

Effects of drift supplementation and altered channel complexity on the foraging distance of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*)

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Abstract

*We studied the foraging distances of resident coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and their relationship to invertebrate drift and channel complexity. Our study tested the hypothesis that invertebrate drift is homogenous by capturing and analyzing drift across different velocities. Our experiment had three distinct trials (1) existing conditions, the control group; (2) supplemented invertebrate drift by 550%, and (3) increased channel complexity. The novelty of our study is the in situ approach we took to experimentally quantify *O. c. clarkii* foraging behavior, unlike previous studies, which have typically taken place in hydraulic flumes or been observational based (Fausch 1984; Hughes et al. 2003). We observed that invertebrate drift was not homogeneous across different velocities ($p = 0.031$). There was a noticeable decrease in foraging distance when invertebrate drift was supplemented. The decline in foraging distance was likely observed because higher prey density allowed individuals to travel shorter distances while feeding. It is likely that foraging distance was greater with increased channel complexity because salmonids were able to forage in lower velocities. Our study provides the framework for future in situ experimental studies attempting to quantify differences in salmonid foraging behavior. Our study and similar investigations will likely be applicable in future habitat conservation and remediation efforts.*

Introduction

Resident coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) are drift-feeding salmonids, dependent on downstream movement of invertebrates for energy gains. Salmonids' primary energy expenditure is from maintaining position or a focal point within the stream (Fausch 1984). It was proposed that salmonids inhabit lower velocity areas, holding focal points, and move into fast-moving currents to forage in order to maximize energy gains (Fausch and White 1981). Salmonids exhibited an inverse relationship between foraging distance and water velocity, and were more selective in their foraging attempts within high velocity areas (Godin and Rangeley 1989; Piccolo et al. 2008; O'Brien and Showalter 1993).

Differences in velocity across streams develop from channel complexity and formulate the basis for salmonid habitat. Within the Pacific Northwest, historic removal of large woody debris simplified stream channels, decreasing habitat suitability (Swanson and Lienkaemper 1978). Remediation efforts include additions of large wood, which can restore fish habitat via increasing channel complexity (Beechie et al.

2000). In this study, we utilized a pool generated from anthropogenic supplementation of large woody debris that formed a logjam.

The downstream movement of invertebrates affects salmonid foraging behavior, and represents a major focus for bioenergetics analysis. Our study scrutinized drift density across a velocity gradient to determine the validity of longstanding assumptions regarding invertebrate distribution within the water column (Fausch 1984). Previous literature states that drift density is fairly homogenous despite variance in streamflow (Müller 1963 (1); Elliot 1970). We hypothesize that invertebrates would be more prevalent in areas of higher velocity.

Our study quantified the *O. c. clarkii* foraging distance during periods of supplemented invertebrate drift, with the intent of observing reactions to larger and more abundant prey. We propose that foraging distance will increase with larger prey and decrease with prey abundance.

We attempt to quantify the relationship between channel complexity and salmonid foraging distance. We observed behavior downstream of a logjam that provided channel complexity. Channel characteristics were altered to empirically study differences in foraging distance.

Defining salmonid feeding strategies, through quantifying fish behavior and spatial-temporal modeling, provides a framework for successful habitat restoration practices and applications (Nislow *et al.* 1999). We aim to clarify the foraging distance, invertebrate drift composition and distribution, and influence of velocity during adult *O. c. clarkii* feeding.

First, we observed existing conditions, where no alterations were made to the stream environment. Second, we supplemented the invertebrate drift. Third, we observed the pool after increasing channel complexity. Numerous studies have empirically studied salmonid foraging patterns within hydraulic flumes under laboratory settings or completed observational studies within streams (Fausch 1984; Hughes *et al.* 2003). Our study takes an *in situ* approach to experimentally quantifying *O. c. clarkii* foraging behavior, to advance understanding the impact of drift density and flow complexity on salmonid foraging windows in the field setting.

Methods

Study Site

We studied a pool in Lookout Creek, located within HJ Andrews Experimental Forest, Oregon, USA (Figure 1). Lookout Creek is a third order stream (wetted width = 8.95 m), and the riparian setting remains a largely undisturbed old growth temperate rainforest. The pool was positioned below an anthropogenic addition of large woody debris (old growth Douglas Fir) that led to a logjam (Figure 2A). The pool's area was 11.36 m², with an average depth of 0.556 m.

Experimental Setup

Before any measurements were taken, we surveyed the bathymetry and velocity of the pool and decreased the population size of the fish. The pool bathymetry was surveyed with a Nikon DTM-352 Total Station. We measured one-dimensional (upstream to downstream) velocity every 0.3 meters horizontally,

longitudinally, and vertically within the pool using a Hach FH950 electromagnetic velocimeter. We utilized electrofishing to decrease the fish density and estimate the fish population in the pool. We removed 43 fish and left 9 fish of varying sizes in the pool. Although 9 fish were released, approximately 20 fish inhabited the pool. All electrofishing data was analyzed with MicroFish 3.0.

