AN ABSTRACT OF THE THESIS OF

Kelly A. Muething for the degree of Master of Science in Marine Resource Management presented on May 23, 2018.

Title: On the Edge: Assessing Fish Habitat Use Across the Boundary between Pacific Oyster Aquaculture and Eelgrass in Willapa Bay, WA.

Abstract approved: ____

Brett R. Dumbauld

Estuaries are an important ecological link between terrestrial, freshwater, and marine systems, but are also subject to a variety of human pressures. Along the West Coast of the United States, shellfish aquaculture is one extensive use of estuarine tidelands. Specifically, Pacific oyster (*Crassostrea gigas*) aquaculture has been practiced for almost 100 years, significantly contributing to the culture and economy of the region. However, this activity does not exist in isolation. Oyster aquaculture commonly occurs in intertidal areas where native eelgrass (*Zostera marina*) is also present. Seagrasses provide valuable nursery habitat for many commercially-harvested species (e.g. salmonids, English sole, and Dungeness crab) and have recently garnered more conservation interest because they are declining in many locations. For these reasons, eelgrass is protected as “essential fish habitat” under the Magnuson-Stevens Fishery Conservation and Management Act. This protection restricts or prohibits oyster aquaculture within or near eelgrass. To help inform management decisions around this issue, questions were addressed regarding the use of both aquaculture and eelgrass as habitat for fish and crabs. Specifically, I was interested in quantifying and distinguishing whether the edge between these two habitats supported a different number of fauna. Information about edge effects could help elucidate potential consequences of aquaculture expansion at the scale of the whole estuary. Due to a recent shift towards off-bottom culture methods, in part to protect seagrasses, this comparison was made in both long-line and on-bottom aquaculture. Direct (underwater video) and indirect (e.g. predation tethering units) measures of fish and invertebrate community composition and behavior were used to quantify effects along a transect that ran between aquaculture and eelgrass in each type of aquaculture.

Results suggest that species use long-line oyster aquaculture and eelgrass habitats similarly with minimal effect of the edge. However, habitat use of the on-bottom aquaculture was less than both the long-line aquaculture and eelgrass beds. This is consistent with an expected positive relationship between faunal abundance and the amount of vertical structure within a habitat. These conclusions add to the best available science regarding aquaculture and eelgrass interactions and provide valuable insight to managers and permitting agencies as they consider requests to expand culture operations.

On the Edge: Assessing Fish Habitat Use Across the Boundary between Pacific Oyster Aquaculture and Eelgrass in Willapa Bay, WA

by
Kelly A. Muething

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented May 23, 2018
Commencement June 2018

Master of Science thesis of Kelly A. Muething presented on May 23, 2018

APPROVED:

Major Professor, representing Marine Resource Management

Dean of the College of Earth, Ocean, and Atmospheric Sciences

Dean of the Graduate School

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

Kelly A. Muething, Author

ACKNOWLEDGEMENTS

There are so many who have both directly and indirectly helped me to reach this point in my educational career. I would first like to thank my advisor, Dr. Brett Dumbauld, for guiding me through the research process and introducing me to the complexities of shellfish aquaculture in the Pacific Northwest. I admire your dedication to your work and ability to engage with relevant stakeholders. I am also extremely grateful for the time and advice of the rest of my thesis committee. Dr. George Waldbusser, thank you for pushing me to think critically about the development and communication of the research. Dr. Scott Heppell, I appreciate your ability to see different perspectives and question the reasoning behind the methodology. And Dr. Fiona Tomas-Nash, thank you for your encouragement, funding support, and patience as I navigated the world of seagrass research. I would also like to express sincere gratitude to all those who helped in the field and lab: Allie Blanchette, Katie Houle, Dacey Mercer, Mary Middleton, Jonathan Minch, and Grant Schwinge. I could not have done this without you all, and it would definitely not have been as much fun. This research and my time were funded in part by a 2016-2017 Provost Fellowship from Oregon State University, two NOAA NMFS Saltonstall-Kennedy grants (2014/2015 NOAA-NMFS-FHQ-2015-2004246 and 2016/2017 NA16NMF4270254), a 2016-2018 Oregon State University Agricultural Research Foundation grant to Dr. Fiona Tomas-Nash, and project funds of the USDA Agricultural Research Service (CRIS Project 2072-63000-004-00D).

I would also like to thank those associated with the Marine Resource Management program. Thank you to Flaxen Conway, Lori Hartline, and Robert Allan for answering my questions, listening to my concerns, and having faith in me. I learned so much during my time here and am so grateful for having been given this opportunity. My MRM cohort and the MRM program were a source of great support as I navigated the challenges of graduate school – thank you to all for the many soup lunches, office chats, and for pushing me out of my comfort zone when necessary. Finally, I would like to thank those who have supported me personally and made me the scientist that I am today. Thanks to Ms. Arbona, Ray, Kevin, and the many others who encouraged my inquisitiveness and taught me about the wonders of the natural

world. Thank you to my parents and siblings for always being there in the midst of busy and challenging lives. And thank you to Joe for the countless phone calls, long flights, and for believing in me even when I did not.

TABLE OF CONTENTS

Page

TABLE OF CONTENTS (Continued)

Page

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

CHAPTER 1: GENERAL INTRODUCTION

To function ecologically, estuarine organisms must adapt to pressure from a variety of human activities, including industry, recreation, and fisheries. Historically, human populations have flourished around these productive ecosystems and that trend has continued into the present day (Lotze et al. 2006). As of 2010, about 40% of the population of the United States lived within shoreline counties (NOAA 2017). Estuaries provide a wide array of ecosystem services and constitute an ecologically and economically important link between terrestrial, freshwater, and marine systems (Costanza et al. 1997). Along the West Coast of the United States, estuarine tidelands have been extensively used for shellfish production for over a century. This is a culturally and economically significant practice within the Pacific Northwest but comprises just one of many uses of the intertidal zone. Aside from the shellfish industry, many other stakeholder groups exist, including those interested in the protection and conservation of seagrasses native to this region. Because of the limited space within estuarine tidelands, conflict arises. To explore the regulatory and ecological relationships between these two interests, the issue will be examined within a coastal estuary in Washington State. Shellfish aquaculture is dominated by oyster production in Washington, a state where both oyster aquaculture and seagrasses are strongly rooted in the economy and culture (Washington Sea Grant 2015). Further exploration of the key social and ecological questions illuminates the challenges of this issue.

1.1 HISTORY OF OYSTER PRODUCTION IN WILLAPA BAY, WA

Commercial harvest of oysters has occurred within Willapa Bay, WA since the 1850s. The native Olympia oyster (*Ostrea lurida*) was initially harvested, but populations were quickly depleted and the Eastern oyster (*Crassostrea virginica*) was introduced in 1893 (Townsend 1896, Dumbauld et al. 2011). Around this same time, the State of Washington was working to prioritize shellfish production and aquaculture in the tidal zone of its estuaries. In 1895, the Bush and Callow Acts were passed, authorizing the sale of a large portion of state-owned intertidal lands into private ownership for shellfish production (RCW 79.135*)*. The sale of tidelands into private ownership ceased with the Gissberg Amendment in 1971 (RCW

79.125.200(2)). Nonetheless, these lands have retained their designation for shellfish production, evidence that, according to state legislators, shellfish aquaculture is a use of tidelands that falls within the public interest (Johnson et al. 1991). If this was not the case, the policy would be in violation of the Public Trust Doctrine, which holds all lands between the mean lower low water (MLLW) line and the mean higher high water (MHHW) line in public trust.

Following the decline of Eastern oysters in 1919, Pacific oysters (*Crassostrea gigas*) were introduced in 1928 to Willapa Bay from Japan for use in oyster aquaculture (Dumbauld et al. 2011). This species has been introduced around the world and continues to be the primary oyster farmed in Washington State and throughout estuaries along the Pacific Coast of the United States (Washington Sea Grant 2015). Today, Willapa Bay is the largest single production site of oysters in the country, with about 20% of the intertidal zone devoted to oyster aquaculture (Dumbauld et al. 2011). Commercial landings surveys indicate the State of Washington produced about 5.7 million pounds of Pacific oysters in 2016, valued at ~$32.4 million (NMFS 2016). As of 2013, 25% of that statewide production could be attributed to Willapa Bay. In addition, due to this productivity, Pacific County which encompasses Willapa Bay was found to be the most aquaculture-dependent county in the state, with 20% of the economy based in aquaculture (Washington Sea Grant 2015). Throughout the state, 2,710 jobs were generated by the shellfish industry in 2010 (NOAA 2016). Thus, not only does the oyster aquaculture industry help to meet demand for seafood, but it also contributes substantially to the state and local economy through jobs and revenue.

Due to the rising demand for seafood, attention has focused on the growth of aquaculture production (FAO 2014). Currently, aquaculture within the United States contributes just 5% of seafood consumed domestically (NOAA 2011). Thus, there is great potential for the expansion of shellfish aquaculture to help meet some of the national demand. The State of Washington has taken steps to recognize the importance of the shellfish industry. Under the Shoreline Management Act of 1971, aquaculture was denoted as a “water-dependent use” of state coastal zones (RCW 90.58). Such policy indicates that shellfish aquaculture is a preferred use of the state’s shorelines. Following national policy initiatives, the guidelines given for counties to develop their specific Shoreline Master Programs also specify that aquaculture is of statewide interest, making it an activity of top priority (Washington State Department of Ecology 2015). To combine these goals, the Washington Shellfish Initiative was established in 2011, following the principles of the National Oceanic and Atmospheric Administration’s (NOAA) National Shellfish Initiative that has the simple goal of putting more bivalves in US coastal waters (NOAA 2018). As a partnership among local and state governments, tribes, non-profit organizations, and the shellfish industry, the Washington Shellfish Initiative is meant to promote the ecosystem and social services provided by shellfish production (Washington State Department of Ecology 2015). Thus, within the State of Washington, shellfish aquaculture is recognized as a beneficial economic and cultural practice that helps to provide seafood for people across the country.

1.2 EELGRASS HABITAT AND PROTECTION

While shellfish aquaculture is a significant use of estuarine tidelands in Washington, it is not the only human interest that exists there. Around the world, seagrasses are recognized as significant ecosystem engineers and contributors to ecosystem services, including carbon sequestration, water current reduction, water quality improvement, and mitigation of ocean acidification (Jones et al. 1994, Costanza et al. 1997, Orth et al. 2006, Hendriks et al. 2014). Pertinent to the issue described here, seagrass beds have been noted as important nursery habitats for many juvenile marine fish and invertebrates (Beck et al. 2001, Heck et al. 2003, Sheaves et al. 2015, Nagelkerken et al. 2015). The native eelgrass (*Zostera marina*) can be found in intertidal and shallow subtidal regions of estuaries. Eelgrass provides a structured habitat within the estuarine habitat matrix, supporting a more diverse community of species than unvegetated areas (Orth et al. 1984, Ferrell and Bell 1991, Jenkins et al. 1997, Pinnix et al. 2005, Hosack et al. 2006, Ferraro and Cole 2010). In Willapa Bay, *Z. marina* naturally occurs at tidal elevations between –1m and +0.5m relative to MLLW (Ruesink et al. 2010). Eelgrass often grows in large monospecific meadows, due to asexual, clonal reproduction through rhizomes. Reproduction can also occur through flowering and seed production, allowing the species to colonize new areas (den Hartog 1970). Nonetheless, this expansion through sexual reproduction is infrequent, limiting the ability of the species to populate areas distant from established beds (Rasheed 2004). Eelgrass also experiences an annual growth cycle, with highest biomass and shoot density during the summer months (Orth and Moore 1986, Thom et al. 2003, Ruesink et al. 2010, Zhang et al. 2016). This coincides with increased abundances of many estuary-dependent species, suggesting a correlation with eelgrass as habitat (Hosack et al. 2006). Because of this habitat use and the recognition that seagrass is declining in many areas, there is great interest in eelgrass conservation and protection (Short and Burdick 1996, Orth et al. 2006, Waycott et al. 2009). To add to this, these ecological concerns are combined with an economic significance in the Pacific Northwest.

Eelgrass is economically significant because it provides nursery habitat for commercial fisheries species like salmonids, Dungeness crab, and English sole (Rooper et al. 2003, Holsman et al. 2006, Dumbauld et al. 2015). Similar to shellfish production, these fisheries make up a significant monetary and cultural contributions to the region. For example, commercial salmon landings in Washington had a value of about $26.1 million (NMFS 2016). Regionally, the decline of salmon populations and interest in protection of future stocks has encouraged action to conserve habitats used at various life stages. Because salmon are anadromous, inhabiting both riverine and marine environments, estuaries are significant points of interaction and habitat use. For these reasons, estuaries have been designated as “essential fish habitat” (EFH) under the Magnuson-Stevens Fishery Conservation and Management Act (USC 16.38). In fact, for salmon in the Pacific region, EFH makes up most of the exclusive economic zone (200 nautical miles) off the West Coast (Pacific Fishery Management Council 2016). While the Magnuson-Stevens Act originally emphasized the economic future of commercial fisheries, subsequent passage of the Sustainable Fisheries Act in 1996 shifted the focus to preservation of fishery stocks and the habitats they rely on, including designation as EFH. This designation restricts the activities that can occur within and adjacent to the protected habitat. In this capacity, fisheries management becomes important for spatial planning within estuaries, influencing activities not directly connected with fishing grounds. Under EFH, “habitat areas of particular concern”

(HAPC) can also be designated. Both estuaries and estuarine submerged aquatic vegetation, like eelgrass, are considered to be HAPC for salmon due to the important nursery functions they provide (Pacific Fishery Management Council 2014). Estuaries and the three-dimensional structure added by submerged aquatic vegetation are recognized as refugia from predators and give juvenile salmon time to acclimate to a saline environment (Simenstad et al. 1982, Semmens 2008, Dumbauld et al. 2015). Thus, these HAPC play a significant role in a crucial life stage of salmon but are under increasing pressure from other human interests within estuaries.

