Shoaling Behavior as a Tool to Understand Microhabitat Use by Juvenile Chum Salmon, *Oncorhynchus keta*

Carl Douglas Young

A thesis submitted in partial fulfillment
of the requirements for the degree of

Master of Science

University of Washington

2009

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington
Graduate School

This is to certify that I have examined this copy of a master's thesis by

Carl Douglas Young

and have found that it is complete and satisfactory in all respects,
and that any and all revisions required by the final
examining committee have been made.

Committee Members:

____
Charles Simenstad

____
Jeffery Cordell

____
Julia Parrish

____
Sandy Wyllie-Echeverria

Date: ____

In presenting this thesis in partial fulfillment of the requirements for a master's degree at the University of Washington, I agree that the Library shall make its copies freely available for inspection. I further agree that extensive copying of this thesis is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Any other reproduction for any purposes or by any means shall not be allowed without my written permission.

Signature ________________________

Date ____________________________

University of Washington

Abstract

Shoaling Behavior as a Tool to Understand Microhabitat Use by Juvenile Chum Salmon, *Oncorhynchus keta*

Carl Douglas Young

Chair of the Supervisory Committee:
Research Professor Charles Simenstad
School of Aquatic and Fishery Sciences

Density is most often used to compare estuarine microhabitats to determine if they are nurseries for juvenile marine fishes and invertebrates. But using only density fails to determine how organisms are using, or meeting life requirements, each microhabitat. Measuring *in situ* behavior of organisms is a tool that can complement density to better clarify how organisms are using estuarine microhabitats. Juvenile chum salmon, *Oncorhynchus keta*, is an example of an organism where behavior in nearshore estuarine microhabitats can be used to understand how they are using these microhabitats. Two estuarine microhabitats where juvenile chum salmon are found are the cobble/gravel beaches of the upper intertidal and eelgrass beds, *Zostera marina*, in the lower intertidal. The upper intertidal is about 2 – 3 times steeper than the lower intertidal. Eelgrass beds have long been thought to be particularly important because prey preferred by juvenile chum salmon are often found in higher densities in lower intertidal eelgrass beds. This study developed an *in situ* method of observing juvenile chum salmon shoaling behavior in nearshore microhabitats by video recording a 0.25 m^2 quadrat nested inside a larger 8-m x 6-m rope grid divided into 2-m x 2-m squares. Shoaling behavior was used as a method to examine microhabitat use because predation and foraging are the two main factors that structure fish shoals. A number of quantitative metrics of shoal cohesiveness were developed and 4 of the 7 of these metrics produced significant results that indicated shoals were more cohesive in the lower intertidal than in the upper intertidal. From shoal movements and the depth

distribution of fish in the upper and lower intertidal microhabitats it was discovered that there is a "stay shallow" mandate for juvenile chum salmon that likely developed as a way to avoid predators. This stay shallow mandate possibly limits microhabitat availability of the lower intertidal microhabitats when the tidal level is high. Also, because of the combination of differences in slope between upper and lower intertidal microhabitats and the stay shallow mandate, any interpretations of only density are likely to be flawed because fish concentrate in areas with the steeper beach slope. Possible explanations are increased predation in the lower intertidal or decreased foraging in the lower intertidal. One site, Tabook Point, in Dabob Bay had the lowest indices of shoal cohesiveness for both years as well as higher than expected density in the lower intertidal. This indicates that this site may be an important potential foraging ground during low tides.

TABLE OF CONTENTS

List of Figures iii
List of Tables v
Introduction 1
- Estuaries as Nurseries 1
- Juvenile Chum Salmon 3
- Upper and Lower Intertidal Microhabitats 4
- Shoaling Behavior and Microhabitat Use 5
- Hypotheses 7
- Objectives 7

Methods 9
- Tidal Zone and Tidal Series Definitions 9
- Study Sites 9
- Site Descriptions 10
- Field work – 2004 13
- Observational Set-Up – 2004 13
- Field work – 2005 14
- Observational Set-Up – 2005 14
- Behavioral Observations – 2005 15
- Audio Analysis 19
- Video Analysis 19
- Fish Length, Depth Distribution, and Deeper/Shallower 20
- Shoal Cohesiveness Metrics 22
- Statistical Analyses 26

Results 28
- Beach Slope 28
- Fish Length, Depth Distribution, and Deeper/Shallower Metrics 29
- Shoal cohesiveness 41
- Shoaling Strength and Occurrence 50
- Individual Fish Orientations 51
- Shoal Movements 52

Discussion 56
- Density – Take One 57
- Stay Shallow Mandate 57
- Implications of Stay Shallow Mandate 60
- Density – Take Two 62
- Microhabitat Shoaling Behavior 62
- Shoal Cohesiveness and Predation Risk 63
- Shoal Cohesiveness and Foraging 65
- To Shoal or Not, That is the Question 67

“Preferred Prey” Bias? 68
Site Differences 68
Landscape Differences 70
Migration pattern 71
Covariates 72
Summary 72
References 75
Appendix A - Density and Shoal Compactness Relationships 81
Appendix B - Shoal Velocity 83

List of Figures

Figure 1. Location of sites in Hood Canal, WA. 10
Figure 2. Frenchman's Cove aerial photo and beach profile 11
Figure 3. Tabook Point aerial photo and beach profile 11
Figure 4. State Timberlands aerial photo and beach profile 12
Figure 5. Barber Sand aerial photo and beach profile 12
Figure 6. Setting the observational equipment 15
Figure 7. On the ladder during the observation 17
Figure 8. View from top of ladder 18
Figure 9. Layout of the 8-m x 6-m grid and the location of the 0.25-m^2 quadrat 19
Figure 10. Raw image and rubbersheeted image with digitized fish 20
Figure 11. 2005 mean fish length (mm) by site and date. 30
Figure 12. Fish length boxplot for 2005 by julian day 31
Figure 13. Percent of fish for each shoal size class for 2005 32
Figure 14. Mean density, fish per minute, throughout the 2005 sampling season from the 0.25-m^2 quadrat (± 1 SE) 33
Figure 15. Mean juvenile chum salmon densities by site in 2005 34
Figure 16. Mean site fish density (± 1 SE) in 2004 35
Figure 17. Mean densities based in the 0.25-m^2 quadrat during spring tides in 2005 36
Figure 18. Spring tidal series mean densities from 0.25-m^2 quadrat in 2004 37
Figure 19. Depth distribution (cm) of juvenile chum salmon in 2005 38
Figure 20. Total proportion of shoal movements shallower or deeper by row from 8-m x 6-m grid in 2005. 39
Figure 21. Proportion of shoal movements deeper or shallower in upper intertidal from 2005 40
Figure 22. Proportion of shoal movements deeper or shallower in lower intertidal from 2005 41
Figure 23. Mean nearest neighbor distances (± 1 SE) between juvenile chum salmon in 2005 43
Figure 24. Mean neighbor distance for spring tidal series (± 1 SE) in 2004. 44
Figure 25. Fish per image (± 1 SE) from 0.25-m^2 quadrat during spring tides in 2005 45
Figure 26. Fish per image from 0.25-m^2 quadrat during spring tides in 2004 46
Figure 27. Shoal size for shoals between 8 April and 13 May 2005 47
Figure 28. Mean shoal size (± 1 SE) in 2004 48
Figure 29. Mean intertidal circular variance (± 1 SE) in 2005. 49
Figure 30. Percent of fish occurring in a shoaling based on 0.25-m^2 quadrat during spring tides in 2005 51
Figure 31. Individual fish orientations from 0.25-m^2 quadrat in 2005. 52
Figure 32. Relative movements for tidal elevation and tidal month combinations in 2005 53

Figure 33. Relative movement (m) per fish shallower or deeper in 8-m x 6-m grid in 2005 54
Figure 34. Relative movement (m) per fish toward mouth or away from mouth in 8-m x 6-m quadrat in 2005 55
Figure 35. Amount of shallow water available at the upper intertidal and lower intertidal 60
Figure 36. Distribution of tidal levels for Seattle between 1993 and 2001 61

List of Tables

Table 1. 2004 shoal specific metrics recorded in the field. 14
Table 2. 2005 information dictated into digital voice recorder. 16
Table 3. Metrics and how they were generated. 25
Table 4. Shoal cohesiveness metrics, their transformations, and problems with ANOVA assumptions. 27
Table 5. Mean beach slope by site and tidal elevation. 29
Table 6. Summary of shoal cohesiveness metrics 50
Table 7. Distribution of individual fish orientations from 0.25-m^2 quadrat in 2005 52

Acknowledgements

I want to offer my thanks and appreciation to my committee: Charles “Si” Simenstad, Jeff Cordell, Julia Parrish, and Sandy Wyllie-Echeverria. Without their support, encouragement, insight, and ultimately patience I would not have been able to finish what I had begun.

I also want to thank all the people that made this project possible. Thank you to Kurt Fresh for insight in early planning. Also thanks to Miles Logsdon and Jen Burke for help with the GIS work. Without each of you I would not have been able to use GIS for the spatial measurements of fish shoals. Property access was granted by the Western Oyster Company as well as the Hunt and Barber families. I appreciate the knowledge I gained from talking with Larry Telles at the Quilcene National Fish Hatchery as well as his help in securing lodging during the first year of study. Also, I wish to thank Steve Todd and Chris Weller of the Point No Point Treaty Council for their help in developing the project.

I thoroughly enjoyed being a member of the Wetland Ecosystem Team and want to thank everyone I worked with while a part of this lab. Thank you for the friendship and the science I learned. Thank you to Ayesha Gray for her continual support and help during the writing process.

Writing my thesis was a difficult process. Thank you to all friends and family who supported me, but kept graciously reminding me to finish.

Funding was provided by Washington Sea Grant.

Introduction

Estuaries as Nurseries

For many marine fishes and invertebrates, estuaries and the variety of microhabitats within them have long been recognized as nurseries, environments that significantly contribute to their adult populations (Heck & Thoman 1984). The nursery value of estuarine microhabitats to organisms, including economically important species, has led to countless studies, but the highly dynamic nature of estuaries complicates their study. Like all natural systems they experience circadian, seasonal, and annual variation, but unlike other systems they also experience variation through tidal cycles, salinity changes, and water clarity. Location within an estuary can also further complicate any investigation. A microhabitat may appear similar in certain ways, but because of location it may be very different. When put together these factors makes finding any true microhabitat replicates difficult if not impossible. This dynamic nature of estuaries often requires creative ways to assess the nursery value of microhabitats.

A microhabitat is considered a nursery when compared to other microhabitats if it has a higher contribution per unit-area in at least one of four criteria: 1) density; 2) growth; 3) juvenile survival (often through decreased predation); and, 4) recruitment to adult populations (Beck *et al.* 2001). Although there are four criteria to identify nurseries, most studies examining estuarine microhabitats as nurseries have only used density to evaluate their nursery value (Beck *et al.* 2001, Heck *et al.* 2003).

Simply using density can be problematic because density is not always an accurate indicator of microhabitat nursery value. Density shows that organisms are present in a microhabitat, but it says nothing about why they are there and any biotic advantages of that microhabitat. The assumption is a microhabitat with higher density contributes a greater proportion of adults to the population. This may be true at times but it is rarely tested and has been shown at times to be false (Beck *et al.* 2001, Heck *et al.* 2003). Densities in juvenile habitat may be largely influenced by their location relative to adult spawning sites and this higher density may not reflect the quality of the juvenile habitat (Lipcius *et al.* 1997). Studies that also address the other three nursery criteria are more valuable than studies that focus on density alone because they explain why the organisms are found there. Differences in density among microhabitats may reflect a trade-off between opposing biological imperatives. For example, certain microhabitats may have higher foraging value but also increased risk of predation and organisms may thus be forced to relocate to areas with a lower predation risk (Werner *et al.* 1983, Power 1984, McDonald *et al.* 1992). In situations such as these, the higher densities reflect a trade-off because avoiding being eaten usually takes precedence over foraging (Krebs & Davies 1993). In summary, sampling for only density is problematic because it says very little about how the organisms are using the microhabitat.

Habitat use is the way an organism uses the environment to meet its life requirements. It can be thought of in a general, collective sense or broken down into specific acts, or behaviors, such as foraging, mating, or avoiding predators (Block & Brennan 1993). These different life requirements may be met differently in various microhabitats, but they all contribute to the growth, survival, and ultimately reproduction of an organism. An organism's microhabitats can be quite different and each microhabitat may be contributing to a different life requirement. As an organism meets a different life requirement its behavior is likely to change so comparing an organism's behavior among microhabitats is an approach to understanding how organisms use microhabitats. Additionally, microhabitat use may reflect a trade-off because one microhabitat may offer a biological advantage in one life requirement where another microhabitat may offer an advantage in another life requirement. Thus an organism's density and behavior may be used to understand this trade-off. An advantage to using density complemented by behavior in microhabitats is that it can convey how organisms are using them, or in other words meeting their life requirements. This combination will more directly address the other three nursery criteria of growth, juvenile survival, and recruitment to adult populations better using only density.

Juvenile Chum Salmon

Juvenile chum salmon, *Oncorhynchus keta*, is an opportune organism for analyzing *in situ* behavior to reveal how they are using estuarine microhabitats as nurseries. They are easily observable in planar shoals surface-oriented shoals in shallow water nearshore microhabitats. Chum salmon are a species of Pacific salmon, *Oncorhynchus* spp., found from Northern California around the Pacific Rim into Russia and Japan. They also occur in the Artic areas of North America and Asia (Salo 1991). They are found in Hood Canal, a branch of Puget Sound in Washington state, USA, and Hood Canal stocks include summer chum, those where adults return to spawn in the late summer/early fall, and fall chum, those where adults return to spawn in fall. Understanding how juvenile chum use microhabitats is particularly important because the Hood Canal and Strait of Juan de Fuca summer chum Evolutionarily Significant Unit (ESU) is listed as threatened under the Endangered Species Act (Ames *et al*. 2000). Although this study will focus primarily on fall chum, results may be relevant to summer chum.

Of the Pacific salmon juvenile chum salmon are generally considered the second most reliant on estuaries as nurseries (Healey 1982b, Simenstad *et al.* 1982, Thorpe 1994). Shortly after emergence from their natal streams, juvenile chum move into estuarine microhabitats (Salo 1991). These can occur in the natal stream deltas or the nearshore environments between deltas (Mason 1974, Bax 1982, Bax 1983, Simenstad *et al.* 2008). Until juvenile chum reach approximately 55-65 mm FL they typically reside in shallow nearshore waters (Bax 1983). While in the estuaries, chum have high growth rates adding an average of 6% body weight per day (Healey 1979, Healey 1982a, Simenstad *et al.* 1982, Salo 1991). These higher growth rates may alleviate intense size-selective mortality during this estuarine phase (Healey 1982c), allowing faster growing fish to utilize areas unavailable to the smaller fish. There may also be decreased predation while in estuaries (Simenstad *et al.* 1982).

Many studies attempting to resolve the correlation of higher estuarine growth and microhabitat use have used stomach content analysis and at times compared it to prey distribution. While in shallow nearshore microhabitats they primarily feed on relatively few of the prey organisms that are presumably available to them. Small epibenthic crustaceans, particularly the harpacticoid copepod *Harpacticus uniremis,* as well as other harpacticoids like *Tisbe* spp. and *Zaus* spp., gammarid amphipods, and other epibenthic organisms have repeatedly been dominant in chum diets (Kaczynski *et al*. 1973, Schreiner *et al*. 1977, Healey 1979, Sibert 1979, Salo *et al*. 1980, Simenstad *et al*. 1980, Landingham 1982, D'Amours 1987, Macdonald & Chang 1993). These epibenthic organisms are disproportionately distributed among estuarine benthic microhabitats with highest abundances found in complex microhabitats with high organic matter such as diatom microalgae and eelgrass, *Zostera marina* (Cordell 1986, D'Amours 1987, Simenstad *et al*. 1988, Webb 1991a, Webb 1991b, Hosack *et al*. 2006). This concentrated distribution of apparently “preferred” prey organisms has led to the belief that certain microhabitats such as eelgrass are more important for foraging by juvenile chum salmon than other microhabitats (Simenstad *et al.* 1982, Simenstad *et al.* 2008).

Upper and Lower Intertidal Microhabitats

Eelgrass and other complex microhabitats are found in the lower intertidal and subtidal elevations of Pacific Northwest estuaries. In Hood Canal the microhabitats found in the upper intertidal are quite different from the microhabitats found in the lower intertidal. The upper intertidal beach is usually cobble or gravel and has less vegetation than the lower intertidal. It also has a steeper beach gradient than the lower intertidal. The lower intertidal is primarily silt/sand and has more vegetation such as eelgrass, macroalgae, and microalgae. It also has a low-tide terrace which has a less steep slope than the upper intertidal (Downing 1983). Again, the eelgrass of the lower intertidal are considered important for juvenile chum salmon because they often have higher densities of chum salmon prey. Despite these striking differences in microhabitats between the upper intertidal and the lower intertidal and the associated differences in prey resources it is still unclear how juvenile chum are using different estuarine microhabitats irrespective of preferred prey concentrations, and how each microhabitat contributes to growth and survival. Must they feed in areas with the highest density of prey or are they feeding in areas regardless of prey density? Are there other factors that influence chum distribution and thus affect microhabitat use?

Questions remain as to the extent to which prey are transported from the epibenthos where they are produced to another microhabitat where juvenile chum salmon feed on them. It is currently unproven if the chum salmon feed directly off the substrate or if there is another way that they obtain epibenthic crustaceans that are important in their early diets.

Juvenile chum salmon behavior is one tool that can be used to understand how they are using estuarine microhabitats. Because of the disproportionate distribution epibenthic prey the chum may forage differently in different microhabitats. The initial plan of this study was to record individual foraging events or at least when the chum were in a feeding "mode", but I found that the small size of the fish and their small mouths made feeding behavior impossible to accurately classify in the field. It is at times possible to say with certainty that the fish are feeding but it is impossible to say for certain when they are not feeding. Instead, I chose shoaling behavior as a proxy for foraging because predators and foraging are the two keys to understanding shoaling behavior (Pitcher 1986, Pitcher & Parrish 1993).

Shoaling Behavior and Microhabitat Use

If differences in shoaling (see methods for definition of shoal) behavior can be measured then these differences may reflect differences in predation threat or foraging. Generally, increased predation risk results in shoals aggregating closer together, increase in size, and increase in polarity (Magurran & Pitcher 1987, Magurran 1990, Hager & Helfman 1991, Pitcher & Parrish 1993, Pavlov 2000). If shoals become more cohesive it may reflect an increase in predation risk.

Unfortunately, shoaling response to foraging is not as clear as it is for predation risk. In the simplest case, shoals will break down and lose their cohesion as fish turn and dart to capture food (Pavlov 2000). The (nearest neighbor) spacing between fish will increase and become more variable and the shoals will become less polarized. There have been studies that confirm that shoals do lose cohesion as they forage. This can be a decrease in shoal size (Hoare *et al.* 2004) or it can decrease other aspects of shoal cohesion such as near-neighbor distances as well as polarity(Ryer & Olla 1996). A series of mesocosm studies using juvenile chum indicated that shoal cohesion decreased while foraging, where isolated chum were more attracted to shoals of eight fish when the shoal was not feeding compared to when it was feeding (Ryer & Olla 1991). Another mesocosm study showed that for both chum exposed to a predator and not exposed to a predator, shoal cohesion was greatest at pre-feeding and then decreased after feeding for both predator treatments (Ryer & Olla 1996). Based on these studies, it is possible that for juvenile chum salmon lower shoaling cohesiveness reflects increased foraging and anti-predation behavior is not an overriding influence.

If foraging is the primary factor structuring juvenile chum shoals, factors beyond simple prey presence/absence are probably operating. Food distribution may also affect fish shoals. Fish in larger shoals have been shown to find food faster when it is patchy or clumped compared to when the shoal is dispersed (Eggers 1976, Pitcher *et al.* 1982, Street & Hart 1985, Baird *et al.* 1991). Ryer & Olla (1996, 1998) found that there was a tendency for juvenile chum salmon in mesocosms to shoal more cohesively when food was dispersed compared to when it was clumped. Clumped food also increased agonistic behavior as single fish guarded the food source (Ryer & Olla 1996). An arena study with juvenile walleye pollock, *Theragra chalcogramma*, has shown the opposite effect. When food was clumped, pollock had a stronger tendency to shoal compared to when food was dispersed (Ryer & Olla 1995, Ryer & Olla 1998). This tendency was maintained even when predators were introduced. Other studies have also shown that shoals are able to find food more quickly when it is clumped because more searchers find it more quickly, and fish respond to the finder (Eggers 1976, Pitcher *et al.* 1982, Baird *et al.* 1991).

Furthermore, at times being in a larger shoal can facilitate increased foraging. For certain species of fish, larger shoals spend more time foraging (Magurran & Pitcher 1983) or they may have more feeding attempts (Ranta & Kaitala 1991). Fish shoals may also be able to exploit foraging areas that smaller shoals do not (Sackley & Kaufman 1996). Or, under certain conditions, individual fish grow more rapidly when they are part of a shoal (Peuhkuri *et al.* 1995). These results are at least partially explained by the fact that being in a group allows increased protection from predators through increased vigilance or predator defense mechanisms (Magurran & Pitcher 1983).

Hypotheses

This study will test two null hypotheses:

1) Juvenile chum salmon shoaling behavior is the same between the upper intertidal and lower intertidal microhabitats.

2) There is no difference in juvenile chum salmon density between the upper and lower intertidal (specifically eelgrass) microhabitats.

Objectives

I have divided this study into two objectives. The first is: Can a meaningful method be developed to measure *in situ* shoaling and movement behavior of nearshore juvenile chum salmon. The second part of the study was to use the method to complement density to see if there are differences in shoaling behavior among microhabitats and determine if observed differences were meaningful.

To approach the first objective an observational system was developed that used an 8-m x 6-m grid divided into 2-m x 2-m squares. Inside this grid was a 0.25 m^2 quadrat that was video recorded. The second objective was tested by using movements of shoals from the 8-m x 6-m grid and quantitative shoal cohesiveness metrics based on the still images from the video.

Methods

Tidal Zone and Tidal Series Definitions

For this study, the upper intertidal zone was classified as above +0.50 m MLLW and the lower intertidal as +0.50 MLLW and below. The spring tide series was defined as having a daytime low tide that fell below +0.50 MLLW before 16:00.

Study Sites

I conducted this study in Hood Canal, WA, a long glacial fjord that is a branch of Puget Sound. Compared to the main basin of Puget Sound, Hood Canal has less tidelands, coves, and embayments and most of the shoreline is beach (Burns 1985). Puget Sound beaches are typically composed of three parts: the backshore, the beach face, and the low-tide terrace. The backshore is above tidal indundation except during severe storms. The beach face is the upper to middle intertidal and is usually composed of cobble, gravel and coarser sand. The low-tide terrace on average begins at 0.0 MLLW and has finer sediments than the beach face. Additionally, the low-tide terrace has a more gradual slope than the beach face (Downing 1983).