Underwater Videogrammetry

We observed foraging behavior using four pairs of side-by-side mounted GoPro Hero 3 cameras between 16:00-17:30. Filming duration (referred to as an “observation period”) was a minimum 60-minute timespan. Camera pairs were mounted on bricks, to allow submergence and stability in the flow. A diver positioned cameras so that we had a complete view of the pool (Figure 2A). Foraging behavior was filmed during all three trials: existing, supplemented drift (550%), and altered velocity conditions.

Invertebrate Drift

Drift of invertebrates was determined for the upstream flow and across multiple velocities within the pool. We measured the overall drift into the pool with two rectangular drift nets (47 cm length x 31 cm height), which were placed upstream of the sampling location. The nets were positioned to collect both surface and subsurface samples, theoretically gathering all passing invertebrates. The rectangular drift nets intercepted flow to the downstream pool between 17:00-17:30. The drift was determined across multiple velocities via 3 D-nets (32 cm diameter x 25 cm radius) that collected invertebrates at 0.08, 0.22, and 0.27 m/s. To determine drift at several velocities, D-nets were suspended across the stream surface from 16:00-17:00; the flat edge was placed 1 cm above the surface with the rounded portion submerged.

In the second trial, drift was supplemented in order to evaluate the impact of varying drift density on foraging distance. The increased drift was comprised of macroinvertebrates collected from rocks downstream of the pool. We supplemented the existing drift by approximately 550% ($n = 570$ invertebrates). The percent drift increase was based on the quantity of macroinvertebrates upstream of the pool, numerated by the two rectangular nets. We supplemented drift over a one-hour period, adding pulses of 95 invertebrates at ten-minute intervals. Additions of invertebrates occurred upstream of the pool.

The composition of supplemental drift was determined by the random sampling of 104 invertebrates. Composition of the naturally occurring drift was determined by 67 invertebrates collected in drift nets upstream of the pool (from 16:00-17:30). Invertebrate dry mass calculations were based on exponential length-mass functions from Sabo *et al.* (2002). Invertebrate size was based on length because it was assumed fish detect prey length more easily than prey mass.

Channel Complexity

In the third trial, we increased the channel complexity in order to evaluate foraging behavior under different velocities. To increase channel complexity, we introduced a colluvial boulder, which modified flow fields within the pool and changed the habitat complexity (Figure 2B).

Analytical Methods

We triangulated the location of fish using 3D videogrammetry in VidSync 1.34-1. Out of the 607 recorded foraging attempts available from filming, we selected and measured 15 from each trial (total $n = 45$),

using simple random selection in R 3.2.0. All measurements of salmonid position were based on the subject's eye location and were recorded in VidSync. For each foraging attempt, a focal point was measured prior to the attempt, and then the foraging location was measured. Focal points were recorded as the location fish held before a foraging attempt. At each focal point, the location of the subject's eye was documented. Foraging attempts were determined by movement away from the fish's focal point and then an opening and closing of the mouth. Immediately following the closing of the subject's mouth, the location of the eye was taken again, and defined as the forage location. The foraging distance was calculated with the formula for three-dimensional distance:

$$d = \sqrt{(F_x - A_x)^2 + (F_y - A_y)^2 + (F_z - A_z)^2}$$

where F_x , F_y , and F_z are the three-dimensional x , y , and z coordinates of the eye at the focal point, respectively. A_x , A_y , and A_z are the three-dimensional x , y , and z coordinates of the eye immediately following the foraging attempt, respectively.

The fork length of fish was measured at each observed focal point by determining the locations of the snout and the middle of the caudal ray. Coordinates of the aforementioned body parts were used to calculate fork length, utilizing the three-dimensional distance formula:

$$L_{fork} = \sqrt{(S_x - C_x)^2 + (S_y - C_y)^2 + (S_z - C_z)^2}$$

where S_x , S_y , and S_z are the three-dimensional x , y , and z coordinates of the snout, respectively. C_x , C_y , and C_z are the three-dimensional x , y , and z coordinates of the caudal fork, respectively.

Results

Pool Population

Before fish removal, the population estimate was 61, and the total salmonid biomass was estimated at 1311 g. The mean length and mass of sampled fish was 12.7 cm and 21.3 g, respectively. We are 95% confident that the true population in the pool was between 9 and 39 after fish were removed.