Within Willapa Bay, the designation of eelgrass as HAPC has implications for the shellfish aquaculture industry. Eelgrass and shellfish aquaculture often occur within the same tidal range in estuaries. Shellfish aquaculture and the presence of eelgrass beds are often considered to be mutually exclusive due to the practice of mechanically harvesting oysters grown directly on the bottom (Neckles et al. 2005, Tallis et al. 2009). While this is not the case, there is a general regulatory understanding that activities involved in shellfish aquaculture limit the range of the native eelgrass (Everett et al. 1995, Wisehart et al. 2007, Tallis et al. 2009, Wagner et al. 2012, Skinner et al. 2013). At the very least, shellfish aquaculture comes into conflict with eelgrass through a competition for space. The cooccurrence of these two stakeholder interests within estuaries creates a complex management issue that requires sufficient scientific understanding to alleviate.

1.3 IMPACTS OF OYSTER AQUACULTURE

In order to inform managers and design regulations to maintain shellfish aquaculture and surrounding estuarine habitats, there has been interest in investigating the ecological impacts of these practices on the functionality of nearby habitats. Oyster aquaculture can be viewed as both a long-term and short-term disturbance to the estuarine system (Dumbauld et al. 2009). The addition of biological and physical material (i.e. shellfish and associated gear for aquaculture) can affect a continual (press) impact on the surrounding environment while the processes associated with harvest and maintenance of the beds are discrete (pulse) events (Simenstad and Fresh 1995, Dumbauld et al. 2009). The addition of the oysters themselves can affect biodeposition, nutrient cycling, and local sedimentary processes (Newell 2004). As filter feeders, oysters take suspended particulate matter out of the water column, potentially improving water quality (Dumbauld et al. 2009). However, the addition of oysters for aquaculture can cause issues with shell accumulation, accretion of sediment, and shading by the physical structure associated with off-bottom methods (Newell 2004, Ruesink et al. 2005, McKindsey et al. 2006, Forrest et al. 2009). Although these changes to the physical and chemical processes within the bed are often limited to the local areas under culture, the interactions between oyster aquaculture and other habitats within the habitat matrix can potentially expand the reach of these impacts (Crawford et al. 2003, Forrest and Creese 2006). Viewing oyster aquaculture in the context of the larger estuarine ecosystem illuminates possible larger-scale consequences of converting tidelands to commercial culture.

While oyster reefs provide an important habitat for many estuarine species, the production and regular harvest of oysters does not typically allow these reefs to develop (Coen et al. 1999). All methods of oyster aquaculture create relatively novel habitats, as compared to oyster reefs or other natural structured habitats. As noted above, habitats with more three-dimensional structure in estuaries support higher abundances and a greater diversity of organisms than unstructured habitats due to trade-offs between resource availability and refuge from predators (Orth et al. 1984, Jenkins et al. 1997, Heck et al. 2003). When compared to eelgrass and unstructured habitats, oyster aquaculture is often intermediate with regards to habitat structure. Because of the structure and resources provided by the oysters, the diversity and abundance of organisms is generally higher in aquaculture beds than in mudflats, including for epibenthic species (Castel et al. 1989, Pinnix et al. 2005, Hosack et al. 2006, Ferraro and Cole 2007). However, the comparison is more complicated between eelgrass and aquaculture beds. The structure provided by oyster aquaculture may be functionally similar to that provided by eelgrass, so responses are often species-specific. Benthic invertebrates were more dense in eelgrass than oyster aquaculture beds, but for fish and other mobile species, the abundances were either similar or greater within aquaculture beds (Dealtris et al. 2004, Pinnix et al. 2005, Hosack et al. 2006). This result suggests that the habitat structure is comparable between eelgrass and oyster aquaculture beds, but more work is necessary to fully capture the impact of aquaculture at the estuary scale.

1.4 SEASCAPE ECOLOGY AND EDGE EFFECTS

Eelgrass and aquaculture both exist within an estuarine habitat mosaic consisting of varying types and quality of habitat. Exploration of the relationships between these habitats and their effects on organisms has been based in concepts originating on land. The field of landscape ecology has sought to investigate how the arrangement of different habitats at the spatial scale of the landscape affects the distribution of organisms in terrestrial systems (Forman and Godron 1986, Turner 1989, Wiens and Milne 1989). These inquiries ultimately led to questions about the effects of edges or boundaries between habitats. Edges represent abrupt changes in resource availability, refugia, and predation risk that can influence the abundance and diversity of organisms through a variety of mechanisms (Gates and Mosher 1981, Ewers et al. 2007). In general, edge effects result from ecological trade-offs, including those between predation risk and foraging potential (Macreadie et al. 2010, 2012, Smith et al. 2011, Carroll and Peterson 2013). Recently, particular attention has been paid to edge effects in terrestrial systems because of increased fragmentation of natural habitats due to human development (Debinski and Holt 2000). Fragmentation increases the amount of edge that exists relative to the core or interior of the habitat (i.e. edge-to-area ratio; Ewers and Didham 2007). This can be especially important for conservation because certain species rely heavily on interior habitat area for growth and survival (Bender et al. 1998, Bogaert et al. 2001).

Seascape ecology adapts the tenets of landscape ecology and applies them to estuarine, coastal, and open ocean ecosystems (Bartlett and Carter 1991). Just as in terrestrial systems, marine organisms must navigate a complex mosaic of habitat type and quality, often leading to a distinct effect of the boundary between habitats. Research on edge effects within marine ecosystems has focused on seagrasses because of their natural propensity to form disconnected patches within estuaries (Boström et al. 2006, 2011). This patchiness leads to straightforward investigations of the difference in habitat use between seagrass beds and surrounding unstructured habitat. As noted above, there are generally higher abundances of fish in seagrass beds than in unstructured habitat, but this pattern becomes more complicated when the edge is considered. Some studies have documented greater densities of organisms at the edge as compared to the core habitat (Bologna and Heck 2002, Tanner 2005, Smith et al. 2008), while others have shown no relationship or even the opposite response (Bell et al. 2001, Jelbart et al. 2006). Mahoney and colleagues (2018) provide a useful summary highlighting the variety of conclusions around responses at seagrass edges across a number of studies. They note the type of seagrass, location, taxa, edge distance, and response variable from these studies, showing just a few variables that could explain the differences in overall conclusions about edge and interior habitats. Other work has supported the possibility that the response may be species-specific (Eggleston et al. 1998, Smith et al. 2010) and that additional factors may be important for determining the distribution of organisms within a habitat matrix. One such factor that has been investigated is the size of the habitat patch. Patch size relates to the edge-to-area ratio, impacting the amount of core habitat relative to edge. In general, faunal density is higher in larger patches but there is an interaction between patch size and effect of the edge (Bowden et al. 2001, Smith et al. 2010). This means that the response of species to the edge depends on the size of the patch, with smaller patches potentially not providing enough interior space for edge effects to occur (Harwell et al. 2011). Other factors that have been shown to influence the direction and strength of edge effects at the boundary of seagrass beds include habitat complexity (Hovel and Lipcius 2001, Pinna et al. 2013), body size and life stage of organisms (Hovel and Lipcius 2001, Selgrath et al. 2007), and the sharpness of the habitat transition (Matias et al. 2013). The type of habitat itself also plays a role; the habitats surrounding oyster reefs influenced the densities of macrofauna found near the edge (Gain et al. 2017). Thus, edge effects are a complex issue with information needed at specific locations and for particular species to make management decisions. In Willapa Bay and other West Coast estuaries, established shellfish aquaculture often occurs adjacent to eelgrass beds. Expected growth of the oyster aquaculture industry to help meet rising demand for seafood could mean an increase in the number of aquaculture/eelgrass edges. Because of the current relationship and anticipated change in the spatial extent of aquaculture, information about the faunal community dynamics at the edge between the two habitat types is thus essential.

1.5 SHELLFISH AQUACULTURE METHODS

While research has been conducted to compare fish and crab use of oyster aquaculture and eelgrass beds as habitat, little has addressed the effect of the edge between them (but see Clarke 2017). In addition, much of the work cited thus far has focused on traditional, on-bottom methods of oyster aquaculture. Increasingly, off-bottom methods are being used to address the half-shell restaurant trade. Suspending the oysters within the water column can result in a more aesthetically-pleasing oyster for this half-shell market, improve survival and growth rates, and increase product consistency (Walton et al. 2012). These practices can also reduce effects on eelgrass by avoiding the impacts of mechanical harvest, which can be destructive to eelgrass (Tallis et al. 2009). While there are clear benefits for the industry, the community influences are less understood. Compared to on-bottom methods, these newer techniques require greater infrastructure (PVC, poles, racks, lines, etc.) to be placed in the estuary. This changes the type of habitat provided by the aquaculture activity and affects the frequency of maintenance. Because of these differences, the impacts of off-bottom aquaculture methods on estuaries are beginning to be evaluated. Erbland and Ozbay (2008) found a greater abundance of fish at an off-bottom aquaculture site as compared to a restored oyster reef. Potential influences on the benthic environment have also been documented and research has shown a negative impact on two species of molluscivorous sea ducks (Mallet et al. 2006, Žydelis et al. 2009). However, direct comparisons between different types of aquaculture are limited. One challenge to this objective is that there are many different types of off-bottom culture, including hanging or floating bags, racks, and long-lines. On the West Coast of the United States, long-lines are commonly used, for which the oysters are woven into a polypropylene line suspended on PVC pipe poles about 0.5m off the bottom. Compared to on-bottom oyster aquaculture, long-lines create a three-dimensional structured habitat within the estuary that could potentially provide similar structure to that of eelgrass.

1.6 MOTIVATIONS AND POTENTIAL IMPLICATIONS

Combining concepts about edge effects with an interest in the ecological functioning of off-bottom oyster aquaculture beds has motivated questions about the differences in habitat use between the two types of aquaculture and eelgrass. The differences in the habitats provided by each has been explored, but this has largely focused on traditional, on-bottom methods of aquaculture. The lens of seascape ecology gives perspective on how differences between the two habitats could affect their function at the estuary scale. Currently, a number of federal and state agencies in Washington have established buffers around existing eelgrass beds in which establishment of new aquaculture is prohibited (Pacific Fishery Management Council 2014, US Army Corps of Engineers 2017a). However, these policies are not based on a strong scientific foundation. This regulatory relationship between oyster aquaculture and eelgrass necessitates a greater understanding of the ecological relationship. Thus, I sought to answer three main questions:

1) Do oyster aquaculture and eelgrass habitats support different abundances of fish and crabs? How does this compare to the edge between them?
2) Does the aquaculture method affect any difference seen amongst habitats?
3) Are fish communities distinct across the different habitats and between aquaculture methods?

Based on the role of habitat structure in influencing the distribution of species, I hypothesized that long-line aquaculture would harbor similar densities of fish and crabs as eelgrass, but greater densities than on-bottom aquaculture. The edge effects between the aquaculture and eelgrass beds could exhibit three potential trends: a) no effect, b) a decrease relative to the habitat interiors, or c) an enhancement relative to the habitat interiors (Figure 1). No effect of the edge would occur if organisms do not sense a habitat transition at the boundary. A decrease in abundance at the edge would suggest that species primarily relied on interior habitat while edge enhancement might be observed if the species using each habitat are combined at the border (Salita et al. 2003, Selgrath et al. 2007). Edge effects are expected to vary depending on the species or specific metric in question due to the variety of driving mechanisms (Mahoney et al. 2018). Nonetheless, I anticipate that there will be recognizable patterns in faunal distribution among the habitat types and will use measurements of environmental characteristics to posit mechanisms driving the patterns.

Because of the close connection between this issue and both state and federal legislation, this type of work could provide key information for managers and policy makers. This work can help provide an ecological foundation to policies which seek to balance these various stakeholder interests within estuaries.

CHAPTER 2

2.1 INTRODUCTION

As intersections of terrestrial, freshwater, and marine systems, estuaries are under pressure from human development and activity (Lotze et al. 2006). Along the West Coast of the United States, shellfish production has been an extensive use of estuarine tidelands for over a century. It constitutes an economically- and ecologically-significant practice that supports a diverse industry and provides seafood for people throughout the country. In Washington state alone, commercial aquaculture of Pacific oysters (*Crassostrea gigas)* brought in $32.4 million in 2016 (NMFS 2016). Currently, aquaculture within the United States amounts to just 5% of the seafood consumed domestically (NOAA 2011). Thus, there is great potential for expansion of oyster aquaculture to help meet increasing national and global demand for seafood. However, growth of shellfish production could have implications for other human interests or activities within West Coast estuaries.

Seagrasses provide a variety of ecosystem services and have been recognized as important ecosystem engineers (Jones et al. 1994, Costanza et al. 1997). Pertinent to the issue of concern here, seagrass beds are also nursery habitats for juvenile fish and invertebrates (Beck et al. 2001, Heck et al. 2003, Sheaves et al. 2015, Nagelkerken et al. 2015). The native eelgrass (*Zostera marina*) of the U.S. West Coast provides a habitat for early life stages of commercial species like salmonids, Dungeness crab, and English sole (Rooper et al. 2003, Holsman et al. 2006, Dumbauld et al. 2015). Thus, there is a clear but indirect connection between eelgrass and the economic success of certain profitable fisheries and eelgrass has therefore been protected as “essential fish habitat” (EFH) under the Magnuson-Stevens Fishery Conservation and Management Act (USC 16.38). This designation prohibits the damage or destruction of eelgrass and forces consideration of trade-offs between certain interests. Within West Coast estuaries, eelgrass and oyster aquaculture occur at similar tidal elevations and often overlap spatially. While the two are not always mutually exclusive, certain aquaculture practices can limit the extent of eelgrass (Wisehart et al. 2007, Tallis et al. 2009, Wagner et al. 2012, Skinner et al. 2013). Expansion of oyster aquaculture could mean loss of eelgrass beds that are important habitat for a wide range of estuarine species. For this reason, there is interest in understanding ecological relationship between aquaculture and eelgrass, specifically how the two relate in the quality of habitat that they provide. The co-occurrence of these two interests within estuaries creates a complex management issue that requires sufficient scientific understanding to inform future decisions.