Because most of the tidelands in Hood Canal are privately owned, I required sites that had a combination of access and eelgrass in the lower intertidal. During the summer I scouted potential sites that had variation of the lower intertidal eelgrass patterns. I then gained access to these sites because they were public property (Frenchman’s Cove and State Timberlands), or I gained access from property owners (Tabook Point and Barber Sand). Sites were also chosen that were protected from different wind directions so that sampling could still proceed at alternative sites if one site was exposed on a given sampling day. In 2004 two sites were sampled, Tabook Point (TP) and Frenchman’s Cove (FC). In 2005 these two sites were again sampled but two more sites, State Timberlands (ST) and Barber Sand (BS), to bring the total to four sites: 1) Frenchman’s Cove (FC); 2) Tabook Point (TB); 3) State Timberlands (ST); and 4) Barber Sand (BS)

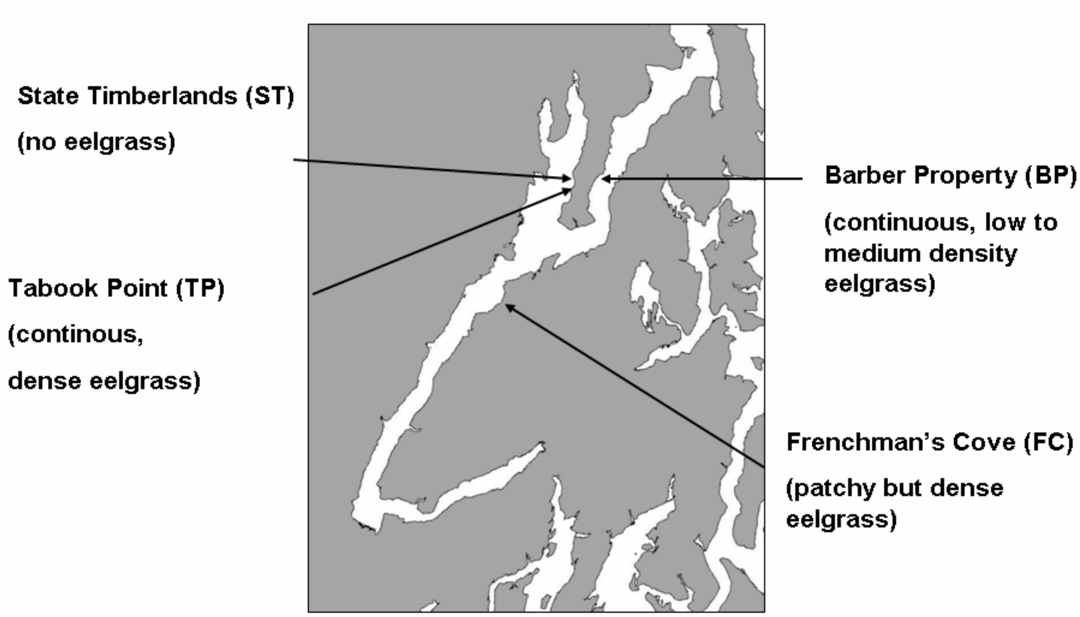


Figure 1. Location of sites in Hood Canal, WA.

Site Descriptions

1. Frenchman's Cove is located at Guillemot Cove Nature Preserve in Kitsap County, WA. It is about 1.8 km south of Hood Point on the east side of the main body of Hood Canal. The upper intertidal is much steeper than the lower intertidal, and there is a pronounced change in slope at the position of the low-tide terrace, about 0.0 m MLLW. The upper intertidal is cobble and gravel and has a large numbers of oysters, Crassostrea gigas, attached to the substrate. Substrate in the lower intertidal is silt/sand, with about half of it covered with medium-sized (≈10-30-m2), dense eelgrass patches. It was sampled both years.

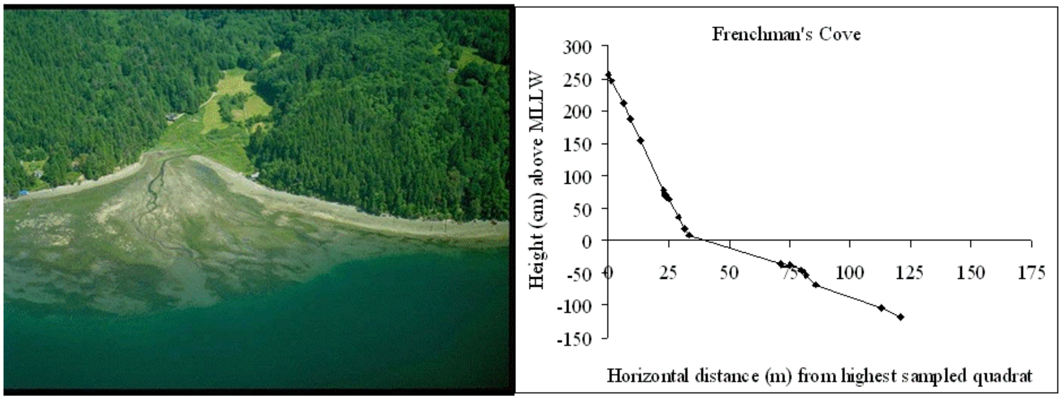


Figure 2. Frenchman's Cove aerial photo and beach profile.
Photo source: http://apps.ecy.wa.gov/shorephotos/scripts/bigphoto.asp?id=KIT0519

2. Tabook Point, is in Dabob Bay on the west side of the Toandos Peninsula south of Tabook Point. The upper intertidal is cobble and gravel and the lower intertidal is a large, continuous and dense eelgrass bed. The intertidal slope is more gradual that then other sites with the transition from gravel/cobble to silt/sand at about +1.0 m MLLW. It was also sampled both years.

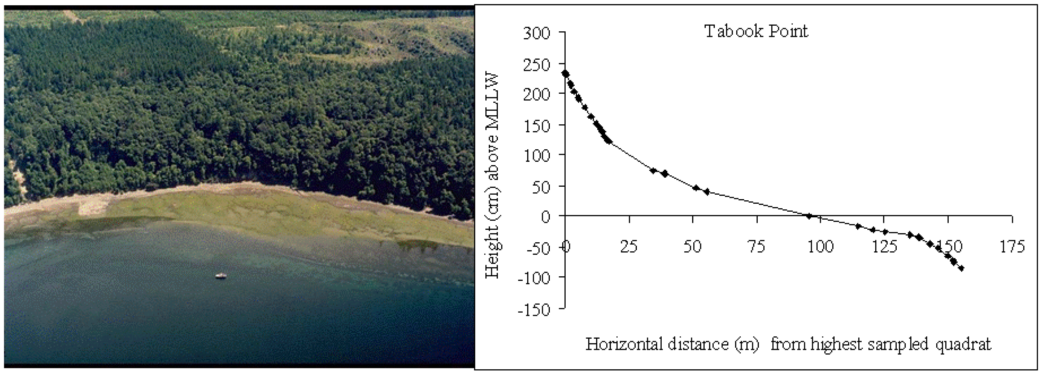


Figure 3. Tabook Point aerial photo and beach profile.
Photo source: http://apps.ecy.wa.gov/shorephotos/scripts/bigphoto.asp?id=JEF0201

3. Approximately 1.5 km north of Tabook Point is the State Timberland site and also in Dabob Bay. This site has very sparse eelgrass in the lower intertidal (at about – 0.5 m MLLW). Most of the lower intertidal substrate is silt/sand and the upper intertidal is cobble and gravel.

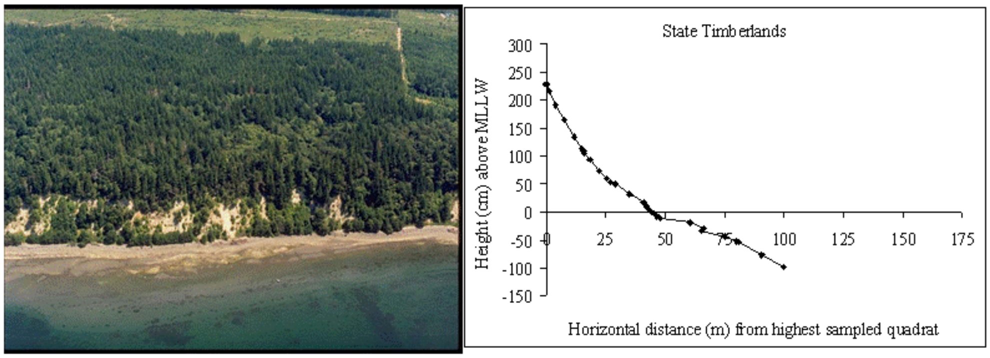


Figure 4. State Timberlands aerial photo and beach profile.
Photo source: http://apps.ecy.wa.gov/shorephotos/scripts/bigphoto.asp?id=JEF0198

4. The fourth site was Barber Sand. It is located at approximately the same latitude as the Tabook Point site but is on the east shore of the Toandos Peninsula on the main arm of Hood Canal. The substrate is gravel in the highest intertidal that quickly transitions to silt/sand in the upper/middle intertidal. This is the only site that had sand instead of gravel/cobble in the upper intertidal. This is also the only site where the upper intertidal had a similar slope to the lower intertidal. In the lower intertidal (about +0.5 m MLLW), there is continuous eelgrass although the eelgrass bed is not as dense as at Tabook Point and Frenchman's Cove.

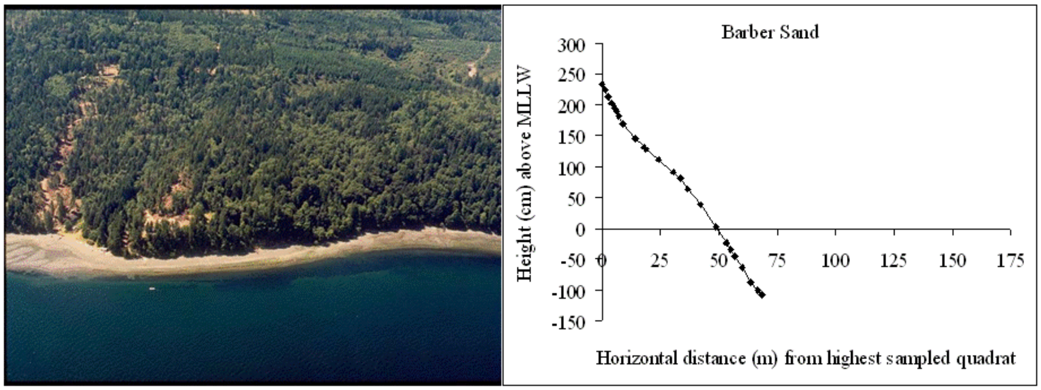


Figure 5. Barber Sand aerial photo and beach profile.
Photo source: http://apps.ecy.wa.gov/shorephotos/scripts/bigphoto.asp?id=JEF0242

Field work – 2004

In 2004, sampling began on 16 April and continued until 25 May.

Observational Set-Up – 2004

The observation method was developed in 2004 so the field work was less extensive than in 2005. There were only two sites compared to four and only a 0.25-m^2 quadrat was used. Sites were only sampled on spring tidal series. Each morning the weather forecast was checked to determine which site was most likely to be protected from the wind. In the morning, a boat was used to access the site. After checking a tide table, a 0.25-m^2 quadrat was placed in the water so that it would be between 0.25 m and 0.50 m deep during the observation. A 3.0 m step ladder was placed 3.5 m shoreward of the quadrat. At the top of the ladder was mounted a tripod with a Sony digital video camera with a polarized filter.

After the quadrat and ladder were set up, I waited 12 minutes until I climbed the ladder. While on the ladder, I waited another 3 minutes before the observation began. The quadrat was filmed with a video camera and shoal specific information was recorded in a data book whenever a shoal entered the quadrat. Each observation lasted 10 minutes.

Table 1. 2004 shoal specific metrics recorded in the field.

Metric	Shoal ID	Shoal Size	Degree of shoaling	Movement Pattern	Direction of Movement
Information recorded in data book	Unique identifier for each shoal	1, 2-10, 11-25, 26-50, 51-100, 101-200, 200+	High, Low, None	Linear, Directed but non linear, No general direction	Towards mouth, Away from mouth

After the observation was over, the same process was repeated. Because of the spring tidal pattern in the Puget Sound, the tide was high in the morning so the first observations occurred in the morning in the upper intertidal. As the tide fell during the day, each observation followed the falling tide down the beach into the lower intertidal zone. Often the wind would increase in velocity around 1400 and the observations would end for the day. But if the wind did not increase velocity then observations would continue up the beach elevations as the tide rose.

Field work - 2005

For 2005 sampling began on 10 March and went through 16 May.

Observational Set-Up – 2005

Because over-water observations can only be useful when the water surface is relatively calm, each morning the marine weather forecast was checked to determine which site would likely be most protected from the wind. The extended forecast was also used to attempt to balance the numbers of times each site was sampled although complete balance of samples was not possible. After a site was chosen, I traveled by boat to access the selected site on the morning high tide. A starting location was haphazardly chosen along the shore and a random number table used to indicate whether to move 0-10 m left or right from the initial chosen spot.

Prior to observations, an 8-m x 6-m rope grid that had been divided into 2-m x 2-m squares was staked out in the water so that the middle row would be located between 0.25 m and 0.50 m deep during the observation period. The 0.25-m^2 quadrat was leveled and staked to the bottom in one of the two middle 2-m x 2-m squares. A 3.0-m step ladder was set up 1.0 m shoreward from the edge of the 8-m x 6-m gird, 3.5 m from the smaller quadrat. A tripod was mounted on the ladder and the digital video camera with a polarized filter was attached. After waiting ten minutes, I climbed the ladder and waited three minutes before observation began.

Figure 6. Setting the observational equipment. The equipment could be set on a rising or falling tide. In this case it is being set on the rising tide. The observation would begin when the grid and quadrat were covered by 0.25 m to 0.50 m of water. The 0.25-m^2 quadrat was placed in the middle row of the grid.

Behavioral Observations - 2005

Each observation lasted 15 minutes. For 2005, data was recorded in two ways. The video camera was once again focused on the 0.25-m^2 quadrat to capture video of the shoals, but all the shoal specific information was dictated into a digital voice recorder instead of recording it in a data book. Whenever a shoal of juvenile chum salmon entered the larger grid, its cell specific location was immediately dictated into the voice recorder. Location was specified by coding the 2-m x 2-m grid (Fig. 9). The categorical size (number of fish) of the shoal (1, 2-10, 11-25, 26-50, 51-100, 101-200, 200+) as well other shoal specific information (e.g., feeding, shoaling or not shoaling) were also dictated (Table 2). Movements within the 8-m x 6-m grid were recorded by dictating into the voice recorder when a shoal transferred from one cell into another. For the analysis of the data, the location of the shoal was assumed to be in the middle of each 2-m x 2-m square. Whenever a shoal passed over the 0.25-m^2 quadrat this was noted on the voice dictation so the shoal specific information could be correlated with the video.

Table 2. 2005 information dictated into digital voice recorder.

Metric	New shoal	Shoal size	Shoaling?	Movement Pattern
Information dictated into digital voice recorder	Yes or no	1, 2-10, 11-25, 26-50, 51-100, 101-200, 200+	Yes or no	Movement from what grid cell into what grid cell and when they moved from cell to cell

After the 15 minute observation was over, I conducted environmental measurements, including: (1) depth of 0.25-m^2 quadrat; (2) light level; (3) water temperature; (4) salinity; (5) beach slope; and (6) wind speed. Light level and wind speed were measured with a Mini Environmental Quality Meter - SPER Scientific 850070 (Anemometer, %RH, Temp, Lux). Salinity and water temperature were measured with a YSI 30. The slope of the beach was measured by laying a 2 m PVC pipe perpendicular to the shore. The water depth was measured at both ends of the pipe and the difference between the two depths and the length of the PVC pipe was used to calculate the slope of the beach. Also, a small lemon was floated through the camera's field of view and recorded to be used to estimate surface current speed based on analysis of the video record.

Figure 7. On the ladder during the observation. As fish entered the 8-m x 6-m grid the information was dictated into a digital voice recorder.

Figure 8. View from top of ladder. Video camera is focused on 0.25-m^2 quadrat. 2-m x 2-m squares are part of larger 8-m x 6-m grid.

Depending on the tidal stage, after an observation period the equipment was moved up or down the beach face and the next observation was repeated as above. Ideally the observations would occur in the upper intertidal zone and then follow the dropping tide into the lower intertidal, and ultimately track the rising tide. However, afternoon observations were typically not possible due to afternoon winds.

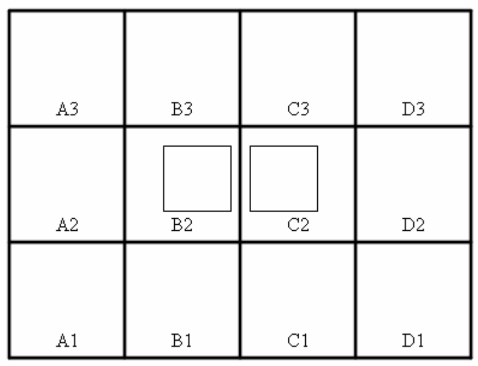


Figure 9. Layout of the 8-m x 6-m grid and the location of the 0.25-m^2 quadrat. The 0.25-m^2 quadrat was placed in either B2 or C2. Row 1 is the nearest to shore.

Audio Analysis

The audio dictation was transcribed so that each shoal's movement was recorded as a time spent in each square and into which square they moved. For example, a movement from cell B2 to C2 would be recorded as a movement right. Left and right movements were adjusted in the lab to indicate movement toward the mouth of Hood Canal or away from it. Movements deeper or shallower and diagonal movements were recorded as well. The time of these movements was also recorded. Velocity, movement pattern, and average shoal depth were calculated from this transcribed data. These calculations were based on when they first entered the grid or were first noticed to when they left the grid. The total distance moved by the shoal was calculated from this data.

Video Analysis

The videos of the 0.25-m^2 quadrat were reviewed in the lab using Adobe Premiere. Whenever a shoal entered the 0.25-m^2 quadrat, the number of fish entering the quadrat was recorded and the shoal specific information from the dictation was correlated with it. Additionally, the time code from the video detailing when they were in the quadrat was recorded.

For spatial measurements of the shoal from the 0.25-m^2 quadrat, I randomly selected a single frame from the video for each shoal and converted it to a still image by using the video software to export it as a TIF image. This still image was then "rubbersheeted" using ERDAS Imagine 8.6 software similarly to how oblique aerial photographs are rubbersheeted. The known dimensions of the corners of the 0.25-m^2 quadrat were used as control points. This corrected image was then imported into ArcGIS 9.1 and each fish was digitized by hand (Fig. 10). The length of the fish were digitized with a line and the heads of each fish were delineated with a point. In 2004 not every shoal was analyzed with GIS for 2004 so shoals were first randomly selected then the frames were randomly selected from these shoals. All 2005 shoals were spatially analyzed.

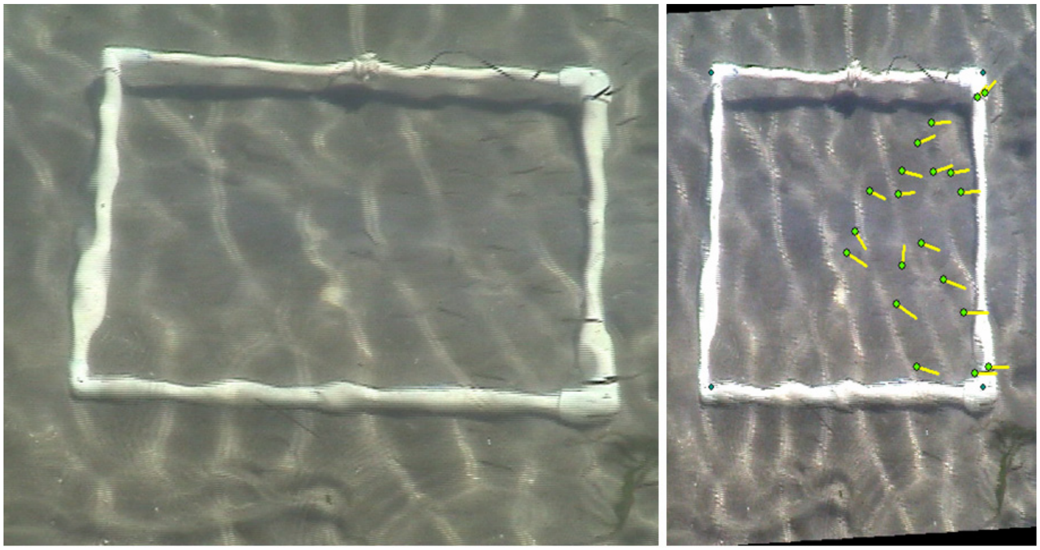


Figure 10. Raw image and rubbersheeted image with digitized fish. The rubbersheeted image was used to calculate spatial measurements of the shoal.

Fish Length, Depth Distribution, and Deeper/Shallower

Fish length was calculated using an ArcGIS model that calculated the length of the digitized fish from the rubbersheeted images captured from the video.

<u>Percent of fish in each shoal size</u>

The percent of fish occurring in each size class was taken from data from both the quadrat and the grid. To get the total number of fish, the number of shoals in each shoal size class was multiplied by the average size of the shoal class (e.g. if there were 10 shoals of size 11-25 then the total number of fish in that size class would be 180 fish). After the number of fish in each size class was found the proportion of total fish in each size class was calculated. The dates used are from 13 March 2005 to 13 May 2005 and include only spring tides.

Fish density

Fish density was calculated by counting the number of fish that entered the 0.25-m^2 quadrat and dividing by the minutes of the video clip for a density metric of number of fish per 0.25-m^2 per minute. This unusual density metric was used because it is not a direct measurement of how many fish are in a specified area at any given one time, but is a measure of how many fish entered an area (0.25 m^2) in an amount of time (usually 15 minutes). Additionally, dividing by the time allowed different observations to be compared that had different durations. Video clips in 2004 were 10 minutes long and they were 15 minutes long in 2005. Fish density will be reported as "fish per minute," but it is actually fish per minute that entered the 0.25-m^2 quadrat.

Fish depth distribution

Average shoal depths were calculated from audio dictation of shoal movements through the 8-m x 6-m grid. Depths of each cell in the gird were calculated from the depth of the 0.25-m^2 quadrat at the end of the observation and the slope of the beach. Based on these two measurements, the depth of each grid cell could be calculated. Then based on which cells the shoal occupied the average shoal depth was calculated. If the shoal occurred in multiple cells, depths of occupied cells were averaged for that shoal. The number of fish in each shoal was used to calculate the overall depth distribution for fish. Because the 8-m x 6-m quadrat did not extend into water deeper than about 1.0 m (often the case for lower tidal elevations), apparent depth distribution may have been underestimated in some cases. For the depth distribution analysis, I used both spring and neap tidal series for the dates between 9 April 2005 and 13 May 2005.