Salmonid Foraging

The overall mean foraging distance was 16.4 cm, and the max foraging distance was 39.4 cm. The average foraging distances were 15.8, 13.8, and 19.6 cm for the existing conditions, supplemented drift, and increased channel complexity trials, respectively. There was not a statistically significant difference in the mean foraging distance across the three trials ($p = 0.240$; from a one-way analysis of variance (ANOVA)). Between the existing conditions and the supplemented drift trials, we observed a 23.3% decrease in median foraging distance from 13.6 cm to 10.4 cm (Figure 4). There was not a significant difference in the mean foraging distances between the existing conditions and increased channel complexity ($p = 0.289$). There was a 33.0% increase in median foraging distance from 13.6 cm to 18.0 cm.

We observed a mean fish fork length of 11.7 cm with a range of [5.9, 18.7] cm for the fish observed during video analysis. There was not a significant correlation between fish length and foraging distance ($p = 0.114$; Figure 5).

Invertebrate Drift

We found that a majority of the invertebrates added during the supplemented drift trial were composed of Ephemeroptera, while the composition of the naturally occurring drift was distributed between Ephemeroptera, Plecoptera, and Diptera (Table 1). We found large disparities within invertebrate life stage between the supplemented and naturally occurring drift. In the supplemental drift, all invertebrates were immature, larva or pupa. The naturally occurring drift contained approximately 46.2% mature or terrestrial invertebrates. The individual invertebrates used for supplementation were 52.0% longer (length excluding antennae and cerci) and 16.8% lighter by dry mass on average. The average dry mass per foraging attempt was calculated at 2.07 mg, based on sampling of the naturally occurring drift.

A one-way analysis of variance (ANOVA) yielded a significant difference in the mean count of invertebrates captured across different water velocities ($p = 0.031$; Figure 6). The mean number of invertebrates captured in low, medium, and high velocities were 3.25, 1.75, and 5.50, respectively.

Velocity

We observed an overall decline in velocities across the majority of the pool, due to declining discharge over the summer. Discharge in our pool decreased from 6.6 m³/s to 3.3 m³/s over the course of our study. Addition of the boulder altered velocity patterns within the pool by shifting the main velocity core farther in the downstream right direction (Figure 7). Fish utilized the velocity shelters directly upstream and downstream of the introduced boulder.

Discussion

Study limitations

Foraging activity may have been influenced by human disturbance during sampling, particularly during drift supplementation. The invertebrates used to supplement drift were different in both size and species, which may have limited the scope of the study. The increased size and mass of drift may have augmented initiative to capture prey, enlarging foraging distances. The change in species could have influenced feeding behavior, if species-specific feeding preferences existed. The naturally occurring drift contained a larger diversity of invertebrate species, as well. The differences in composition of supplemental drift and naturally occurring drift likely took place because of sampling practices. Ephemeroptera appeared more likely to remain on substrate following its removal from the stream bottom, whereas other invertebrates (i.e. Plecoptera) fled from human capture.

Invertebrate drift and velocity

The significant difference in the mean number of invertebrates captured between several velocities rejects the previous assumption that drift is evenly distributed across streams ($p = 0.031$). There was not a linear correlation between water velocity and drift captured. This suggests that our results conflict with the assumption made within Fausch's laboratory model (Fausch 1984). We observed more foraging attempts

than the amount of captured invertebrates. This may have been induced by trout foraging in front of our drift nets.

Foraging distances

While the 23.3% decrease in foraging distance between existing conditions and supplemented drift was not statistically significant, there is a possibility of ecological significance. We originally hypothesized that increased drift density would decrease foraging distances, but larger invertebrate prey would increase foraging distances. The supplementation of drift in our pool increased the density of prey more so than size of prey, which is a possible explanation for shorter foraging distances.

With the addition of channel complexity, we observed a 33.0% increase in foraging distance. The increase was not statistically significant, however. Two possible explanations for the increased foraging distances during the third trial are (1) lower velocities in front and behind the introduced boulder or (2) the 50% reduction of discharge over the course of the summer.

Conclusion

Restoration of stream habitat is critical in restoring salmonid populations. Understanding salmonid foraging behavior is crucial if restoration efforts are to be efficient. Our study helped provide part of this understanding, as well as a framework for future endeavors to improve knowledge in this field.

We observed a heterogeneous distribution of invertebrate drift capture across the pool, which is inconsistent with previous literature on the subject (Fausch 1984). This provides a framework for potential research.

We found that *O. c. clarkii* foraging distance decreased with the supplementation of invertebrate drift, but increased with the alteration of channel complexity. The foraging distance likely decreased with drift supplementation because of a higher density of food availability. The increased foraging distance observed with the alteration of channel complexity could be due to low velocity areas created in front of and behind the introduced boulder or an overall decrease in velocity throughout the pool.