Oyster aquaculture can be viewed as both a long-term (press) and short-term (pulse) disturbance to the estuarine system. Pulse disturbances occur as discrete events often related to harvest or maintenance of the beds, while press disturbances result from the addition of the oysters and associated gear over longer periods (Simenstad and Fresh 1995, Dumbauld et al. 2009). Eelgrass and its function as habitat can be impacted by both of these types of disturbances. Pulse disturbances associated with harvest practices like mechanical dredging can damage or destroy eelgrass within the aquaculture beds (Dumbauld et al. 2009). But while pulse disturbances are often limited to the local areas under culture, the interactions between oyster aquaculture and other habitats within the matrix can potentially expand the reach of these impacts (Crawford et al. 2003, Forrest and Creese 2006). By considering oyster aquaculture as another habitat type within the estuarine habitat mosaic, the wider-reaching impacts can be seen.

Oyster aquaculture creates relatively novel habitat within estuaries, even compared to natural oyster reefs because Pacific oysters are non-native and not typically grown in a reef arrangement. However, some methods of oyster aquaculture, especially off-bottom methods, do provide structure similar to that provided by natural structured habitats (Dealtris et al. 2004). Habitat three-dimensional structure is an important factor in determining the community of organisms within a location. In estuaries, habitats with more vertical structure have been shown to support higher faunal abundances and more diverse groups of species (Orth et al. 1984, Jenkins et al. 1997, Heck et al. 2003). This phenomenon has largely been attributed to behavioral choices about resource availability and refuge from predators. Eelgrass provides a natural structured habitat that hosts a diverse assemblage of organisms, especially when compared to unvegetated areas (Ferrell and Bell 1991, Pinnix et al. 2005, Hosack et al.

2006, Ferraro and Cole 2007). Oyster aquaculture generally falls somewhere in between these habitat types with regards to habitat structure. Because of the structure and resources provided by the oysters, diversity and abundance of organisms is generally higher in aquaculture beds than in adjacent mudflats (Castel et al. 1989, Pinnix et al. 2005, Hosack et al. 2006, Ferraro and Cole 2007), but the comparison with eelgrass beds is less clear. When looking at eelgrass and aquaculture beds, the relationship was often species-specific. Higher densities of benthic invertebrates were found in eelgrass than oyster aquaculture beds, but for fish and other mobile species, abundances were either similar or greater within aquaculture beds (Dealtris et al. 2004, Pinnix et al. 2005, Hosack et al. 2006). Thus, it is possible that oyster aquaculture provides a functionally similar habitat to that provided by eelgrass, but more work is necessary to fully characterize the ecological relationship.

The relatively new field of seascape ecology provides an interesting lens through which to view the connection between oyster aquaculture and eelgrass (Hinchey et al. 2008, Wedding et al. 2011). Seascape ecology is based in concepts of landscape ecology that have described how the arrangement of different habitats at the spatial scale of the landscape affects the distribution of organisms (Forman and Godron 1986, Turner 1989, Wiens and Milne 1989). Both of these disciplines have paid particular attention to the effects of edges or boundaries between habitats. Edges represent abrupt changes in resource availability, refugia, and predation pressure that can influence the abundance and diversity of organisms through a variety of mechanisms (Gates and Mosher 1981, Sisk and Haddad 2002, Ewers et al. 2007). In marine systems, seagrasses have been a focal system for research on edge effects because of their natural propensity to form discrete patches (Boström et al. 2006, 2011). While it is well-known that structured estuarine habitats support higher abundances of organisms, this pattern becomes more complicated when the edge is considered. Some studies have documented greater densities of organisms along habitat edges as compared to the core habitat (Bologna and Heck 2002, Tanner 2005, Smith et al. 2008), while others have shown no relationship or even the opposite response (Bell et al. 2001, Jelbart et al. 2006). This suggests that the response may be species-specific (Eggleston et al. 1998, Smith et al. 2010) or depend on any number of factors that influence species distributions within a habitat mosaic. These include patch-size (Bowden et al. 2001, Smith et al. 2010), habitat complexity (Hovel and Lipcius 2001, Pinna et al. 2013), body size and life stage of organisms (Hovel and Lipcius 2001, Selgrath et al. 2007), and the type of habitat transition (Matias et al. 2013). Thus, edge effects are complex and may require species- and location-specific information to be fully understood. Due to the spatial overlap between oyster aquaculture and eelgrass and the regulatory ramifications of that overlap, edge effects are a pertinent question within West Coast estuaries. Growth of this industry could mean an increase in the number of aquaculture/eelgrass edges due to fragmentation of eelgrass beds. Thus, information about the ecological relationship between aquaculture and eelgrass is necessary to inform regulations and management.

While some work has been done to characterize fish and crab use of oyster aquaculture and eelgrass beds, little has addressed the effect of the edge between them (but see Clarke 2017). These investigations are further complicated by the wide range of aquaculture methods that exist in these locations. To date, research has focused on on-bottom methods of aquaculture because this has been the primary technique for growing oysters. However, off-bottom methods are becoming increasingly popular because of regulatory constraints and to address a higher quality product for the half-shell market (Walton et al. 2012). These methods have also been shown to reduce effects on eelgrass, as they do not involve mechanical harvesting through dredging (Tallis et al. 2009). While some characteristics of off-bottom oyster aquaculture provide clear benefits to the industry, the ecological impacts of such practices are less well-understood. In contrast to on-bottom aquaculture, off-bottom methods require a large amount of gear to be placed in the estuary. This can include cages, floats, rafts, lines, and supporting structures. Because of this associated structure, the habitat provided by these new types of aquaculture is distinct from that provided by oysters alone in on-bottom aquaculture. This difference in habitat structure has the potential to affect the strength or presence of edge effects when aquaculture is found adjacent to eelgrass beds. In this study, I sought to compare the habitat transition from both on-bottom and off-bottom aquaculture into eelgrass beds. The method of off-bottom aquaculture present at the study locations was long-lines, in which the oysters are woven into a line suspended on PVC pipe about 0.5m off the bottom. Approaching these issues from the perspective of seascape ecology could help to highlight the potential trade-offs involved at the estuarine scale when converting tideflat area to oyster aquaculture.

Under current regulations implemented by the Pacific Fishery Management Council, new aquaculture is prohibited within 25-30ft of existing eelgrass beds (Pacific Fishery Management Council 2014). Thus, there is a clear regulatory relationship between these two interests. In order to explore the ecological relationship more closely, I sought to answer three main questions within Willapa Bay, WA:

1) Do oyster aquaculture and eelgrass habitats support different abundances of fish and crabs? How does this compare to the edge between them?
2) Does the aquaculture method affect any difference seen amongst habitats?
3) Are fish communities distinct across the different habitats and between aquaculture methods?

Due to the influence of habitat structure, I hypothesized that long-line aquaculture would support similar abundances of fish and crabs to eelgrass, but greater than on-bottom aquaculture. Edge effects could result three primary trends (see Figure 1), but will likely vary with the species or metric in question. Nonetheless, I anticipated recognizable patterns in faunal abundance across the habitat transition between aquaculture and eelgrass.

This research is geared at advancing the best available science for both managers and policy makers. Oyster aquaculture and eelgrass are ecologically, economically, and culturally important within estuaries along the West Coast of the United States. By investigating use of the transition between these two habitats, a more informed and balanced management approach can be obtained.

2.2 MATERIALS AND METHODS

2.2.1 STUDY SITES

Willapa Bay is a macrotidal estuary located in Washington State, USA (46.5395° N, 123.9888° W). It is the third largest estuary along the US Pacific Coast with an area of 358 km^2. The bay is strongly tidally-influenced, with 62% of the area (227 km^2) considered intertidal (Hedgpeth and Obrebski 1981). Of that 227 km^2, 20% is devoted to oyster aquaculture (Dumbauld et al. 2011). Recent surveys have shown that *Z. marina* occupies approximately 32% of the tide flat (Dumbauld and McCoy 2015), often at similar tidal elevations to oyster aquaculture (Ruesink et al. 2006, 2010).

Sampling occurred at three sites within the bay: Russell Channel, Tokeland, and Nemah (Figure 2). These sites were chosen based on four factors: 1) presence and appropriate configuration of necessary habitats (on-bottom aquaculture, long-line aquaculture, and eelgrass), 2) similar tidal elevation within each site, 3) structural consistency of oyster and eelgrass habitats (e.g. similar density of eelgrass, similar size of oysters), and 4) accessibility at low and high tide. Sampling occurred twice at each site; once in July 2017, and a second time approximately 4 weeks later in August 2017. Sampling was constrained to the summer months to target the season with peak eelgrass density and also fish abundance and diversity (Orth and Moore 1986, Thom et al. 2003, Hosack et al. 2006, Ruesink et al. 2010, Zhang et al. 2016).

2.2.2 SAMPLING DESIGN

A 60m transect was laid perpendicular to the boundary between the aquaculture and eelgrass habitats at each site. This transect was aligned parallel to the nearest channel at two of the sites (Tokeland and Nemah), but eelgrass density did not allow for this directionality at Russell Channel. This resulted in a large tidal range at Russell Channel (0.90m) versus Nemah (0.11m) and Tokeland (0.06m). An array of sampling methods was used to characterize the differences in species presence and behavior at each of five, evenly-spaced positions (15m apart) along the transect (Figure 3). These five positions were considered to represent different parts of the habitat matrix: (A) aquaculture interior, (B) aquaculture intermediate, (C) edge, (D) eelgrass intermediate, and (E) eelgrass interior. The edge was defined relative to the aquaculture bed and was chosen based on the presence of eelgrass. For long-lines, the edge was simply defined as the location where the culture lines ended. For on-bottom aquaculture, however, the edge was more diffuse and was designated by visually assessing the location where the density of oysters dramatically decreased. The edge was always the middle of the transect, so the interior habitats were each 30m into the respective habitat.

Environmental Data

Four HOBO® Onset Data Loggers UA-002-64 were used to measure water temperature (°C) and relative changes in light intensity (lux or lumens/m^2). One logger was attached to a minnow trap deployed in each interior habitat region and the edge between long-line aquaculture and eelgrass. Data collected were used to assess environmental differences between sites and anecdotally corroborate the underwater visibility in the videos.

Eelgrass Sampling

Eelgrass metrics were collected every 3m along the transect, resulting in a total of 21 data points at each site. At each sampling location, a 0.0625m^2 quadrat was used to assess percent cover, shoot density of *Z. marina*, and percent cover of epiphytes on *Z. marina* blades. Eelgrass morphology was measured on 10 eelgrass shoots from each of the five main sampling positions along the transect. These shoots were placed in a cooler and stored at -20°C until processing. The length and width of the longest blade and epiphyte load (dry mass of epiphytes/dry mass shoot) were measured. Length was defined as the distance from the last nodule on the rhizome to the end of the blade. Epiphyte load was determined by scraping the epiphytes off the blade using a microscope slide, and then drying the blades and epiphytes separately in an oven at 60°C for 48 hours or until a constant weight was reached (Terrados and Pons 2008). Taken together, these data help to provide a quantitative measure of the surface area and food provided by eelgrass.

Predation Tethering Units

Predation intensity was measured with predation tethering units (PTUs; Duffy et al. 2015). Bamboo stakes with small pieces of dried squid attached as bait were used and the presence or absence of the squid at predetermined time points was recorded. PTUs are used widely in a variety of systems to estimate how much predation is occurring within a given habitat or area. Two different PTU treatments (“high” and “low”) were deployed. Squid bait (diameter = ½ in, 1.27cm) was superglued to a 10cm monofilament line and tied at 30cm above the substrate for the High treatment and 10cm above the substrate for the Low treatment, so that the bait was suspended 20cm above and just above the substrate, respectively. These two treatments were designed to assess different types of predators within the system: those that were swimming and predating within the water column and those that were searching for prey along the bottom. At each of the five main positions along the transect, 5 PTUs of each treatment were deployed at low tide. The stakes were placed in two rows approximately 2m apart, alternating High and Low treatment within each row. The first set at each point was placed about 4m from the transect tape, so as to not influence other sampling techniques. Presence of the squid bait was checked at two points: once the water had reached a depth of about 30cm (height of the knot on the high treatment) and then approximately 24 hours later.

Minnow Traps

Minnow traps (approximately 60cm x 60cm x 46cm, with a ~15mm opening) were used to sample the fish and crab species and were placed about 5-6m from the transect tape at each of three transect positions: (A) aquaculture interior, (C) edge, and (E) eelgrass interior (Figure 3). Traps (un-baited) were deployed at low tide and retrieved approximately one hour after the local high tide. Captured fish and crabs within the traps were identified, counted, and then returned to the water.

Digital Video

To complement the other sampling techniques, digital video data was gathered using GoPro HERO4® cameras placed at each of the five main positions along the transect. Camera mounts were constructed out of 1” PVC pipe, which included an arm on which the camera was attached and a 0.25m^2 quadrat that lay on the bottom (Figure 4). The camera was affixed approximately 30cm off the bottom and a makeshift Secchi disk was mounted on one corner of the quadrat, approximately 1m away from the camera. In traditional application, Secchi disks are a way to estimate turbidity by lowering the disk into a body of water and recording the depth at which the disk can no longer be seen. In this case, the Secchi disk was used for a quantitative analysis of the visibility in the video using image analysis software. Its placement also acted as a point of reference beyond which organisms were not counted because it was determined that identification and simple detection of fish and crabs was not reliable beyond one meter.

The cameras were deployed by snorkeling the mount out to a buoy that had been placed at low tide and were retrieved from a boat approximately two hours after deployment (when the cameras ran out of battery).

2.2.3 VIDEO PROCESSING

Because of issues with video quality and inconsistencies between the gear used for video data collection between the two sampling trips, only video from the August 2017 trip was included in the analysis presented here (30 2-hour videos). All other data collected were analyzed over the two timepoints (July and August).

