition.

Measured Responses

Hypothesized Interaction		Growth	Day/Night Sculpin Cover-Use	Cutthroat Trout Aggressive Interactions	Piscivory
	Exploitative Competition	X	X		
	Interference Competition	X	X	X	
	Intraguild Predation				X

Table 1. Table of hypothesized interactions and measured responses from an artificial stream channel experiment investigating competitive interactions between cutthroat trout and sculpins. Predicted responses from the hypothesized interactions are denoted with an "X".



Materials and Methods

Experimental design

A response surface design was used to select the treatments for this experiment (Inouye 2001); (Figure 2). The experimental design included eight treatments ranging from each species in isolation at low densities to species in combinations at high densities. Each treatment was replicated twice, yielding a total of 16 treatments for this experiment.

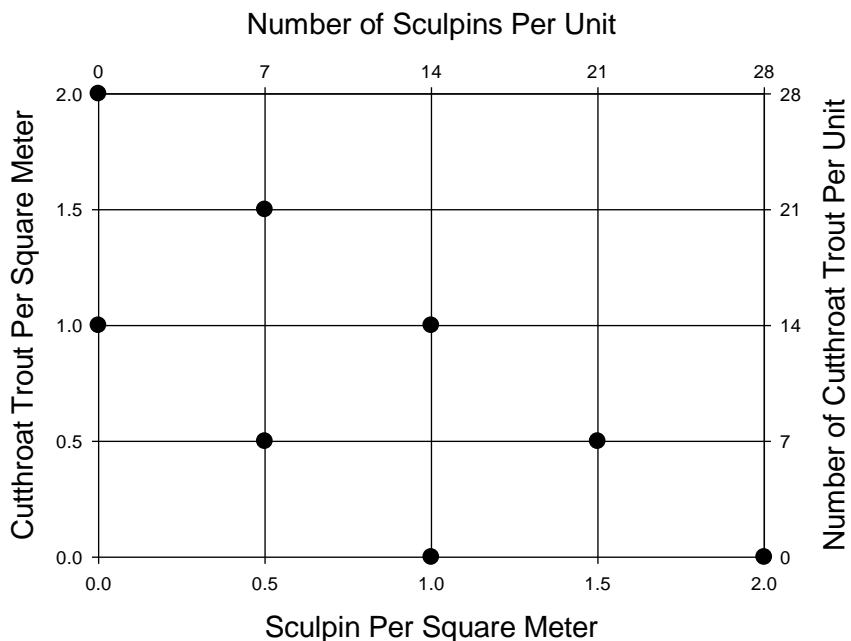


Figure 2. Response surface design showing the various treatments for an experiment investigating interactions between cutthroat trout and sculpins. Each point represents a treatment in the experiment. The left and bottom axes show the treatments based on density of fish per unit while the top and right axes show the resulting numbers of each species required for an experimental unit measuring 14 m^2 .

Fish collection and tagging

For this experiment, two species of sculpins (riffle sculpin – *Cottus gulosus*: reticulate sculpin – *Cottus perplexus*) and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) were collected from two watersheds in the Coast Range Mountains of Oregon. For the purposes of this experiment, both species of sculpins were collected, as they cannot be discerned from one another in the field (D. Bateman, Oregon State University, pers. comm.) and they both play similar ecological roles in nature (Patten 1975, Reimers and Bond 1967).

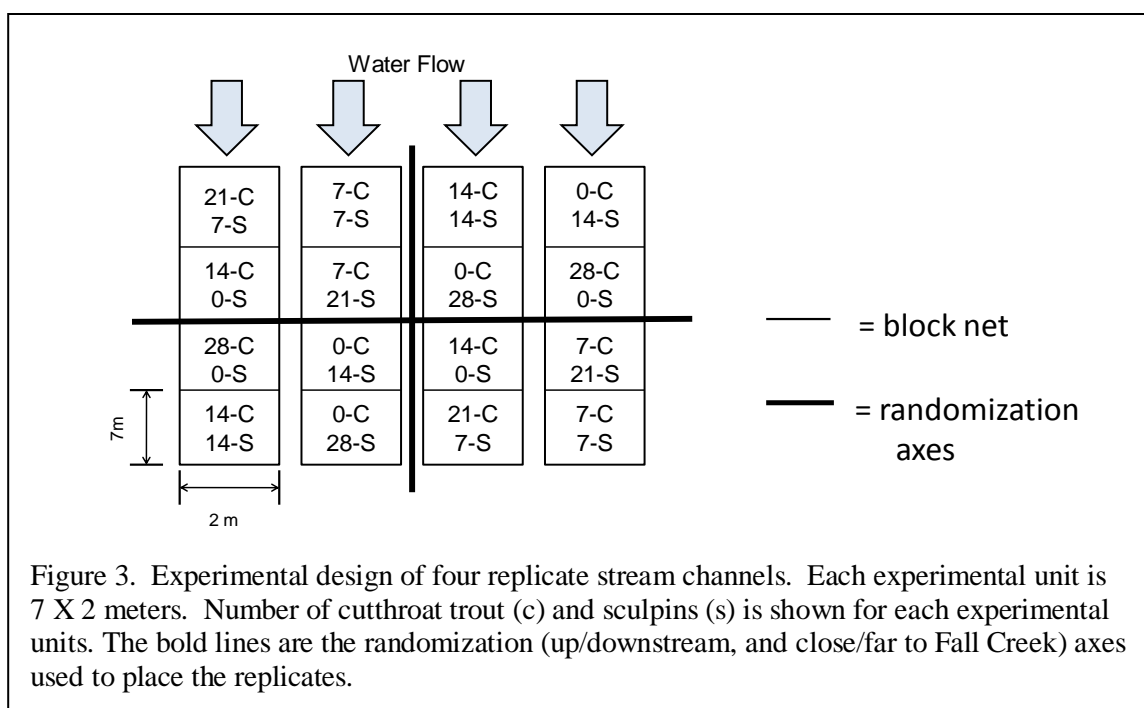
Fish were collected from two streams in the central Oregon coast range: Rocky Creek (44°46'38.96"N, 124°04'01.32"W) and Euchre Creek (44°47'34.53"N, 123°52'42.85"W). Fish collection took place between 8 June and 8 July 2010. Fish were captured using standard electrofishing techniques (Dunham et. al. 2009) and with the use of downstream seine nets to capture stunned individuals. Only fish large enough to receive an internally implanted 8.5 mm passive integrated transponder (PIT) tag (Texas Instruments, Dallas, Texas) were collected. This included coastal cutthroat trout larger than 55 mm fork length (Bateman et. al. 2009) and sculpins greater than 50 mm standard length (Bruyndoncx et. al. 2002). For larger fish, only individuals within the size range commonly observed in headwater streams of western Oregon (Raggon 2010) were collected. Fish were placed in tanks containing only conspecifics

and supplied with aerated water while being transported to the holding tanks at the laboratory facility (Oregon Hatchery Research Center, <http://www.dfw.state.or.us/OHRC/>). At the laboratory facility, fish were placed in holding tanks containing only conspecifics and supplied with circulating water and cover until the start of the experiment. While held in these tanks, fish were implanted with PIT tags to allow for individual identification. Tags were read with an Allflex Model RS601-3 handheld scanner (Allflex USA, Dallas, Texas).

Experimental setup

This experiment was conducted in four outdoor experimental stream channels located at the Oregon Hatchery Research Center (OHRC). The artificial stream channels consist of four parallel fish raceways filled with river gravels. Average gravel size for the channels was 35 ± 3 mm (based on standard b-axis measurements; B. Penaluna, unpublished data). Water was provided through a settling pond at the top of the stream channels supplied with water from nearby Fall Creek, a tributary to the Alsea River. To mimic shade found in headwater streams, a nylon shade cloth (3.8 mm diameter) was used to cover the enclosure. Coupled with the nylon shade cloth, a nylon mesh fence (3 cm diameter) fully enclosed the channels to deter potential predators from entering the streams.

During late June through early July, gravel in the artificial channels was excavated to form four replicate stream channels. Block screens (3 mm diameter mesh) were placed in the stream channels to prevent fish movement and partition each individual stream channel into four experimental units of equal length (Figure 3). Experimental units had a mean length of 6.99 ± 0.09 m, a mean wetted width of 2.04 ± 0.03 m, and a mean surface area of 14.28 ± 0.27 m². Streams depths were kept shallow (mean depth: 0.15 ± 0.01 m), which mimicked conditions commonly observed during low flows in headwater streams in summer (Andersen 2008). Discharge from the four stream channels over the duration of the experiment ranged from 0.02 to 0.03 m³s⁻¹ (mean: 0.02 ± 0.004 m³s⁻¹) while temperatures ranged from 9.72 to 18.61°C (mean temperature: 13.9 ± 1.6 °C).



Experimental units were supplied with equal amounts of in-stream cover and age 0+ steelhead trout (*Oncorhynchus mykiss*) to provide a semi-natural set of physical and biotic conditions. All steelhead trout were provided by the OHRC and were introduced into the experimental units on 8 August 2010. At this time, each experimental unit received a stocking of 40 steelhead trout, averaging $47 \text{ mm} \pm 4$ in length across all units. In-stream cover within each experimental unit was provided at a density of 0.14 per m^2 (a total of 2 units of cover per experimental unit), a low level based on results of prior experiments on cover use by coastal cutthroat trout in the experimental stream channels (B. Penaluna, unpublished data). Each unit of cover consisted of a 30.5 X 30.5 X 5.8 cm cement block set on top of a 30.5 X 20.3 X 5.8 cm block, thus creating two overhanging sides that provided a combined total surface area of 622.2 cm^2 that can be used as refuge.