Additions of large woody debris may work to augment habitat complexity and enhance ability for trout to have higher net energy gains. The pool demonstrates salmonid foraging behavior within an anthropogenic induced logjam, and provides information regarding the usefulness of woody debris inputs for stream remediation.

This study helps to show the validity of remediation efforts that reduce velocities, since they allow salmonids to increase foraging distances. More future research should be conducted into best practices of increasing channel complexity and providing areas of decreased velocity for salmonids. Our study provides a framework for *in situ* experiments on salmonid foraging distances, and our approach may provide the basis for similar studies. Future studies should implement a larger sample size; however, which may provide a more robust dataset and improve statistical analysis. Our study and similar investigations will likely be applicable in future habitat conservation and remediation efforts.

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Figures

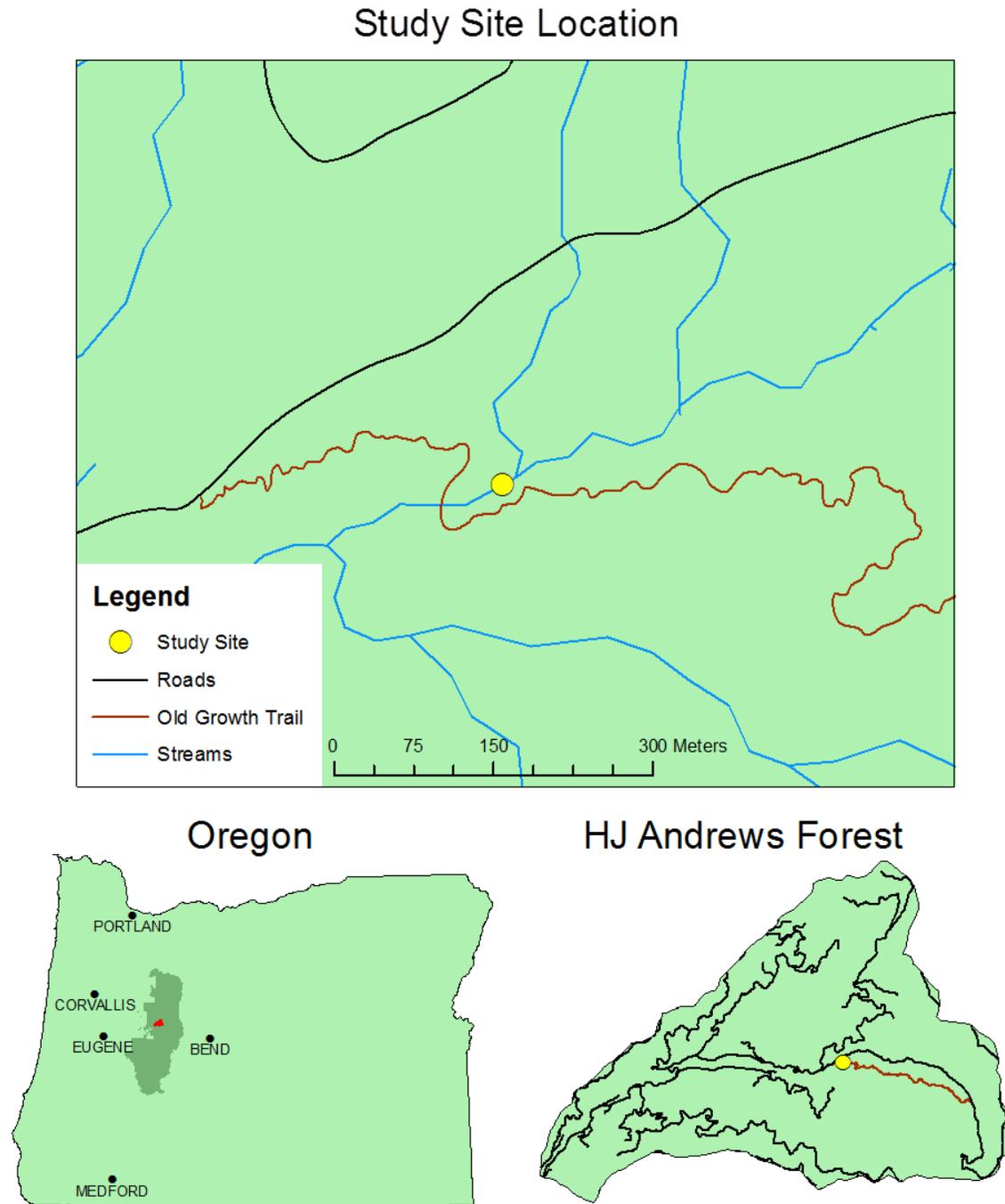


Figure 1. Location of the study site within the HJ Andrews forest, and location of the HJ Andrews forest within Oregon in relation to major cities and the Willamette National Forest.