Video footage was first assessed for water clarity by using the difference in the average pixel values between the black and white quadrants of the Secchi disk. Theoretically, as the turbidity increases, the contrast between these two sections of the image should decrease. At a high turbidity level, the Secchi disk would not even be visible and the contrast would be zero. Grayscale pixel values are assessed on a range from zero (black) to 255 (white), so a maximum contrast would be 255, although this value would not be realistic in natural conditions. ImageJ (https://imagej.nih.gov/ij/index.html), was used to assess the contrast in five stills taken from each two-hour video (Schindelin et al. 2015). An image was analyzed for water clarity every twenty minutes within a given 2-hour video, starting at the time of mount placement. Within the software, a horizontal line was drawn from one quadrant of the disk to the other and the grayscale values along this line were exported. The minimum and maximum of the second derivative of the curve were determined and used as the bounding points to obtain average values for the white and black sections of the Secchi disk. These averages were then subtracted to get a contrast for the given image. However, eelgrass often limited the view of the Secchi disk and all five measurements were not possible. In these cases, as many measurements as possible were made. Only two videos did not have any images that were usable to assess visibility with the Secchi disk. The average of the calculated contrast values was then taken to provide a water clarity score for each video. Obstruction by eelgrass or macroalgae was also assessed at each 20-minute time point and the video was given an average score based on the percentage of the field-of-view that was blocked. The frame was roughly divided into thirds, and obstruction was assessed in these increments. Before fitting models, the contrast and obstruction scores were used to measure correlation between visibility and the number of fish seen within each video.

Analysis of the species composition and behavior within each video was completed using BORIS, a free behavioral coding software (Friard and Gamba 2016). Because of the time taken to place the camera and previous examination of video quality, it was determined that the middle hour of video was appropriate for analysis (Clarke 2017). Thus, observation was started at 30 minutes into the recording and stopped at 1.5 hours. Within the software, any sighting within a video was logged with the species identification and behavior category. Clarke (2017) described a list of behavior categories that was applied to each fish or crab sighted (Table 1). Each time a fish or crab was sighted, the species and behavior category were recorded. Because it was difficult to know if an individual reentered the frame once it had left, our response variable is termed as “sightings”, rather than counts. For individuals that were unidentifiable, the observation was still recorded as such and included in the calculation of total sightings. In addition to sightings, Time in View (TiV) was also recorded (Smith et al. 2011). By quantifying the amount of time a given species spends in each habitat, TiV gives an estimate of how different species are using the habitats. The same rules mentioned above regarding fish leaving the frame were used. An additional guideline was used for fish that were lost from view: if a fish that had entered the frame was lost from view and not seen again after 5 seconds, it was assumed to have left the screen. This was only updated if the organism again became visible and had clearly not re-entered the frame. All videos were watched by the same individual to decrease observer bias.

2.2.4 STATISTICAL ANALYSES

All data analysis was completed using R© (R Core Team 2016). Generalized linear mixed models (GLMMs; Bolker et al. 2009) were first used to assess the significance of the position along the transect and aquaculture type according to the following equation:

$$\mu(\text{response variable}) = \text{Transect Position} + \text{Aqua. Type} + \text{Transect Position:Aqua. Type} + \text{Date}$$

Both Transect Position and Aquaculture Type were treated as categorical fixed effects. Transect Position (5 levels = A, B, C, D, or E) represents the main sampling position along the transect between oyster aquaculture and eelgrass habitats. Aquaculture Type (two levels = long-line (LL) or on-bottom(OB)) is the method of aquaculture being practiced along that transect. The interaction indicates whether the effect of Transect Position depends on Aquaculture Type. For all data that were collected at both time points, Date was included as a random effect (two levels = July or August). Thus, the data structure included three replicates (Site) of a two-factor design with the random effect of Date (N=3). Models were fit using the *lme4* package (Bates et al. 2015). Presence/absence data from the PTUs was analyzed using logistic regression with two additional factors: Treatment (high/low) and Check Time (first/24hour). Count data from the minnow traps was fit using a Poisson distribution. After checking the reasonability of assumptions by examining residuals and leverage of the data, all other data (eelgrass survey parameters, epiphyte load, etc.) were fit using a Gaussian distribution. The GLMMs were followed with a Type II Wald χ^2-test (Analysis of Deviance) using the Kenward-Roger degrees of freedom approximation to assess overall significance of the factors (Schaalje et al. 2002).

When the interaction term between Transect Position and Aquaculture Type was significant in the original model, multiple pairwise comparisons were completed to explore the drivers of the significant interaction. Simultaneous z-tests were used to examine all pairwise comparisons between the ten habitats (LL-A, OB-A, LL-B, etc.) using the *multcomp* package (Hothorn et al. 2008, Wright et al. 2014). Contrasts of interest included those between the edge and other habitats within each aquaculture type, in addition to differences between the aquaculture types at each transect position. Significant comparisons of interest were included in associated figures to highlight these differences.

Video data was analyzed using a generalized linear model (GLM) because it only included one timepoint. Video sightings were fit to a Poisson distribution and time in view (TiV) fit with a Gaussian distribution. These univariate methods were then followed with a multivariate faunal community analysis.

Non-metric multidimensional scaling (NMDS) of the Bray-Curtis dissimilarity matrix was also used to evaluate the video sighting data with the *vegan* package in R (Oksanen et al. 2018). Unidentified individuals were excluded from the analysis. The coefficient of variation (CV) and skew were used to explore the shape of the data. To bring these values within acceptable thresholds (<200 for CV and between ±2 for skew), species that occurred in less than 5% of videos (i.e. in only one video) were excluded from the analysis (Sund 2015). No other data transformations were required. The number of dimensions for NMDS was chosen through an iterative process to minimize the stress below 0.2 (McCune and Grace 2002). Two dimensions reduced the stress below this threshold and while further reduction was possible, two was used for ease of visualization. Analyses were followed with a permutational multivariate analysis of variance (PERMANOVA) test to assess the significance of Aquaculture Type, Transect Position, and their interaction. The significance of individual species was also assessed with an Indicator Species Analysis (ISA) using the *labdsv* package (Roberts 2016). Combined with the univariate analysis, this analysis helped to highlight how the community differed across the habitats and aquaculture types explored.

2.3 RESULTS

2.3.1 ENVIRONMENTAL DATA

Temperature data were only available for two sites in July (Tokeland and Russell Channel) and all three sites in August. Across the three sites and two timepoints, the average water temperature was approximately 18°C, with little variation in time and space (SE = 0.35°C). The water was about 1°C warmer in August than at the July sampling point. Light intensity measurements varied by an order of magnitude, even at a single site (397.08 lux vs. 4,742.26 lux). Based on literature about logger sensitivity, this was assumed to be due to a calibration error, making comparisons between loggers unreliable (Long et al. 2012). This change of light intensity within a single logger dataset was used to approximate the time period when the logger was underwater and determine average water temperature but light intensity data was not otherwise used.

2.3.2 EELGRASS SURVEY AND SAMPLING DATA

Both percent cover and shoot density of *Z. marina* varied with Transect Position and the interaction between Transect Position and Aquaculture Type (Table 3, Figures 5 and 6, Appendix Tables A.1 and A.3). For percent cover, post-hoc analyses (Appendix Table A.2) indicated that the two eelgrass habitats on the long-line transect (LL-D and LL-E) were significantly greater than the long-line edge (LL-C) by a factor of about two (LL-C and LL-D: z-value=4.592, p-value<0.001, LL-C and LL-E: z-value=3.363, p-value=0.027). Eelgrass cover in the on-bottom eelgrass habitats (OB-D and OB-E) was also significantly greater than that at the edge (OB-C) by a similar factor of two (OB-C and OB-D: z-value = 6.176, p-value<0.001, OB-C and OB-E: z-value=6.176, p-value<0.001). Within the on-bottom aquaculture, the intermediate habitat (OB-B) harbored significantly less eelgrass than the on-bottom edge (OB-C; OB-B and OB-C: z-value=3.169, p-value=0.049). Similar patterns were seen in post-hoc analyses of the shoot density data (Appendix Table A.4). Shoot density in the eelgrass habitats along the on-bottom transect (OB-D and OB-E) were significantly greater than that at the on-bottom edge (OB-C) but there was no significant difference between density in these habitats on the long-line transect (OB-C and OB-D: z-value=5.173, p-value<0.001, OB-C and OB-E: z-value=3.946, p-value<0.01). Shoot density at the long-line edge (LL-C) differed significantly from density in the aquaculture habitat 30m from the edge (LL-A), showing an average shoot density about four times higher than in the interior of the aquaculture bed (LL-C and LL-A: z-value=3.595, p-value=0.012). The two aquaculture types also differed in shoot density at the intermediate eelgrass habitat (D; Transect Position D: z-value=3.946, p-value<0.01).

Transect Position, Aquaculture Type, and their interaction were significant for percent cover of epiphytes on the eelgrass blades (Table 3, Figure 7). Post-hoc analyses revealed that the eelgrass in on-bottom aquaculture habitats (OB-A and OB-B) had significantly less epiphyte percent cover than that at the on-bottom edge (OB-C; OB-A and OB-C: z-value=4.689, p-value<0.01, OB-B and OB-C: z-value=5.260, p-value<0.01). In addition, the eelgrass in these habitats had significantly less epiphyte cover than the eelgrass in associated long-line habitats (LL-A and LL-B; OB-A and LL-A: z-value=-3.422, p-value<0.01, OB-B and LL-B: z-value=-4.848, p-value<0.01). Eelgrass samples did not show a significant difference in epiphyte load across Transect Position or by Aquaculture Type (Table 3, Appendix Figure A.2). However, multiplying epiphyte load by shoot density to estimate the total epiphyte biomass across the transect did show the significance of Transect Position, with more biomass available in the eelgrass beds than the aquaculture beds (Table 3). Blade surface area (length*width of longest blade of each shoot) depended significantly on Transect Position, Aquaculture Type and their interaction (Table 3, Figure *Figure 8*8). Post-hoc analyses indicated a significant difference in blade area between the long-line edge (LL-C) and long-line eelgrass habitat 30m from the edge (LL-E), as well as between the two aquaculture types at the eelgrass interior (OB-E and LL-E; LL-C and LL-E: z-value=4.564, p-value<0.001, Transect Position E: z-value=-3.452, p-value=0.020). In both cases, blade area at LL-E was significantly greater than that in the habitat to which it was compared. As with epiphyte load, when surface area was multiplied by shoot density to estimate the emergent surface area provided by eelgrass (sensu Dealtris et al. 2004), Transect Position was significant (Table 3, Figure 9).

2.3.3 PREDATION TETHERING UNITS

Both Treatment and Check Time significantly affected the presence of bait, with the Low treatment being predated upon more and almost all of the bait absent at the 24hr check. Aquaculture Type was also significant with more predation in long-line habitats but there was no significant interaction with Transect Position (Table 4, Figure 10).

2.3.4 MINNOW TRAPS

Both Aquaculture Type and the interaction between the two fixed factors were found to significantly affect the total number of fish and crab caught in minnow traps (Table 5, Figure 11, Appendix Tables A.5 and A.6), whereas species richness did not differ across the transect or between aquaculture types (Table 5).

Pairwise comparisons showed a significant difference between total catch of fish and crab in aquaculture types at the edge, with the long-line edge (LL-C) being greater than the on-bottom edge (OB-C; LL-C and OB-C: z-value=-4.103, p-value<0.001). The high average catch seen at the long-line edge (LL-C) was mainly driven by a large catch of three-spined sticklebacks (*Gasterosteus aculeatus*) at one site (Tokeland, 36 in LL-C traps across both sampling points). Evidence of edge effects were most apparent in the on-bottom aquaculture as both the aquaculture and eelgrass habitats were significantly greater than the edge (OB-A and OB-C: z-value=-2.979, p-value=0.031, OB-C and OB-E: z-value=3.290, p-value=0.012).

2.3.5 DIGITAL VIDEO

Videos had an average Secchi contrast score of 14.6, with values ranging from 0 to 23.9 (SE=0.79). While the values themselves do not have any practical meaning, they give a sense of the range of visibility among the videos. The low values (~0-8) represent videos in which the Secchi disk was barely visible at the one-meter distance. However, the videos with above average values have relatively clear visibility out to one-meter and even slightly beyond. For eelgrass obstruction, the videos were about 25% obstructed on average, with values ranging from 0 to 67% (SE=0.35). Neither of these visibility metrics was highly correlated with total fish sightings in a given video (Secchi contrast: R=0.07, eelgrass obstruction: R=0.17) and were therefore not included in subsequent models.

Analysis of total fish and crab sightings in video data revealed the significance of both main factors and their interaction (Table 6, Figure 12, Appendix Table A.7). Pairwise comparisons of the interaction (Appendix Table A.8) showed that sightings in the long-line aquaculture habitats (LL-A and LL-B) were both statistically greater than the associated on-bottom habitats (OB-A and OB-B; Transect Position A: z-value=-5.376, p-value<0.001, Transect Position B: z-value=-6.765, p-value<0.001). For long-lines, edge effects were detected, as the habitats 30m (LL-A) and 15m (LL-B) into aquaculture and 30m (LL-E) into eelgrass were all significantly greater than the long-line edge (LL-C; LL-A and LL-C: z-value=-4.711, p-value<0.001, LL-B and LL-C: z-value=-3.729, p-value=0.007, LL-E and LL-C: z-value=4.152, p=0.001). No significance was seen in the comparisons between the edge and the other habitats for on-bottom aquaculture. There were also no significant differences in species richness or TiV among the transect positions or between aquaculture types (Table 6).

Shiner perch (*Cymatogaster aggregata*; 58% of sightings) and Pacific staghorn sculpin (*Leptocottus armatus*; 12% of sightings), the two most frequently sighted species, were separated out for further analysis (see Appendix Figures A.3 and A.4 for Dungeness crab and pile perch sightings). Shiner perch and Pacific staghorn sculpin sightings were each significantly related to both Transect Position and Aquaculture Type, along with their interaction (Table 6, Figure 13 and Figure 14). Thus, for these two species, it appears that the method of aquaculture significantly affects how individuals use the five different habitats along the transect. For shiner perch, sightings in both long-line aquaculture habitats (LL-A and LL-B) were significantly greater than in on-bottom habitats (OB-A and OB-B; Transect Position A: z-value=-5.173, p-value<0.001, Transect Position B: z-value=-6.037, p-value<0.001). In addition, sightings at the on-bottom edge (OB-C) were significantly greater than those at the habitat 15m into the aquaculture bed (OB-B; OB-B and OB-C: z-value=4.188, p-value<0.001). For Pacific staghorn sculpins, sightings in the long-line habitat 15m into the bed (LL-B) were significantly greater than in on-bottom aquaculture (OB-B), but this was the only habitat with a significant difference (Transect Position B: z-value=-3.512, p-value=0.013). On the long-line transect, sightings in both of the aquaculture habitats (LL-A and LL-B) were significantly greater than the edge (LL-C; LL-A and LL-C: z-value=-3.850, p-value<0.01, LL-B and LL-C: z-value=-4.241, p-value<0.001).