Experimental units were randomly allocated along two gradients, representing lateral and longitudinal gradients potentially present within the experimental stream channels (Figure 3). The lateral gradient was utilized to control for potential effects of increasing shade associated with riparian vegetation along Fall Creek, while the longitudinal gradient was needed to control for the effects of the unidirectional flow of water and resulting prey availability. Experimental units were assigned to ensure that both lateral and longitudinal gradients were represented for each pair of replicated treatments. For example, the treatment involving 28 cutthroat trout and 0 sculpins

was assigned to a downstream quadrant that was close to Fall Creek. The replicate of this treatment was assigned to the quadrant that was away from Fall Creek and representing an upstream location (Figure 3). With only two replicates, this ensured that both lateral and longitudinal gradients were represented for each treatment (densities of cutthroat trout and sculpins; Figure 3).

Fish were randomly assigned to each experimental unit, based on numbers determined by the response surface design (Figure 2, 3). Before placing the fish in the channels, each individual's PIT tag identification, wet weight (g), standard length (mm) for sculpins and a fork length (mm) for cutthroat trout was recorded. The fish were then transported to the artificial channels in plastic buckets and carefully released into the streams. The sculpins were placed in the units first on 29 July 2010 and cutthroat trout the following day, due to logistical constraints of introducing both species on the same day. All fish were removed from the experiment on 7 October by electrofishing (see appendix A for number of fish recovered from each experimental unit). Total time spent in the experimental units was 67 days for cutthroat trout and 68 days for sculpins.

Daily experiment maintenance

Natural prey within the stream channels was supplemented with a ration (5 g) of oligochaetes (*Eisenia fetida*) administered to each experimental unit every other day, as previous work in these artificial streams has shown fish to lose weight (B. Penaluna, unpublished data). Feeding times were alternated between 1000 hours and 2200 hours. To prevent fish from conditioning to the presence of the investigator, a cup fixed to the end of a three meter rod was used to deliver food while the investigator remained hidden. To maintain adequate flow in the artificial channels, all screens (block nets, intake screens, and outflow screens) were cleaned daily in the morning. At this time, units were scanned for any deceased fish, which were immediately removed if found. Tag number, wet weight (g) and length (mm) were recorded for any deceased fish.

Response measures

To assess effects of conspecific and heterospecific fish within each experimental unit, two rapid behavioral responses (aggressive interaction and cover use) and one slower phenotypic response (growth) were measured over the duration of the experiment. Behaviors were observed on six occasions during the experiment (Appendix B) with each observation period lasted four days, with one day of observations per stream channel (four experimental units per stream channel) and two

days between observation periods. This allowed me to randomize the order of observations at the stream channel scale for each of the six observation periods and to alternate feeding between the stream channels. By alternating the feeding rotations, I was able to exclude observations on fish that were fed the same day as they were to be observed. This was to avoid potential impacts of feeding on fish behavior.

Aggressive interactions – cutthroat trout only. I anticipated that territorial behavior of cutthroat trout would be important in driving species interactions (e.g., Jenkins 1969, Kalleberg 1958, Puckett and Dill 1985), and quantified aggressive interactions involving cutthroat trout to assess effects of density treatments. To conduct an observation, blinds were erected within each of the four units in the chosen stream channel at 0800 hours. Blinds consisted of a wooden framed panel measuring 2.4 X 0.9 m, and covered with nylon mesh (2 cm diameter) and 3D camouflage netting (CamoSystems Inc., Marietta, Georgia). After setting up the blinds, I would leave the enclosure and allow two hours for fish to resume normal activity patterns. Upon returning to the enclosure at 1000 hours, I would stealthily crawl behind the blind in the downstream unit of the stream channel and remain motionless for 15 minutes before beginning the observation. After the waiting period, I would visually separate the experimental unit into three sections (upstream, middle, downstream) and begin recording the total number of visible fish in the downstream section first and then progressing to the middle and upstream sections. After I

obtained a count of the fish in each section, I would record the number of nips and chases or mouth fighting that occurred within a five minute observation window. I utilized 7 X 35 mm power binoculars to assist with visual observation of fish numbers and behaviors.

Cover use – sculpins only. Due to the cryptic nature of cottids (Bond 1963, Moyle 1977), direct visual observations of sculpin behavior were not feasible. To address behavioral responses of sculpins, day- and night-time sculpin use of cover was quantified to assess any effects of density treatments. As cutthroat trout are active during the day (Kalleberg 1958) and sculpins are often active at night (Bond 1963, Moyle 1977), patterns of cover use might differ between day- and night-time observations. I assumed cover was a limiting resource for sculpins in the face of interactions with larger cutthroat trout. To conduct observations on sculpin cover use, I approached the downstream unit in the selected stream channel and, using an Allflex ISO RFID Stick Reader (Allflex USA, Dallas, Texas), scanned the perimeter of the downstream unit of artificial cover and recorded all tag numbers detected. I then scanned the unit again to verify all recorded tag numbers. I did this for the next unit of artificial cover to complete the unit. For a complete observation, sculpin cover use was recorded twice, once during the day (1100 h; directly following cutthroat trout observation in the same experimental unit) and then again at night (2200 h).

Cutthroat trout cover use was not quantified, as their use of cover was infrequent and sporadic, especially in the presence of an observer.

Growth – cutthroat trout and sculpins. To assess the effect of treatments on fish growth, wet weights (g) and fork length (mm) for cutthroat trout and standard length (mm) for sculpins were recorded prior to introduction into the experimental units and directly following removal at the end of the experiment.

Data analysis

All statistical analyses were conducted using R v 2.12.1 (<http://www.r-project.org/>). I utilized regression analyses and investigated density and biomass for possible effects on each response measure. For each response measure, I investigated a full model of the form; $Y_1 = \beta_0 - \beta_1 X_1 - \beta_2 X_2 - \beta_3 X_1 X_2$ that included an intercept term (β_0), a term describing the conspecific fish effect ($\beta_1 X_1$), and a term describing the heterospecific fish effect ($\beta_2 X_2$). As conspecific and heterospecific effects might differ in strength in relation to each other, I also investigated a term describing the statistical interaction of the two ($\beta_3 X_1 X_2$). I utilized an alpha (α) level of 0.05 and dropped all insignificant interaction terms from the analysis. Along with the possible effects of species abundance and biomass, I also investigated correlations between two to uncover any potentially confounding issues.

To evaluate effects of cutthroat trout and sculpin density and biomass on aggressive behavior of cutthroat trout, I calculated per capita aggressive interactions (total aggressive interaction / total cutthroat trout) for each unit and for each of the six observation periods. Mean and median per capita aggressive interactions were analyzed for all observation periods combined, as they are both measures of central tendency and the median is not affected by potential outliers. Similarly, to evaluate use of cover by sculpins, I calculated the proportional cover use (sculpins using cover / total sculpins in unit) for each unit during day and night for each of the six observation periods. Here again, mean and median proportional cover use was analyzed to describe the central tendency and deal with extreme values.

To determine any effect of treatments on cutthroat trout and sculpin growth rates, the mean and median relative instantaneous growth rates (Guy and Brown 2007) were analyzed using regression analysis. For short term fish growth (days to months), instantaneous growth rates (growth per unit time) are preferred (Guy and Brown 2007). By calculating the relative instantaneous growth rate, I was able to quantify the rate of change in fish mass (mg) per day per unit of initial fish mass (mg). By utilizing relative instantaneous growth rates, I was able to account for the potential effect of initial fish size when analyzing growth over the duration of the experiment.

Results

Initially, I intended to manipulate and analyze the numbers of competitors per experimental unit (density), but upon further investigation, it was discovered that size and density were confounded, by chance (Hurlbert 1984) in this experiment. As a result, I considered biomass, as well as density as an indicator of the influence of competitors. Biomass was estimated as the product of mean mass and total number of individuals present at the beginning of the experiment. An investigation of the correlations between cutthroat trout or sculpin biomass per experimental unit and density (total number of fish per unit) indicated that the two were highly correlated (Pearson's, $r = 0.99$, $p < 0.001$) and results from both analyses were similar. Here, I present only the results from the analyses based on biomass (see Appendix C for density results). In addition to investigating correlations, I also investigated the variance of the behavioral responses (cover use, aggressive interactions), as visual trends of heterogeneity (Figures 4, 5) might have prevented models from detecting effect. Although visual trends of heterogeneity were present, Levene's tests for equality of variances were all insignificant.

Juvenile steelhead

Age 0+ steelhead were introduced into the experimental units on 8 August 2010 and all individuals were consumed by cutthroat trout and sculpins prior to the

initial observations that occurred on 12 August 2010. A thorough check of the experimental units prior to this initial observation period resulted in no detections of steelhead. Given the small size of age 0+ steelhead and gape widths of cutthroat trout and sculpin (Raggon 2010), steelhead could have been easily consumed by sculpin or cutthroat trout. I was unable to determine which individuals or species were responsible for predation upon age 0+ steelhead, except to note that all fish were rapidly consumed, even in treatments where only one species (sculpin or cutthroat trout) were present. In essence, age 0+ steelhead served as additional food for the cutthroat trout and sculpins in the experiment.