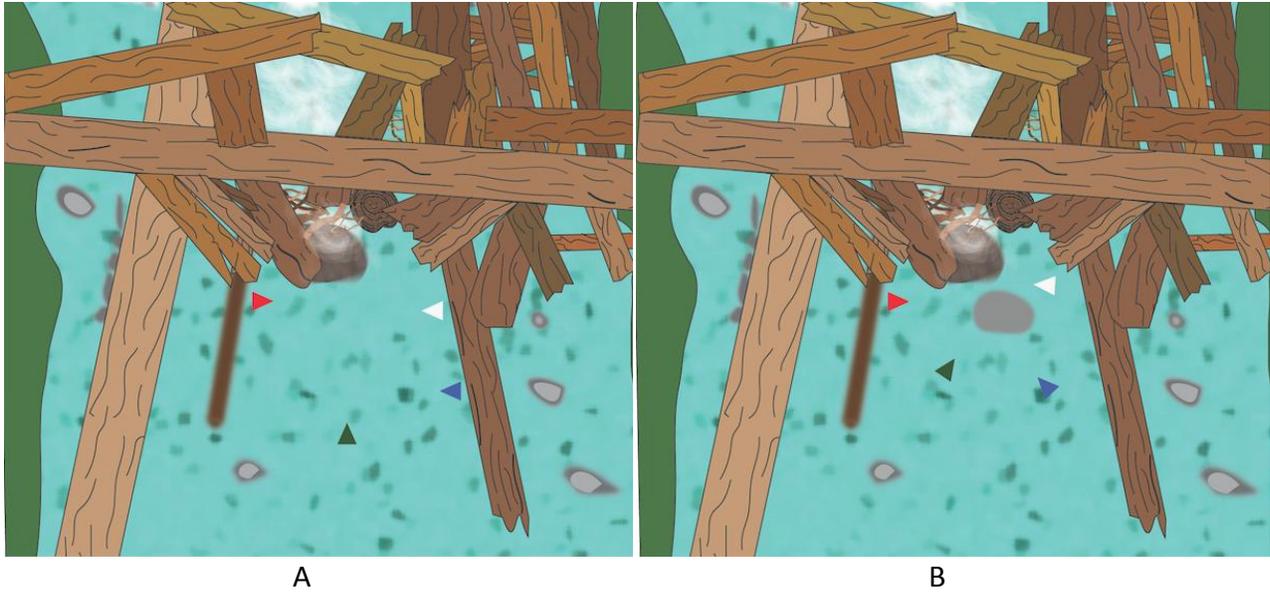


Figure 2. A. The study pool within Lookout Creek (HJ Andrews Experimental Forest, OR) during the existing conditions and supplemented drift (Trial 1 & 2). **B.** The study pool within Lookout Creek (HJ Andrews Experimental Forest, OR) during the increased channel complexity trial (Trial 3).

Table 1. The proportion by count represents the amount of each invertebrate order. Dry mass (DM) was estimated using the exponential allometric equation $DM = aL^b$, where L is invertebrate length. The constants a and b were obtained from Sabo *et al.* (2002). R^2 values from previous literature demonstrate the fit of length-mass conversions used for DM calculations. Terrestrial Trichoptera and terrestrial Plecoptera DMs were produced from constants given for all terrestrial invertebrates, since no order specific constants exist in the literature.

		Invertebrate Order	Proportion by Count	a	b	Mean DM (mg)	Proportion by DM	R²
Supplemented Drift	}	Ephemeroptera	0.98	0.014	2.49	1.57	0.89	0.89
		Plecoptera	0.020	0.26	1.69	9.47	0.11	0.95
Naturally Occurring Drift	}	Ephemeroptera	0.18	0.014	2.49	0.87	0.076	0.89
		Plecoptera	0.31	0.26	1.69	2.25	0.34	0.95
		*Diptera	0.25	0.040	2.26	1.08	0.13	0.67
		†Coleoptera	0.075	0.040	2.64	0.73	0.026	0.95
		†Trichoptera	0.015	0.032	2.63	7.10	0.051	0.81
		†Plecoptera	0.15	0.032	2.63	4.28	0.31	0.81
		†Hymenoptera	0.015	0.56	1.56	8.69	0.063	0.75