Shoal movements shallower or deeper

This represents the proportion of movements by shoals, not the proportion of movements of fish. Shoal movements shallower or deeper were based on the audio transcription of shoal movements through the 8-m x 6-m grid. They included spring and neap tidal series for the dates between 9 April 2005 and 13 May 2005. The total movements any direction out of each 2-m x 2-m cell were tallied by row. Then the total number of shoal movements either shallower or deeper (if a movement was a diagonal, e.g. shallower and to the right, that movement was included in the total for movements shallower or deeper) were tallied. These total movements shallower or deeper in each row were then divided by the total shoal movements within that row to get the proportion of movements shallower or deeper by row. These row by row movements were then broken down by total, upper intertidal, and lower intertidal.

Shoal Cohesiveness Metrics

There is frequent confusion between the terms shoal and school. For this paper, a fish shoal is any social aggregation of fish. The term school will not be used, but is most commonly defined as a type of shoal characterized by coordinated movement, similar between fish spacing, and high polarity (Pitcher 1983, Pitcher & Parrish 1993). I use the concept of shoal cohesiveness, in which shoal cohesiveness will be reflected in smaller near neighbor distances as well as shoal polarity (all fish pointing the same direction). If shoal cohesiveness increases it becomes more “school-like.”

Mean nearest neighbor distance

Near neighbor distances were based on rubbersheeted images captured from the video of the 0.25-m^2 quadrat. They were calculated using an ArcGIS model that found the mid-points of each fish and then calculated near neighbor distances using these mid-points. The mean nearest neighbor distance for each shoal was calculated by averaging the nearest neighbor distance for all members of the shoal in each image.

Fish per image

The number of fish in each randomly selected frame can also be used to assess how closely fish are associated in a shoal. This metric not only reflects within shoal spacing of fish but also reflects shoal size. One advantage the fish per image metric has over the nearest neighbor index is that images with a single fish can be included in the analysis because randomly selected frames with only a single fish can be used. Data were log (x) transformed.

Shoal size

For shoal size, the mean size of the shoal size class (e.g., 2-10 would be 6) was used for every shoal that entered the quadrat or grid. If the fish were not in shoals then shoal size for those fish was not used for these calculations. Again, the same dates for the other upper intertidal vs. lower intertidal comparisons were used. In this comparison the Barber Sand was able to be included because fish did enter the 8-m x 6-m quadrat at the upper intertidal elevations.

Shoal polarity

I used circular variance to test for shoal polarity. This is a metric that ranges from 0 to 1. Scores closer to 0 indicate more uniform orientation whereas scores closer to 1 indicate dispersion of orientations (Mardia 2000). An ArcGIS model was also used to calculate orientations on digitized fish from the rubbersheeted 0.25-m^2 quadrat image. Shoal circular variance was then calculated for each shoal that had more than one fish in the still image.

Shoaling strength and occurrence

Not all fish were part of shoal. In the field whenever a fish entered either the grid or the quadrat a subjective determination was made if the fish were part of a shoal. Fish were not considered part of a shoal if there was very little to no coordinated movement between fish. A single fish was not considered to be in a shoal. The proportion of fish occurring in a shoal was calculated by taking the total number of fish that entered the 0.25-m^2 quadrat as part of a shoal, and then dividing by the total number of fish that entered the quadrat. Again, no metric could be generated for Barber Sand because no fish entered the 0.25-m^2 quadrat. Only spring tides from 2005 were analyzed.

Individual fish orientation distribution

Individual fish orientations were calculated from the digitized fish using the ArcGIS model that was used to generate orientations for the shoal polarity. Because different sites were located on opposite sides of Hood Canal their orientations from the ArcGIS had to be standardized. Individual fish orientations were standardized to have the following meaning: 0º, parallel to the shore and pointing toward the mouth of Hood Canal; 90º, perpendicular to the shore with the head pointing away from shore; 180º, parallel to shore and pointing away from the mouth of Hood Canal; 270º, perpendicular to the shore and pointing toward deeper water. Fish were placed in these categories if they were oriented within 45º of these angles. For example, a fish with an orientation of 347º was considered oriented toward the mouth of Hood Canal.

Relative movement per fish

The audio transcription was also used to calculate the relative distance the shoal moved shallower vs. deeper and toward Hood Canal's mouth vs. away from during the time they were observed in the quadrat. These relative distances were then multiplied by the shoal size to arrive at total relative meters moved for fish in that shoal. This number could then be summed for any category of interest and divided by the total number of fish in that category to arrive at an average relative distance moved per fish. Spring and neap tidal series were analyzed for the dates between 9 April 2005 and 13 May 2005.

Table 3. Metrics and how they were generated.

Metric	Year	From	Based on	How it was generated
Fish length	2005	0.25-m^2 quadrat	Rubbersheeted image from video	GIS analysis of digitized fish from video still image
Percent of Fish in Each Shoal Size	2005	0.25-m^2 quadrat	Video and audio transcription	Based on the total number of fish that entered 0.25 m^2 quadrat and what size shoal they were in.
Fish density	2004, 2005	0.25-m^2 quadrat	Video	Number of fish that entered quadrat on video
Fish depth distribution	2005	8-m x 6-m grid	Audio transcription	Mean depth of the shoal times the number of fish in shoal
Shoal movements – shallower or deeper	2005	8-m x 6-m grid	Audio transcription	Proportion of total movements of shoals in each row shallower or deeper
Mean nearest neighbor	2004, 2005	0.25-m^2 quadrat	Rubbersheeted image from video	ArcGIS model to calculate nearest neighbor distances from midpoint of fish
Fish per image	2004, 2005	0.25-m^2 quadrat	Rubbersheeted image from video	The number of fish that occurred in a single randomly selected image.
Shoal size	2004, 2005	Both quadrat and grid	Shoal size was estimated in field	The shoal size was the average shoal size for each shoal size class (e.g. 2-10 would be 6)
Shoal polarity	2005	0.25-m^2 quadrat	Rubbersheeted image from video	ArcGIS model to calculute individual fish orientation then circular variance used to figure polarity for the shoal
Shoaling Strength and Occurrence	2005	0.25-m^2 quadrat	Video and field dictation	In the field it was dictated if a fish was in a shoal or not for all fish that entered the quadrat. The number of fish not in shoals was divided by the total number of fish that entered the quadrat
Individual fish orientation distribution	2005	0.25-m^2 quadrat	Rubbersheeted image from video	ArcGIS model to calculate individual fish orientation. Mean angle was used to for the mean orientation of all fish.
Relative movements per fish while in grid	2005	8-m x 6-m grid	Audio transcription	Based on when fish first entered the grid (or were noticed) to when they left the grid their relative movement was calculated based on the in field audio dictation.

Statistical Analyses

Data was analyzed using R version 2.3.1. Type II ANOVAs were performed using the *Companion to Applied Regression (car)* package. Circular data was analyzed with R using the *Circular Statistics (circular)* package.

The four sites used in 2005 are BS, FC, TP, and ST although BS was not included in an ANOVA of any shoal cohesiveness metric based on fish in the video of the 0.25-m^2 quadrat. Fish were never captured on the video of the BS upper intertidal and because of this the BS upper intertidal was not able to be used for any comparisons between upper and lower intertidal. For shoal metrics based on the 0.25-m^2 quadrat (with the exception of the fish per image), images containing a single fish were not used in the ANOVA analysis. Data presented for 2005 upper interidal vs. lower intertidal shoal cohesiveness comparisons included only the spring tidal series from 8 April 2005 to 13 May 2005. For the 2004 data, upper vs. lower intertidal comparisons include spring tide data from 21 April 2004 to 9 May 2004 at only FC and TP. This data represents the analysis from the peak of the chum migration as well as when complete coverage of all sites occurred.

It was not possible to obtain a balanced sample of the number of shoals between each treatment combination because the number of shoals entering the grid or quadrat were uncontrolled. Type II ANOVAs were used to account for this lack of balance. Data was transformed (either log(x+1) or log(x)) to come as close as possible to meeting the assumptions. Although some of the data did not meet the assumptions of normal distribution or constant variance, ANOVAs were used because an analagous two-factor nonparametric test is lacking (Zar 1999).

Table 4. Shoal cohesiveness metrics, their transformations, and problems with ANOVA assumptions.

Metric	**Type of transformation**	**Assumptions met?**
2005 mean nearest neighbor	log (x + 1)	Maybe constant variance
2004 mean nearest neighbor	log (x)	
2005 fish per image	log (x)	Maybe heteroscedasity
2004 fish per image	log (x)	No - heteroscedasity
2005 shoal size	log (x + 1)	
2004 shoal size	log (x + 1)	No - heteroscedasity
2005 shoal circular variance	log (x)	

Results

Fish densities were significantly different between sites, but tidal elevation was not a significant factor. There was significant site by tidal elevation interaction. Some sites had higher densities in the upper intertidal and some had lower densities in the lower intertidal.

Data from the depth distribution and the movements shallower or deeper indicate that in the upper intertidal fish are more likely to be closer to the shore than in the lower intertidal.

In this study shoal cohesiveness was used to compare behavior between the upper intertidal and the lower intertidal. Most of the metrics to do this were spatial measurements of digitized fish in a shoal using ArcGIS. These measurements were based on still images taken from the video of the 0.25 m^2 quadrat. Between the two years, 4 of these 7 metrics indicated that shoal cohesiveness was higher in the lower intertidal than in the upper intertidal. The only shoal cohesiveness metric not based on the 0.25 m^2 quadrat was the shoaling or not shoaling field assessment. This metric showed that only Tabook Point had a large proportion of the fish not occurring in shoals.

Beach Slope

With the exception of Barber Sand, the sites had beach slopes that were between 2.3 and 2.7 times steeper in the upper intertidal than in the lower intertidal.

Table 5. Mean beach slope by site and tidal elevation.

Site	Tidal Elevation	Mean beach slope (degrees)
Frenchman's Cove	Upper	3.9
	Lower	1.7
State Timberlands	Upper	3.8
	Lower	1.6
Tabook Point	Upper	3.5
	Lower	1.3
Barber Sand	Upper	3.2
	Lower	3.1

Fish Length, Depth Distribution, and Deeper/Shallower Metrics

Mean fish lengths generally increased throughout the 2005 field season but there was variation from sites and time. The fist day had a mean length of 38.3 mm and the last day a mean length of 43.8 mm. The highest mean length for any day was 57.1 mm on 25 April 2005 at Tabook Point. The lowest mean length was 36.9 mm and occurred on 20 April 2005 at Barber Sand (Fig. 11).

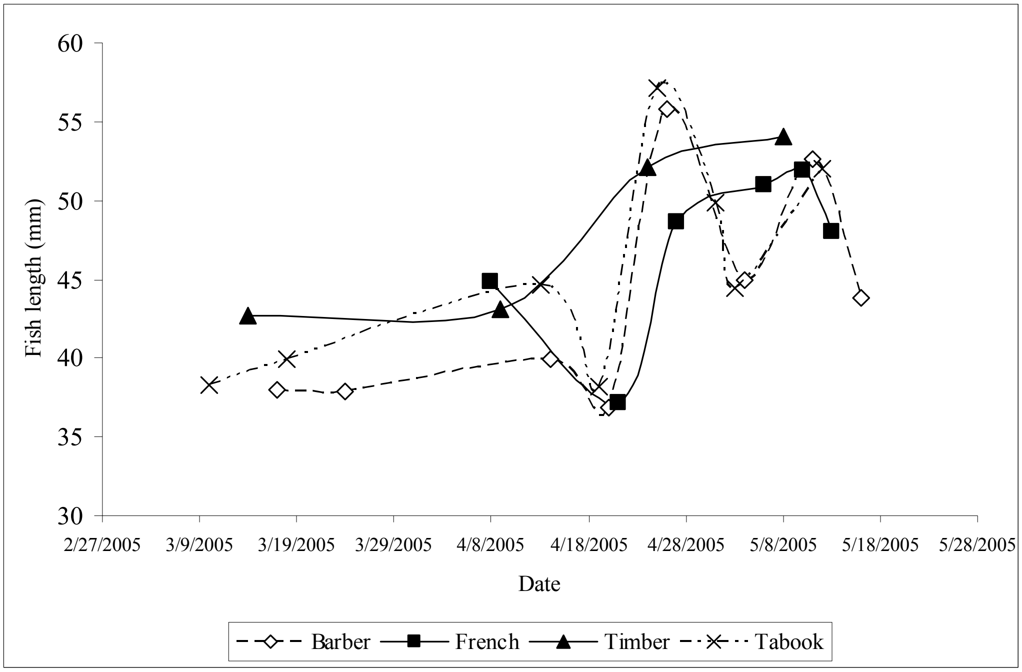


Figure 11. 2005 mean fish length (mm) by site and date.

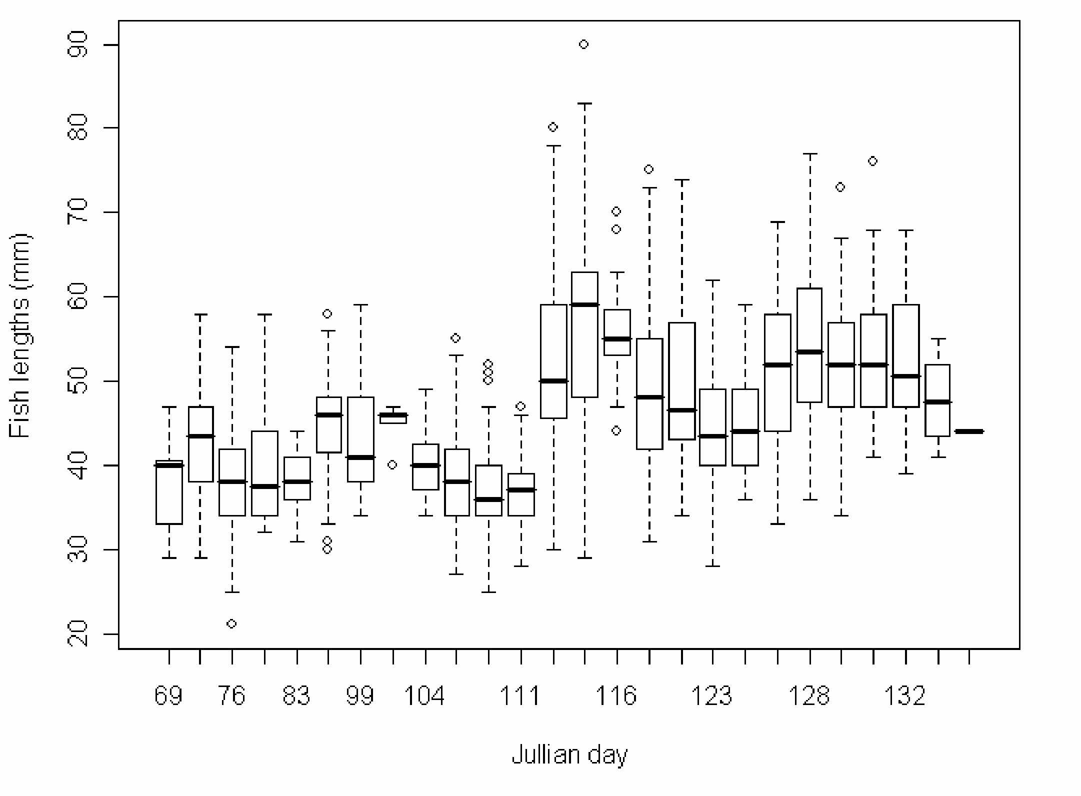


Figure 12. Fish length boxplot for 2005 by julian day. Taken from fish occurring in $0.25\ m^2$ quadrat and measured by ArcGIS.

Percent of Fish in Each Shoal Size

For the fish observed in 2005, 45.5% of them were in shoals of 25 fish or less, and 83.2% were in shoals of 50 fish or smaller (Fig. 13). Breaking it down by site the percent of fish in shoals of 25 or fewer are: 1) Frenchman's Cove – 49.5%, 2) State Timberlands – 39.1%, 3) Tabook Point – 65.4%, and 4) Barber Sand – 27.3%.

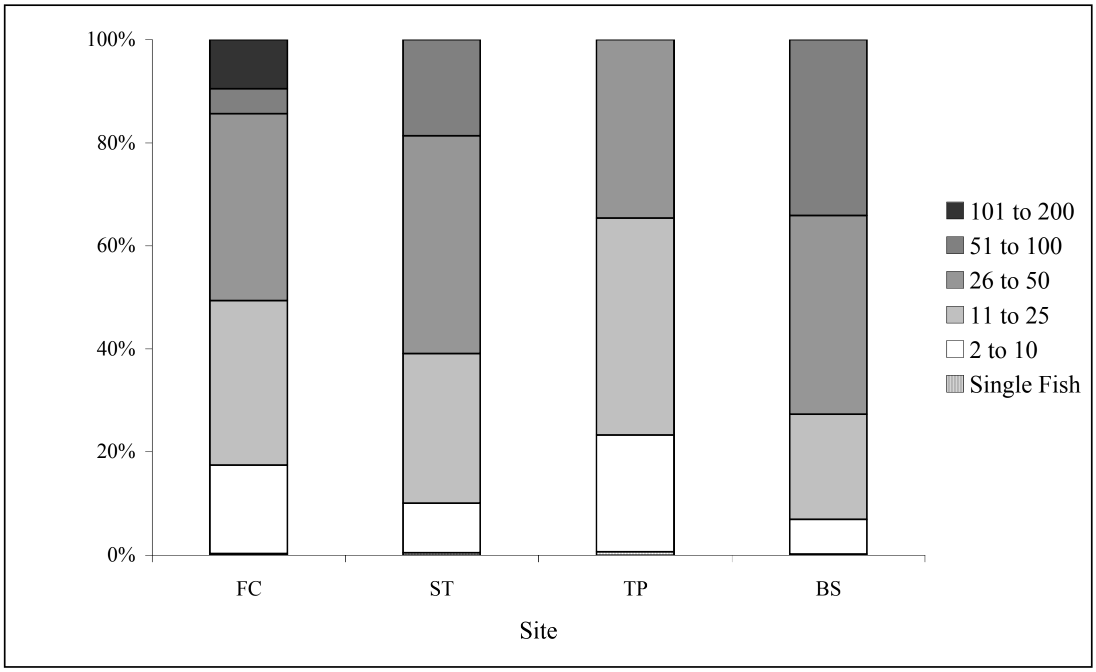


Figure 13. Percent of fish for each shoal size class for 2005. Based on number of fish within shoals that entered the 8-m x 6-m grid or 0.25 m^2 quadrat.

Overall Density - 2005

Juvenile chum salmon densities fluctuated in 2005 (Fig. 14). Much of this variability was associated with the different sampling sites (Fig. 15). Although it may appear that density rises and falls drastically throughout the season, this is primarily driven by sampling different sites on different days, and these sites have lower overall densities than other sites. By mid-May, juvenile chum salmon were not found in the shallowest available water in my study areas.

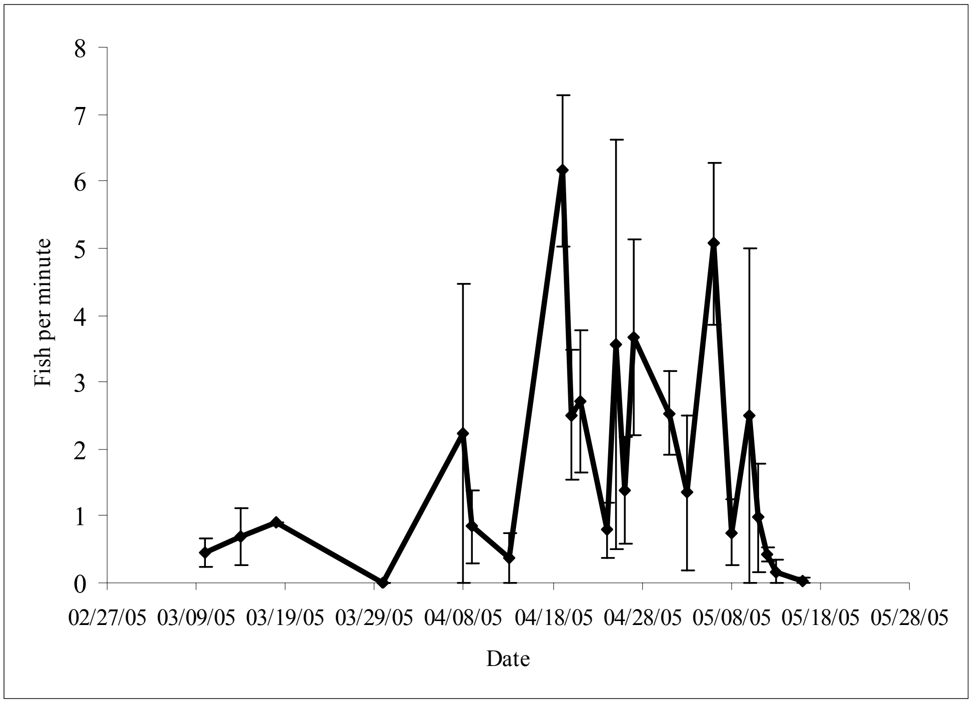


Figure 14. Mean density, fish per minute, throughout the 2005 sampling season from the 0.25-m^2 quadrat (± 1 SE). All tidal elevations are combined for the given day and this includes spring and neap tidal series. Means are based on these sequential n = 6, 11, 1, 9, 2, 6, 2, 6, 7, 6, 9, 6, 6, 7, 4, 4, 2, 4, 2, 7, 7, 2, 2.

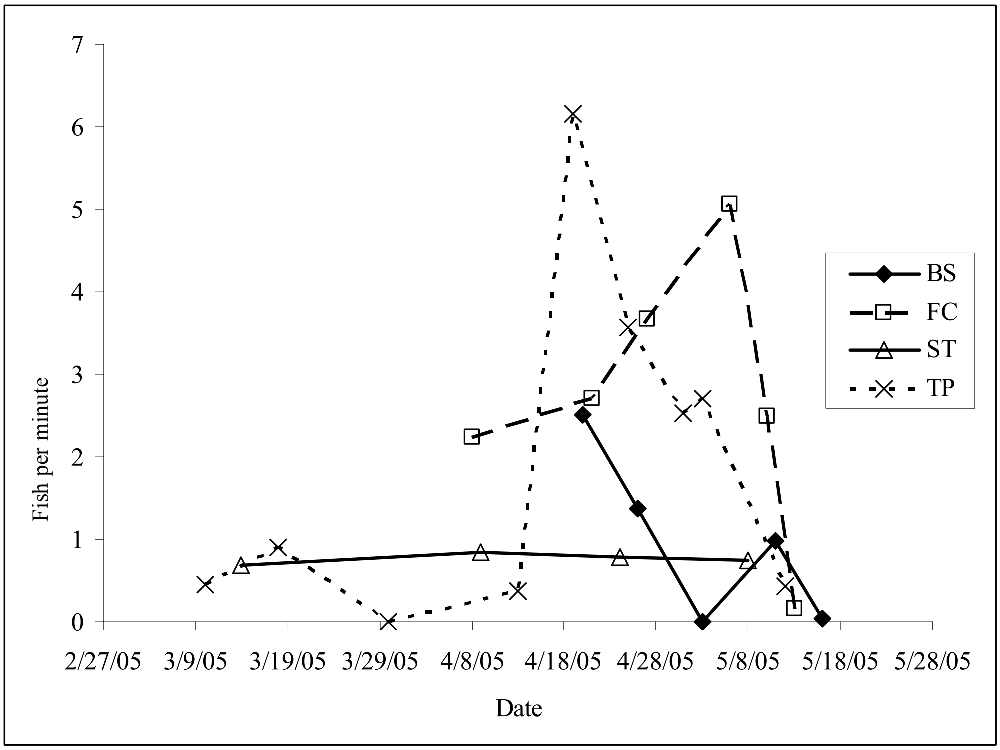


Figure 15. Mean juvenile chum salmon densities by site in 2005. Error bars not included for clarity of graph. Includes both spring and neap tidal series. Upper intertidal and lower intertidal densities have been combined for each date.