Aggressive interactions

The mean per capita cutthroat trout aggressive interactions for all treatments during this experiment was 0.159 (95% confidence interval: 0.101-0.217) for the five minute observation periods. There was sufficient evidence to suggest that cutthroat trout biomass had a positive intraspecific effect on the mean and median per capita aggressive cutthroat trout interactions (Table 2, Figure 4). Conversely, there was no evidence to suggest any interspecific effect of sculpin biomass on the mean or median per capita aggressive interactions (Table 2, Figure 4). There was no evidence to suggest a significant statistical interaction between sculpin and cutthroat trout biomass for any of the per capita aggression models, so all interaction terms were dropped from

analysis and all models took on the form of $Y_1 = \beta_0 - \beta_1 X_1 - \beta_2 X_2$ (see methods for model description).

Cover use

The mean proportional day-time sculpin cover use was 0.098 (95% confidence interval; 0.048-0.148) while the mean proportional night-time sculpin cover use was 0.090 (95% confidence interval: 0.072-0.107) for all treatments over the duration of the experiment. On average, 90.2% of sculpins during the day and 90% of the sculpins at night did not utilize the artificial cover structures. There was no evidence to suggest any intraspecific effects of sculpin biomass on the mean or median proportional day- or night-time sculpin cover use (Table 3.A, 2.B, Figure 5). Although there was no indication of any intraspecific effects, cutthroat trout biomass had a positive interspecific effect on both the mean and median proportional day-time sculpin cover use (Table 3.A, Figure 5). Conversely though, there was no evidence of any interspecific effect of cutthroat trout biomass on the mean or median proportional night-time sculpin cover use (Table 3.B, Figure 5). There was no evidence to suggest a significant statistical interaction between sculpin and cutthroat trout biomass for any of the proportional sculpin cover use models, so all interaction terms were dropped from analysis and all models took on the form of $Y_1 = \beta_0 - \beta_1 X_1 - \beta_2 X_2$ (see methods for model description).

Growth

The mean relative instantaneous growth rate was 0.960 ± 1.561 mg/initial mg*total days (95% confidence interval: 0.076 - 1.843 mg) for cutthroat trout and 11.166 ± 2.342 mg/initial mg*total days (95% confidence interval: 9.841 – 12.491 mg) for sculpins for all treatments. There was sufficient evidence to suggest a negative intraspecific effect of cutthroat trout biomass on the mean relative instantaneous cutthroat trout growth rate (Table 4.A, Figure 6), but there was no evidence of any intraspecific effect on the median relative instantaneous cutthroat trout growth rate (Table 4.A, Figure 6). There was no evidence of any intraspecific effects on the mean or median relative instantaneous sculpin growth rates (Table 4.B, Figure 7). There was no evidence to suggest any interspecific effects on sculpin or cutthroat trout growth (Table 4.A, 4.B, Figure 6, 7). For cutthroat trout and sculpin growth, there was no evidence of a significant statistical interaction between cutthroat trout and sculpin biomass, so all interaction terms were subsequently dropped from the analysis and all models took on the form of $Y_1 = \beta_0 - \beta_1 X_1 - \beta_2 X_2$ (see methods for model description).

Table 2. Results from regression analyses on per capita (pc) cutthroat trout aggressive interactions in the artificial stream channel experiment. Coefficient estimates, 95% confidence intervals, and p -values are given for each parameter. F -ratios and numerator (ndf) and denominator (ddf) degrees of freedom are given for the overall model. All coefficient estimates and confidence intervals were multiplied by 100 to make estimates larger and more visible.

Response	Cutthroat Biomass	Sculpin Biomass	F -ratio (ndf, ddf)
Mean pc aggression	0.071 (0.012, 0.130) $p=0.023$	Non Significant ($p=0.085$)	3.87 (2, 9)
Median pc aggression	0.080 (0.016, 0.145) $p=0.021$	Non Significant ($p=0.778$)	5.05 (2, 9)

Table 3. Results from regression analyses on proportional (prop) day-time (A) and night-time (B) sculpin cover use in the artificial stream channel experiment. Coefficient estimates, 95% confidence intervals, and p -values are given for each parameter. F -ratios and numerator (ndf) and denominator (ddf) degrees of freedom are given for the overall model. All coefficient estimates and confidence intervals were multiplied by 100 to make estimates larger and more visible.

A. Day-Time Sculpin Cover Use

Response	Cutthroat Biomass	Sculpin Biomass	F -ratio (ndf , ddf)
Mean prop cover use	0.063 (0.016, 0.111) $p=0.014$	Non Significant ($p=0.269$)	5.08 (2, 9)
Median prop cover use	0.065 (-0.001, 0.131) $p=0.053$	Non Significant ($p=0.283$)	2.53 (2, 9)

B. Night-Time Sculpin Cover Use

Response	Cutthroat Biomass	Sculpin Biomass	F -ratio (ndf , ddf)
Mean prop cover use	Non Significant ($p=0.465$)	Non Significant ($p=0.912$)	0.40 (2, 9)
Median prop cover use	Non Significant ($p=0.777$)	Non Significant ($p=0.293$)	0.76 (2, 9)

Table 4. Results from regression analyses on the relative (rel) instantaneous (inst) cutthroat trout (A) and sculpin (B) growth rates from the artificial stream channel experiment. Coefficient estimates, 95% confidence intervals, and *p*-values are given for each parameter. *F*-ratios and numerator (*ndf*) and denominator (*ddf*) degrees of freedom are given for the overall model. All coefficient estimates and confidence intervals were multiplied by 100 to make estimates larger and more visible.

A. Cutthroat Trout Growth

Response	Cutthroat Biomass	Sculpin Biomass	<i>F</i> -ratio (<i>ndf</i> , <i>ddf</i>)
Mean rel inst growth rate	-0.001 (-0.002, -0.000) <i>p</i> =0.041	Non Significant (<i>p</i> =0.932)	4.21 (2, 9)
Median rel inst growth rate	Non Significant (<i>p</i> =0.173)	Non Significant (<i>p</i> =0.609)	2.38 (2, 9)

B. Sculpin Growth

Response	Cutthroat Biomass	Sculpin Biomass	<i>F</i> -ratio (<i>ndf</i> , <i>ddf</i>)
Mean rel inst growth rate	Non Significant (<i>p</i> =0.711)	Non Significant (<i>p</i> =0.189)	2.32 (2, 9)
Median rel inst growth rate	Non Significant (<i>p</i> =0.980)	Non Significant (<i>p</i> =0.247)	1.22 (2, 9)

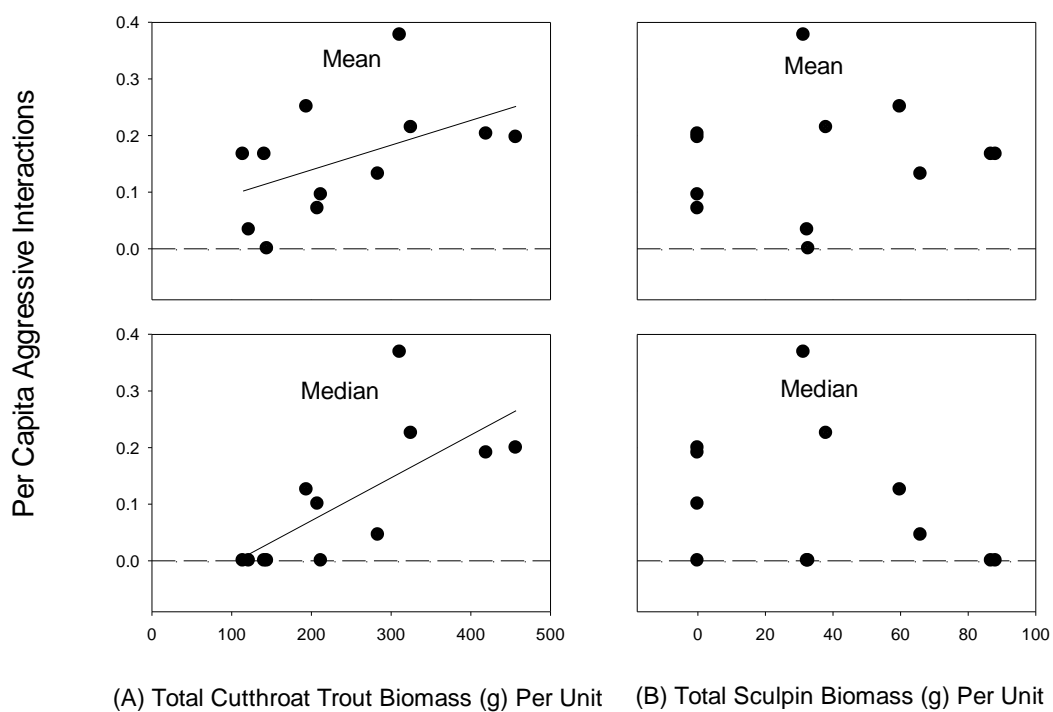
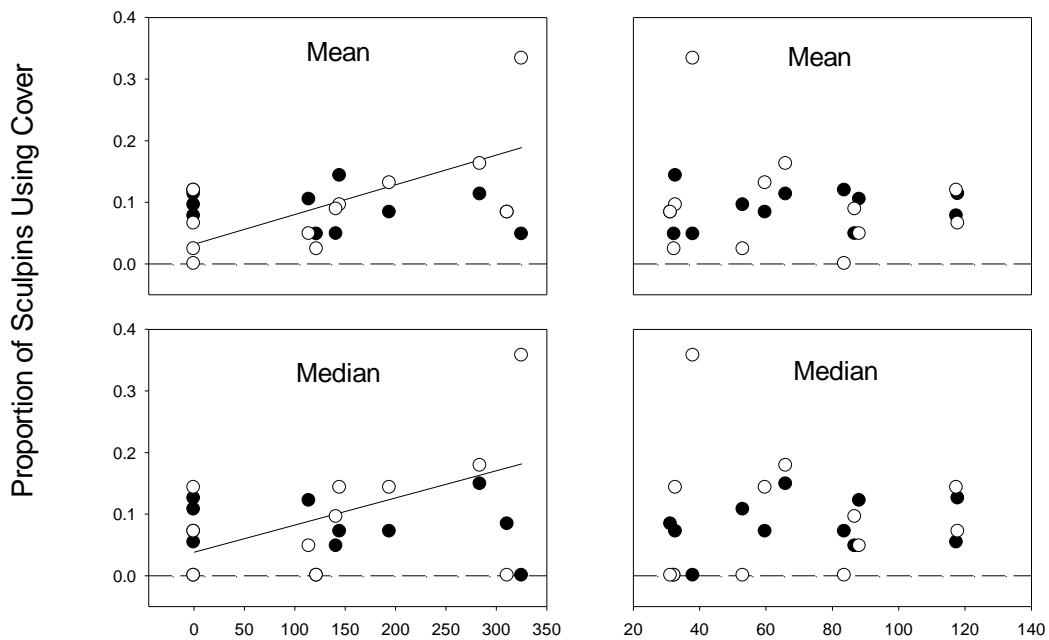