† terrestrial invertebrates

* calculated the same regardless of terrestrial or aquatic

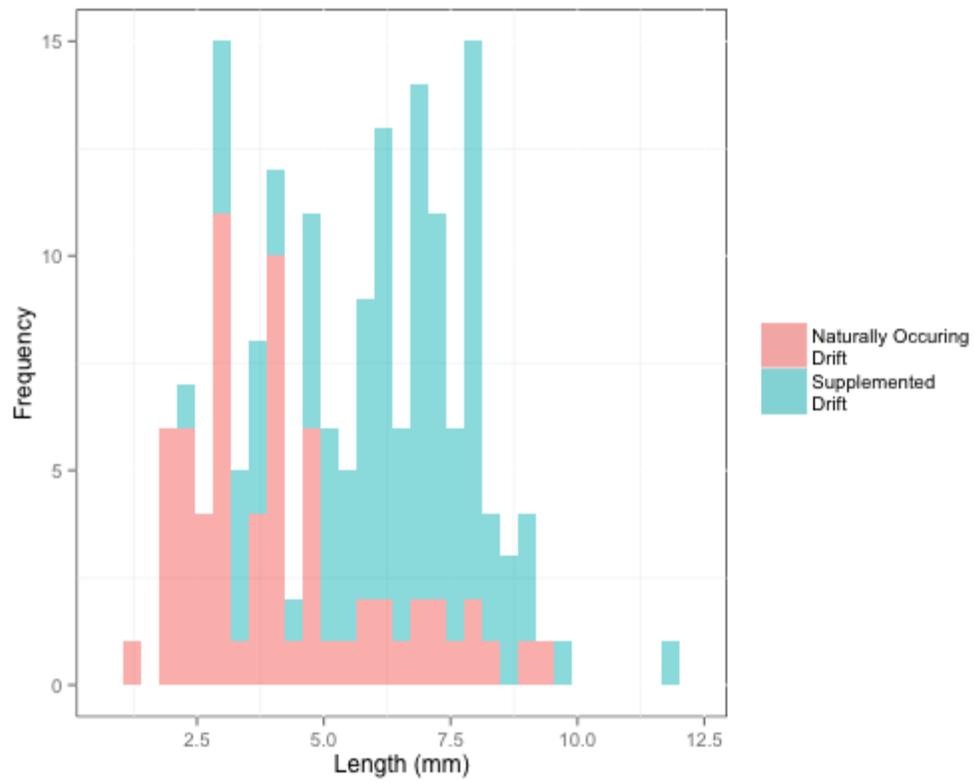


Figure 3. Distribution of invertebrate length for the naturally occurring drift and the supplemented drift.

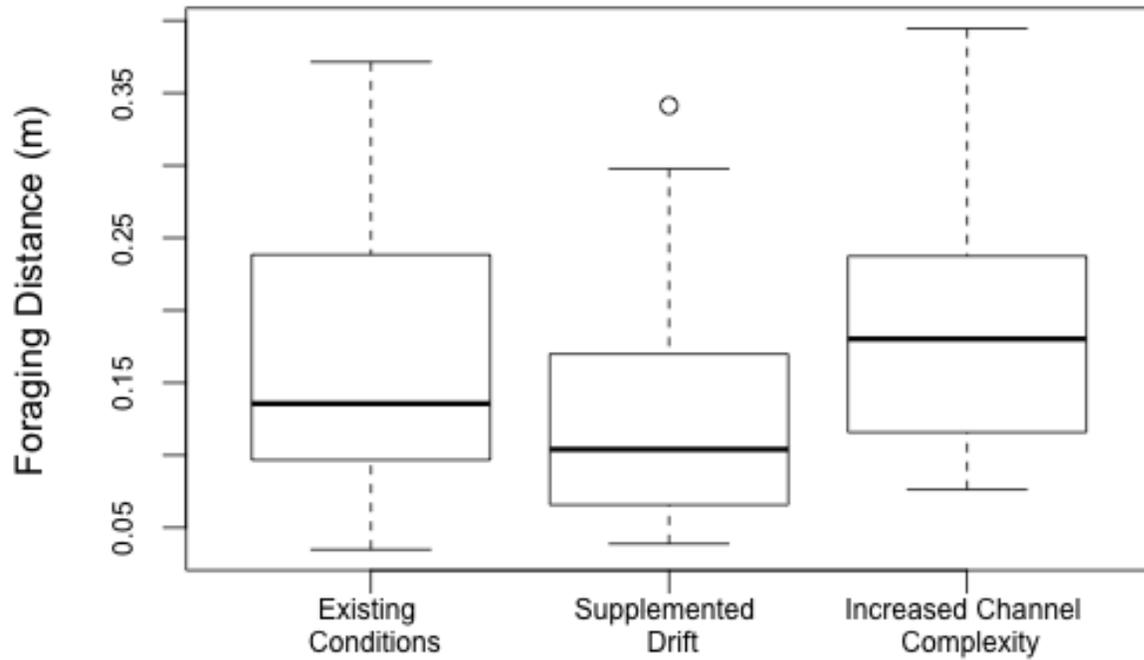


Figure 4. Foraging distances for each of the three trials. The one-way analysis of variance showed no statistical significance in the difference of mean foraging distances across all trials ($p = 0.240$). There was no statistical significance in the difference of mean foraging distances between existing conditions and supplemented drift ($p = 0.548$). There was no statistical significance in the difference of mean foraging distances between existing conditions and increased channel complexity ($p = 0.289$).