Overall density – 2004

The 2004 overall density (Fig. 16) is misleading. The 24 April 2004 and 6 May 2004 sampling dates at Frenchman's Cove were only sampled at the low tide whereas the other FC dates included at least one upper and at least one lower intertidal observation. Because of slope differences, it is not surprising that the density dropped when only the lower intertidal zone was sampled. Like the 2005 data, the fish were not present in the sampling area after mid-May.

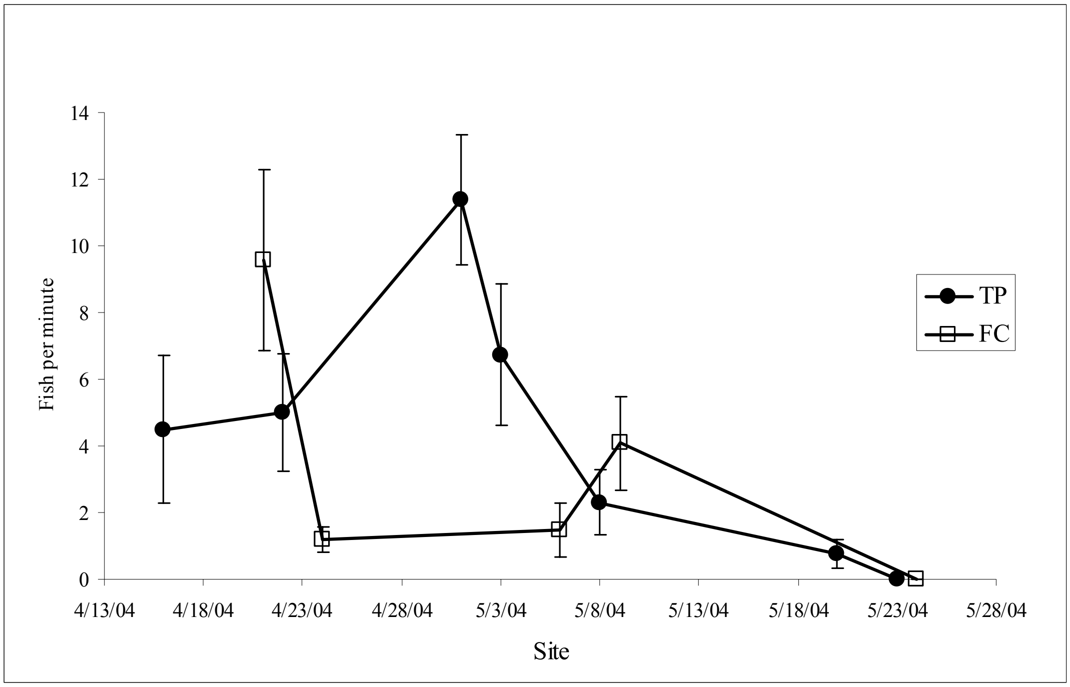


Figure 16. Mean site fish density (± 1 SE) in 2004. Average density for each date. Error bars are standard error. Averages include all video clip density for each date. For each site the sequential date's n is based on: FC - 11, 6, 6, 7, 5; TP - 2, 13, 6, 12, 9, 11, 5

<u>2005 Site and Tidal Elevation Density</u>

In 2005, site significantly affected density ($p < 0.032$) but tidal elevation did not ($p > 0.46$) (Fig. 16). Site by tidal level interaction was significant, primarily driven by higher upper intertidal densities at Frenchman's Cove and a slight increase at State Timberlands, whereas Barber Sand and Tabook Point had higher lower intertidal densities (with no fish observed in the upper intertidal).

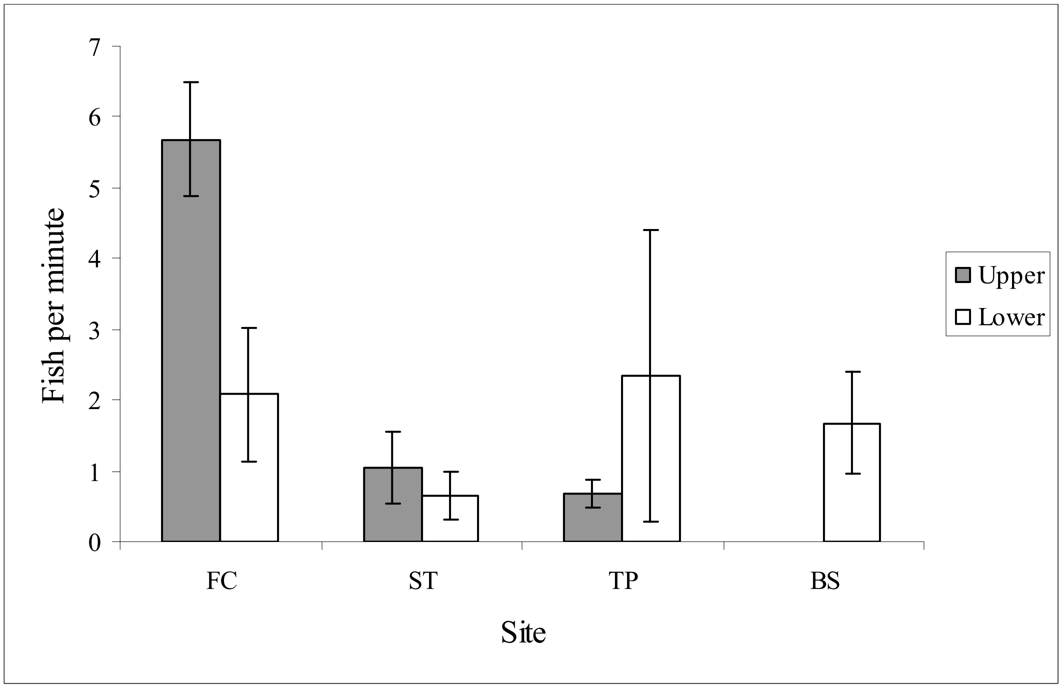


Figure 17. Mean densities based in the 0.25-m^2 quadrat during spring tides in 2005. Number of video clips analyzed: FC - High (4), Low (11); ST - High (6), Low (12); TP - High (6), Low (9); BS - High (4), Low (9)

2004 site and tidal elevation density

In 2004, neither of the main effects, site and tidal elevation, were significnt ($p>0.77$ and $p>0.21$ respectively) but there was a highly significant interaction ($p<0.0001$) (Fig. 17).

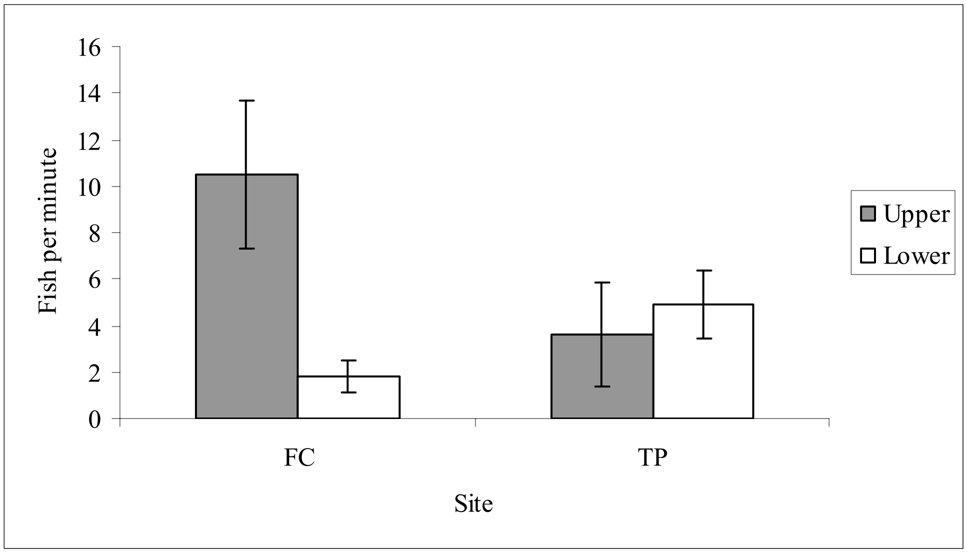


Figure 18. Spring tidal series mean densities from 0.25-m^2 quadrat in 2004. These are two of the sites that were repeated for 2005 sampling. Number of video clips analyzed: FC – High (11), Low (19); TP – High (16), Low (18)

To test if there were density differences (in fish per minute) between spring tidal series and neap tidal series, 2005 data from only the upper intertidal was used (because during neap tide series, the water level did not recede into the lower intertidal). Site effects and interaction were significant ($p < 0.0014$ and $p < 0.004$, respectively) but the tidal series effect was not ($p = 0.067$).

Depth Distribution

The median depth of the 0.25-m^2 quadrat in the upper intertidal zone was 47 cm (Fig. 19). Although the median depth in the upper intertidal zone was 47 cm, 72.6% of the fish were 47 cm or shallower and 97.0% of the fish were 75 cm or shallower. For the lower intertidal zone the median quadrat depth was 45.5 cm and 54.6% of the fish were shallower than this. 93.4% of the fish in the lower intertidal zone were 75 cm or shallower.

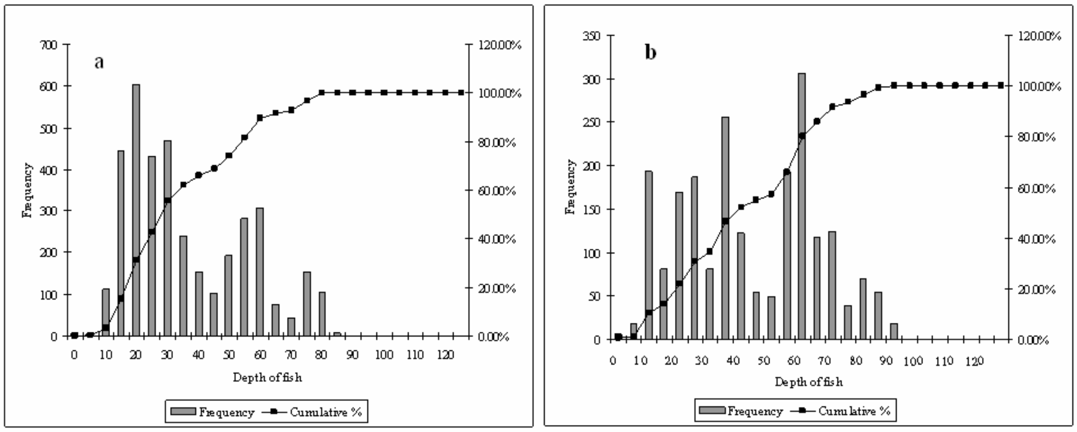


Figure 19. Depth distribution (cm) of juvenile chum salmon in 2005. The upper intertidal zone (a) includes neap tidal series as well as spring tidal series. The lower intertidal zone (b) does not include any neap tidal series. Based on 8-m x 6-m grid. Includes fish from 9 April 2005 to 13 May 2005.

Row Movements Shallower or Deeper

For all shoal movements, including the neap tides in the 8-m x 6-m grid between 8 April and 13 May 2005, shoals moved deeper 33.6% of the time in row 1 (Fig. 20). In row 2, shoals moved deeper 20.2% of the time, and in row 3, the deepest row they moved deeper only 13.0% of the time. In row 1, shoals moved shallower 11.4% of the time, in row 2 they moved shallower 9.6% of the time, and in row 3 they moved shallower 24.3% of the time. In row 3, shoals were 1.87 times more likely to move shallower than they were to move deeper and out of the quadrat.

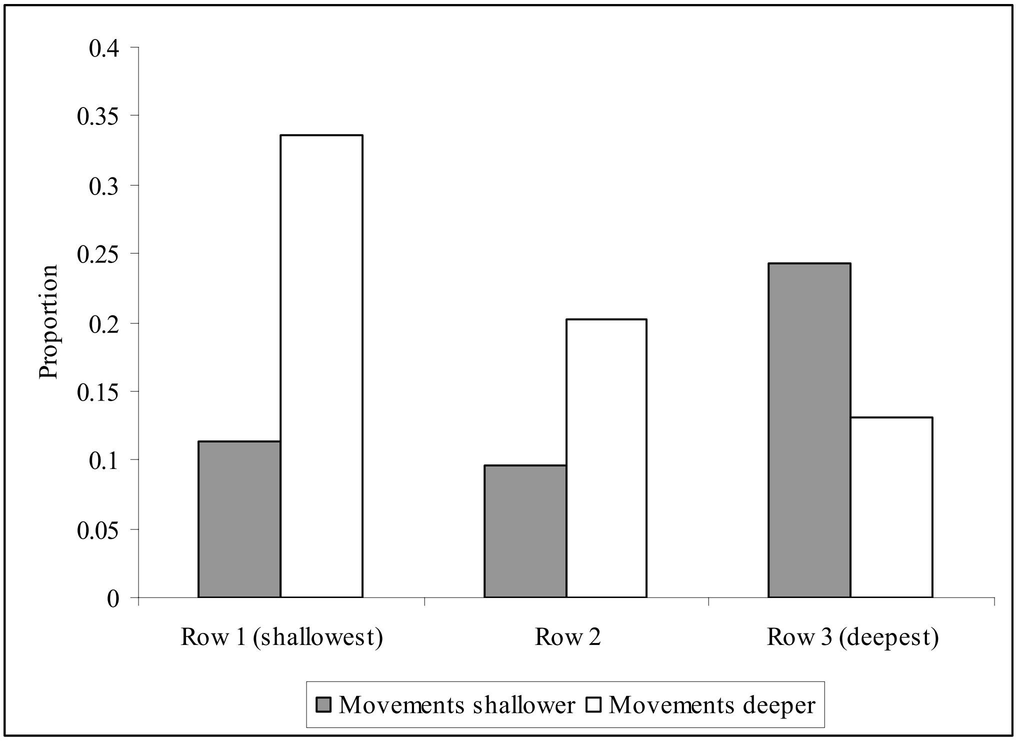


Figure 20. Total proportion of shoal movements shallower or deeper by row from 8-m x 6-m grid in 2005.

Because there is such a pronounced difference in beach slope between the upper and lower intertidal, row by row movements were analyzed for each tidal elevation. For the upper intertidal when the 4 sites were pooled, 19.2% of movements from rows 2 and 3 moved shallower whereas only 15.9% were deeper. Movements in only row 3 were deeper 9.8% of the time and shallower 33.1% (Fig. 21). For the lower intertidal pooled sites, 14.1% of the movements from rows 2 or 3 were shallower and 20.2% were deeper. For only row 3 movements deeper happened 16.1% and movements shallow also happened 16.1% of the time (Fig 22).

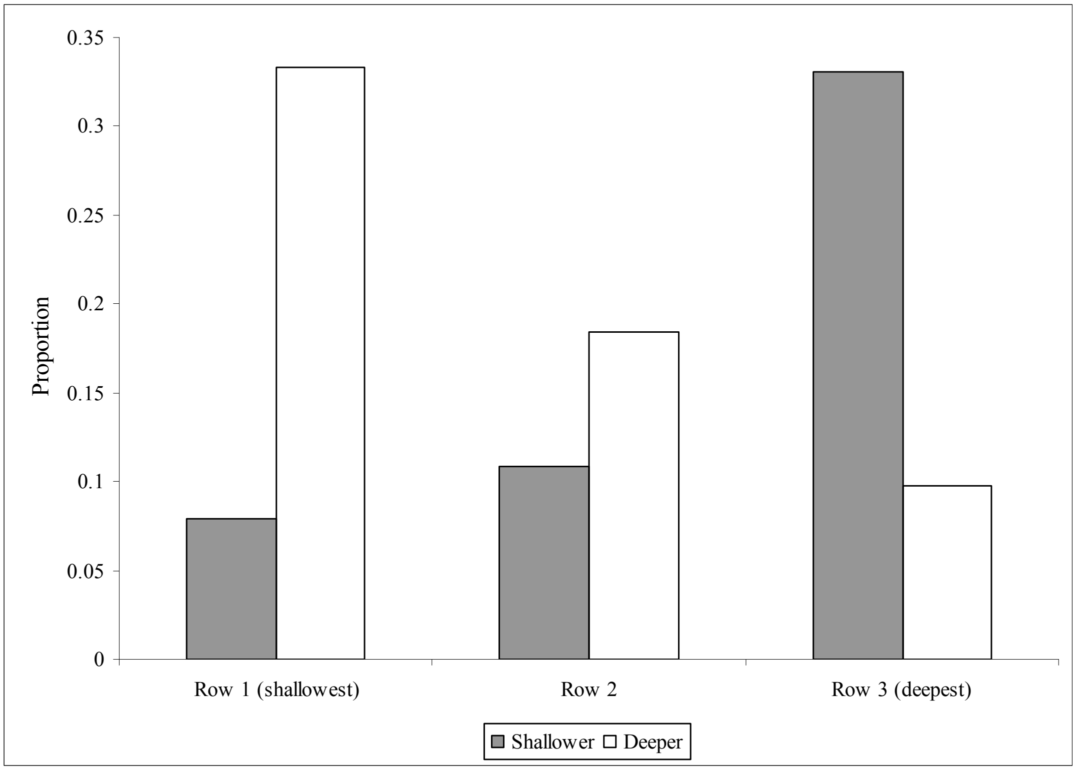


Figure 21. Proportion of shoal movements deeper or shallower in upper intertidal from 2005. Based on shoal movements from 8-m x 6-m grid.

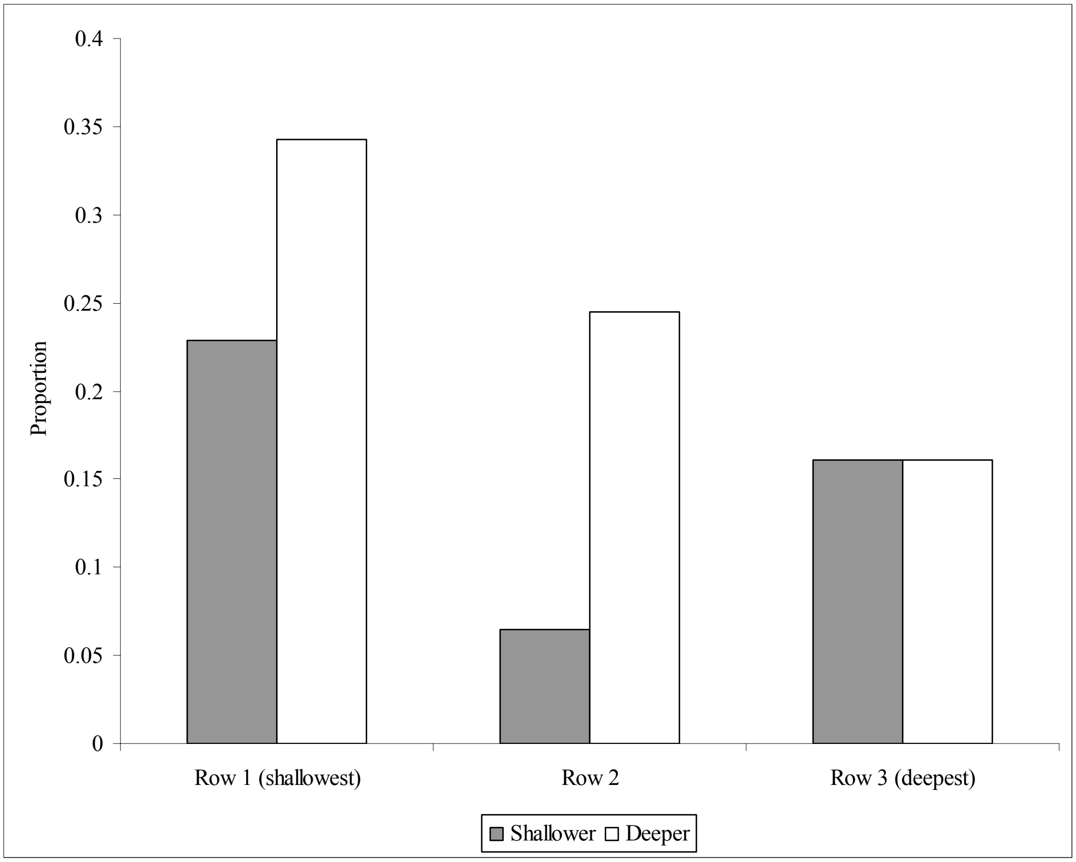


Figure 22. Proportion of shoal movements deeper or shallower in lower intertidal from 2005. Based on shoal movements from 8-m x 6-m grid.

Shoal cohesiveness

Nearest Neighbor Distance

The first shoal cohesiveness metric is nearest neighbor distance. The lower the nearest neighbor distance the tighter and closer the fish are within the shoal. The two 2005 Dabob Bay sites, Tabook Point and State Timberlands, had the highest mean nearest neighbor distances for both intertidal zones meaning fish within shoals are spaced the furthest apart. For the upper intertidal zone, Tabook Point and State Timberlands had mean nearest neighbor distances of 24.3 cm and 23.9 cm. These distances are close to the maximum possible distances for this method because if two fish were in opposite corners of the quadrat they would have a mean nearest neighbor distance of about 35 cm.

For both of these sites, mean nearest neighbor distances decreased in the lower intertidal although the distances did not decrease as drastically for Tabook Point as it did for State Timberlands. The other two sites had cumulative mean nearest neighbor distances of 10.5 cm for Frenchman's Cove and 9.2 cm for Barber Sand. These two distances indicate the fish at these sites were packed together because these distances are roughly twice the mean fish length.

In 2005, mean nearest neighbor distances were highly significant ($p << 0.00001$) at the site level, but not significantly different for tidal elevation ($p = 0.24$) or site by tidal zone interaction ($p = 0.12$) (Fig. 23). Similar to 2005, mean nearest neighbor distances of juvenile chum shoals in 2004 were significantly different at the site level ($p <0.028$), but tidal elevation was also significantly different ($p < 0.0001$) (Fig. 24). So for 2004 at these two sites, fish within shoals were closer to each other in the lower intertidal than they were in the upper intertidal. Site by tidal zone interaction ($p = 0.47$) was not significant in 2004. Mean nearest neighbor distances decreased at both sites in the lower intertidal therefore the fish were closer together in the lower intertidal.