Figure 4. Scatterplots of mean and median per capita (total aggressive interactions/ total fish) aggressive cutthroat trout interactions and total cutthroat trout biomass (A) and total sculpin biomass (B) from experiment in artificial stream channels experiment conducted during summer, 2010.



(A) Total Cutthroat Trout Biomass (g) Per Unit (B) Total Sculpin Biomass (g) Per Unit

Figure 5. Scatterplots of mean and median proportional (total sculpins using cover/ total sculpins in unit) day-time (open circles) and night-time (filled in circles) sculpin cover use versus cutthroat trout biomass (A) and total sculpin biomass (B) from artificial stream channel experiment conducted during summer, 2010. Regression lines are for significant day-time effects only.

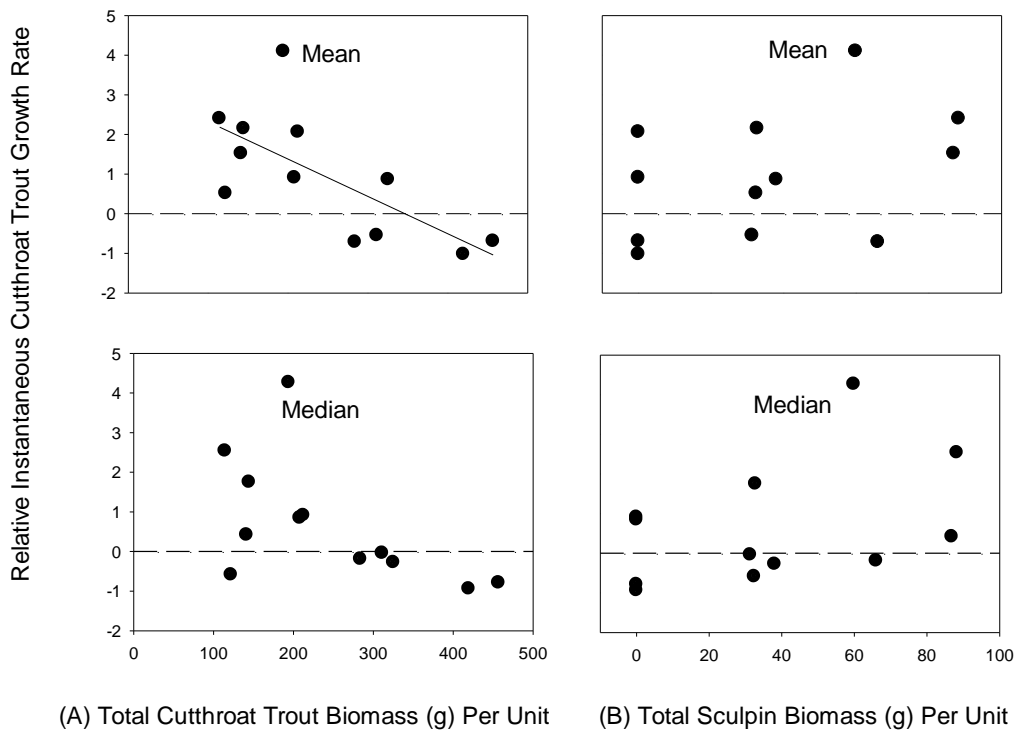
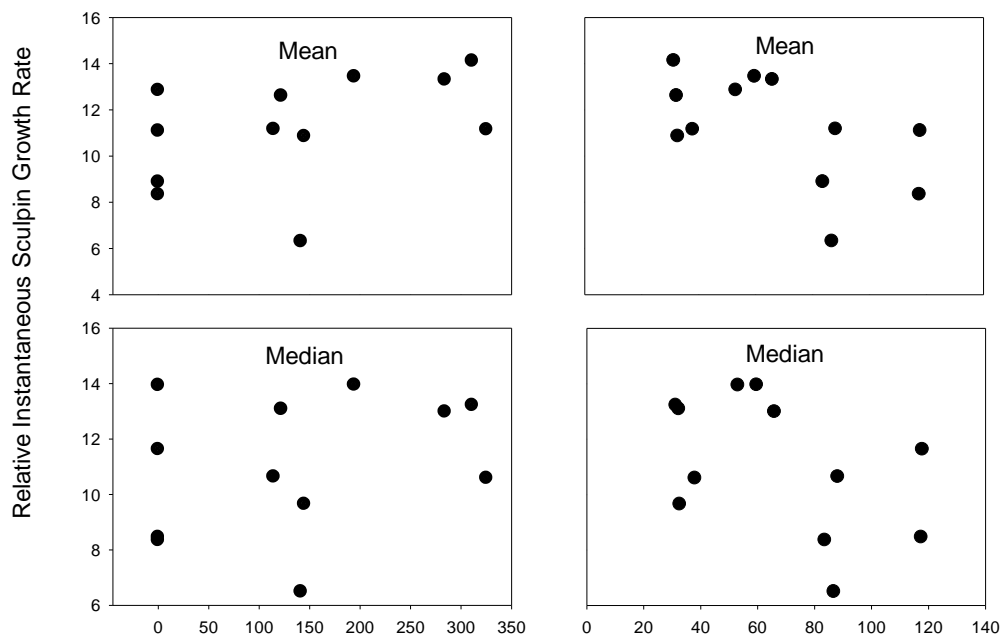


Figure 6. Scatterplots of mean and median relative instantaneous cutthroat trout growth rates ($\Delta\text{mg}/\text{initial mg} \times \text{total days}$) versus cutthroat trout biomass (A) and sculpin biomass (B) from artificial stream channel experiment conducted from 29 July 2010 to 7 October 2010.



(A) Total Cutthroat Trout Biomass (g) Per Unit (B) Total Sculpin Biomass (g) Per Unit

Figure 7. Scatterplots of mean and median relative instantaneous sculpin growth rates ($\Delta\text{mg}/\text{initial mg} \times \text{total days}$) versus cutthroat trout biomass (A) and sculpin biomass (B) from artificial stream channel experiment conducted from 29 July 2010 to 7 October 2010.

Discussion

Results of this experiment yielded evidence of both intra- and interspecific interactions between cutthroat trout and sculpins. Overall the effect of cutthroat trout dominated with little influence of sculpins on either species. These results parallel those of a similarly designed response surface experiment investigating the interactions between coho salmon (*O. kisutch*) and steelhead trout (*O. mykiss*), where coho salmon density explained patterns of habitat selection for both species (Young 2004). In this experiment, cutthroat trout maintained a natural size advantage over sculpins, which could explain the competitive asymmetry I observed, also observed by Young (2004). Results of this work suggest that competition is manifested most strongly as interference, with limited evidence for intraspecific exploitative competition, and little support for the role of intraguild predation.

The only evidence in support of exploitative competition occurring during the experiment was a negative effect of cutthroat trout biomass on cutthroat growth. My results suggested no evidence of any interspecific effects on fish growth. This is contrary to another study, where sculpins exhibited potential to compete exploitatively with cutthroat trout in laboratory streams (Brocksen et. al. 1968). It is possible that fish in relatively confined conditions of laboratory streams may be able to more efficiently deplete prey resources (i.e., food limitation is more likely), thus increasing the likelihood that exploitative competition is realized. The lack of

interspecific effects observed herein could also be the result of different diel activity patterns between cottids and salmonids. Cottids actively feed during the night (Bond 1963, Moyle 1977) whereas salmonines usually actively feed during the day (Bradford and Higgins 2001, Young et. al. 1997). Inspection of trends in growth of cutthroat trout and sculpin in relation to biomass shows a nonsignificant trend of declining growth with increases in intraspecific biomass (Figure 6, 7). I cannot claim these patterns indicate significant biological interactions, but it is possible that the short time span of this experiment (68 days) might have been inadequate to detect influence of biomass on growth. It is important to note that growth may indicate influences of both exploitative or interference competition, as either process could result in reduced growth. However, lack of a strong growth response observed herein indicates that factors other than food limitation played a greater role within the timeframe of this study. Finally, it is important to note that the relative abundance of sculpins and cutthroat trout may not represent abundances realized in natural streams. If sculpins strongly outnumber cutthroat trout, as seems likely based on many field observations (Bond 1963, Moyle 1977), then exploitative competition could be a strong possibility, particularly during times of the year when resource scarcity is pronounced (Raggon 2010).