Four behaviors were observed for fish and crabs in the video: foraging, seeking refuge, schooling (sensu Keenleyside 1955), and transiting (Table 1, Figure 15). By far, the most common behavior was transiting (88% of sightings). When the transiting data was analyzed separately, both of the main factors and their interaction were found to significantly affect the number of sightings (Table 6, Figure 16). This is consistent with the analysis of the complete dataset. The post-hoc analyses also follow the same patterns as the dataset of all the behaviors combined. Analysis of the foraging observations (8% of sightings) revealed that Transect Position was significant (Table 6, Figure 17). Neither of the other behaviors were observed frequently enough for separate analysis.

Since the CV and skew of the raw data were 187.78 and 2.07, respectively, species that occurred in less than 5% of videos [lingcod (*Ophiodon elongatus*) and tube-snout (*Aulorhynchus flavidus*)] were removed from the dataset for multivariate analysis. Removing these species brought the CV down to 166.11 and the skew to 1.74. Because these values were below the specified thresholds, no further transformations were performed on the data. The NMDS that was used in subsequent analyses had a stress value of 0.187 with two dimensions. A square root transformation and Wisconsin double standardization were automatically performed when the model was fit. PERMANOVA revealed the significance of Aquaculture Type (p-value=0.041). While there was a high degree of overlap, on-bottom aquaculture deviated slightly (Table 7, Figure 18). ISA analysis of the aquaculture types exposed a significant association between shiner perch and long-line aquaculture, but there were no other significant relationships between species and habitats (shiner perch: p-value=0.023, I-value=0.650). Pacific staghorn sculpin had the second highest I-value related to long-lines (I-value=0.440), but this was not statistically significant. No species associations with the different habitats were significant using ISA. Nonetheless, cursory exploration of site differences with ISA showed significant associations of five of the ten species to specific sites. Four of these five species were associated with Tokeland, suggesting that it might have been the most distinct site of the three.

2.4 DISCUSSION

Through sampling of the fish community and habitat characteristics in oyster aquaculture beds and eelgrass, I sought to characterize the function of these habitats for fish and crabs. Results from this survey suggest that off-bottom long-line aquaculture is similar to eelgrass in habitat use and could provide habitat akin to that provided by eelgrass, while on-bottom aquaculture beds support a less abundant assemblage. Average sightings of fish and crab in video in long-line aquaculture were comparable to sightings within eelgrass and were statistically greater than sightings in on-bottom aquaculture (Figure 12). Based on previous research, this is consistent with the increased level of habitat structure provided by eelgrass and aquaculture gear within long-line beds, as compared to on-bottom aquaculture (Figure 9, Orth et al. 1984, Ferraro and Cole 2010). Predation intensity and food availability metrics further characterize how fish and crabs were using these habitats; combined with observations of foraging activity in the video footage, long-line aquaculture supported predation and foraging rates analogous to those measured in eelgrass. Although edge effects were not broadly detected across these metrics, consideration of the edge provides context for expansion of this work to the broader estuarine seascape. Aquaculture type can affect the distribution of fish and crabs across the habitat transition into eelgrass. Examining the specifics of this result could elucidate implications for best management practices.

2.4.1 FISH AND INVERTEBRATE COMMUNITY

Both minnow traps and underwater video were used to assess the distribution of species and organisms across the habitat transition from aquaculture into eelgrass. Trap catches confirmed the species that were sighted in the video. For example, the high catch of three-spined sticklebacks at Tokeland was corroborated through frequent sightings of this species in the video. By combining these two methods, the bias of either one individually was reduced. Because of the consistency of the species caught by each method, video was used primarily to examine the differences in abundance across the habitat transition. The significance of the interaction between Transect Position and Aquaculture Type in the generalized linear model results for total video sightings indicates that aquaculture method influenced the distribution of species across the habitat transition (Table 6). Sightings were statistically greater in long-line aquaculture than in on-bottom aquaculture and were more similar to those in eelgrass. While there has been little work that directly compares the habitat provided by these two methods of aquaculture, each has been separately compared to eelgrass. Relative to unvegetated mudflats, the number of organisms found in on-bottom aquaculture has been found to be statistically indistinguishable from that in eelgrass (Pinnix et al. 2005, Hosack et al. 2006, Ferraro and Cole 2007). However, off-bottom aquaculture harbored a greater number of species than nearby eelgrass in an estuary in southern Rhode Island (Dealtris et al. 2004). The results presented here, however, suggest that differences can be distinguished when the comparison between aquaculture types occurs within a single estuary and at specific sites. While on-bottom aquaculture might support similar faunal abundances to eelgrass, this work was done primarily in contrast to unvegetated substrate. Adding off-bottom aquaculture to the comparison instead resulted in a significant difference in the number of organisms sighted between the two aquaculture types. Community analysis of the sightings data corroborated this difference.

Further exploration of these patterns provides more detail about the distribution of species across the habitat transition. While edge effects were not broadly apparent across multiple metrics, there seems to be a decrease of abundance at the edge in the video sightings data (Figure 1b). This is especially apparent on the long-line transect, where edge sightings were statistically fewer than sightings in both the aquaculture and eelgrass interior habitats. This suggests that the edge was perceived to have a high predation risk or perhaps have less food available. Because of the potential for the edge to affect individual species differently the two most common species were separated out for further analysis. Shiner perch were approximately equally abundant across the long-line transect but were less abundant in on-bottom aquaculture (Figure 13). However, Pacific staghorn sculpins were sighted primarily in aquaculture and less frequently in eelgrass (Figure 14). Thus, the edge did not seem to affect the distribution of shiner perch, but sightings of Pacific staghorn sculpin dramatically decreased once the edge was crossed into the eelgrass bed. In Samish Bay (Washington, USA), Pacific staghorn sculpins were also seen more frequently in underwater video in long-line aquaculture and at the edge than in eelgrass (Clarke 2017). In contrast, shiner perch were more abundant in eelgrass beds and at the edge between vegetated and unvegetated sediments in Willapa Bay (Gross et al. 2017). Pacific staghorn sculpins have been recognized as avid predators of juvenile crabs, shrimp, and other fish within these estuaries, while shiner perch rely on zooplankton and mesograzers for food (Clarke 2017, Motley 2017). This suggests that the contrasting use of the edge may relate to the primary foraging behavior of each species. Pacific staghorn sculpins could make use of the refuge along the edge to capture prey. Shiner perch, on the other hand, rely on the structure and food available in the interior of structured habitats. It is important to note that these differences may also relate to biases of the sampling method; shiner perch are often obvious swimming within the water column while Pacific staghorn sculpins swim along the bottom in a slow and cryptic manner. Regardless, the marked differences in the distribution patterns of these two species highlight the complexities of edge effects between aquaculture and eelgrass.

2.4.2 HABITAT STRUCTURE

Considering established ecological relationships regarding habitat complexity, characterization of eelgrass structure provides a potential driving mechanism for the distribution of organisms observed in the video. Habitats with more three-dimensional structure support higher densities of organisms and more diverse communities, as compared to nearby unstructured habitats (Orth et al. 1984, Pinnix et al. 2005, Hosack et al. 2006, Ferraro and Cole 2007). Eelgrass constitutes the natural structured habitat in this study. There is a clear increase in percent cover and shoot density of eelgrass moving from the aquaculture to eelgrass bed, as expected given the sampling design (Figures 5 and 6, Appendix Figure A.1). The significance of the interaction term in the models for these variables also indicates the influence of aquaculture type on this change along the transect (Table 3). Notably, the increase from aquaculture to eelgrass was less extreme on the long-line transect than the on-bottom transect. Although pairwise comparisons were not significant, percent cover and shoot density were greater in the long-line aquaculture than in on-bottom culture. This difference between aquaculture types is consistent with previous research that showed little impact of long-line aquaculture on shoot density (Wisehart et al. 2007, Tallis et al. 2009), while on-bottom mechanical harvest methods can reduce eelgrass (Dumbauld et al. 2009). Estimation of eelgrass emergent surface area (blade surface area*shoot density) confirms the higher measures within long-line aquaculture than on-bottom aquaculture beds (Figure 9). As it relates to habitat use, these measurements of eelgrass structure help to explain the patterns seen in the video sightings. More fish and crabs were sighted within long-line aquaculture than on-bottom aquaculture, consistent with the greater emergent surface area of eelgrass. In addition, the long-lines themselves provide vertical structure that contributes to the overall complexity of the habitat. In the future, it might be possible to adapt imagery techniques used to estimate seagrass habitat structure to quantify the structure provided by the oysters and associated aquaculture gear (Leslie et al. 2017). Similar work was done by Dealtris and colleagues (2004) to quantify the emergent surface area (cm^2 m^{-2}) of both off-bottom aquaculture gear and eelgrass. Such measurements would allow for a more complete understanding of the total structure that is potentially shaping the distribution of species across the habitat mosaic.

This difference in eelgrass structure also relates to the potential strength of edge effects between the aquaculture and eelgrass beds. For both aquaculture types, the edge was defined based on where the aquaculture stopped; this did not always equate to the edge of the eelgrass bed. By this definition, the edges were not always dramatic changes in habitat. This fact could have an impact on the detectability of edge effects and where they occurred. Matias and colleagues (2013) found that the type of edge (sharp vs. gradual transition) influenced the magnitude of the interactions for the distribution of marine molluscs across experimental landscapes. Their results suggest that edge effects may be more pronounced given a sharper transition between aquaculture and eelgrass. This adds a layer of complexity to management because the actual extent of eelgrass within an aquaculture bed changes over time and this progression could affect the distribution of organisms within both habitats (Dumbauld and McCoy 2015). Further research on the effect of the type of edge in this context could help to clarify how this factor affects habitat use.

2.4.3 PREDATION AND RESOURCE AVAILABILITY

Characterization of predation intensity and food availability provides further information about how organisms are using the aquaculture and eelgrass habitats. By considering these data alongside the video sightings data, we can achieve a more complete understanding of the functionality of aquaculture and eelgrass beds. These metrics have also been implicated as mechanisms driving edge effects and thus help to explain edge effects detected here.

Predation tethering units (PTUs) have been used in habitats throughout the world and are a straightforward way to approximate predation intensity. This method is helpful for comparing predation intensity in habitats across time and space. Differences in relative predation intensity are correlated with abundance and species richness of fish measured through visual surveys, making this an appropriate method to pair with video sightings of the fish and crab community (Duffy et al. 2015). The bait in the Low treatment (bait directly on bottom) was absent more often than the bait in the High treatment (bait 20cm off bottom) at both check times, but especially at the 24-hr check, when almost all the Low treatment bait was gone. These results are consistent with other data that have been collected in similar locations and habitats (Clarke 2017, Gross et al. in press). While the data at the first check (when water level reached 30cm) is slightly misleading because of the difference in immersion time of the bait between the two treatments, the 24-hr check provides evidence of greater levels of predation within the long-line habitats than on-bottom habitats for both treatments (Figure 10). The increased predation intensity observed within the long-line aquaculture is consistent with more sightings of fish and crabs in long-lines. This correlation suggests that the increased sightings were at least in part sightings of predators that consumed the bait. The large numbers of Pacific staghorn sculpins sighted in long-line aquaculture corroborates this connection. However, research also suggests a potentially conflicting relationship with habitat structure or emergent surface area. Some researchers have found that the presence of structure, but not the relative amount of structure, has an influence on prey survival (Mattila et al. 2008), while others have seen a clear decrease in predation risk with increased shoot density (Reynolds et al. 2018). This decrease is attributed to a reduction in detection and capture of mobile prey within more complex habitats. Contrary to this conclusion, we saw an increase in predation with increasing habitat structure, suggesting that the complexity was not great enough to reduce detection of prey (i.e. squid bait). The increased structure was correlated with an increase in overall abundance of organisms within these habitats but did not seem to alter the ability of predators to find the bait. There did appear to be an edge effect for the High treatment, where predation was less in the on-bottom edge than within the eelgrass bed, but this difference was not significant. While edge effects were not clear, the distinction between the two aquaculture types suggests potential for differences in how each relates to adjacent eelgrass beds.

Epiphytes are known to be an important food source for mesograzers within seagrass meadows (Jernakoff et al. 1996, Cullen-Unsworth and Unsworth 2013, Motley 2017). Quantification of epiphyte percent cover and load (dry mass of epiphytes/dry mass shoot) therefore provides one estimate of food availability among the habitat types. Values for epiphyte load in this study fell within the ranges of those found in other bays along the West Coast of the United States (Clarke 2017, Motley 2017). While epiphyte load did not significantly vary across the transect or between aquaculture types, the percent cover of epiphytes on eelgrass blades was significantly influenced by these factors (Table 3, Figure 7, Appendix Figure A.2). This significance was primarily driven by the high percentage of epiphyte cover observed in long-line aquaculture as compared to on-bottom. Epiphyte cover was statistically equivalent throughout the rest of the habitats, suggesting that food availability was similar among these habitats. Nonetheless, neither of these measurements (epiphyte load or cover) quantifies the total epiphyte biomass along the transects. Epiphyte biomass is obtained as an intermediate step in the epiphyte load calculation, but this only represents ten blades sampled at each of the five main transect positions. Thus, it is not an absolute comparison between the total epiphyte biomass available in each habitat. To estimate how the total biomass would vary across the transect, the average epiphyte load at each position along the transect was multiplied with the average shoot density. This manipulation revealed the significance of Transect Position but not Aquaculture Type in determining total biomass (Table 3), suggesting an imperfect relationship between epiphyte cover and epiphyte biomass. Epiphyte cover may not accurately characterize the food availability provided by epiphytes within a habitat. Nonetheless, analyses of epiphyte cover and load help show how the habitats could differ relative to each other in the amount of resources that are available.