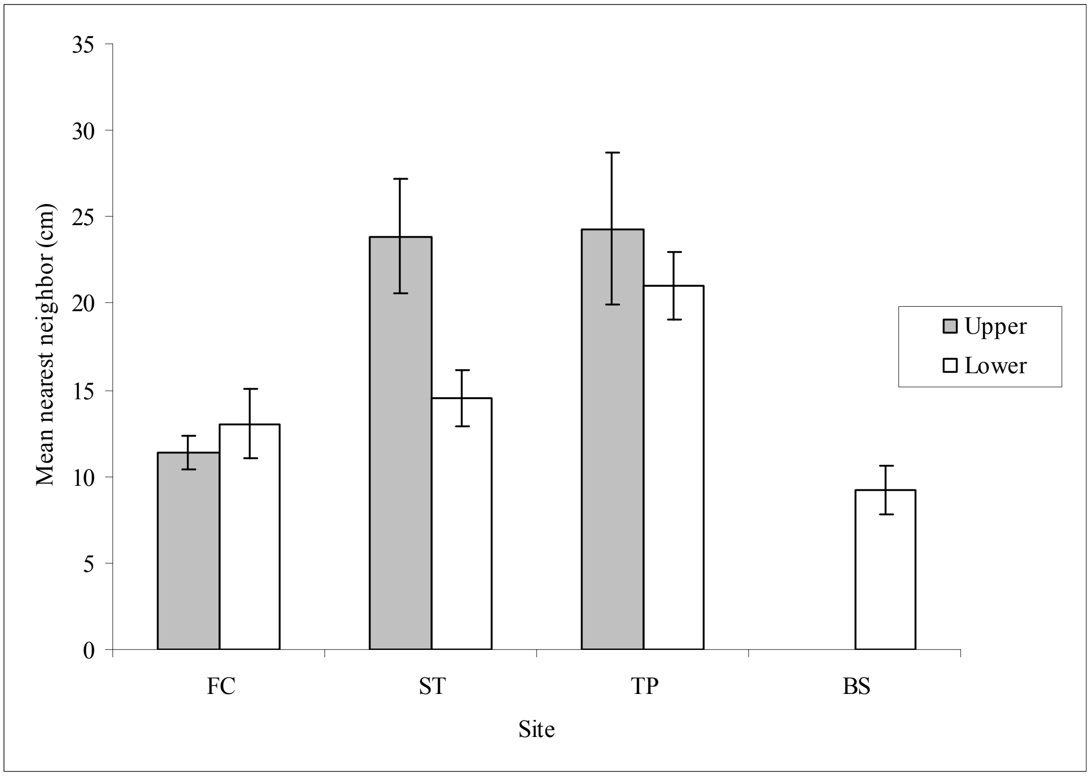


Figure 23. Mean nearest neighbor distances (± 1 SE) between juvenile chum salmon in 2005. For shoals from 8 April 2005 to 13 May 2005 spring tidal series only. Numbers of shoals based on: FC - High (24); Low (18); ST - High (8), Low (14); ST - High (4), Low (11); BS - High (0); Low (13)

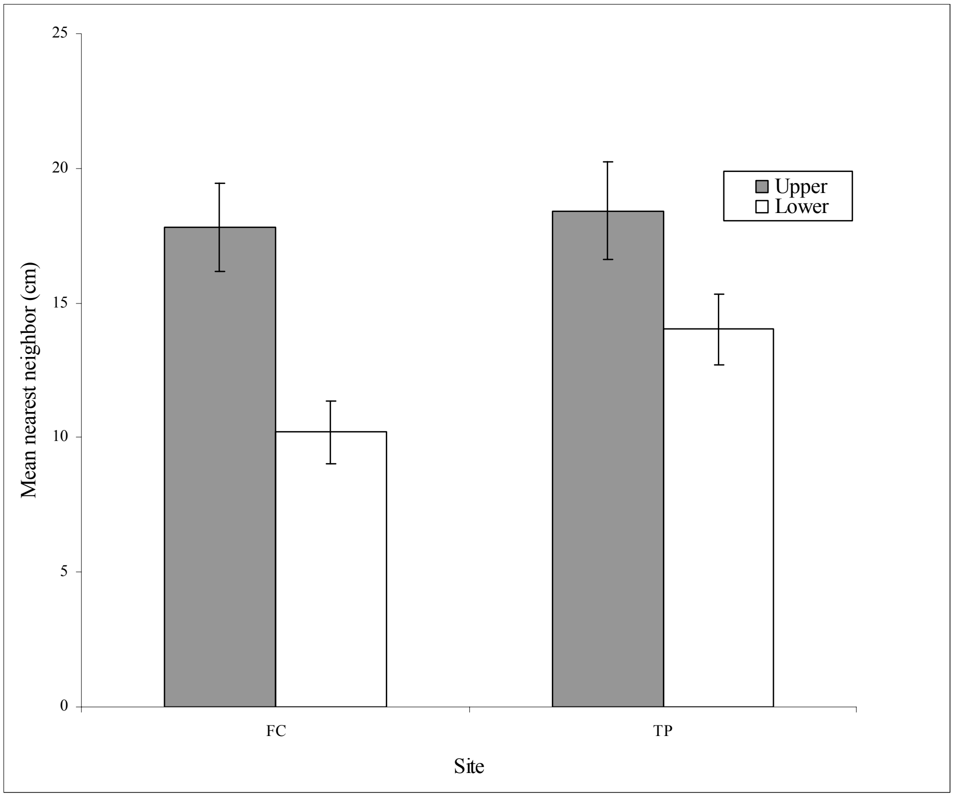


Figure 24. Mean neighbor distance for spring tidal series (± 1 SE) in 2004. Numbers of shoals based on: FC - Upper (60), Lower (37); TP - Upper (29), Lower (63)

Fish per Image

Like 2004 mean nearest neighbor distance, this metric indicated that the fish were closer together in the lower intertidal than they were in the upper intertidal. Overall Frenchman's Cove and Barber Sand had the most fish per image and the two other Dabob Bay sites had lower fish per image. For this metric site effect was significant ($p << 0.0001$), and tidal elevation was also significant ($p < 0.007$) (Fig. 25). The tidal elevation by site interaction effect was not significant, however.

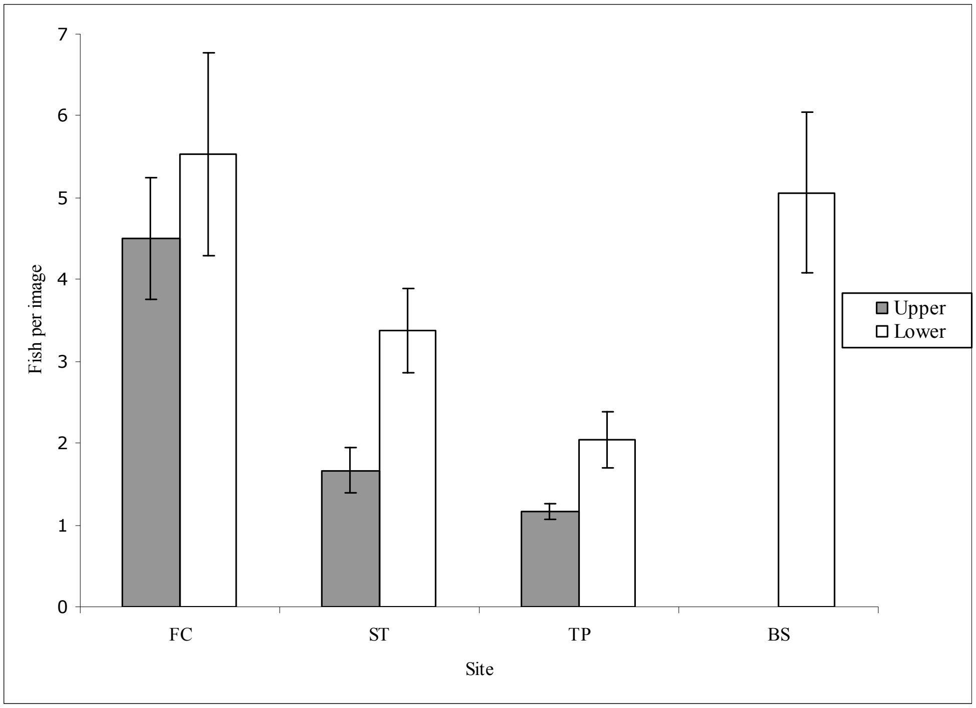


Figure 25. Fish per image (± 1 SE) from 0.25-m^2 quadrat during spring tides in 2005. Numbers of images based on: FC - High (30), Low (21); ST - High (18), Low (16); TP - High (18), Low (24); BS - High (0), Low (17)

In 2004, differences in fish per image were highly significant for site ($p < 0.00001$), but tidal zone ($p = 0.72$) and interaction were not ($p = 0.059$). Once again Frenchman's Cove had more fish per image than Tabook Point indicating fish packed tighter to each other (Fig. 26). The type II ANOVA did not meet the assumption of heteroscedasity.

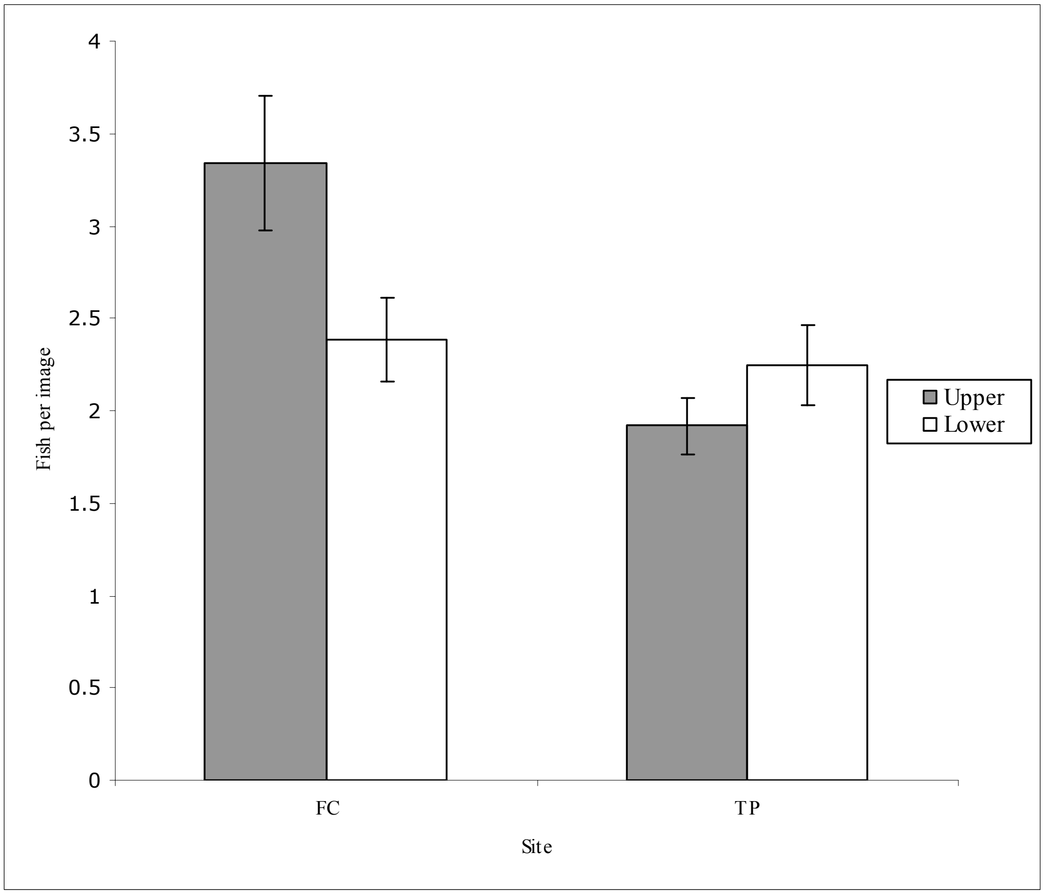


Figure 26. Fish per image from 0.25-m^2 quadrat during spring tides in 2004. Numbers of images based on: FC - upper (100), lower (62); TP - upper (133); lower (131)

Shoal Size

The shoals in the lower intertidal were larger than in the upper intertidal for both 2005 and 2004. In 2004, both sites had larger shoals in the lower intertidal although these differences in size were not as pronounced as they were in 2005. In 2005 all sites except State Timberlands had larger shoals in the lower intertidal than in the upper intertidal. In 2005 shoal size was significantly different for site ($p < 0.012$) and also nearly significant for intertidal zone ($p = 0.05004$) (Fig. 27). There were no significant interaction effects ($p = 0.62$).

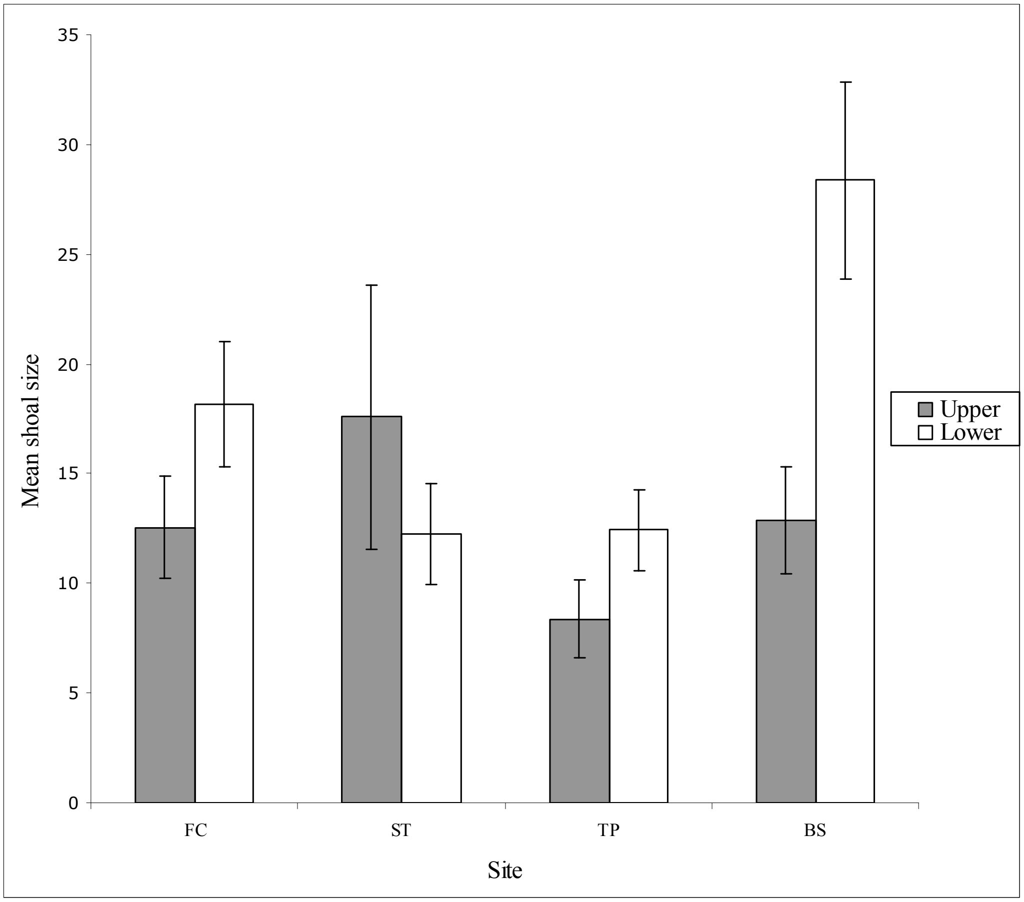


Figure 27. Shoal size for shoals between 8 April and 13 May 2005 (± 1 SE). From field estimates of shoal size for shoals that entered quadrat or grid. Based on numbers of shoals: FC - upper (34), lower (58); ST - upper (12), lower (17); TP - upper (14), lower (34); BS - upper (7), lower (28)

Although the differences between upper intertidal and lower intertidal were not that pronounced and despite not meeting the assumption of homoscedasity, the behavioral response of shoal size in 2004 was also significantly different for site ($p < 0.006$) and tidal elevation ($p < 0.03$) (Fig. 9). Interaction effects were not significant ($p = 0.31$).

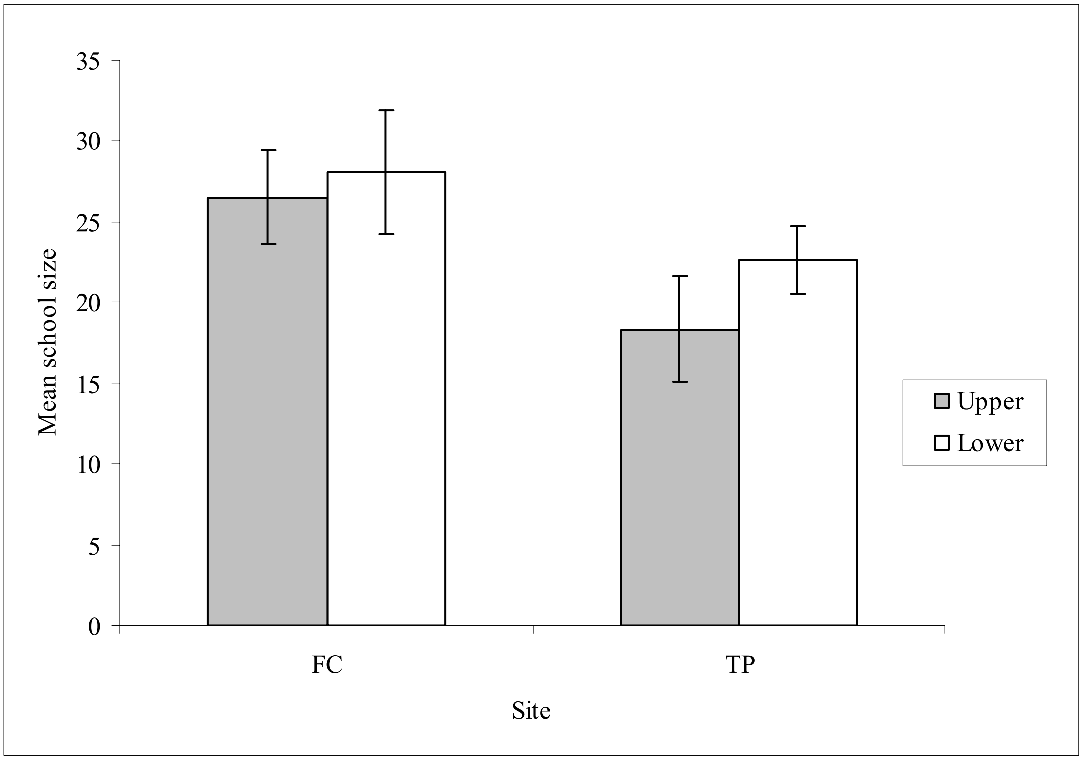


Figure 28. Mean shoal size (± 1 SE) in 2004. Based on fish that entered the 0.25-m^2 quadrat for 21 April 2004 - 9 May 2004 spring tides only. Based on numbers of shoals: FC - upper (97), lower (55); TP - upper (70), lower (98)

Shoal Polarity

Differences in shoal polarity were significant at the site level ($p < 0.011$), but neither for tidal elevation ($p = 0.33$) nor interaction ($p = 0.98$) (Fig. 10). Although tidal elevation effect was not significant, for all sites mean shoal polarity was higher in the lower intertidal zone.

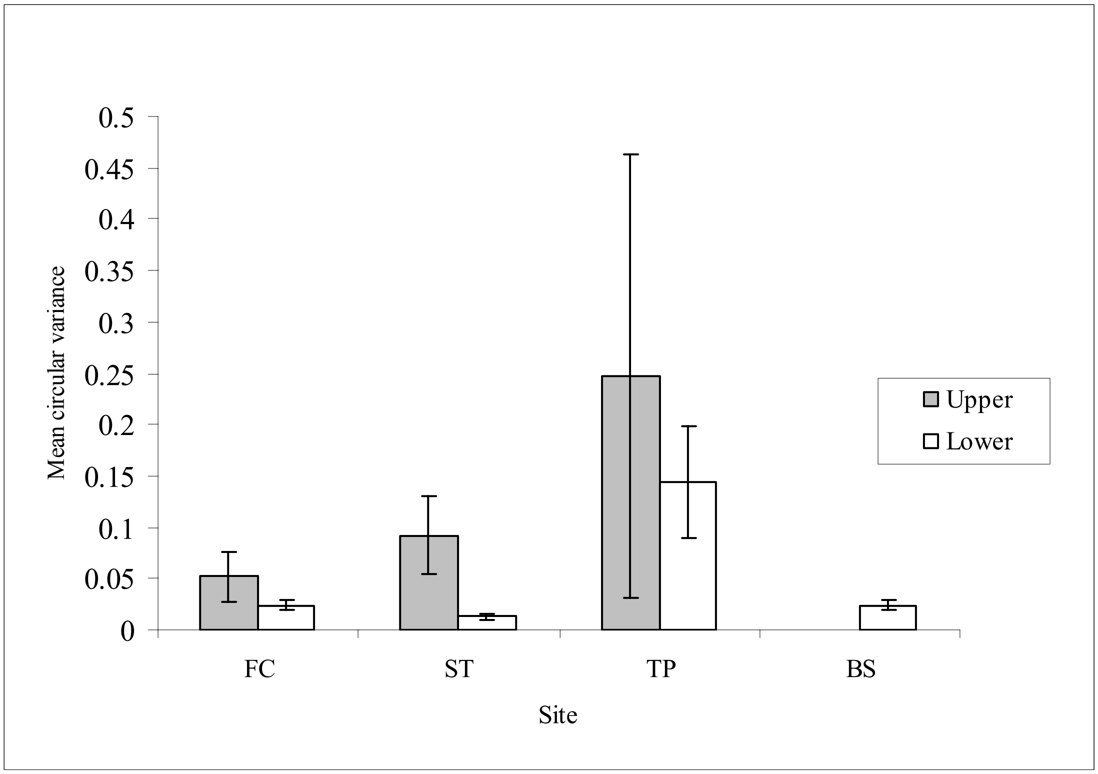


Figure 29. Mean intertidal circular variance (± 1 SE) in 2005. Scores closer to 0 means higher shoal polarity. Scores closer to 1 indicate lower shoal polarity. Based on these numbers of shoals FC - upper (24), lower (18); ST - upper (8), lower (14); TP - upper (4), lower (11); BS - upper (0), lower (13)

For all shoal cohesiveness metrics, the tidal elevation had no significant effect or the fish shoals were less organized and cohesive in the upper intertidal zone (Table 6).

Table 6. Summary of shoal cohesiveness metrics. If it was significant the p-value is listed. For the intertidal zone factor, if it was significant the p-value is listed as well as which intertidal zone had the least shoal cohesiveness. NS means not significant and a blank means that metric was not used.