With respect to evidence for interference competition, results indicated that cutthroat trout biomass had a significant effect on the day-time proportional sculpin

cover use, but no effect on night-time proportional sculpin cover use. Although a significant interspecific effect was evident, the implications of increasing day-time sculpin cover use with increasing cutthroat trout are somewhat unclear. During the day, increased cover use by sculpins could translate into decreased foraging activity, yet I observed no impacts of either species on growth of sculpins. Accordingly, sculpins must have been able to forage effectively at night, a common observation for fishes in this family, noted for the ability of individuals to forage in low light conditions (Bond 1963, Moyle 1977) and to use non-visual means of locating prey (Hoekstra and Janssen 1985, 1986). Sculpins were almost never observed day (B. Ramirez, personal observations), yet the majority of individuals did not use the cover structures provided. This leaves non-structural refuge (hiding in the substrate) as the likely alternative to cover use by sculpins. Alternatively, some individuals may have relied on cryptic coloration behaviors to avoid detection. Overall, it appeared important that sculpins can use different forms of refuge (cover structures, substrate, crypsis; Berryman and Hawkins 2006) during the day-time, particularly in the presence of a potentially superior competitor, such as cutthroat trout

Although use of cover by sculpins was significantly influenced by cutthroat trout, cutthroat trout were not influenced by sculpin, as revealed through impacts on growth of aggressive interactions. During the experiment, cutthroat trout competed with other conspecifics for space, as was evidenced by increases in agonistic

interactions coupled with increases in cutthroat trout biomass. These results are consistent with previous research indicating intraspecific agonistic interactions to play a major role in the structuring of trout distributions (Jenkins 1969, Volpe et. al. 2001). Declines in growth of cutthroat trout as a function of increasing biomass could have resulted at least in part from the cost of increased aggression (Boisclair and Leggett 1989, Raggon 2010). Thus, growth may have been suppressed in the absence of food limitation, not requiring exploitation as a competitive process (Anholt 1990, Schoener 1983).

Although intraspecific interactions appeared very important for cutthroat trout, interactions among sculpins were conspicuously absent. This is contrary to other experiments involving mottled sculpins (*Cottus bairdi*), that found density dependence (Grossman et. al. 2006) and size based territoriality (Freeman and Stouder 1989, Petty and Grossman 2007) to be influential in population regulation. These studies were able to evaluate conspecific effects on the full range of sculpin sizes, whereas my experiment was bounded by the minimum size required for PIT tag insertion (50 mm standard length). In focusing on larger individuals, important effects on smaller sculpins might have been missed. It is also possible that the short duration of the experiment (68 days) might have been inadequate to detect an intraspecific effect.

This experiment yielded no evidence of the occurrence of intraguild predation, whilst other studies have identified its importance in structuring fish populations

(Browne and Rasmussen 2009, Polis and Holt 1992, Taniguchi et. al. 2002). Survival was high over the duration of the experiment and ingested PIT tags were never detected in any recovered fish stomachs. Additionally, a thorough check of the experimental units directly following fish removal and de-watering of the streams failed to detect any lost tags. The lack of intraguild predation during the experiment might have been a result of the experimental design. This experiment focused on relatively larger individuals of both species, potentially limiting opportunity for predation via gape limitation. For a process that is based on size-structured interactions such as intraguild predation (Browne and Rasmussen 2009, Taniguchi et. al. 2002), an experiment void of smaller size class fish might not adequately detect its occurrence. For example, small age 0+ steelhead juveniles were completely consumed by sculpins and cutthroat trout in only a few days after this experiment was initiated. Although use of larger fish could have limited intraspecific predation, many sculpins were well within the sizes that could be consumed by cutthroat trout, yet this was not observed. These findings parallel lack of predation by coastal cutthroat trout on sculpins in headwater streams (Raggon 2010).

Conclusion

This experiment provides insights into species interactions and the mechanisms that may allow sculpins and salmonines to coexist in nature. These species commonly coexist in streams across the northern hemisphere (Adams and Schmetterling 2007),

often representing the dominant vertebrate consumers, particularly in small streams (Bond 1963, Finger 1979, Reeves et. al. 1998). As such, understanding factors controlling the distribution and abundance of sculpins and salmonines can have important implications for understanding the consequences of species interactions for both aquatic and terrestrial food webs (Baxter et. al. 2005). Often, salmonines and sculpins are studied in isolation of each other, but this study and the work of others (Brocksen et. al. 1968, Hesthagen and Heggenes 2003, Zimmerman and Vondracek 2007) show that both direct and indirect interactions can be critical in term of influencing consumer behaviors, distributions, and abundance. Failing to acknowledge these interactions, and the importance of sculpins, which are poorly understood in general, may lead to a very narrow and biased view of the role of fishes in north-temperate stream ecosystems (Bond 1963, Moyle 1977).

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Appendices

Appendix A – Recovered Fish

Table A.1. Numbers of initial coastal cutthroat trout (CCT) and sculpins at the beginning of the experiment and number of coastal cutthroat trout and sculpins recovered at the end of the experiment are given for each treatment (Replicates of the same treatment are denoted by number followed by an A or B).

<u>Treatment</u>	<u>Initial CCT</u>	<u>Initial Sculpins</u>	<u>Recovered CCT</u>	<u>Recovered Sculpins</u>
1A	14	0	9	0
1B	14	0	11	0
2A	7	7	5	5
2B	7	7	4	7
3A	0	14	0	7
3B	0	14	0	12
4A	28	0	16	0
4B	28	0	9	0
5A	21	7	8	4
5B	21	7	10	4
6A	14	14	9	11
6B	14	14	7	5
7A	7	21	6	13
7B	7	21	6	15
8A	0	28	0	20
8B	0	28	0	20

Appendix B

Table B-1. Schedule of observation and feeding rotations

Month	Day	Observation	Channel A	Channel B	Channel C	Channel D
August	12	1	Observation	Feeding PM	Feeding PM	
	13	1	Feeding PM	Observation		Feeding PM
	14	1		Feeding AM	Feeding AM	Observation
	15	1	Feeding AM		Observation	Feeding AM
	18	2	Feeding PM	Observation	Feeding PM	
	19	2	Observation	Feeding PM		Feeding PM
	20	2	Feeding AM		Feeding AM	Observation
	21	2		Feeding AM	Observation	Feeding AM
	24	3		Feeding PM	Observation	Feeding PM
	25	3	Feeding PM	Observation	Feeding PM	
	26	3	Observation	Feeding AM		Feeding AM
	27	3	Feeding AM		Feeding AM	Observation
	30	4	Feeding PM		Feeding PM	Observation
	31	4		Feeding PM	Observation	Feeding PM
	September	1	4	Feeding AM	Observation	Feeding AM
2		4	Observation	Feeding AM		Feeding AM

5	5	Feeding PM		Feeding PM	Observation
6	5	Observation	Feeding PM		Feeding PM
7	5	Feeding AM	Observation	Feeding AM	
8	5		Feeding AM	Observation	Feeding AM
11	6	Observation	Feeding PM		Feeding PM
12	6	Feeding PM		Feeding PM	Observation
13	6	Observation	Feeding AM		Feeding AM

Appendix C – Result tables for density analyses

Table C.1. Results from regression analyses on per capita (pc) cutthroat trout aggressive interactions in the artificial stream channel experiment. Coefficient estimates, 95% confidence intervals, and *p*-values are given for each parameter. *F*-ratios and numerator (*ndf*) and denominator (*ddf*) degrees of freedom are given for the overall model. All coefficient estimates and confidence intervals were multiplied by 100 to make estimates larger and more visible.

Response	Cutthroat Density	Sculpin Density	<i>F</i> -ratio (<i>ndf</i> , <i>ddf</i>)
Mean pc aggression	1.415 (0.661, 2.169) <i>p</i> =0.002	0.943 (0.232, 1.655) <i>p</i> =0.015	9.17 (2, 9)
Median pc aggression	1.496 (0.634, 2.358) <i>p</i> =0.003	Non Significant (<i>p</i> =0.488)	9.80 (2, 9)

Appendix C – Result tables for density analyses (cont.)

Table C.2. Results from regression analyses on proportional (prop) day-time (A) and night-time (B) sculpin cover use in the artificial stream channel experiment. Coefficient estimates, 95% confidence intervals, and p -values are given for each parameter. F -ratios and numerator (ndf) and denominator (ddf) degrees of freedom are given for the overall model. All coefficient estimates and confidence intervals were multiplied by 100 to make estimates larger and more visible.