Foraging behavior varied significantly by Transect Position, with less foraging occurring at the edge than in the interior habitats (Figure 17). Observations of foraging behavior in the video show whether organisms were consuming the food that was available in a given habitat, but it should be noted the potential error in these observations could be relatively large because of the small number of sightings (8% of total). Edge effects are largely driven by trade-offs between predation risk and foraging potential (Macreadie et al. 2010, 2012, Carroll and Peterson 2013). In an Australian estuary, predators made use of edges between seagrass beds and open sand, while prey species were more common within the seagrass (Smith et al. 2011). As applied to the study presented here, predator presence on the edge may have discouraged foraging in this habitat. However, sightings of a known predator (Pacific staghorn sculpin) were low on the edge. Thus, it may have been a combination of food availability and predation risk (influenced by habitat structure) that shaped the decrease in foraging observed at the edge.

2.5 CONCLUSIONS

My research sought to characterize how different oyster aquaculture techniques compare to natural habitats like eelgrass in Pacific Northwest estuaries as habitat for fish and crabs. Based simply on habitat structure and complexity, I hypothesized that long-line aquaculture would provide a habitat more similar to eelgrass than on-bottom aquaculture. Through observation of fish presence and behavior, this effect was mostly confirmed. Abundance of fish and crabs was higher in long-line oyster aquaculture than in on-bottom oyster habitat, correlating with the greater habitat structure provided by eelgrass and by the long-lines themselves. Thus, there is evidence for a difference in how estuarine fauna use these different aquaculture beds.

The sampling design also allowed for exploration of edge effects between aquaculture and eelgrass, contrasting these two habitat types within the larger estuarine seascape. Although there was a clear difference in fish use between the two aquaculture types, edge effects were not as distinct for the metrics collected. This was especially apparent when examining patterns of abundance for individual species. The difference in these patterns helps to highlight the complexities of edge habitat use. Further work will be necessary to fully characterize the impact of these edges, most likely focusing on specific taxa to detect a clear signal.

This type of information could be used to inform management of shellfish aquaculture and eelgrass. Regulations already exist prohibiting the establishment of new aquaculture beds within, and in buffer zones around, native eelgrass beds. However, there are inconsistencies in these regulations, and research into the effects of edges and the pervasiveness of these effects could help to align regulations. For example, the US Army Corps of Engineers (USACE), with input from the NOAA National Marine Fisheries Service, prohibits new aquaculture within a 16-horizontal foot buffer around eelgrass, while a buffer of 25-30ft is used under the Magnuson-Stevens Act (Pacific Fishery Management Council 2014, US Army Corps of Engineers 2017a). Understanding the breadth and strength of edge effects could be a foundation for setting scientifically-appropriate buffer widths and inform those concerned with eelgrass bed fragmentation. In addition, studies such as this that compare different types of aquaculture add to the body of information about the impacts of these altered areas and inform best management practices. Increasingly, shellfish aquaculture is being recognized as a beneficial use of United States coastal waters (NOAA 2018). As the industry is only expected to grow in the coming years, it is necessary to understand how that growth could impact estuarine function. Expanding the knowledge base concerning similarities between shellfish aquaculture and eelgrass will help give managers the tools to appropriately balance these two stakeholder interests.

2.6 TABLES AND FIGURES

Table 1. Ethogram of behaviors used for classification within BORIS software.

Behavior	Description
Transit	moving through the frame with no other detectable behaviors
Forage	acting to ingest or seek out food
School	two or more fish of the same species moving together (sensu Keenleyside 1955)
Refuge	using structure to hide from predators

Table 2. List of species sighted in underwater video footage. Note: there were an additional 191 sightings for which species was not identified.

Common Name	Scientific Name	Total Sightings
Shiner perch	*Cymatogaster aggregata*	675
Pacific staghorn sculpin	*Leptocottus armatus*	138
Three-spined stickleback	*Gasterosteus aculeatus*	76
Dungeness crab	*Metacarcinus magister*	30
Pile perch	*Rhacochilus vacca*	29
Bay pipefish	*Syngnathus leptorhynchus*	13
English sole	*Parophrys vetulus*	6
Saddleback gunnel	*Pholis ornata*	5
Lingcod	*Ophiodon elongatus*	1
Tube-snout	*Aulorhynchus flavidus*	1

Table 3. Results of analysis of deviance tests following GLMMs on eelgrass presence and structure metrics. N=3 for all tests.

	Fixed Effect		
Metric	Transect Position	Aquaculture Type	Interaction
Z. marina percent cover	$\chi^2(4) = 240.54$	$\chi^2(1) = 0.00$	$\chi^2(4) = 13.08$
	$p<0.001$	$p=0.952$	$p=0.011$
Shoot density	$\chi^2(4) = 104.70$	$\chi^2(1) = 0.26$	$\chi^2(4) = 25.14$
	$p<0.001$	$p=0.610$	$p<0.001$
Epiphyte percent cover	$\chi^2(4) = 91.76$	$\chi^2(1) = 9.72$	$\chi^2(4) = 31.01$
	$p<0.001$	$p=0.002$	$p<0.001$
Blade surface area	$\chi^2(4) = 25.80$	$\chi^2(1) = 15.11$	$\chi^2(4) = 12.56$
	$p<0.001$	$p<0.001$	$p=0.014$
Epiphyte load	$\chi^2(4) = 7.69$	$\chi^2(1) = 0.49$	$\chi^2(4) = 6.00$
	$p=0.104$	$p=0.485$	$p=0.199$
Structural complexity	$\chi^2(4) = 35.15$	$\chi^2(1) = 0.18$	$\chi^2(4) = 5.44$
	$p<0.001$	$p=0.672$	$p=0.246$
Total epiphyte biomass	$\chi^2(4) = 18.44$	$\chi^2(1) = 0.13$	$\chi^2(4) = 6.53$
	$p=0.001$	$p=0.716$	$p=0.163$

Table 4. Analysis of deviance results following a GLMM fit for the predation tethering unit (PTU) data (N=3).

Fixed Effects	χ^2	**Degrees of freedom**	**Pr ($>\chi^2$)**
Transect position	5.7743	4	0.21665
Aquaculture type	6.3637	1	0.01165
Treatment	57.8562	1	<0.001
Check time	330.5039	1	<0.001
Transect position X Aquaculture type	6.9406	4	0.13906

Table 5. Results of analysis of deviance tests following associated GLMMs on minnow trap data metrics. N=3 for all tests.

Metric	**Fixed Effect**		
	Transect Position	Aquaculture Type	Interaction
Total Abundance	χ^2 (2) = 0.45	χ^2 (1) = 7.62	χ^2 (2) = 11.94
	p=0.799	p=0.006	p=0.003
Species Richness	χ^2 (2) = 0.38	χ^2 (1) = 0.12	χ^2 (2) = 1.91
	p=0.827	p=0.732	p=0.385

Table 6. Results of analysis of deviance tests following associated GLMs on digital video data metrics. N=3 for all tests.

Metric	**Fixed Effect**		
	Transect Position	Aquaculture Type	Interaction
Total Sightings	χ^2 (4) = 24.79	χ^2 (1) = 57.16	χ^2 (4) = 36.35
	p<0.001	p<0.001	p<0.001
Species Richness	χ^2 (4) = 1.68	χ^2 (1) = 0.15	χ^2 (4) = 1.09
	p=0.794	p=0.700	p=0.859
Time in View	χ^2 (4) = 2.87	χ^2 (1) = 0.27	χ^2 (4) = 2.99
	p=0.580	p=0.606	p=0.560
Shiner Perch Sightings	χ^2 (4) = 38.41	χ^2 (1) = 62.01	χ^2 (4) = 39.23
	p<0.001	p<0.001	p<0.001
Pacific staghorn sculpin Sightings	χ^2 (4) = 70.59	χ^2 (1) = 14.28	χ^2 (4) = 19.13
	p<0.001	p<0.001	p<0.001
Transiting behavior	χ^2 (4) = 25.18	χ^2 (1) = 55.13	χ^2 (4) = 55.69
	p<0.001	p<0.001	p<0.001
Foraging behavior	χ^2 (4) = 13.82	χ^2 (1) = 0.00	χ^2 (4) = 2.71
	p=0.008	p=0.948	p=0.608

Table 7. PERMANOVA results after NMDS of video community data.

Fixed Effects	**Degrees of Freedom**	**Mean Squares**	**F Model**	**R^2**	**Pr(>F)**
Transect position	4	0.14601	0.9295	0.12888	0.545
Aquaculture type	1	0.45486	2.89563	0.10037	0.034
Transect position X Aquaculture type	4	0.08775	0.55861	0.07746	0.899
Residuals	20	0.15708		0.69329	
Total	29			1	

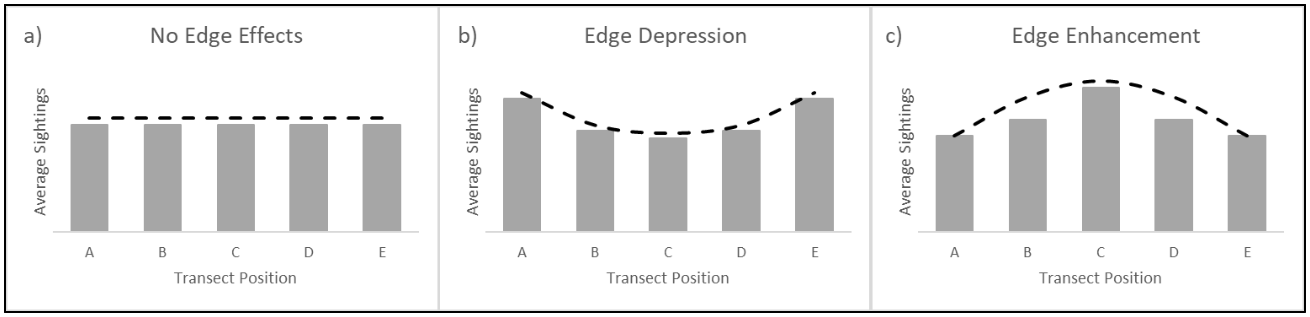

Figure 1. Possible patterns of edge effects across the habitat transition from aquaculture to eelgrass.

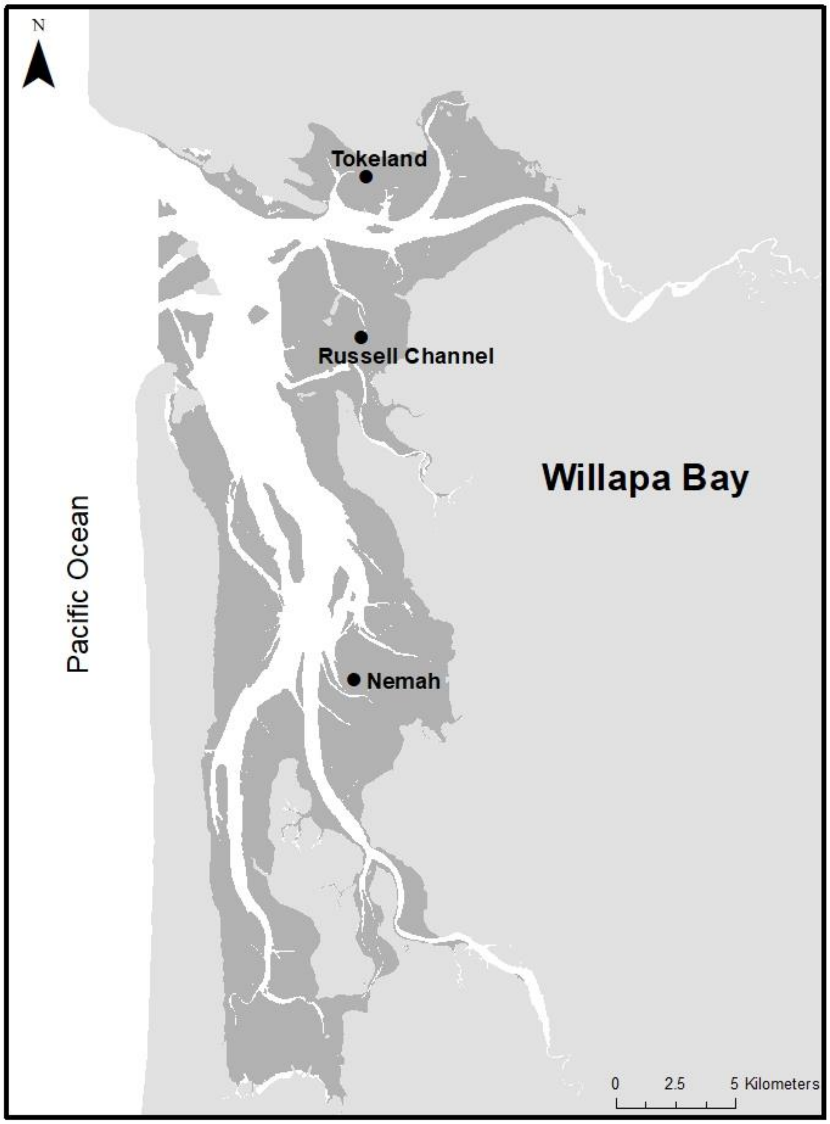

Figure 2. Sampling points within Willapa Bay, WA.