Metric	**Year**	**Site factor**	**Intertidal factor**	**Interaction**
Mean nearest neighbor	2005	$p << 0.00001$	NS	NS
	2004	$p < 0.028$	Upper $p < 0.0001$	NS
Fish per image	2005	$p << 0.0001$	Upper $p < 0.007$	NS
	2004	$p < 0.00001$	NS	NS
Circular variance	2005	$p < 0.011$	NS	NS
	2004			
Shoal size	2005	$p < 0.012$	Upper $p = 0.05004$	NS
	2004	$p < 0.006$	Upper $p < 0.03$	NS

Shoaling Strength and Occurrence

Overall, 80.4% of the fish observed in the 0.25-m^2 quadrat during the 2005 spring tides were in a shoal (Fig. 30). Of the fish that were not in shoals, 89.7% (226 of 252) were observed at the Tabook Point site. At this site, 25.9% (10 of 39) of the non-shoaling fish were in the upper intertidal and 81.2% (216 of 266) were in the lower intertidal. For the other three sites nearly all the fish, 97.3% (955 of 981) were in a shoal.

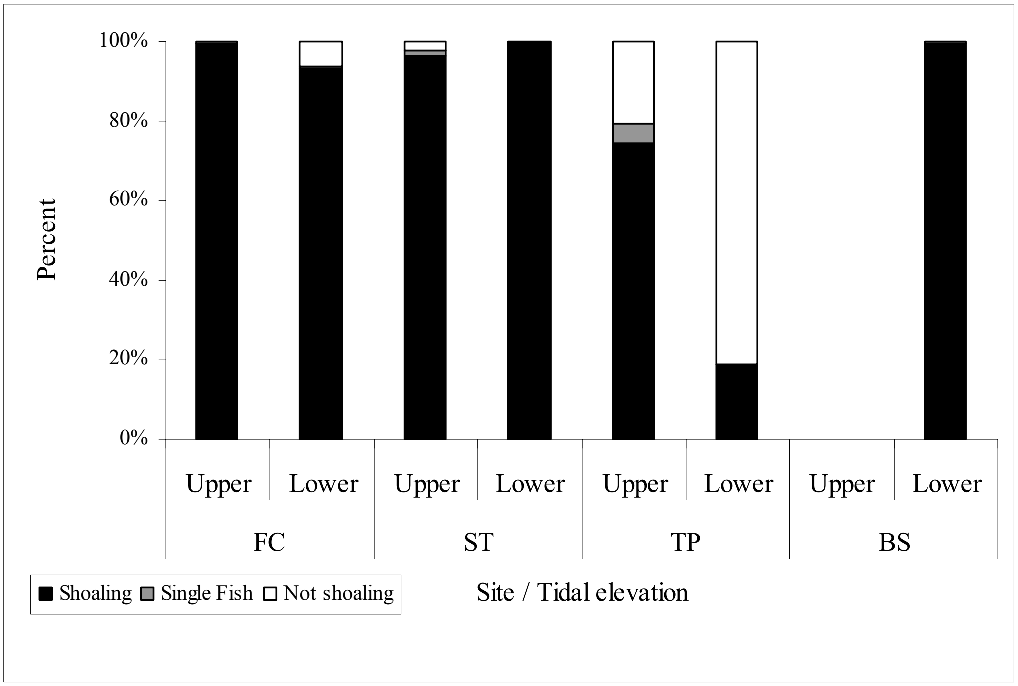


Figure 30. Percent of fish occurring in a shoaling based on 0.25-m^2 quadrat during spring tides in 2005.

Individual Fish Orientations

The mean orientation for all fish in the upper tidal elevation/spring tidal group was -8.9°, -22.0° for the upper tidal elevation/neap tide group, and -3.5° for the lower tidal elevation/spring tide group (Figure 31; Table 7). Thus, on average individual fish were oriented toward the mouth of Hood Canal and slightly away from the shore.

Table 7. Distribution of individual fish orientations from 0.25-m^2 quadrat in 2005. Fish totals are listed with the proportion of fish in parentheses. Fish are from 8 April 2005 to 13 May 2005.

Orientation	**Upper Spring**	**Upper Neap**	**Lower Spring**	**Total**
Toward mouth	95 (0.53)	189 (0.42)	149 (0.49)	433 (0.46)
Deeper	28 (0.16)	53 (0.12)	24 (0.08)	105 (0.11)
Away from mouth	45 (0.25)	154 (0.34)	103 (0.34)	302 (0.32)
Shallower	12 (0.07)	51 (0.11)	31 (0.10)	94 (0.10)
Total	180	447	307	934

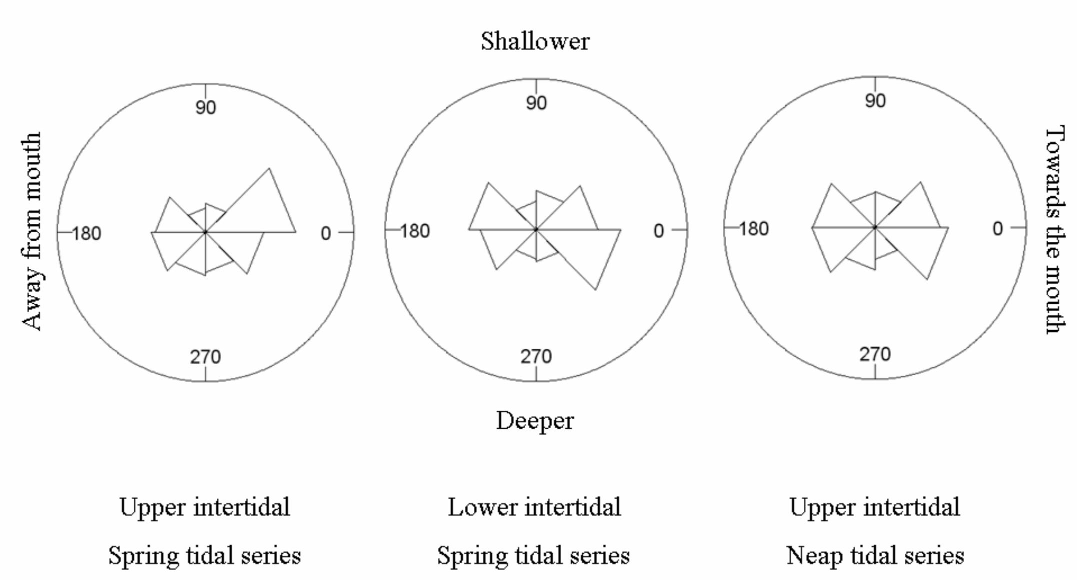


Figure 31. Individual fish orientations from 0.25-m^2 quadrat in 2005.

Shoal Movements

Overall, fish moved relatively deeper by an average of 0.32 m per fish while in the 8-m x 6-m grid (Figure 32). This only accounts for relative movement while they were in the grid and does not account for time spent in the grid. They generally moved toward the mouth of Hood Canal by an average of 0.63 m per fish (Fig. 32). The average absolute distance traveled for a fish while in the grid was 7.33 m per fish.

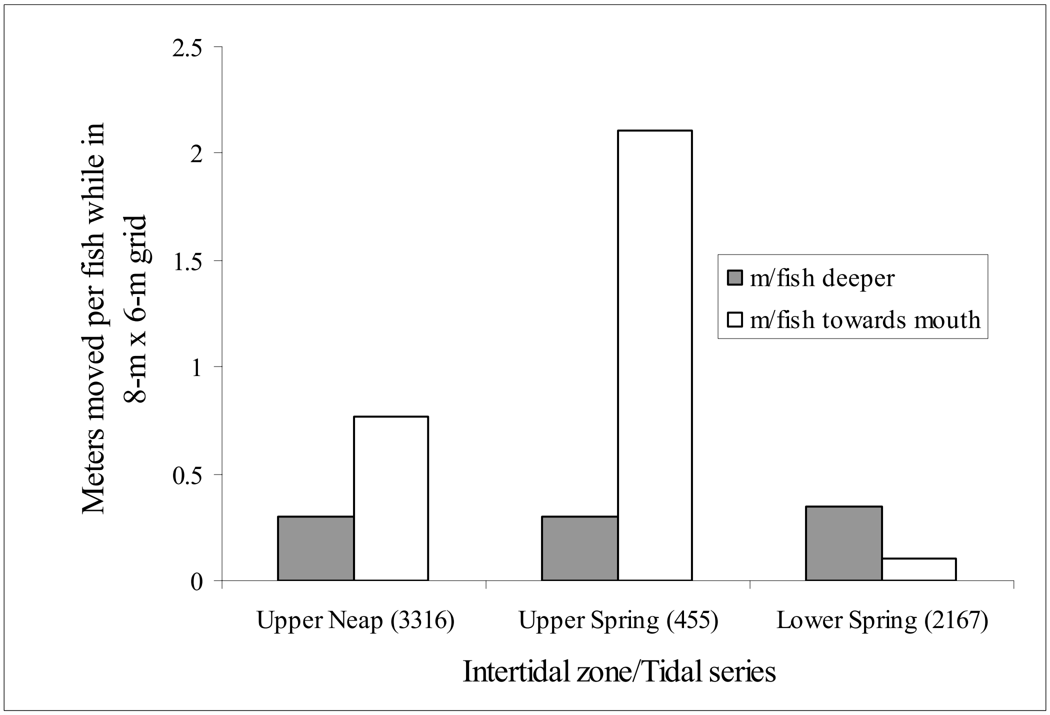


Figure 32. Relative movements for tidal elevation and tidal month combinations in 2005. Numbers in parentheses are numbers of fish.

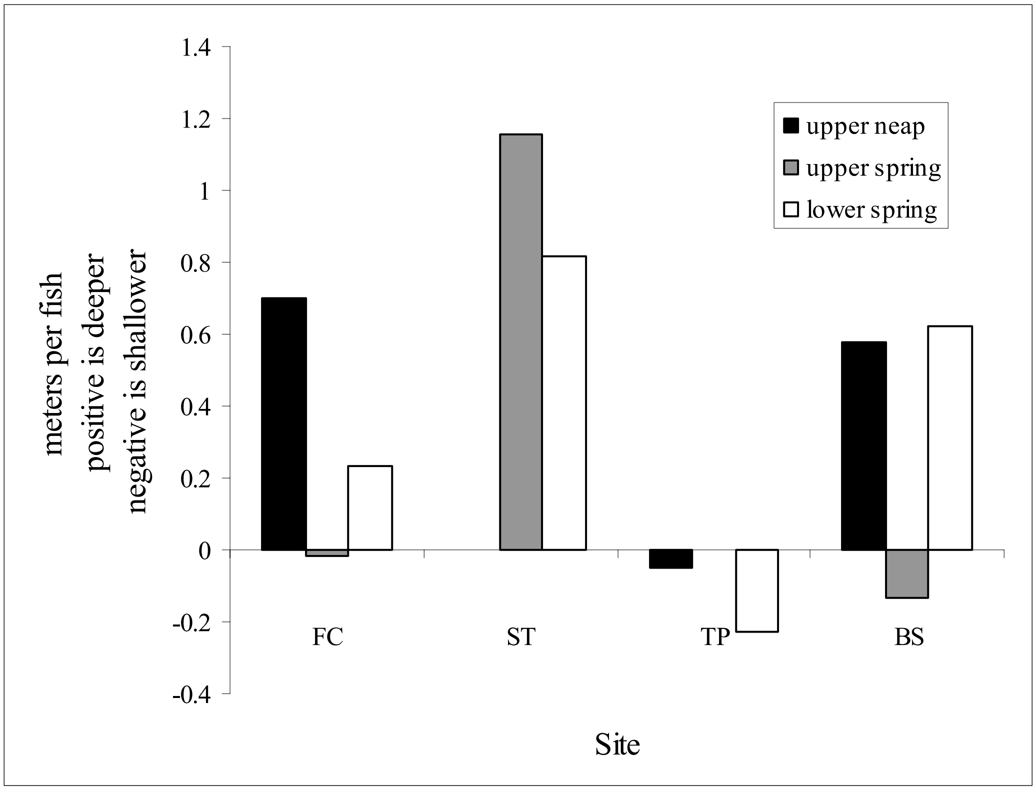


Figure 33. Relative movement (m) per fish shallower or deeper in 8-m x 6-m grid in 2005. Positive values deeper movement; negative values indicate shallower movement. Based on numbers of fish: BS – FC – upper neap (361), upper spring (112), lower spring (780); ST – upper neap (never sampled), upper spring (130), lower spring (208); TP – upper neap (1531), upper spring (123), lower spring (385); BS – upper neap (1424), upper spring (90), lower spring (794).

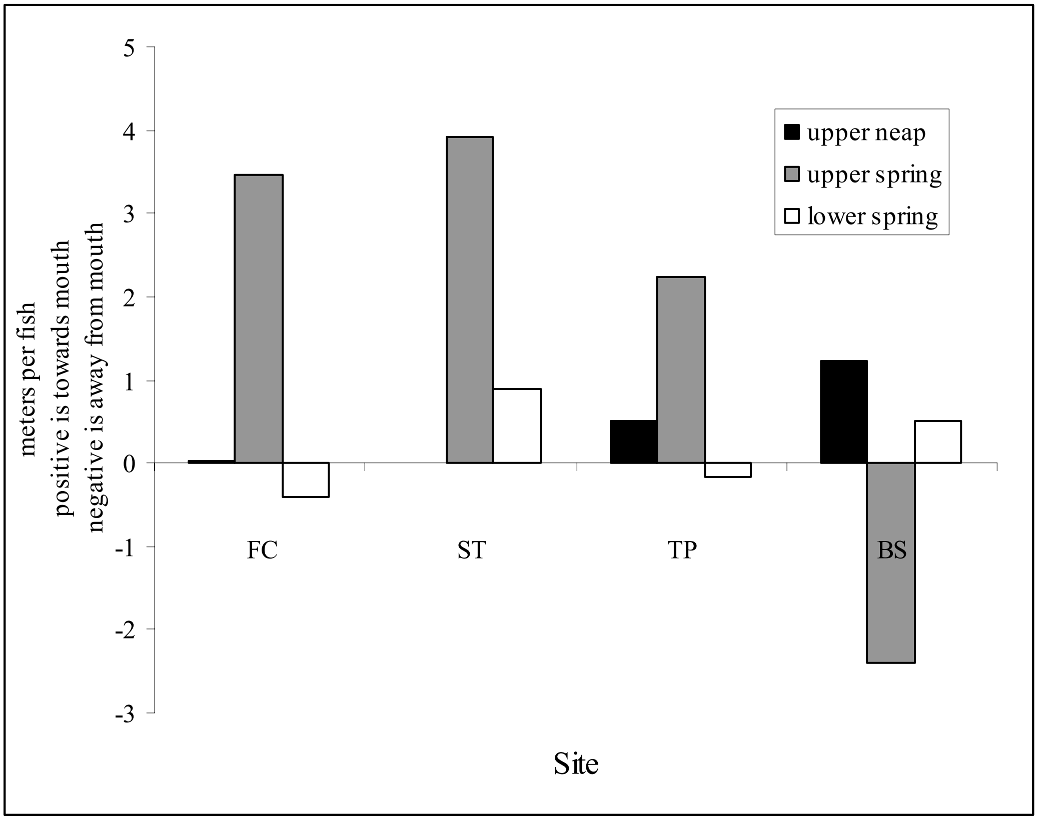


Figure 34. Relative movement (m) per fish toward mouth or away from mouth in 8-m x 6-m quadrat in 2005. Positive values indicate movement toward the mouth; negative values indicate movement away from the mouth. Based on numbers of fish: FC – upper neap (361), upper spring (112), lower spring (780); ST – upper neap (never sampled), upper spring (130), lower spring (208); TP – upper neap (1531), upper spring (123), lower spring (385); BS – upper neap (1424), upper spring (90), lower spring (794).

Discussion

The method I developed in this study appears to successfully quantify *in situ* juvenile chum behavior when then occupy shallow water microhabitats early in their estuarine migration in Hood Canal. I was able to use a variety of derived metrics from these observations and measurements to analyze and statistically test two basic hypotheses about microhabitat use.

This study is an example of how if only fish density is examined the results could be easily misinterpreted. In the case of juvenile chum salmon in nearshore microhabitats, density had a significant interaction effect, with some sites having a higher density in lower intertidal microhabitats and other sites having higher densities in the upper intertidal. In situations like this, it is difficult to get a clear picture of how important one microhabitat is relative to another one and how organisms may be using each microhabitat.

In this particular case, using behavior not only provides insight into why the fish are found where they are, but also how they may be using, or fulfilling life requirements, in different microhabitats. The first piece of behavioral information from this study is that there is a "stay shallow" mandate operating for juvenile chum salmon. It is not entirely clear how strict this mandate may be, but it likely limits access to lower intertidal microhabitats at high tides.

The other piece of behavioral information is that shoaling cohesiveness is higher in the lower intertidal compared to the upper intertidal. In other words, the shoals become larger and fish within these shoals get closer together in the lower intertidal. This may be related to foraging.

Behavioral information is then used in conjunction with density to get a better understanding how juvenile chum salmon are using intertidal microhabitats.

Density – Take One

The case of juvenile chum salmon is an instance where using only density to infer microhabitat value or use is potentially problematic. Initially, the density seems confusing and may not provide any relevant information. Sites had significantly different density (Fig. 17), but this is not surprising because each site was chosen to be different, and the sites are located different places along Hood Canal. The different locations in Hood Canal give each site a unique supply of fish with a unique prehistory.

But density provides little information on how juvenile chum are using upper intertidal microhabitats relative to lower intertidal eelgrass microhabitats. Both years had significant site by tidal elevation interaction with some sites having higher densities in the upper intertidal and other sites having higher densities in the lower intertidal. In 2005, two of the sites, Tabook Point and Barber Sand, had higher densities in the lower intertidal, and two sites, Frenchman's Cove and State Timberlands, had higher densities in the upper intertidal. The two 2004 sites exhibit the same density pattern in both years, with Tabook Point having a higher density in the lower intertidal and Frenchman's Cove having a higher density in the upper intertidal.

At this point it may be tempting to speculate on the reason for the density differences, maybe the different landscape patterns of the lower intertidal eelgrass causes the intertidal differences, but really without further information it is just speculation. But this study uses behavior to understand microhabitat use, and the first behavior is the stay shallow mandate.

Stay Shallow Mandate

Although this study was not specifically designed to specifically assess a mandate to stay shallow it does provide evidence that there is a behavioral mandate for the fish to continually seek shallow water microhabitats. Although it is partially an artifact of my sampling design, I found that the majority of fish were found in water depths less than 75 cm. This is particularly pronounced in the steeper upper tidal elevation of beaches, where 72.6% of the fish were found shallower than the median depth of 47 cm. In the lower gradient, lower tidal elevations, juvenile chum salmon were more dispersed, with only 54.6% of the fish shallower than the median depth (Fig. 12).

Data on shoal movement from the 8-m x 6-m grid also reflect a behavioral mandate to stay in shallow water. For the data pooled between upper and lower intertidal, shoals were less likely to move into deeper water in row 3 (the deepest row) than they were in row 1 (the shallowest) with row 2 in between the other two (Fig. 19). Row 3 was also the only row in which fish were more likely to move shallower than deeper. It is not surprising that fish in the shallower rows were more likely to move deeper because there is a limit to how shallow the fish can move whether it is the emergent shoreline, as was at times the case in row 1 or just water deep enough to swim in.

The results are even stronger when the movements are separated into upper and lower intertidal. The upper intertidal shoal movements provide the strongest evidence for the stay shallow mandate because it has a steeper beach gradient (Table 5). If movements from row 1 are not included because of the often impossibility of them moving shallower, there are more combined movements shallower in rows 2 and 3 than combined movements deeper (19.2% compared to 15.9%). Additionally, in row 3 shoals were 3.4 times more likely to move shallower than deeper (33.1% movements shallower/9.8% movements deeper) (Fig. 21). The stay shallow mandate is not as relevant in the lower intertidal because row 1 was rarely more shallow than row 3 and this is shown by the equal occurrence of movements shallower and deeper in row 3 (16.1%) (Fig. 22).

What is uncertain is how strict this stay shallow mandate is. Certainly juvenile chum salmon of the same size class in this study are at times found in deeper water

(Bax 1983, Fukuwaka & Suzuki 1998), but since this study only focused on the nearshore immediately adjacent to shore it is impossible to clearly discern how strict the rule is. Surface activity from fish in deeper water was rarely observed, but this certainly does not preclude their presence because fish in deeper water could be just below the surface or possibly the distance from the observer to the fish made it impossible to discern surface activity on all but the calmest days.

Again, this study was not designed to test the stay shallow mandate, but it does provide strong evidence that the stay shallow mandate exists. Other studies that are explicitly designed to determine the stay shallow rule could easily be developed that could better define this mandate. They could be ladder based, video, or snorkeling. For example, the question could be asked, do juvenile chum "always stay shallower than 1.0 m" or do they "stay as shallow as possible?"

The present study suggests the mandate is more likely similar to "stay shallower than 1.0 m" than the alternative "stay as shallow as possible" mandate. Individual fish orientations from the 0.25-m^2 quadrat show that while in row 2 fish are on average oriented slightly pointing into deeper water. There are not strong movements shallower until the fish are in row 3 and this is particularly pronounced in the upper intertidal for both the fish depth distribution (fig. 18) and the movements shallower or deeper (Figs. 20 & 21). Based on the fact that the deepest row of the study area was about 0.75 – 1.0 m deep and in this row fish were more likely to move shallower than deeper, a best guess for the stay shallow mandate is "stay more shallow than 1.0 – 1.5 m deep." The likely reason for the stay shallow mandate is juvenile chum salmon are likely using this shallow water as a refuge from predators like other fish have been known to do (Blaber & Blaber 1980, Werner *et al.* 1983, McDonald *et al.* 1992, Ruiz *et al.* 1993, Ellis & Bell 2003).

Implications of Stay Shallow Mandate

Effects on density

This mandate to stay shallow has implications for analysis depending on how rigid the mandate is. The first thing it is likely to affect is fish density. Because of differences in slopes between the upper and lower tidal elevations (Fig. 24), fish would be expected to concentrate in the water immediately adjacent to the shoreline. In the lower elevations, the fish would have more shallow water to disperse and thus, on an areal basis, lower fish densities would be expected in lower tidal elevations even though the same amount of fish may be there (Toft *et al.* 2007). As a consequence, in this study if the same numbers of juvenile chum are present between upper and lower intertidal microhabitats expected densities would be much greater in the upper intertidal.

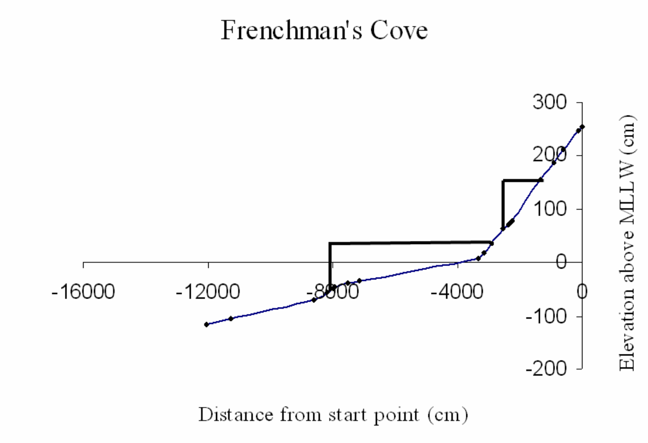


Figure 35. Amount of shallow water available at the upper intertidal and lower intertidal. The theoretical behavioral "stay shallow" mandate is stay shallower than 1.0 m deep. "Triangles" in drawn in show the amount of available water at different tidal elevations.