A. Day-Time Sculpin Cover Use

Response	Cutthroat Density	Sculpin Density	F -ratio (ndf , ddf)
Mean prop cover use	0.996 (0.242, 1.749) $p=0.015$	Non Significant ($p=0.275$)	4.86 (2, 9)
Median prop cover use	Non Significant ($p=0.077$)	Non Significant ($p=0.345$)	2.04 (2, 9)

B. Night-Time Sculpin Cover Use

Response	Cutthroat Density	Sculpin Density	F -ratio (ndf , ddf)
Mean prop cover use	Non Significant ($p=0.283$)	Non Significant ($p=0.640$)	0.69 (2, 9)
Median prop cover use	Non Significant ($p=0.920$)	Non Significant ($p=0.326$)	0.78 (2, 9)

Appendix C – Result tables for density analyses (cont.)

Table C.3. Results from regression analyses on the relative (rel) instantaneous (inst) cutthroat trout (A) and sculpin (B) growth rates from the artificial stream channel experiment. Coefficient estimates, 95% confidence intervals, and *p*-values are given for each parameter. F-ratios and numerator (*ndf*) and denominator (*ddf*) degrees of freedom are given for the overall model. All coefficient estimates and confidence intervals were multiplied by 100 to make estimates larger and more visible.

A. Cutthroat Trout Growth

Response	Cutthroat Density	Sculpin Density	F-ratio (<i>ndf</i> , <i>ddf</i>)
Mean rel inst growth rate	Non Significant (<i>p</i> =0.128)	Non Significant (<i>p</i> =0.816)	2.68 (2, 9)
Median rel inst growth rate	Non Significant (<i>p</i> =0.378)	Non Significant (<i>p</i> =0.494)	1.73 (2, 9)

B. Sculpin Growth

Response	Cutthroat Density	Sculpin Density	F-ratio (<i>ndf</i> , <i>ddf</i>)
Mean rel inst growth rate	Non Significant (<i>p</i> =0.496)	Non Significant (<i>p</i> =0.340)	2.00 (2, 9)
Median rel inst growth rate	Non Significant (<i>p</i> =0.687)	Non Significant (<i>p</i> =0.487)	0.85 (2, 9)

Appendix D – Raw data

Table D.1. Raw growth data collected from July 29 to October 7, 2010 during an experiment in artificial stream channels at the Oregon Hatchery Research Center. For each fish, tag id, species (CT – cutthroat trout, SC – sculpin), treatment, initial and final lengths (fork length for cutthroat trout, standard length for sculpins) and weights, and the date of introduction and removal are given.

Tag ID	Species	Treatment	Initial Length (mm)	Final Length (mm)	Initial Weight (g)	Final Weight (g)	Initial Date	Final Date
73568	CT	6B	141	139	25.01	22.75	7/30/2010	10/5/2010
73530	CT	6B	154	155	31.72	31.31	7/30/2010	10/5/2010
73518	CT	6B	119	118	15.6	14.04	7/30/2010	10/5/2010
72745	CT	6B	148	146	29.34	25.03	7/30/2010	10/5/2010
70693	CT	6B	104	105	10.68	10.55	7/30/2010	10/5/2010
73502	CT	6B	121	122	16.01	16.3	7/30/2010	10/5/2010
72793	CT	6B	108	110	11.83	11.94	7/30/2010	10/5/2010
71077	SC	6B	54	60	3	4.87	8/9/2010	10/5/2010
70633	SC	6B	51	63	2.89	5.64	7/29/2010	10/5/2010
71015	SC	6B	64	76	5.43	10.22	7/29/2010	10/5/2010
74080	SC	6B	52	65	2.88	6.96	7/29/2010	10/5/2010
71011	SC	6B	58	66	4.11	6.27	7/29/2010	10/5/2010
73584	CT	4A	94	94	7.72	7.25	7/30/2010	10/5/2010
72798	CT	4A	107	109	11.6	11.66	7/30/2010	10/5/2010
70636	CT	4A	114	104	15.39	14.05	7/30/2010	10/5/2010
73519	CT	4A	121	121	16.96	15.41	7/30/2010	10/5/2010
70608	CT	4A	95	95	8.34	8.8	7/30/2010	10/5/2010
70685	CT	4A	105	106	9.75	9.43	7/30/2010	10/5/2010

66661	CT	4A	148	145	28.69	21.52	7/30/2010	10/5/2010
73515	CT	4A	120	123	16.9	15.91	7/30/2010	10/5/2010
72742	CT	4A	145	145	25.68	26.87	7/30/2010	10/5/2010
73566	CT	4A	117	117	14.11	14.1	7/30/2010	10/5/2010
74867	CT	4A	133	133	22.01	18.87	7/30/2010	10/5/2010
73507	CT	4A	122	120	14.71	13.35	7/30/2010	10/5/2010
70658	CT	4A	100	101	9.75	9.11	7/30/2010	10/5/2010
73553	CT	4A	135	132	19.68	16.29	7/30/2010	10/5/2010
73563	CT	4A	107	106	11.28	10.78	7/30/2010	10/5/2010
73525	CT	4A	96	96	8.15	7.28	7/30/2010	10/5/2010
70674	CT	1B	130	137	18.49	23.65	7/30/2010	10/5/2010
66662	CT	1B	112	115	13.91	13.47	7/30/2010	10/5/2010
73572	CT	1B	130	130	20.33	20	7/30/2010	10/5/2010
70653	CT	1B	89	98	7.14	9.37	7/30/2010	10/5/2010
70697	CT	1B	71	80	3.11	4.58	7/30/2010	10/5/2010
73546	CT	1B	134	138	20.45	22.7	7/30/2010	10/5/2010
73599	CT	1B	116	119	14.1	14.74	7/30/2010	10/5/2010
72794	CT	1B	135	137	22.24	23.59	7/30/2010	10/5/2010
72777	CT	1B	109	110	12.45	12.79	7/30/2010	10/5/2010
70679	CT	1B	126	130	19.9	20.45	7/30/2010	10/5/2010
72776	CT	1B	88	95	6.54	8.04	7/30/2010	10/5/2010
70655	CT	5B	116	115	12.3	14.62	7/30/2010	10/5/2010
72788	CT	5B	145	145	28.96	28.27	7/30/2010	10/5/2010
73549	CT	5B	150	149	32.57	29.92	7/30/2010	10/5/2010
70634	CT	5B	79	89	5.25	6.95	7/30/2010	10/5/2010
72703	CT	5B	140	138	23.55	20.33	7/30/2010	10/5/2010
73526	CT	5B	100	110	9.06	11.6	7/30/2010	10/5/2010

72707	CT	5B	172	171	41.41	39.47	7/30/2010	10/5/2010
73537	CT	5B	114	115	14.11	13.92	7/30/2010	10/5/2010
73510	CT	5B	115	111	11.04	13.95	7/30/2010	10/5/2010
73562	CT	5B	135	134	23.06	18.97	7/30/2010	10/5/2010
71088	SC	5B	59	65	3.6	6.36	7/29/2010	10/5/2010
74055	SC	5B	71	79	6.58	11	7/29/2010	10/5/2010
74047	SC	5B	59	69	4.69	8.28	8/11/2010	10/5/2010
74054	SC	5B	73	80	6.9	11.35	7/29/2010	10/5/2010
73535	CT	2B	103	103	10.43	9.23	7/30/2010	10/5/2010
66663	CT	2B	124	136	18.11	24.12	7/30/2010	10/5/2010
73534	CT	2B	150	150	31.67	29.17	7/30/2010	10/5/2010
72725	CT	2B	120	121	15.17	15.17	7/30/2010	10/5/2010
71003	SC	2B	67	75	5.56	10.72	7/29/2010	10/5/2010
71095	SC	2B	60	71	4.07	8.86	7/29/2010	10/5/2010
70645	SC	2B	64	70	4.23	7.99	7/29/2010	10/5/2010
70649	SC	2B	63	76	4.2	9.71	7/29/2010	10/5/2010
74066	SC	2B	61	66	3.66	6.58	7/29/2010	10/5/2010
71030	SC	2B	64	71	4.88	7.86	7/29/2010	10/5/2010
70601	SC	2B	65	69	5.83	7.48	7/29/2010	10/5/2010
72737	CT	7A	107	110	11.09	11.43	7/30/2010	10/5/2010
72735	CT	7A	123	125	18.01	18.46	7/30/2010	10/5/2010
66664	CT	7A	159	162	26.35	39.72	7/30/2010	10/5/2010
73583	CT	7A	132	136	20.06	21.39	7/30/2010	10/5/2010
72713	CT	7A	133	131	18.78	19.2	7/30/2010	10/5/2010
73513	CT	7A	129	130	21.82	20.9	7/30/2010	10/5/2010
70660	SC	7A	60	65	4.56	5.94	7/29/2010	10/5/2010