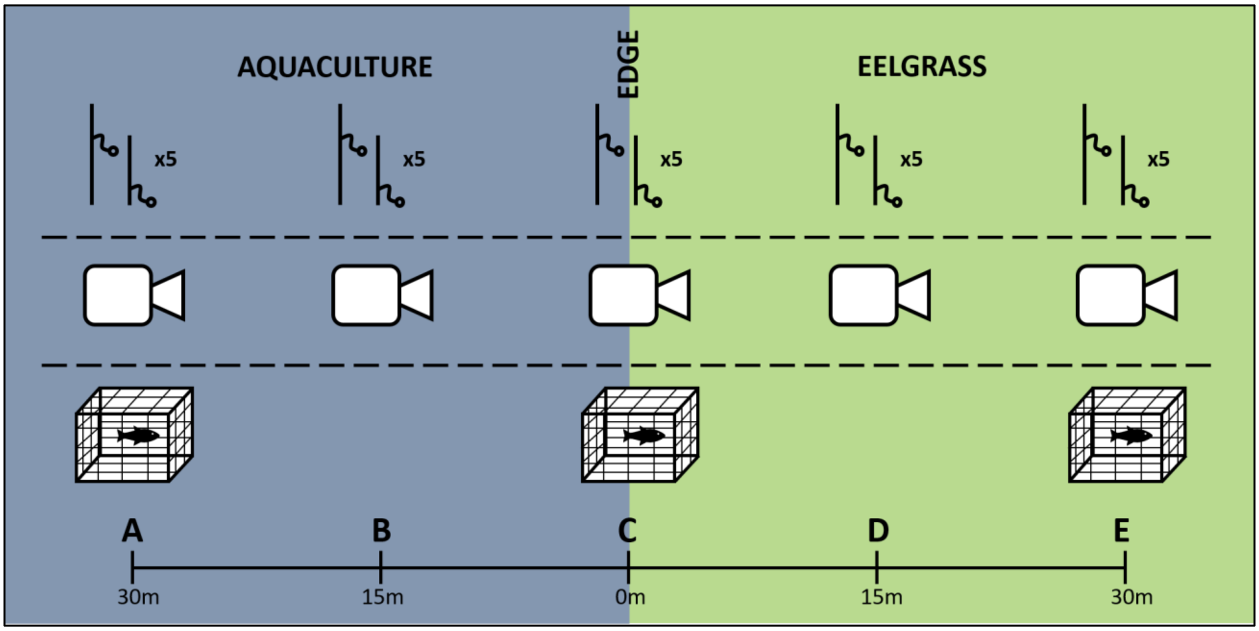

Figure 3. Schematic of sampling design showing PTUs (top), cameras (middle), and minnow traps (bottom). Letters refer to main habitat points along the transect (A=aquaculture interior, B=aquaculture intermediate, C=edge, D=eelgrass intermediate, E=eelgrass interior).

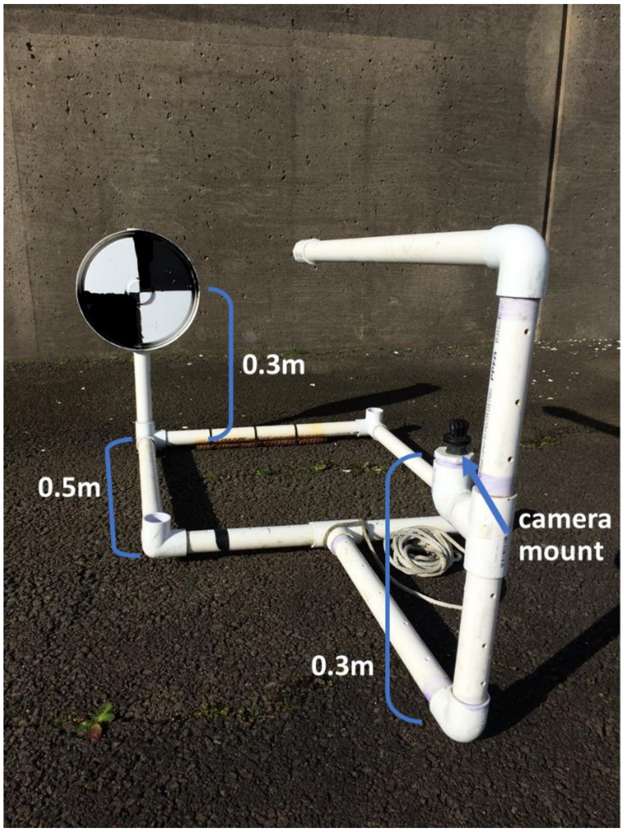

Figure 4. Mount used to deploy GoPro cameras. Quadrat is 0.25m^2. Camera sits about 0.3m off the ground with the Secchi disk approximately 1m away from the camera.

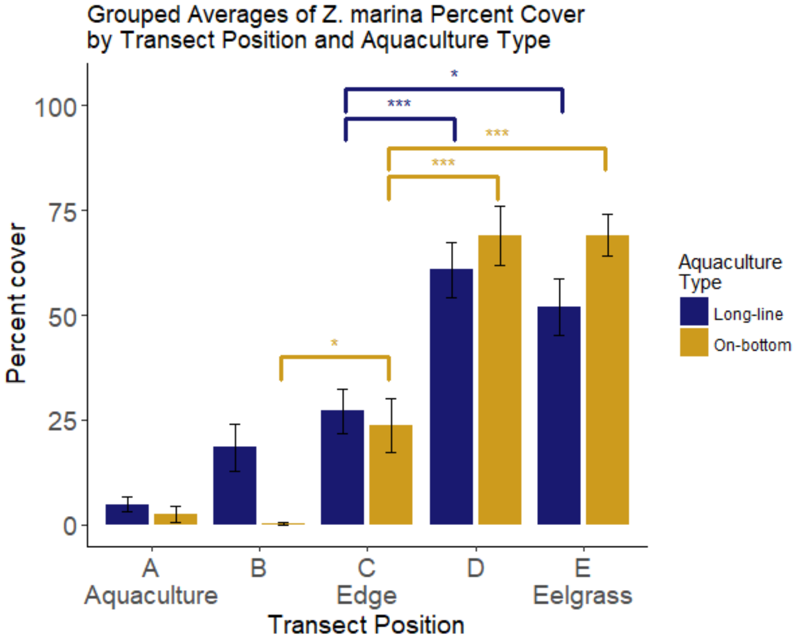

*Figure 5. Averages of Zostera marina percent cover across the transects for both aquaculture types (N=6). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison. Error bars are ±1 SE.*

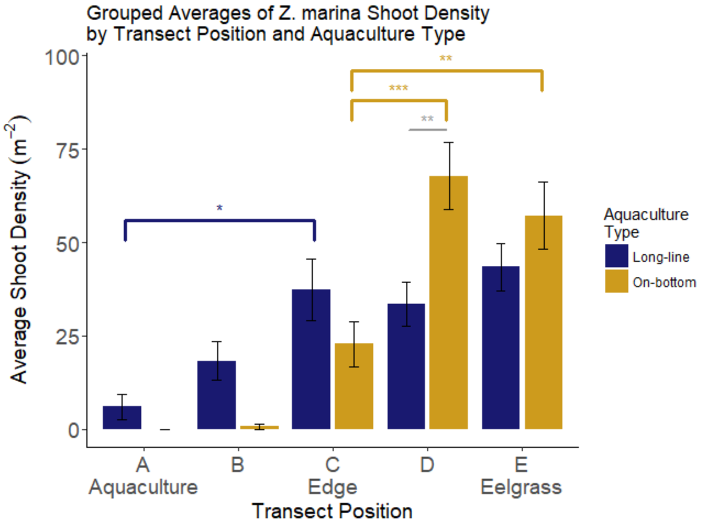

*Figure 6. Averages of Zostera marina shoot density across the transects for both aquaculture types (N=6). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

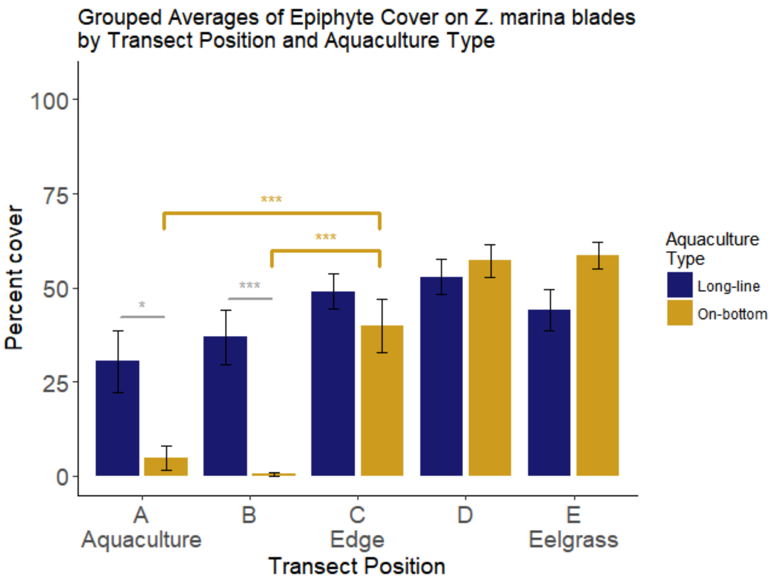

*Figure 7. Averages of epiphyte percent cover on Zostera marina blades from eelgrass survey along transect for both aquaculture types (N=6). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

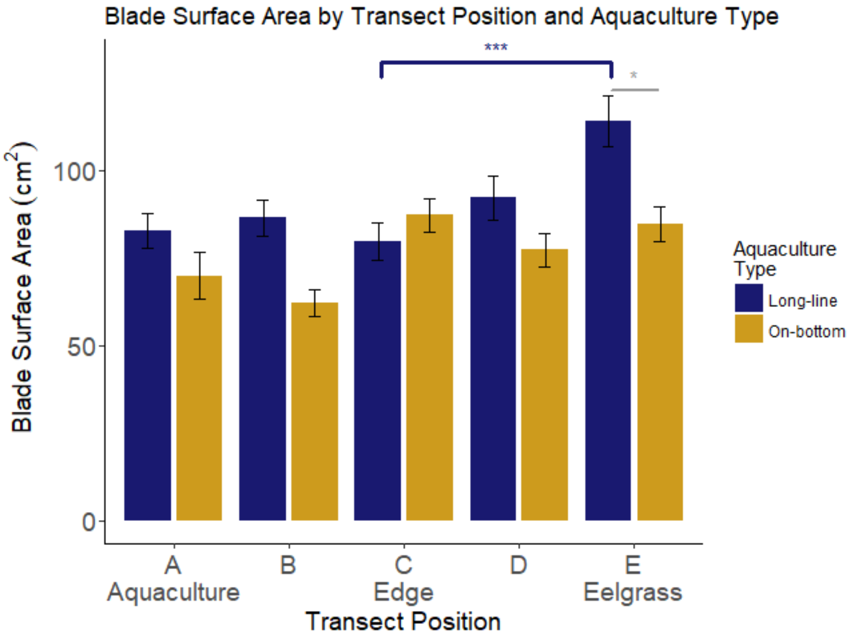

*Figure 8. Averages of blade surface area from measurements of length and width of Zostera marina shoot samples (10 shoots per Transect Position and Aquaculture Type). For most, N=60 but some habitats were missing samples. Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

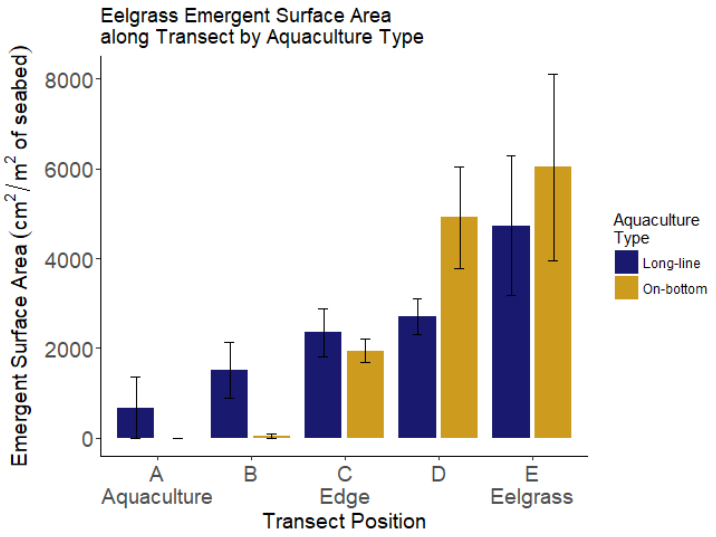

*Figure 9. Emergent surface area of Zostera marina, as calculated by blade surface area*shoot density for each aquaculture type and position along the transect (N=6). Error bars are ±1 SE.*

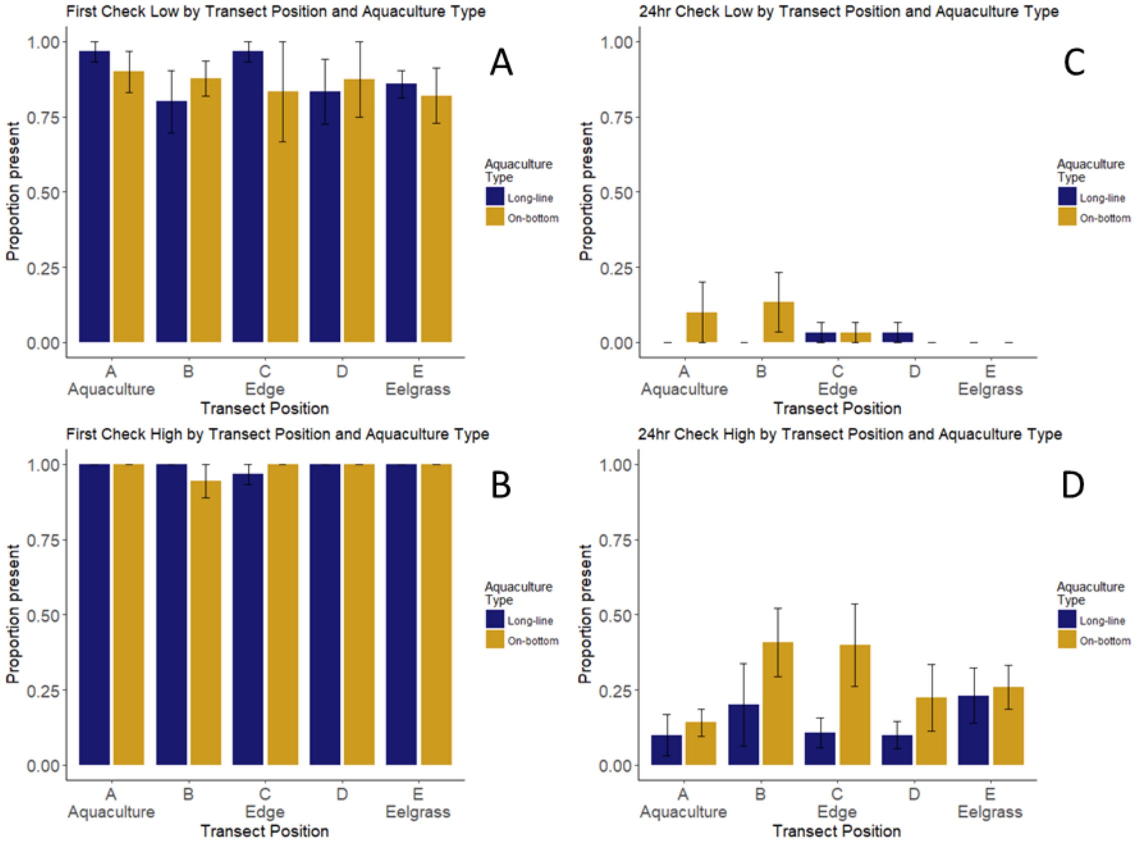

Figure 10. Results of predation tethering unit (PTU) arrays for both the Low treatment (A and C) and High treatment (B and D) at the first check (A and B) and 24hr check (C and D) (N=6). Error bars are ±1SE.