Effects on Microhabitat Access

Another consequence of the stay shallow mandate is the potential limitation of microhabitats that juvenile chum salmon can access. The stricter the stay shallow mandate, the more it limits the fish’s access to lower tidal elevation microhabitats. In this study, lower tidal elevations were defined as +0.50 m MLLW and below. In Hood Canal, the first time the mid-day tides drop into the lower intertidal is early March and the typical spring tides series for this study did not begin until 13 March. This could be relevant for threatened summer chum that move into Hood Canal earlier in the year, often before mid-day tides are dropping into lower tidal elevations.

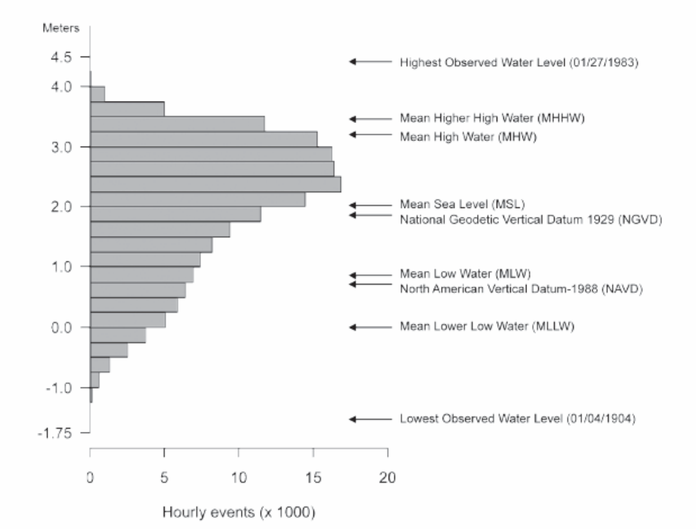


Figure 36. Distribution of tidal levels for Seattle between 1993 and 2001. From Finlayson 2006 p. 18.

The semidiurnal tides of Puget Sound and Hood Canal result in the tides rarely dropping into the lower intertidal zone (Finlayson 2006). Tides in lower tidal elevations are not as rare during the chum salmon outmigration, but in the spring season only about 50% of the days (those of the spring tidal series) have tides that even drop into the lower intertidal. On the days with tides that drop into the lower intertidal the low tides occur mid-morning to mid-afternoon. Consequently even though lower intertidal microhabitats likely have higher prey densities chum may not have direct access to them during prime feeding times. During the neap tidal series, the fish would not have any access to the lower intertidal under a strict stay shallow mandate.

These two potential effects of the stay shallow mandate to juvenile chum salmon, the effects on density and microhabitat access, show similar results to other studies that show that water depth must be considered as an important factor in estuarine studies (Beck et al. 2001, Ellis & Bell 2003).

Density – Take Two

A consequence of the stay shallow mandate is if there are equal numbers of fish between microhabitats, the microhabitat with the steeper slope will have higher density. This effect must be taken into account when evaluating density. In this case, upper intertidal microhabitats with their steeper gradient would be expected to concentrate fish and likely have higher densities than the lower intertidal. This was true at Frenchman's Cove (2004 and 2005) and State Timberlands (2005), but the opposite was true for Tabook Point (2004 and 2005) and Barber Sand (2005). The increase in density in the lower intertidal at Tabook Point seems to be real because the same trend was observed for both years at this site. The Barber Sand density is less clear if the observed densities are accurate or a result of random error. There may be some reason fish avoid the upper tidal elevations compared to lower tidal elevations at this site (e.g., it was the only site with a sand beach). Alternatively, it may be a result of sampling error. Fish entered the 8-m x 6-m grid but never entered the smaller 0.25-m^2 quadrat. There were only four observations made at Barber Sand during the spring tidal series/upper tidal elevation combination, and it may just be random chance that fish did not enter the smaller quadrat.

This study builds upon density by examining shoaling behavior to understand how juvenile chum salmon are using intertidal microhabitats.

Microhabitat Shoaling Behavior

The null hypothesis that shoaling behavior of juvenile chum salmon in Hood Canal is the same between intertidal microhabitats is rejected. When juvenile chum salmon are in shoals, there is significantly less shoal cohesiveness in the upper tidal elevations than in lower elevations of the beach. All shoal cohesiveness metrics that were significant (4 of 7) indicate that shoals were less cohesive along the upper beach. However, the various shoal cohesiveness metrics were only relevant to a portion of the fish populations I surveyed because 19.6% of fish did not occur in shoals and the metrics only partially reflect this non-shoaling. Shoal size could only be used when the fish were actually in shoals, and the average nearest neighbor distance and circular variance could only be used when two or more fish occurred in a randomly selected image. Alternatively, I could use fish per image when any fish occurred in the image.

Given the documented behavioral differences, the next question is: Do these differences in behavior indicate a difference in microhabitat use or its nursery value? There could be several reasons for the juvenile chum survival or performance factors that might explain these differences in shoaling behavior. Among the many internal (within-fish) and external factors that might contribute (Colgan 1993), the two primary factors that influence fish shoals are predation and foraging (Pitcher 1986, Pitcher & Parrish 1993).

Shoal Cohesiveness and Predation Risk

The stay shallow mandate likely exists as a way to avoid predation, and it is possible that the increased shoal cohesiveness is a consequence of increased predation pressure or threat. Although this study was not designed to test predation as a cause of shoaling, it is possible that it is the primary factor causing the observed differences in shoaling cohesiveness of juvenile chum salmon. Generally speaking, shoaling cohesiveness in fishes increases under a higher predation risk (Godin 1986, Magurran & Pitcher 1987, Hager & Helfman 1991, Pitcher & Parrish 1993, Pavlov 2000). If predation risk is causing the observed behavioral differences, occupying the lower tidal elevations of a beach would impose a higher predation risk for juvenile chum salmon, most likely from one or more of fish predators, seabirds, and/or wading birds (Hargreaves 1985, Bayer 1986, Hargreaves & Lebrasseur 1986, Nagasawa & Kaeriyama 1995, Duffy & Beauchamp 2008).

There are a few reasons to think that predation risk is not higher in the lower tidal elevations. The first is predator access. The lower intertidal has a shallower slope than the upper intertidal and consequently any large fish predators would have a harder time or be reluctant to access shallow water in the lower tidal elevations compared to the higher tidal elevations on the steeper face of the beach. Seabirds that forage by diving would also have a difficult time feeding in this shallow water.

Another reason to think that predation risk is not the primary factor causing the increased shoal cohesiveness in the lower intertidal is that no predation events were ever observed in the study area in either the upper or lower tidal elevations. If the lower intertidal truly has a higher predation threat than it would be expected there would be at least some signs of the increase. If predation pressure were the primary factor causing shoals to become more cohesive then at least some predation or predators would expected to be observed. But from the beginning of the study I wanted to see if I ever directly observed a predation event upon the chum by a fish predator. Again, I never did directly witness a chum being eaten by a fish predator. I did see some surface feeding events by fish certainly larger than the chum, but these were in deeper water (≈ 1.0+ m) than I could directly observe so I cannot be certain if these were predation events upon chum.

The chum predators that are most likely to eat the fish in shallow water are wading birds such as the great blue heron, *Ardea herodias*. Herons were present in the study area, but not in large numbers. It is possible that the increased shoal cohesiveness is an evolutionary response to when wading birds were more abundant. There may not currently be higher predation threat from wading birds in the lower intertidal, but the increased shoal cohesiveness may be an evolutionary carryover from when predators were in greater abundance.

The third reason that predation is not likely the cause of the increases shoaling is that although juvenile chum were never observed directly using eelgrass as a refuge like many other fish do, it is more likely that the vegetation does provide increased protection from predators compared to the bare cobble substrates of the upper intertidal (Orth 1984).

The final reason to be suspicious of predation threat causing the increased shoal cohesiveness is results from prior studies with juvenile chum salmon showing that predation threat either did not alter behavior or affected it less than feeding. One aquarium study found that predation threat did not affect either juvenile chum habitat choice, cover or open water, or feeding rate (Magnhagen 1988). Another mesocosm study with juvenile chum salmon found that although mean nearest-neighbor ratios were higher in a non-predator treatment compared to a predator treatment, the predation factor did not increase mean-nearest neighbor ratios as drastically as post-feeding of the chum did (Ryer & Olla 1996).

Shoal Cohesiveness and Foraging

The other primary factor that is documented to structure fish shoaling is foraging. This could be the factor that is causing the behavioral response because the typical prey of chum salmon fry and small fingerlings are disproportionately distributed among microhabitats (Cordell 1986, Simenstad *et al.* 1988, Webb 1991a, Webb 1991b, Hosack *et al.* 2006) and these differences in distribution could cause fish to forage differently while in these microhabitats. The behavioral response of shoal cohesiveness in relation to foraging is much more complicated and less predictable than the response associated with predation risk. Fish shoals respond to both the occurrence and distribution of prey. The two most likely possibilities for foraging structuring fish shoals are that (1) shoals break down while fish are intensively foraging and (2) variability in prey distribution causes observed differences in shoaling behavior.

Shoal cohesiveness decreases while fish are feeding because the homogeneous structure of the shoal cannot be maintained as fish dart to capture individual prey the (Pavlov 2000). This could be the cause of the change in shoaling behavior for juvenile chum. Two mesocosm studies with chum have results consistent with this interpretation. One showed that chum were more likely to join a shoal when it was not feeding compared to when it was (Ryer & Olla 1991), and another study showed that shoal cohesiveness decreased when chum began feeding for both a predator present and the predator absent (Ryer & Olla 1996).

Another foraging factor that can influence the structure of fish shoals is the distribution of prey. When prey are clumped, fish in shoals may forage more effectively than individuals because there are more fish searching for the clumped food (Eggers 1976, Pitcher *et al.* 1982, Mittelbach 1984, Pitcher 1986). When prey is located, fish may respond to their shoalmates and are attracted to the site of the prey. This can result in shoals with higher feeding rates than individuals, despite the increased intraspecific competition (Ranta & Kaitala 1991, Ryer & Olla 1992, Ryer & Olla 1995). If prey are dispersed, individual foraging may be better because prey will likely be consumed before a fish can approach its feeding shoalmate (Ryer & Olla 1995).

While little is known about the distribution of chum prey items in shallow water microhabitats, the observations in this study may indicate possibilities in the prey distribution. Despite typical juvenile chum salmon prey organisms being epibenthic, fish were never observed feeding directly off the substrate although there has been at least one mesocosm study where chum did feed off the bottom of the mesocosm (Ryer & Olla 1991). The lack of direct feeding off the substrate indicates that the prey are natant and are not consumed when they are physically located on the epibenthos. Exaclty how this happens or if it would result in dispersed or clumpy prey is unknown and beyond the scope of this study.

Behavioral observations from this study support that the prey is at least partially dispersed because chum were not observed feeding heavily in one concentrated area. For instance, shoals would not move and then stop to feed, presumably when they found an area of highly concentrated food, and then move on when that source was depleted as is typical when feeding is enhanced by shoaling. If the shoaling response was caused by the prey being highly clumped this kind of behavior would likely have been more obvious. An alternative explanation is that the prey are in fact clumped but the clumps are spatially small. In this case, if a fish found a clump of prey it would not be large enough to attract the entire shoal.

This study is not comprehensive enough to determine if increased foraging or clumped food is responsible for the decreased shoal cohesiveness. More information such as invertebrate sampling would be needed to determine what is causing the observed behavioral differences, but this study can provide insight into how juvenile chum salmon may be responding to prey availability.

If the increased shoal cohesiveness in the lower tidal elevations is a result of less foraging compared to upper elevations then the eelgrass beds located there are not a consistently available foraging microhabitat for juvenile chum salmon. This interpretation is consistent with the stay shallow mandate because the chum would not have as much shallow water access to eelgrass beds compared upper intertidal microhabitats. The other possibility pertaining to foraging to explain the differences is the prey distribution. Because there is increased shoaling cohesiveness in the lower elevations then the prey may be more clumped there than it is in the higher elevations of the beach.

To Shoal or Not, That is the Question

Shoal cohesiveness metrics provide only a partial explanation of how the fish are behaving. Overall, 19.6% of fish were not in shoals; these fish had very little to no social interaction even though they were in the same area. However, nearly all (226 of 252) of the non-shoaling fish occurred just at the Tabook Point site. Non-shoaling could be an indicator of feeding because fish cannot maintain cohesive shoals as they feed. This is the site that had the most shallow slope as well as a large, dense, continuous eelgrass bed in the lower intertidal.

Additionally, low shoaling incidence at this site was also reflected in the shoaling cohesiveness metrics. For instance, the circular variance results indicated that juvenile chum salmon shoals were the least polarized at Tabook Point. At that site, upper tidal elevations had a higher mean circular variance than the lower tidal elevations, but even the mean circular variance in lower tidal elevations was greater than at any other site. The other shoaling cohesiveness metrics showed similar trends. This data indicates that this site definitely had the lowest shoal cohesiveness. The fact that this site had the lowest shoal cohesiveness as well being the only site with a large percentage of non-shoaling fish indicates that Tabook Point may be a place of high feeding. But what are the site-specific characteristics that might make this site a place of high feeding?

"Preferred Prey" Bias?

A large premise of this study is based on results from numerous studies that have shown that juvenile chum salmon consistently feed on only a few of the prey items that are assumed to be available to them. Part of this interpretation of preferred prey items and their microhabitats may be influenced by the timing and tidal elevation of chum capture. Some studies did not detail what tidal elevation the chum were captured (Kaczynski *et al*. 1973, Schreiner *et al*. 1977, Salo *et al*. 1980, Simenstad *et al*. 1980), others captured fish at intermediate tidal levels at mid-afternoon (Macdonald & Chang 1993) and others captured fish at low tide (D'Amours 1987). The stay shallow mandate from this current study indicates that future studies of diet analysis should be sure to capture fish from all tidal elevations.

Site Differences

For density as well as all shoal cohesiveness metrics, site effect was nearly always significant (the lone exception was 2004 density). This is not surprising because sites were chosen to be different based on their eelgrass landscape characteristics. They are also spatially separated and this could cause the observed differences as well. Thus, juvenile chum salmon behavior is likely affected by site-specific differences, which may be quite important in determining how juvenile chum benefit from microhabitat use. These differences could reflect either interior site characteristics or larger landscape settings, such as location of the site relative to the river or stream from which the salmon originated.

This study was conceived in part to assess juvenile chum response to lower tidal elevation microhabitats, specifically eelgrass, because their typical prey were thought to be more highly concentrated in these areas. The Tabook Point is the only of the four sites with a dense, large, continuous eelgrass bed over the low-tide terrace. The other sites, with the exception of State Timberlands, had eelgrass in the lower intertidal that is patchier and of lower density than at Tabook Point. This large eelgrass bed may be a dominant source of prey to which the chum shoals are responding. This site had the lowest shoal cohesiveness when the fish were shoaling, but the majority of fish for both the upper and lower tidal elevations the fish were not shoaling.

If decreased shoaling is mostly due to increased foraging then this site would have the highest foraging, presumably in the large, dense eelgrass bed in the lower intertidal. If this is the case, the lower intertidal eelgrass bed may also be contributing to prey distribution in the upper tidal elevations because less shoaling was evident in the upper tidal elevations at Tabook Point than the other sites and often less shoal cohesiveness than at the lower tidal elevation at Tabook Point.

Another interesting result from Tabook Point is the higher juvenile chum mean density in the lower intertidal compared to the upper intertidal that occurred in both sampling years. Because of the stay shallow mandate and the differences in beach slope, if there are the same number of fish at a site between the upper and lower intertidal the lower intertidal would have a lower density because the fish would have the ability to spread out in more available shallow water. But at Tabook Point the densities increased. It appears that Tabook Point has more fish present in the lower intertidal to compensate for the decreased beach slope. Possibly the reason for this is the dense eelgrass bed is attracting fish to feed during the low tide. With Tabook Point being the only site with a dense, continuous eelgrass bed it cannot be known for sure if this is happening, but further investigation with more replicates could clarify if this is actually happening.

The other site that had increased fish density in the lower intertidal is Barber Sand. This site was unique in two ways, it had sand in the upper intertidal and the lower intertidal was as steep as the upper intertidal (3.1° compared to 3.2°). All the other sites had cobble/gravel in the upper intertidal as well as a pronounced low-tide terrace. It is possible that chum are avoiding this site during the higher tide levels because of the sand substrate, but since this is the only site sampled with upper intertidal sand this is only conjecture. Fish did occur in the upper intertidal during the neap tides at a density of 1.6 fish per minute and this is close to the density during spring tides in the lower intertidal of 1.7 fish per minute. Again, with this being the only site with these conditions and with it being sampled only one year, it is difficult to say why this site had a higher chum density it the lower intertidal.

Another possibility for the observed density and behavioral differences is that there are larger landscape-scale processes operating beyond the upper vs. lower tidal elevation differences in microhabitat. For instance, if a site is closer to a natal chum stream than another site, the fish that encounter that site would have a different prehistory than fish at other sites that had been migrating for a longer time and distance.

Landscape Differences

To address landscape scale questions the two spatially close sites, Tabook Point and State Timberlands, can be compared. These two sites were chosen because they are close together (≈ 1.5 km) but have different microhabitats in the lower intertidal. Because it is close to Tabook Point, fish at the State Timberlands site should share more prehistory with those from Tabook Point than with those from the other two sites. Shoal cohesiveness was always less at Tabook Point, but this only reflects when fish were in shoals. If non-shoaling fish are taken into account, Tabook Point had far less shoaling (0.26 in shoals for Tabook Point with 0.98 in shoals at State Timberlands). Perhaps the most notable difference between Tabook Point and the other sites is the increase in mean chum density in the lower intertidal zone whereas State Timberlands had the expected decrease in lower intertidal density. If decreased shoal cohesiveness is related to increased foraging, then comparing Tabook Point to State Timberlands indicates that the dense, continuous eelgrass bed at Tabook Point may be an important foraging site for juvenile chum salmon at low tide. The increased density in the lower intertidal also provides evidence for this interpretation.

Migration pattern

Supplemental information that developed from the behavior of juvenile chum salmon is the migration pattern. There was an overall signal of migration toward the mouth of Hood Canal. This migration is not focused and linear however; there is a certain amount of wandering. The migration signal as well as the wandering are both reflected in the quadrat as well as the grid. In data from the 0.25 m^2 quadrat, 46% of fish were oriented within 45° of pointing toward the mouth of Hood Canal. While fish were in the 8-m x 6-m quadrat, they moved an average of 0.63 m per fish toward the mouth. If the chum swim at an average of 0.22 m/s (Appendix B) and 46% of their movement is directed toward the mouth, they would migrate at a rate of 8.7 km/day. This estimate agrees quite well with other estimates for chum migration rate. Estimates are 8-10 km/day for smaller April chum and 5-7 km/day for larger June chum (Whitmus & Olsen 1979). Other estimates are as high as 14 km/day (Bax 1983).

Based on the shoal movements while in the 8-m x 6-m grid, juvenile chum salmon migration orientation was generally more toward the mouth of Hood Canal when the fish were in upper tidal elevations during the spring tides. There was less migration toward the mouth in lower tidal elevations and in the upper elevations during the neap tides.

Covariates

If increased shoaling cohesiveness is truly reflective of less feeding then it may seem counterintuitive that fish are foraging less in the lower intertidal where prey densities are presumed to be higher. This study was designed to examine microhabitat use between the upper and lower tidal elevations at four sites in Hood Canal. However, there were other variables that were not explicitly tested that but that could also have predictably covaried with these intertidal zones. During the months of migrations, the low tides that drop into the lower intertidal occur from mid-morning to mid-afternoon. Any observations in the upper intertidal zone were earlier in the morning or later in the afternoon than the lower intertidal observations. Variables that would predictably covary with the tidal zones are time of day, light levels, water temperature, air temperature, currents, and at times, wind levels. The less shoal cohesiveness in the upper tidal elevation could reflect covariation with tidal level and the time of day.

Because of the stay shallow mandate, the chum are located in the upper intertidal in the early morning hours. If the early morning is when chum feed at the highest rates then this is the microhabtiat they will be primarily feeding from even though lower tidal elevations could very well have more available prey items. Then when the water drops into the lower tidal elevations they only top off their already full stomachs when prey is encountered. This would explain why at the three sites besides Tabook Point, the fish were in cohesive shoals in the lower intertidal. But a site such as Tabook Point could potentially be an important low tide feeding site for juvenile chum salmon that actually attracts fish.

Summary

Many studies have only examined density to determine if certain microhabitats are nurseries for juvenile marine fishes and invertebrates, but this says nothing how they are using, or meeting life requirements, in these microhabitats. Nearshore microhabitats are certainly nurseries for juvenile chum salmon. This study used density complemented with behavior to better understand how they are using these microhabitats. Research has suggested that lower intertidal microhabitats, in particular eelgrass beds, are important because they have higher densities of important prey resources for chum salmon, but the stay shallow mandate described in this study suggests there are other factors besides prey density that control juvenile chum salmon distribution and microhabitat use.

The stay shallow mandate encourages chum salmon to stay in shallow water. This mandate is probably in the form of something like “stay more shallow than 1.0 m” as opposed to “stay as shallow as possible.” So although chum prey densities are likely higher in lower intertidal microhabitats at high tide levels these microhabitats are unavailable to chum salmon because of the stay shallow mandate. The mandate likely exists as a way to avoid predation and represents a trade-off. The trade-off is possibly decreased access to foraging opportunities in the lower intertidal for increased protection from predators in the shallow water. Because of this mandate as well as the differences in beach slope between upper and lower intertidal microhabitats (and their associated eelgrass beds, macro and microalgae, etc.) any interpretations of only density are likely flawed.

Shoal cohesiveness increased in the lower intertidal. This may be a reflection of decreased foraging. If this is truly the case then less foraging in the lower intertidal it is likely a consequence of juvenile chum salmon only having access to this microhabitat from mid-morning to mid-afternoon on spring tidal series. This co-occurs with the times of days for lowest foraging.

The Tabook Point site had the lowest shoal cohesiveness metrics and also was the only site that had a large proportion of fish not occurring in shoals. This behavior combined with the unexpected increase in density in the lower intertidal indicate that this site may be an important foraging site for juvenile chum salmon during low tides. It is also the only site with a large, dense continuous eelgrass bed. Further investigation with more replicates would be needed to determine if this is what is actually happening.