70677	SC	7A	69	73	6.16	8.42	7/29/2010	10/5/2010
74001	SC	7A	59	64	3.93	6.06	7/29/2010	10/5/2010
70642	SC	7A	74	81	7.18	12.35	7/29/2010	10/5/2010
74059	SC	7A	60	68	4.92	7.09	7/29/2010	10/5/2010
70618	SC	7A	52	58	3.38	3.97	7/29/2010	10/5/2010
74040	SC	7A	58	70	4.98	7.4	7/29/2010	10/5/2010
71064	SC	7A	64	70	5.67	7.62	7/29/2010	10/5/2010
70682	SC	7A	52	55	2.58	3.74	7/29/2010	10/5/2010
70615	SC	7A	56	62	3.55	4.85	7/29/2010	10/5/2010
71062	SC	7A	55	63	3.55	5.64	7/29/2010	10/5/2010
71075	SC	7A	56	61	3.71	4.44	7/29/2010	10/5/2010
73501	CT	4B	125	127	20.26	19.12	7/30/2010	10/5/2010
70699	CT	4B	153	157	29.71	30.29	7/30/2010	10/5/2010
73554	CT	4B	115	117	15.95	14.41	7/30/2010	10/5/2010
72789	CT	4B	118	122	18.5	17.85	7/30/2010	10/5/2010
73516	CT	4B	174	171	42.29	35.98	7/30/2010	10/5/2010
72772	CT	4B	148	155	30.63	32.78	7/30/2010	10/5/2010
73589	CT	4B	124	124	19.23	19.72	7/30/2010	10/5/2010
72715	CT	4B	127	129	17.77	16.83	7/30/2010	10/5/2010
73538	CT	4B	103	105	10.49	8.97	7/30/2010	10/5/2010
70652	SC	3A	54	68	2.8	8.03	7/29/2010	10/5/2010
74079	SC	3A	70	74	6.5	9.44	7/29/2010	10/5/2010
71033	SC	3A	47	55	2.1	4.09	7/29/2010	10/5/2010
70657	SC	3A	57	70	3.84	8.2	7/29/2010	10/5/2010
70607	SC	3A	55	61	3.45	5.01	7/29/2010	10/5/2010
70670	SC	3A	55	66	3.51	6.87	7/29/2010	10/5/2010
74008	SC	3A	64	65	4.3	5.59	7/29/2010	10/5/2010

73541	CT	5A	142	142	26.31	21.2	7/30/2010	10/5/2010
72733	CT	5A	152	155	33.56	33.58	7/30/2010	10/5/2010
73594	CT	5A	156	155	34.02	31.5	7/30/2010	10/5/2010
72800	CT	5A	128	129	20.36	19	7/30/2010	10/5/2010
73555	CT	5A	90	92	7.88	7.89	7/30/2010	10/5/2010
73528	CT	5A	118	120	15.53	15.6	7/30/2010	10/5/2010
73564	CT	5A	90	95	8.24	8.19	7/30/2010	10/5/2010
70611	CT	5A	94	99	8.53	8.88	7/30/2010	10/5/2010
74035	SC	5A	63	77	5.34	11.05	7/29/2010	10/5/2010
70667	SC	5A	62	76	4.71	11.24	7/29/2010	10/5/2010
70623	SC	5A	53	63	3.3	5.7	7/29/2010	10/5/2010
74092	SC	5A	70	76	5.78	9.57	7/29/2010	10/5/2010
72751	CT	1A	130	129	21.98	19.89	7/30/2010	10/5/2010
66665	CT	1A	130	135	18.62	22.54	7/30/2010	10/5/2010
70683	CT	1A	100	105	10.05	10.62	7/30/2010	10/5/2010
72767	CT	1A	117	122	16.09	18.01	7/30/2010	10/5/2010
72748	CT	1A	125	125	16.86	15.8	7/30/2010	10/5/2010
72747	CT	1A	100	105	10.26	10.61	7/30/2010	10/5/2010
72724	CT	1A	106	109	11.31	11.12	7/30/2010	10/5/2010
72757	CT	1A	101	104	9.2	10.83	7/30/2010	10/5/2010
72763	CT	1A	106	110	10.72	12.05	7/30/2010	10/5/2010
71039	SC	8B	68	73	6.44	10.24	7/29/2010	10/5/2010
70654	SC	8B	54	65	3.17	6.46	7/29/2010	10/5/2010
71045	SC	8B	60	66	4.15	6.7	7/29/2010	10/5/2010
71053	SC	8B	66	78	6.4	11.5	7/29/2010	10/5/2010
71010	SC	8B	59	65	4.2	6.5	7/29/2010	10/5/2010
74021	SC	8B	62	71	4.49	8.23	7/29/2010	10/5/2010

71006	SC	8B	70	79	6.29	11.46	7/29/2010	10/5/2010
70684	SC	8B	70	76	5.74	11.65	7/29/2010	10/5/2010
71090	SC	8B	61	69	4.5	6.81	7/29/2010	10/5/2010
71078	SC	8B	67	74	5.37	10.47	7/29/2010	10/5/2010
71051	SC	8B	60	65	3.86	5.95	7/29/2010	10/5/2010
70669	SC	8B	59	73	4.58	9.49	7/29/2010	10/5/2010
74057	SC	8B	63	71	4.31	7.98	7/29/2010	10/5/2010
71024	SC	8B	53	61	2.98	5.35	7/29/2010	10/5/2010
71094	SC	8B	58	72	3.97	8.32	7/29/2010	10/5/2010
70666	SC	8B	59	61	3.72	5.4	8/11/2010	10/5/2010
71098	SC	8B	51	58	2.27	4.05	7/29/2010	10/5/2010
70635	SC	8B	53	60	2.99	5.13	7/29/2010	10/5/2010
71020	SC	8B	63	66	4.8	7.17	7/29/2010	10/5/2010
70656	SC	8B	55	61	3.3	4.73	7/29/2010	10/5/2010
70664	CT	6A	86	95	5.84	7.95	7/30/2010	10/5/2010
73522	CT	6A	125	135	18.4	25.36	7/30/2010	10/5/2010
72764	CT	6A	117	124	16.56	18.34	7/30/2010	10/5/2010
73586	CT	6A	139	139	22.87	25.1	7/30/2010	10/5/2010
72778	CT	6A	149	166	30.36	45.07	7/30/2010	10/5/2010
73509	CT	6A	94	101	8.81	9.88	7/30/2010	10/5/2010
72770	CT	6A	90	96	7.33	7.89	7/30/2010	10/5/2010
72771	CT	6A	97	111	8.96	13.95	7/30/2010	10/5/2010
72734	CT	6A	102	112	10.43	13.41	7/30/2010	10/5/2010
70644	SC	6A	82	90	10.28	16.26	7/29/2010	10/5/2010
74036	SC	6A	75	85	8.69	17.97	7/29/2010	10/5/2010
70651	SC	6A	62	64	4.78	7	7/29/2010	10/5/2010
70651	SC	6A	52	64	2.7	7	7/29/2010	10/5/2010

71001	SC	6A	77	88	8.48	15.85	7/29/2010	10/5/2010
74085	SC	6A	61	72	4.39	9.77	7/29/2010	10/5/2010
70661	SC	6A	49	60	2.23	4.77	7/29/2010	10/5/2010
71036	SC	6A	63	71	4.42	8.61	7/29/2010	10/5/2010
71004	SC	6A	53	66	3.13	7.29	7/29/2010	10/5/2010
71060	SC	6A	47	51	2.19	3.11	7/29/2010	10/5/2010
71097	SC	6A	51	55	2.74	3.86	7/29/2010	10/5/2010
71047	SC	8A	60	66	4.92	7.05	7/29/2010	10/7/2010
74044	SC	8A	61	70	4.58	7.7	7/29/2010	10/7/2010
74068	SC	8A	58	69	4.89	7.73	7/29/2010	10/7/2010
74098	SC	8A	61	67	4.54	6.96	8/9/2010	10/7/2010
71035	SC	8A	64	71	5.1	8.17	7/29/2010	10/7/2010
71067	SC	8A	74	76	7.06	8.96	7/29/2010	10/7/2010
74050	SC	8A	54	63	3.06	5.65	7/29/2010	10/7/2010
71026	SC	8A	58	66	4.66	7.27	7/29/2010	10/7/2010
71021	SC	8A	60	68	4.26	6.89	7/29/2010	10/7/2010
74018	SC	8A	62	70	5.37	8.28	7/29/2010	10/7/2010
71007	SC	8A	66	75	5.34	9.26	8/5/2010	10/7/2010
71073	SC	8A	62	66	4.33	6.81	7/29/2010	10/7/2010
70665	SC	8A	62	70	5.9	6.97	8/11/2010	10/7/2010
74051	SC	8A	52	60	2.88	5.59	7/29/2010	10/7/2010
70628	SC	8A	53	61	3.38	4.97	7/29/2010	10/7/2010
74043	SC	8A	52	51	3	3.21	7/29/2010	10/7/2010
70620	SC	8A	65	70	4.87	6.85	7/29/2010	10/7/2010
70609	SC	8A	59	66	3.73	6.31	7/29/2010	10/7/2010
74069	SC	8A	52	59	2.54	4.44	7/29/2010	10/7/2010
74091	SC	8A	52	65	3.1	6.05	7/29/2010	10/7/2010