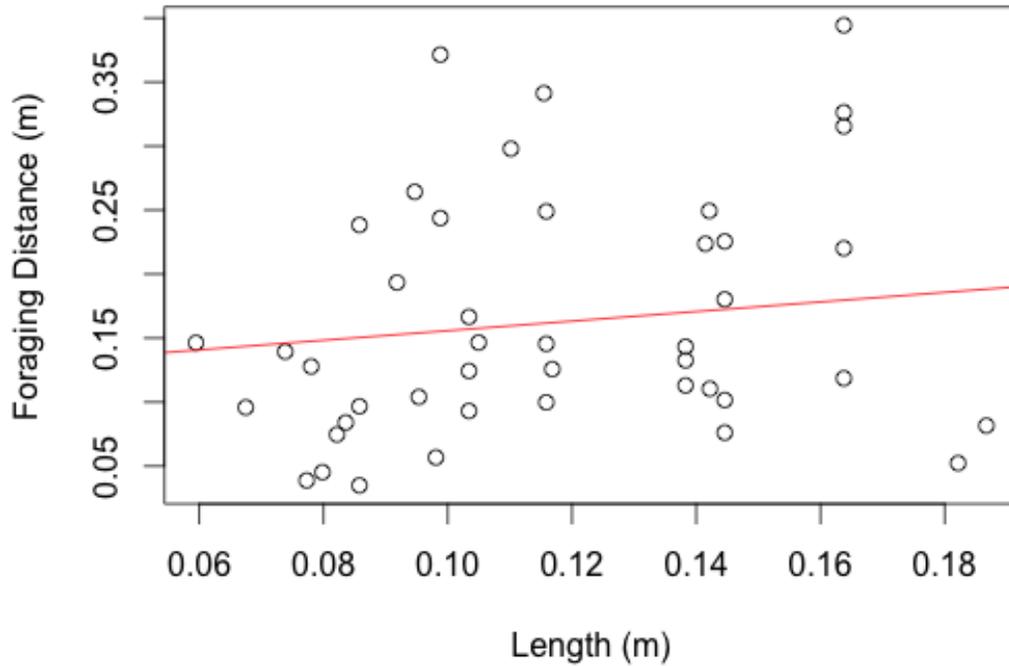


Figure 5. There was not a statistically significant linear relationship between the fish fork length and foraging distance. ($p = 0.114$, $R^2 = 0.058$).

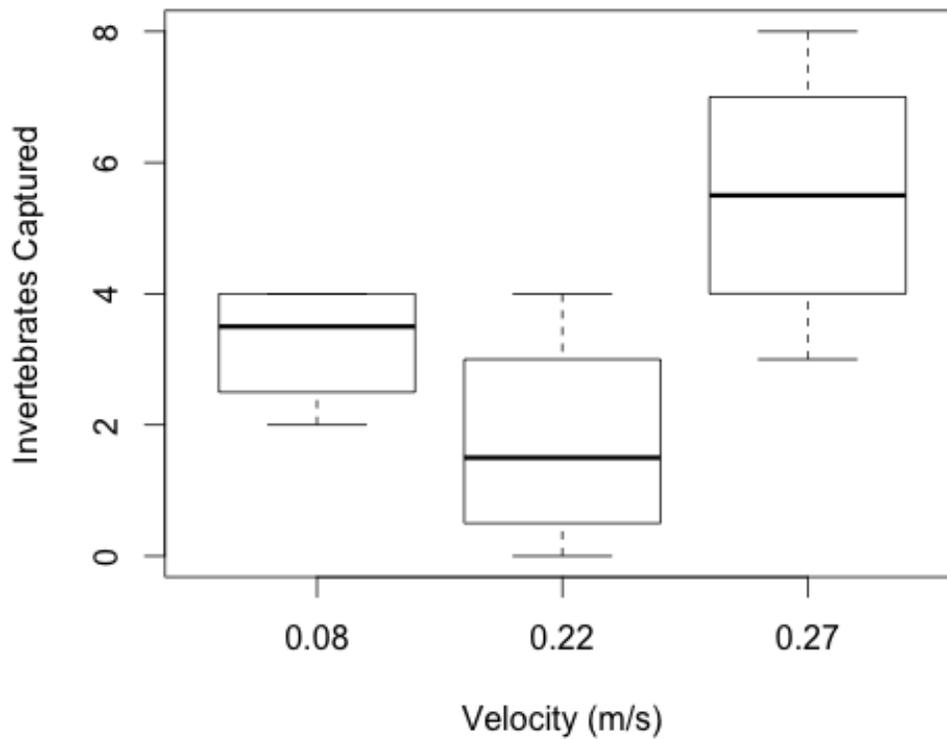


Figure 6. The analysis of variance had a significant difference between the mean count of invertebrates captured at different velocities ($p = 0.031$).