This study also has implications for conservation. Hood Canal and Strait of Juan de Fuca summer chum are currently listed as threatened under the Endangered Species Act. They leave their natal streams and occupy nearshore microhabitats before the daytime tides start dropping into the lower intertidal. If they also follow the stay shallow mandate they will not have access to the lower intertidal. Another application to conservation is shoreline modification. Shoreline modifications (e.g. armoring, bulkheading) often truncate the shallow nearshore, but it is unclear how this affects juvenile chum salmon. This study has documented behavior in natural conditions and it could be compared to behavior in areas of shoreline modification. For instance, shoals sizes in this study were smaller than are found in modified shorelines (Toft *et al*. 2007). The consequences of these differences or lack of differences could then be determined.

References

Ames, J., G. Graves & C. Weller (ed.). 2000. Summer Chum Salmon Conservation Initiative: An Implementation Plan to Recover Summer Chum in the Hood Canal and Strait of Juan de Fuca Region. Wash. Dept. Fish Wildl., Olympia, WA, and Point-No-Point Treaty Tribes, Hansville, WA.

Baird, T.A., C.H. Ryer & B.L. Olla. 1991. Social enhancement of foraging on an ephemeral food source in juvenile walleye pollock, *Theragra chalcogramma*. Environmental Biology of Fishes 31: 307-311.

Bax, N.J. 1982. Seasonal and annual variations in the movement of juvenile chum salmon through Hood Canal, Washington. *In:* E.L. Brannon, E. O. Salo (ed.) Proceedings of the Salmon and Trout Migratory Behavior Symposium, School of Fisheries, University of Washington, Seattle, WA.

Bax, N.J. 1983. The early marine migration of juvenile chum salmon (*Oncorhynchus keta*) through Hood Canal - its variability and consequences, University of Washington, Seattle, WA. 196 pp.

Bayer, R.D. 1986. Seabirds near an Oregon estuarine salmon hatchery in 1982 and during the 1983 El Nino. Fishery Bulletin 84: 279-286.

Beck, M.W., J. Heck, K.L., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan & M.P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51: 633-641.

Blaber, S.J.M. & T.G. Blaber. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. Journal of Fish Biology 17: 143-162.

Block, W.M. & L.A. Brennan. 1993. The habitat concept in ornithology. pp. 35-91. *In:* D.M. Power (ed.) Current Ornithology, Plenum Press, New York, New York.

Burns, R. 1985. The Shape and Form of Puget Sound. Washington Sea Grant, Seattle, WA.

Colgan, P. 1993. The motivational basis of fish behaviour. pp. 31-55. *In:* T.J. Pitcher (ed.) Behaviour of Teleost Fishes, Chapman and Hall, London, UK.

Cordell, J.R. 1986. Structure and dynamics of an epibenthic harpacticoid assemblage and the role of predation by juvenile salmon, University of Washington, Seattle, WA. 186 pp.

D'Amours, D. 1987. Trophic phasing of juvenile chum salmon (*Oncorhynchus keta* Walbaum) harpacticoid copepods in the Fraser River Estuary, British Columbia, University of British Columbia, Vancouver, BC. 163 pp.

Downing, J. 1983. The Coast of Puget Sound. Washington Sea Grant, Seattle, WA.

Duffy, E.J. & D.A. Beauchamp. 2008. Seasonal patterns of predation by juvenile Pacific salmon by anadromous cutthroat trout in Puget Sound. Transactions of the American Fisheries Society 137: 165-181.

Eggers, D.M. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. Journal of the Fisheries Research Board of Canada 33: 1965-1971.

Ellis, W.L. & S.S. Bell. 2003. Conditional use of mangrove habitats by fishes: depth as a cue to avoid predators. Estuaries 27: 966-976.

Finlayson, D. 2006. The geomorphology of Puget Sound beaches. Puget Sound Nearshore Partnership Report No. 2006-02. Published by Washington Sea Grant Program, University of Washington, Seattle, Washington.

Fukuwaka, M.-a. & T. Suzuki. 1998. Role of a riverine plume as a nursery area for chum salmon *Oncorhynchus keta*. Marine Ecology Progress Series 173: 289-297.

Godin, J.G.J. 1986. Antipredator function of shoaling in teleost fishes: a selective review. Le Naturaliste Canadien 113: 241-250.

Hager, M.C. & G.S. Helfman. 1991. Safety in numbers: shoal size choice by minnows under predatory threat. Behavioral Ecology and Sociobiology 29: 271-276.

Hargreaves, N.B. & R.J. Lebrasseur. 1986. Size selectivity of coho, *Oncorhynchus kisutch,* preying on juvenile chum salmon, *Oncorhynchus keta*. Canadian Journal of Fisheries and Aquatic Sciences 581-586: 581-586.

Hargreaves, N.B., R.J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). Canadian Journal of Fisheries and Aquatic sciences 42: 659-668.

Healey, M.C. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: I. Production and feeding rates of juvenile chum salmon (*Oncorhynchus keta*). Journal of the Fisheries Research Board of Canada 36: 488-496.

Healey, M.C. 1982a. The distribution and residency of juvenile salmon in Georgia Strait, British Columbia. pp. 61-69. *In:* B.R. Melteff, R.A. Neve' (ed.) Proceedings of North Pacific Aquaculture Symposium.

Healey, M.C. 1982b. Juvenile Pacific salmon in estuaries: the life support system. pp. 315-341. *In:* V.S. Kennedy (ed.) Estuarine Comparisons, Academic Press, New York, NY.

Healey, M.C. 1982c. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Canadian Journal of Fisheries and Aquatic sciences 39: 952-957.

Heck, K.L., Jr., G. Hays & R.J. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253: 123-136.

Heck, K.L., Jr. & T.A. Thoman. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesepeake Bay. Estuaries 7: 70-92.

Hoare, D.J., I.D. Couzin, J.G.J. Godin & J. Krause. 2004. Context-dependent group size choice in fish. Animal Behaviour 67: 155-164.

Hosack, G.R., B.R. Dumbauld, J.L. Ruesink & D.A. Armstrong. 2006. Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (Zostera marina) and oyster (Crassostrea gigas) habitats. Estuaries and Coasts 29: 1150-1160.

Kaczynski, V.W., R.J. Feller, J. Clayton & R.J. Gerke. 1973. Trophic analysis of juvenile pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*) in Puget Sound. Journal of the Fisheries Research Board of Canada 30: 1003-1008.

Krebs, J.R. & N.B. Davies. 1993. An Introduction to Behavioural Ecology. Blackwell Science Ltd, London, England. 420 pp.

Landingham, J.H. 1982. Feeding ecology of pink and chum salmon fry in the nearshore habitat of Auke Bay, Alaska, University of Alaska, Juneau, Juneau, AK. 132 pp.

Lipcius, R.N., W.T. Stockhausen, D.B. Eggleston, L.S.J. Marshall & B. Hickey. 1997. Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: source-sink dynamics? Marine and Freshwater Research 48: 807-815.

Macdonald, J.S. & B.D. Chang. 1993. Seasonal use by fish of nearshore areas in an urbanized coastall inlet in southwestern British Columbia. Northwest Science 67: 63-77.

Magnhagen, C. 1988. Predation risk and foraging in juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). Canadian Journal of Fisheries and Aquatic Sciences 45: 592-596.

Magurran, A.E. 1990. The adaptive significance of schooling as an antipredator behaviour. Annales Zoologici Fennici 27: 51-66.

Magurran, A.E. & T.J. Pitcher. 1983. Foraging, timidity, and shoal size in minnows and goldfish. Behavioral Ecology and Sociobiology 12: 147-152.

Magurran, A.E. & T.J. Pitcher. 1987. Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. Proceedings of the Royal Society of London, Series B 229: 439-465.

Mardia, K.V., P.E. Jupp. 2000. Directional Statistics. John Wiley and Sons LTD, West Sussex, UK. 429 pp.

Mason, J.C. 1974. Behavioral ecology of chum salmon fry (*Oncorhynchus keta*) in a small estuary. Journal of the Fisheries Research Board of Canada 31: 83-92.

McDonald, M.E., A.E. Hershey & W.J. O'Brien. 1992. Cost of predation avoidance in young-of-year lake trout (*Salvenius namaycush*): growth differential in sub-optimal habitats. Hydrobiologia 240: 213-218.

Mittelbach, G.G. 1984. Group size and feeding rate in bluegills. Copeia 1984: 998-1000.

Nagasawa, K. & M. Kaeriyama. 1995. Predation by Fishes and Seabirds on Juvenile Chum Salmon (*Oncorhynchus keta*) in Coastal Waters of Japan: A Review. Scientific Reports of the Hokkaido Salmon Hatchery 0: 41-53.

Orth, R.J., K.L. Heck, Jr., J.V. Montfrans. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 4A: 339-350.

Pavlov, D.S., A.O. Kasumyan. 2000. Patterns and mechanisms of schooling behavior in fish: a review. Journal of Ichthyology 40: S163-S231.

Peuhkuri, N., E. Ranta, S.K. Juvonen & K. Lindström. 1995. Schooling affects growth in the 3-spined stickleback, *Gasterosteus aculeatus*. Journal of Fish Biology 46: 221-226.

Pitcher, T.J. 1983. Heuristic definitions of shoaling behavior. Animal Behavior 31: 611-613.

Pitcher, T.J. 1986. Predators and food are the keys to understanding fish shoals: a review of recent experiments. Le Naturaliste Canadien 113: 225-233.

Pitcher, T.J., A.E. Magurran & I.J. Winfield. 1982. Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology 10: 149-151.

Pitcher, T.J. & J.K. Parrish. 1993. Functions of shoaling behaviour in teleosts. pp. 715. *In:* T.J. Pitcher (ed.) Behaviour of Teleost Fishes, Chapman and Hall, London, UK.

Power, M.E. 1984. Depth distribution of armored catfish: predator-influenced resource avoidance? Ecology 65: 523-528.

Ranta, E. & V. Kaitala. 1991. School size affects individual feeding success in three-spined sticklebacks (*Gasterosteus aculeatus* L.). Journal of Fish Biology 39: 733-737.

Ruiz, G.M., A.H. Hines & M.H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Cheasepeake Bay. Marine Ecology Progress Series 99: 1-16.

Ryer, C.H. & B.L. Olla. 1991. Information transfer and the facilitation and inhibition of feeding in a schooling fish. Environmental Biology of Fishes 30: 317-323.

Ryer, C.H. & B.L. Olla. 1992. Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. Animal Behaviour 44: 69-74.

Ryer, C.H. & B.L. Olla. 1995. Influences of food distribution on fish foraging behaviour. Animal Behaviour 49: 411-418.

Ryer, C.H. & B.L. Olla. 1996. Social behavior of juvenile chum salmon, *Oncorhynchus keta*, under risk of predation: the influence of food distribution. Environmental Biology of Fishes 45: 75-83.

Ryer, C.H. & B.L. Olla. 1998. Shifting the balance between foraging and predator avoidance: the importance of food distribution for a schooling pelagic forager. Environmental Biology of Fishes.

Sackley, P.G. & L.S. Kaufman. 1996. Effect of predation on foraging height in a planktivorous coral reef fish, *Chromis nitida*. Copeia 1996: 729-729.

Salo, E.O. 1991. Life history of chum salmon (*Oncorhynchus keta*). pp. 564. *In:* C. Groot & L. Margolis (ed.) Pacific Salmon Life Histories, UBC Press, Vancouver, BC.

Salo, E.O., N.J. Bax, T.E. Prinslow, C.J. Whitmus, B.P. Snyder & C.A. Simenstad. 1980. The effects of construction of naval facilities on the outmigration of juvenile salmonids from Hood Canal, WA. UW Fish. Res. Inst. rpt. FRI-UW-8006. Univ. of Wash., Seattle, WA. 159 pp.

Schreiner, J.U., E.O. Salo, B.P. Snyder & C.A. Simenstad. 1977. Salmonid Outmigration Studies in Hood Canal: Final Report, Phase II. UW Fish. Res. Inst. rpt. FRI-UW-7715. Univ. of Wash., Seattle, WA. 64 pp.

Sibert, J. 1979. Detritus and juvenile salmon production in the Nanaimo estuary. 2: meiofauna available as food for juvenile salmon. Journal of the Fisheries Research Board of Canada 36: 497-503.

Simenstad, C.A., J.R. Cordell, R.C. Wissmar, K.L. Fresh, S.L. Schroder, M. Carr, G. Sanborn & M. Burg. 1988. Assemblage structure, microhabitat distribution, and food web linkages of epibenthic crustaceans in Padilla Bay National Estuarine Research Reserve, Washington. UW Fish. Res. Inst. rpt. FRI-UW-8813. Univ. of Wash., Seattle, WA.

Simenstad, C.A., K.L. Fresh & E.O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. pp. 343-364. *In:* V.S. Kennedy (ed.) Estuarine Comparisons, Academic Press, New York, NY.

Simenstad, C.A., R.J. Garono, T. Labbe, A.C. Mortimer, R. Robinson, C. Weller, S. Todd, J. Toft, J. Burke, D. Finlayson, J. Coyle, M. Logsdon & C. Russell. 2008. Assessment of intertidal eelgrass habitat landscapes for threatened salmon in the Hood Canal and Eastern Strait of Juan de Fuca, Washington State. pp. 152, Point No Point Treaty Council, Hansville, WA.

Simenstad, C.A., W.J. Kinney, S.S. Parker, E.O. Salo, J.R. Cordell & H. Buechner. 1980. Prey community structure and trophic ecology of outmigrating juvenile chum and pink salmon in Hood Canal, Washington: a synthesis of three years' studies, 1977-1979. UW Fish. Res. Inst. rpt. FRI-UW-8026. Univ. of Wash., Seattle, WA. 113 pp.

Street, N.G. & P.J.B. Hart. 1985. Group size and patch location by the stoneloach, *Noemacheilus barbatulus*, a non-visually foraging predator. Journal of Fish Biology 217: 785-792.

Thorpe, J.E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17: 76-93.

Toft, J.D., J.R. Cordell, C.A. Simenstad & L.A. Stamatiou. 2007. Fish Distribution, Abundance, and Behavior along City Shoreline Types in Puget Sound. North American Journal of Fisheries Management 27: 465-480.

Webb, D.G. 1991a. Effect of predation by juvenile Pacific salmon on marine harpacticoid copepods. I. Comparisons of patterns of copepod mortality with patterns of salmon consumption. Marine Ecology Progress Series 72: 25-36.

Webb, D.G. 1991b. Effect of predation by juvenile Pacific salmon on marine harpacticoid copepods. II. Predator density manipulation experiments. Marine Ecology Progress Series 72: 37-47.

Werner, E.E., J.F. Gilliam, D.J. Hall & G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540-1548.

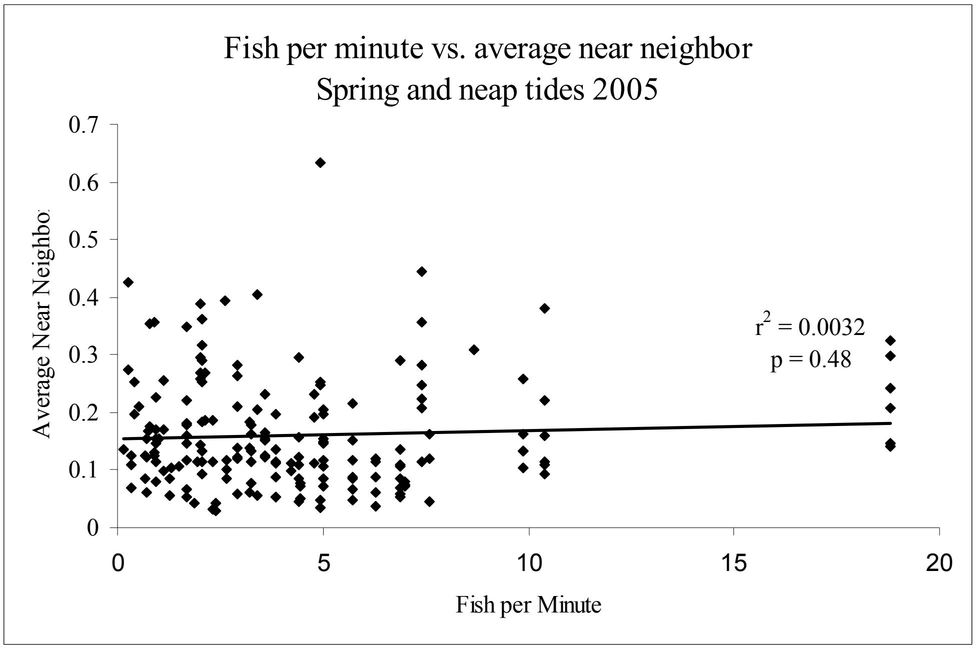
Whitmus, C.J. & S. Olsen. 1979. The migratory behavior of juvenile chum salmon released in 1977 from the Hood Canal Hacthery, Hoodsport, Washington. pp. 46, Fisheries Research Institute, Seattle, WA.

Zar, J.H. 1999. Biostatistical Analysis. Prentice Hall, Upper Saddle River, NJ.

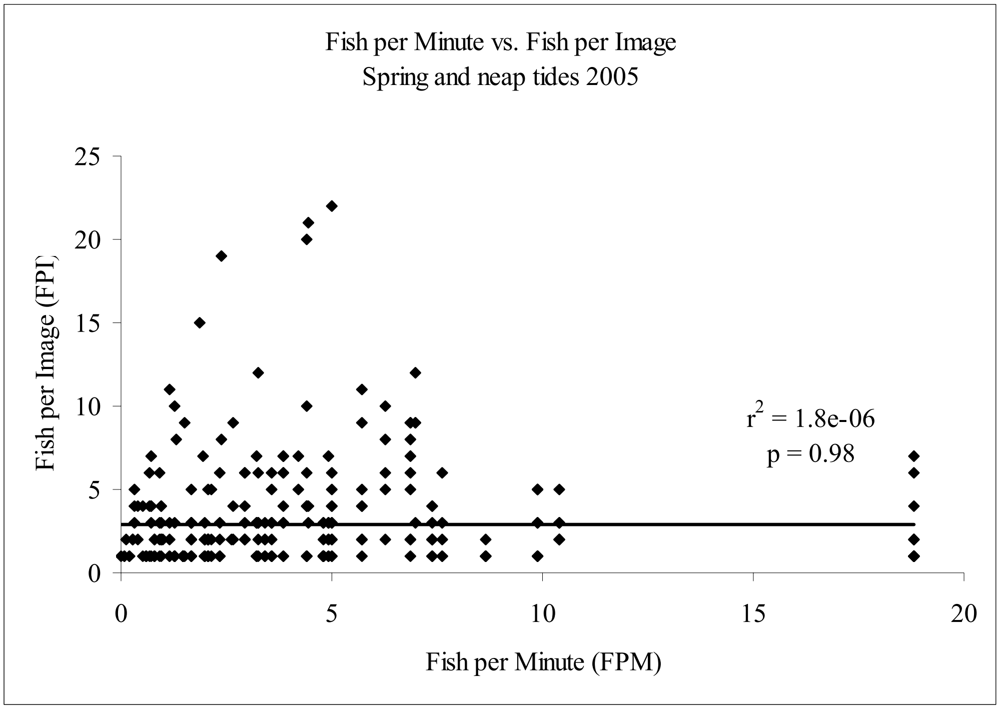
Appendix A - Density and Shoal Compactness Relationships

Density and shoal compactness – FPM vs. ANN and FPM vs FPI regressions

To investigate if the fish are simply become closer together solely because of increased density, regressions were run with fish per minuteFish as the independent variable and mean nearest neighbor and fish per image as the dependent variables. Neither had a significant effect on the slope of the regression line. The fish per minute vs. mean nearest neighbor regression had a p-value of ~ 0.45 and an r^2 of < 0.01. The fish per minute vs. fish per image regression had a p-value of ~ 0.98 and a r^2 of < 0.0001.



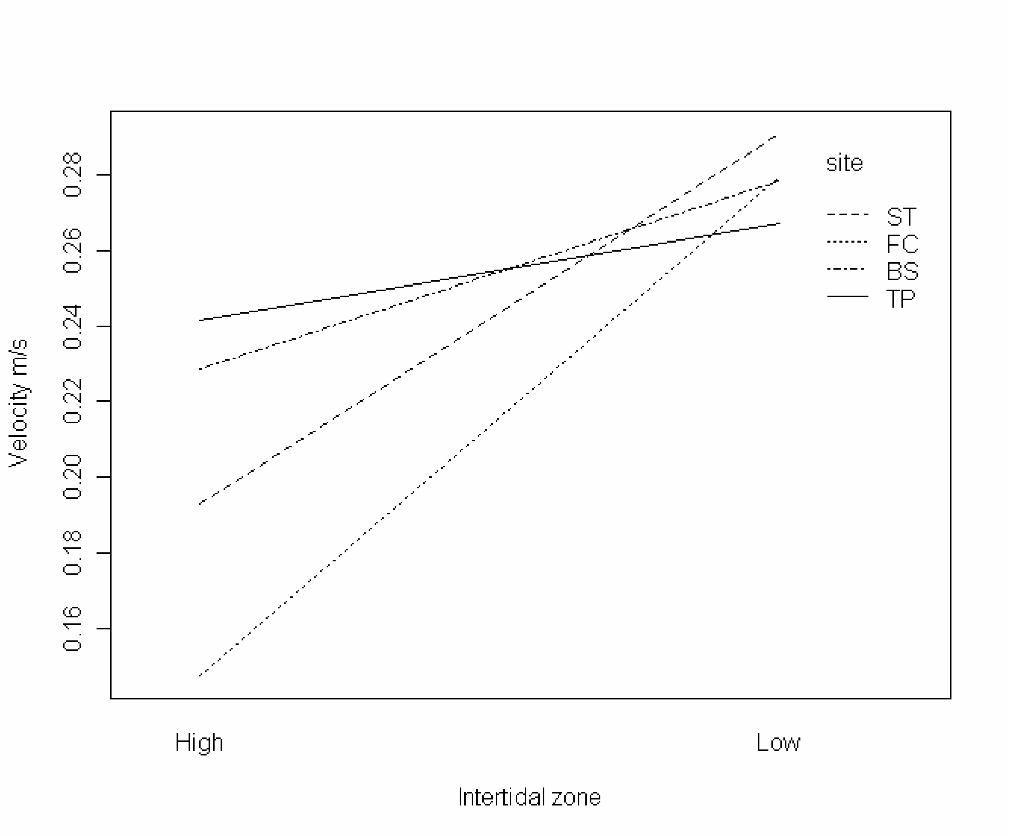
Appendix A. Fish per minute vs. average nearest neighbor distance (m) for spring and neap tides 2005.



Appendix A. Fish per minute vs. fish per image regression for 2005 data. Includes both spring and neap tide series.

Appendix B - Shoal Velocity

Velocity for 2005 was analyzed by taking the total length traveled by a shoal while in the 8-m x 6-m grid and dividing by the time it took to travel this distance. Again the same dates were used, the data was log(x+1) transformed, and a type II ANOVA was performed. None of the factors were significant including interaction.



Appendix B. Velocity calculated from movements within the 8-m x 6-m grid. Spring tide data only from 4/8/2005 and 5/13/2005.