74011	SC	3B	74	77	7.02	10.96	7/29/2010	10/7/2010
71019	SC	3B	57	64	3.58	5.67	7/29/2010	10/7/2010
70695	SC	3B	64	75	5.28	10.49	7/29/2010	10/7/2010
71082	SC	3B	72	76	8.4	11.34	7/29/2010	10/7/2010
71096	SC	3B	80	85	10.09	14.65	7/29/2010	10/7/2010
71081	SC	3B	72	82	8.14	12.72	7/29/2010	10/7/2010
71044	SC	3B	65	74	5.95	10.45	7/29/2010	10/7/2010
70619	SC	3B	58	66	4.29	7.44	7/29/2010	10/7/2010
71031	SC	3B	59	69	4.17	8.19	7/29/2010	10/7/2010
71072	SC	3B	68	72	6.75	8.89	7/29/2010	10/7/2010
71086	SC	3B	57	65	3.84	6.15	7/29/2010	10/7/2010
71085	SC	3B	58	66	4.16	6.59	7/29/2010	10/7/2010
73545	CT	7B	129	130	20.37	22.15	7/30/2010	10/7/2010
70621	CT	7B	101	107	9.19	12.15	7/30/2010	10/7/2010
72718	CT	7B	121	122	16.61	16.37	7/30/2010	10/7/2010
73542	CT	7B	118	125	14.83	18.75	7/30/2010	10/7/2010
72701	CT	7B	105	111	10.03	12.66	7/30/2010	10/7/2010
72787	CT	7B	106	110	12.23	13.11	7/30/2010	10/7/2010
74006	SC	7B	54	66	3.54	7.9	7/29/2010	10/7/2010
70686	SC	7B	59	73	4.13	9.39	7/29/2010	10/7/2010
70691	SC	7B	57	64	3.4	5.93	7/29/2010	10/7/2010
70639	SC	7B	62	74	4.45	9.68	7/29/2010	10/7/2010
71052	SC	7B	62	67	4.78	6.5	7/29/2010	10/7/2010
71083	SC	7B	63	75	5.22	11.24	7/29/2010	10/7/2010
70659	SC	7B	60	65	4.05	6.01	7/29/2010	10/7/2010
71029	SC	7B	66	72	5.02	7.6	7/29/2010	10/7/2010
70692	SC	7B	56	70	3.63	7.9	7/29/2010	10/7/2010

74094	SC	7B	66	76	6.04	9.66	7/29/2010	10/7/2010
74031	SC	7B	59	66	4.3	6.52	7/29/2010	10/7/2010
74003	SC	7B	54	63	2.83	5.36	7/29/2010	10/7/2010
71100	SC	7B	57	64	3.45	5.48	7/29/2010	10/7/2010
74041	SC	7B	74	82	6.64	12.05	7/29/2010	10/7/2010
70640	SC	7B	51	53	2.84	3.36	7/29/2010	10/7/2010
73557	CT	2A	122	126	18.28	19.2	7/30/2010	10/7/2010
73548	CT	2A	112	113	12.47	13.14	7/30/2010	10/7/2010
73598	CT	2A	108	112	12.53	14.04	7/30/2010	10/7/2010
70605	CT	2A	150	161	34.52	45.6	7/30/2010	10/7/2010
70603	CT	2A	149	152	28.53	34.09	7/30/2010	10/7/2010
74078	SC	2A	67	71	5.63	8.02	7/29/2010	10/7/2010
74056	SC	2A	60	74	4.64	9.72	7/29/2010	10/7/2010
71022	SC	2A	55	62	3.57	5.77	7/29/2010	10/7/2010
74087	SC	2A	58	69	3.87	7.68	7/29/2010	10/7/2010
74060	SC	2A	65	72	4.8	8.04	7/29/2010	10/7/2010

Table D.2. Raw sculpin cover use data collected August 12 to September 14, 2010 during an experiment in artificial stream channels at the Oregon Hatchery Research Center. Number of sculpins detected in artificial cover during day-time (Cover Day) and night-time (Cover Night) observations are given for each observation period (6 total) for each treatment containing sculpins.

Treatment	Cover Day	Cover Night	Observation Period	Date
2A	1	1	1	8/13/2010
2A	1	3	2	8/18/2010
2A	1	0	3	8/25/2010
2A	1	0	4	9/1/2010
2A	0	0	5	9/7/2010
2A	0	2	6	9/14/2010
2B	0	0	1	8/14/2010
2B	1	0	2	8/20/2010
2B	0	0	3	8/27/2010
2B	0	0	4	8/30/2010
2B	0	0	5	9/5/2010
2B	0	2	6	9/12/2010
3A	1	0	1	8/14/2010
3A	0	3	2	8/20/2010
3A	0	2	3	8/27/2010
3A	1	1	4	8/30/2010
3A	0	0	5	9/5/2010
3A	0	2	6	9/12/2010
3B	0	4	1	8/13/2010
3B	0	1	2	8/18/2010
3B	0	3	3	8/25/2010
3B	0	1	4	9/1/2010
3B	0	0	5	9/7/2010
3B	0	1	6	9/14/2010
5A	0	1	1	8/15/2010
5A	0	0	2	8/21/2010
5A	0	0	3	8/24/2010
5A	0	0	4	8/31/2010
5A	1	1	5	9/8/2010
5A	2	1	6	9/13/2010

5B	2	0	1	8/16/2010
5B	3	1	2	8/19/2010
5B	3	0	3	8/26/2010
5B	3	1	4	9/2/2010
5B	1	0	5	9/6/2010
5B	2	0	6	9/11/2010
6A	2	1	1	8/15/2010
6A	1	1	2	8/21/2010
6A	2	0	3	8/24/2010
6A	2	0	4	8/31/2010
6A	1	1	5	9/8/2010
6A	3	4	6	9/13/2010
6B	3	0	1	8/16/2010
6B	0	1	2	8/19/2010
6B	2	2	3	8/26/2010
6B	3	2	4	9/2/2010
6B	1	2	5	9/6/2010
6B	4	2	6	9/11/2010
7A	3	0	1	8/14/2010
7A	2	1	2	8/20/2010
7A	2	1	3	8/27/2010
7A	0	1	4	8/30/2010
7A	2	1	5	9/5/2010
7A	2	2	6	9/12/2010
7B	1	4	1	8/13/2010
7B	1	3	2	8/18/2010
7B	1	3	3	8/25/2010
7B	1	0	4	9/1/2010
7B	1	2	5	9/7/2010
7B	1	1	6	9/14/2010
8A	4	5	1	8/13/2010
8A	4	5	2	8/18/2010
8A	4	2	3	8/25/2010
8A	2	0	4	9/1/2010
8A	2	0	5	9/7/2010
8A	4	1	6	9/14/2010
8B	1	4	1	8/15/2010
8B	2	1	2	8/21/2010
8B	2	3	3	8/24/2010

8B	2	2	4	8/31/2010
8B	2	5	5	9/8/2010
8B	2	4	6	9/13/2010

Table D.3. Raw coastal cutthroat trout aggressive interactions data collected August 12 to September 14, 2010 during an experiment in artificial stream channels at the Oregon Hatchery Research Center. The total visible cutthroat trout (Total Cutthroat) and total acts of aggression (Total Agg) are given for each treatment for each observation period.

Treatment	Total Cutthroat	Total Agg	Observation Period	Date
1A	8	1	1	8/15/2010
1A	10	1	2	8/21/2010
1A	10	1	3	8/24/2010
1A	10	0	4	8/31/2010
1A	10	0	5	9/8/2010
1A	10	1	6	9/13/2010
1B	7	3	1	8/16/2010
1B	7	1	2	8/19/2010
1B	8	0	3	8/26/2010
1B	7	0	4	9/2/2010
1B	8	0	5	9/6/2010
1B	9	0	6	9/11/2010
2A	1	0	1	8/13/2010
2A	2	0	2	8/18/2010
2A	3	0	3	8/25/2010
2A	2	0	4	9/1/2010
2A	2	0	5	9/7/2010
2A	3	0	6	9/14/2010
2B	2	0	1	8/14/2010
2B	5	1	2	8/20/2010
2B	1	0	3	8/27/2010
2B	2	0	4	8/30/2010
2B	1	0	5	9/5/2010
2B	2	0	6	9/12/2010
4A	17	2	1	8/16/2010
4A	19	5	2	8/19/2010
4A	22	10	3	8/26/2010
4A	20	6	4	9/2/2010
4A	25	2	5	9/6/2010
4A	23	0	6	9/11/2010
4B	19	5	1	8/14/2010

4B	18	4	2	8/20/2010
4B	16	2	3	8/27/2010
4B	17	3	4	8/30/2010
4B	19	3	5	9/5/2010
4B	17	4	6	9/12/2010
5A	13	15	1	8/15/2010
5A	19	7	2	8/21/2010
5A	19	7	3	8/24/2010
5A	17	0	4	8/31/2010
5A	16	6	5	9/8/2010
5A	17	0	6	9/13/2010
5B	12	3	1	8/16/2010
5B	10	0	2	8/19/2010
5B	10	4	3	8/26/2010
5B	10	1	4	9/2/2010
5B	9	3	5	9/6/2010
5B	10	2	6	9/11/2010
6A	9	9	1	8/15/2010
6A	9	1	2	8/21/2010
6A	7	1	3	8/24/2010
6A	8	1	4	8/31/2010
6A	9	0	5	9/8/2010
6A	8	1	6	9/13/2010
6B	5	2	1	8/16/2010
6B	8	0	2	8/19/2010
6B	11	1	3	8/26/2010
6B	10	3	4	9/2/2010
6B	9	0	5	9/6/2010
6B	8	0	6	9/11/2010
7A	2	0	1	8/14/2010
7A	3	3	2	8/20/2010
7A	3	0	3	8/27/2010
7A	2	0	4	8/30/2010
7A	1	0	5	9/5/2010
7A	2	0	6	9/12/2010
7B	2	2	1	8/13/2010
7B	2	0	2	8/18/2010
7B	3	0	3	8/25/2010
7B	2	0	4	9/1/2010

7B	2	0	5	9/7/2010
7B	4	0	6	9/14/2010