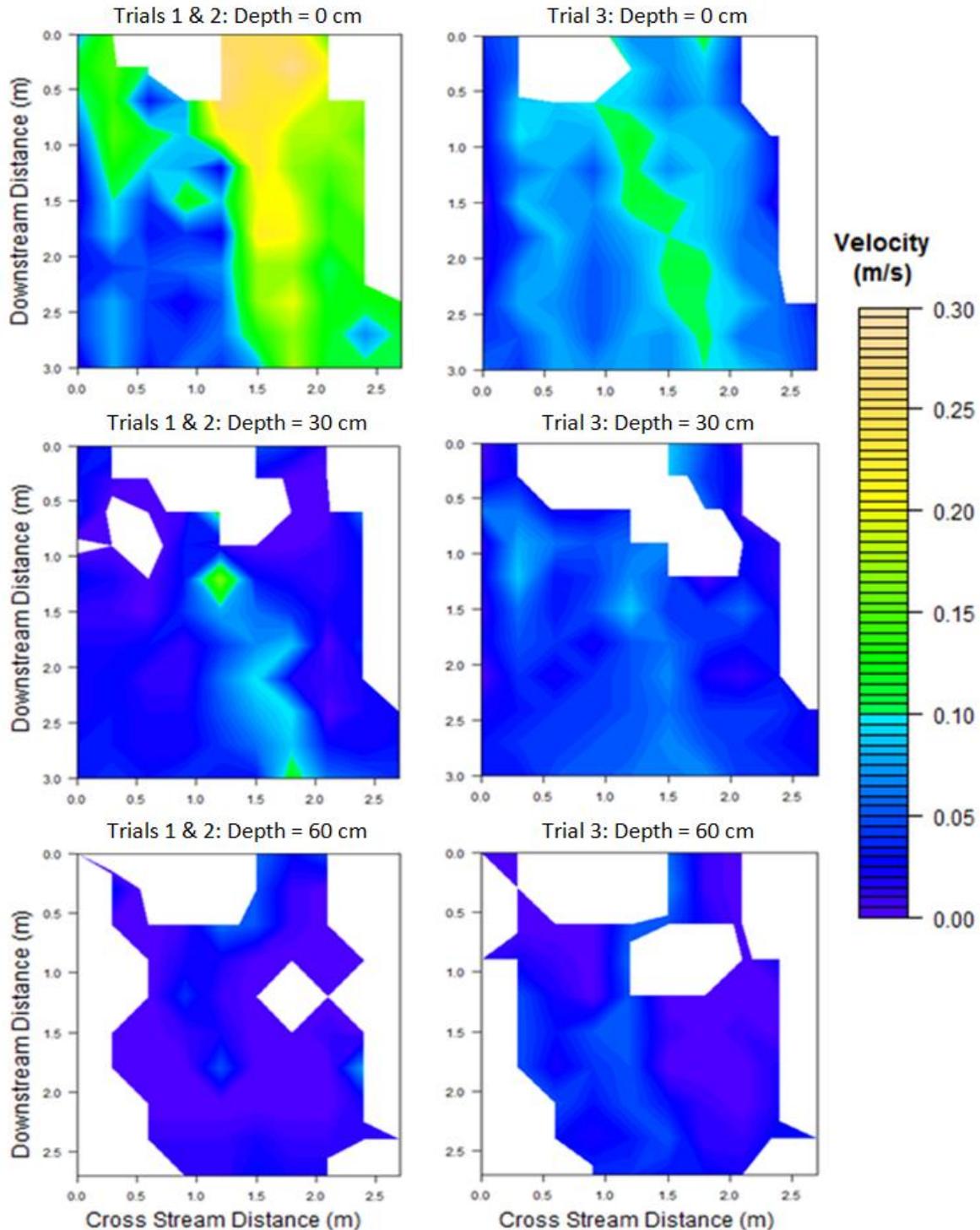


Figure 7. Velocity contours from before and after the boulder addition. All plots are plan view of the pool. The flow direction is from top to bottom. The plots in the left column show velocity conditions before the boulder addition, and the plots in the right column show conditions after. Each row shows a different water depth. The boulder was located at approximately 1 meter downstream distance and 1.75 meters cross stream distance in trial 3.