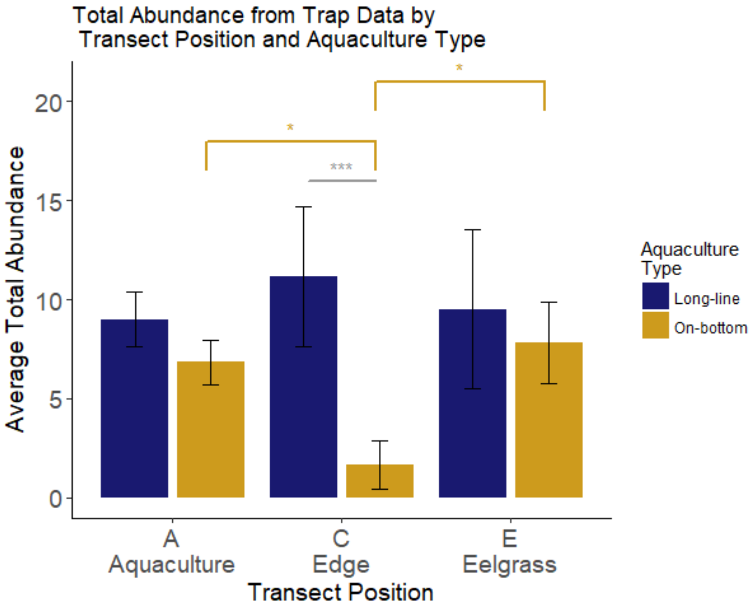

*Figure 11. Average catch of fish and crab in minnow traps across the transects and between aquaculture types (N=6). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

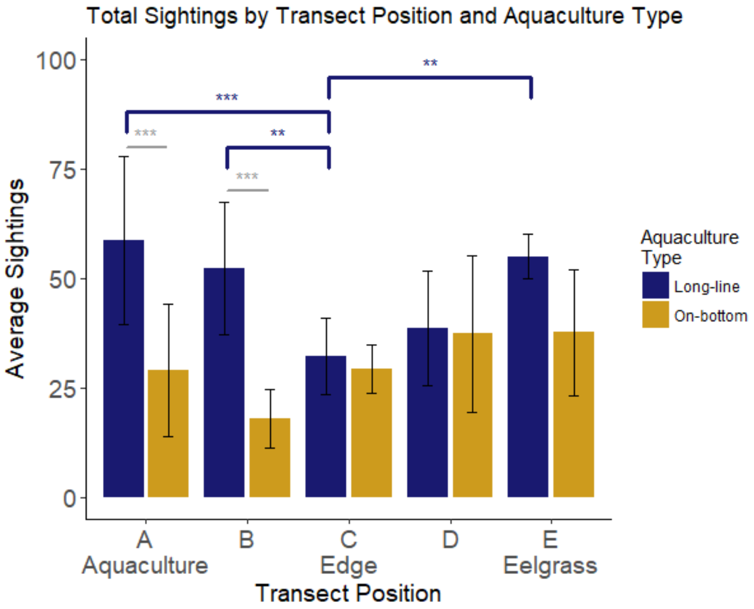

*Figure 12. Average total sightings of fish and crab from video data across transects and between aquaculture types (N=3). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

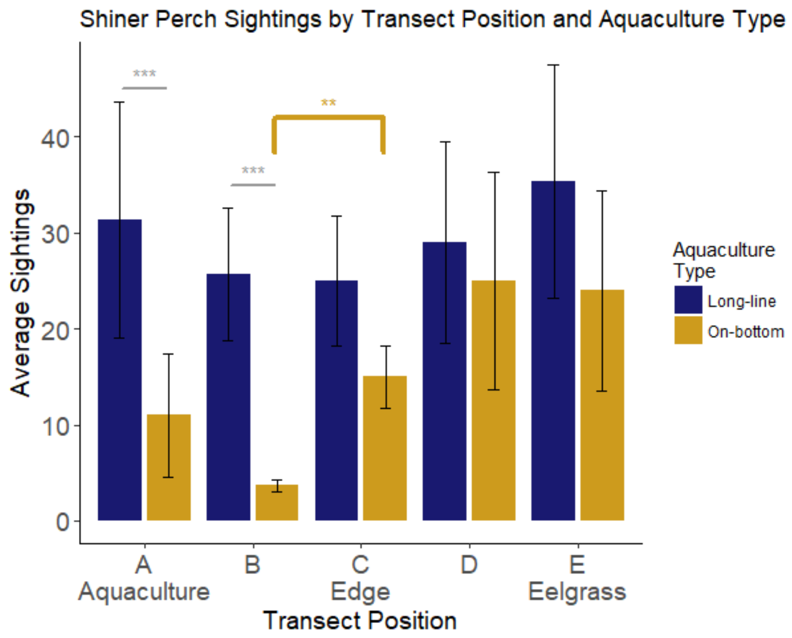

*Figure 13. Sightings of shiner perch across the transect and between aquaculture types (N=3). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

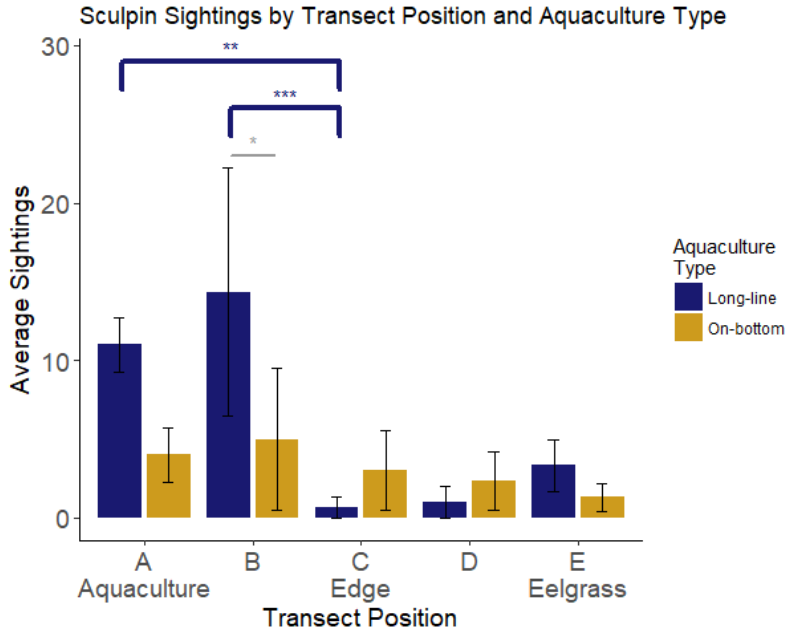

*Figure 14. Sightings of Pacific staghorn sculpin across the transect and between aquaculture types (N=3). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

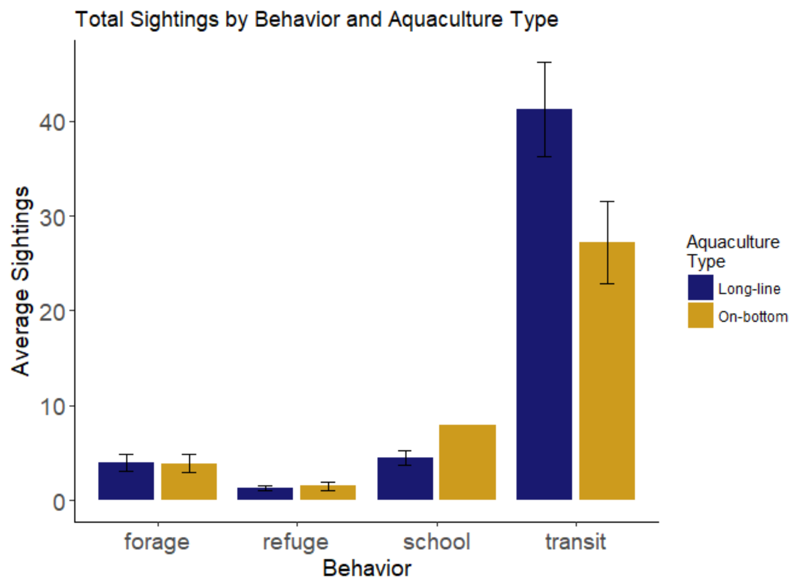

Figure 15. Sightings separated by behavior and aquaculture type. Transiting was by far the most common behavior (88% of sightings). Error bars are ±1 SE.

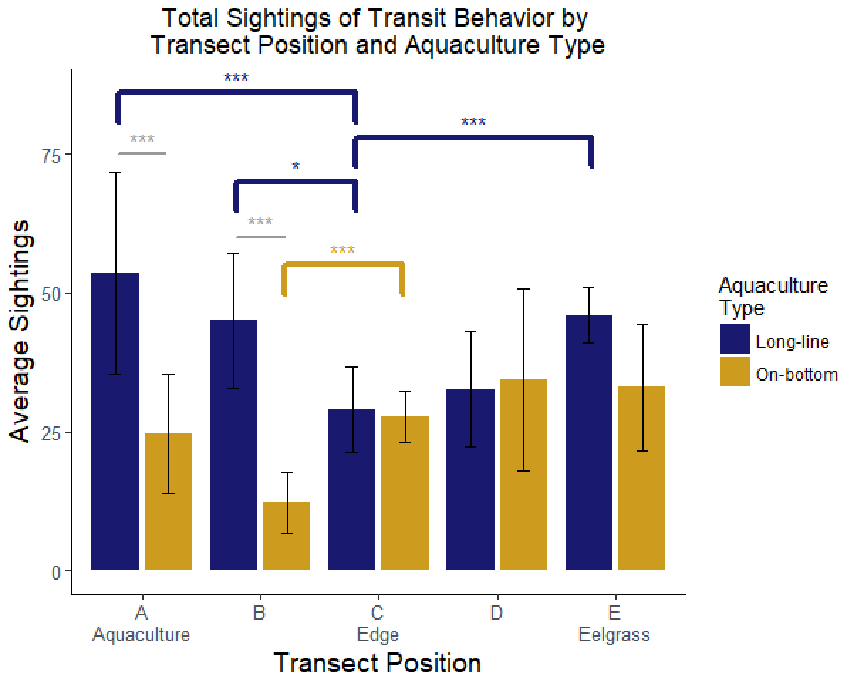

*Figure 16. Sightings of transiting behavior by transect position and aquaculture type (N=3). Brackets show significant contrasts of interest from simultaneous comparisons of all pairs (significance levels: 0 "***" 0.001 "**" 0.01 "*" 0.05). Colors correspond to aquaculture type of the comparison, grey designating comparisons between type. Error bars are ±1 SE.*

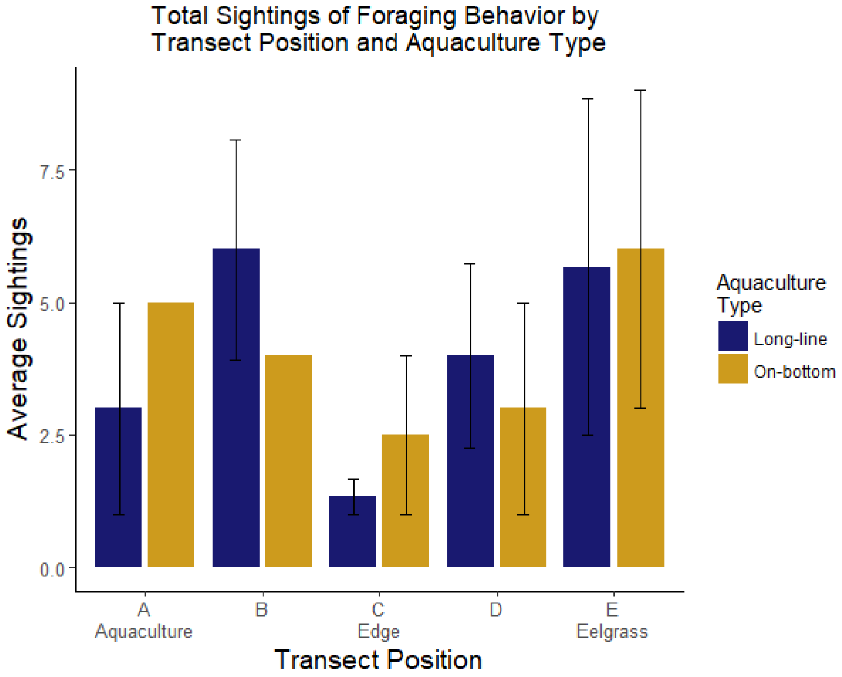

Figure 17. Average sightings of foraging behavior by transect position and aquaculture type (N=3).

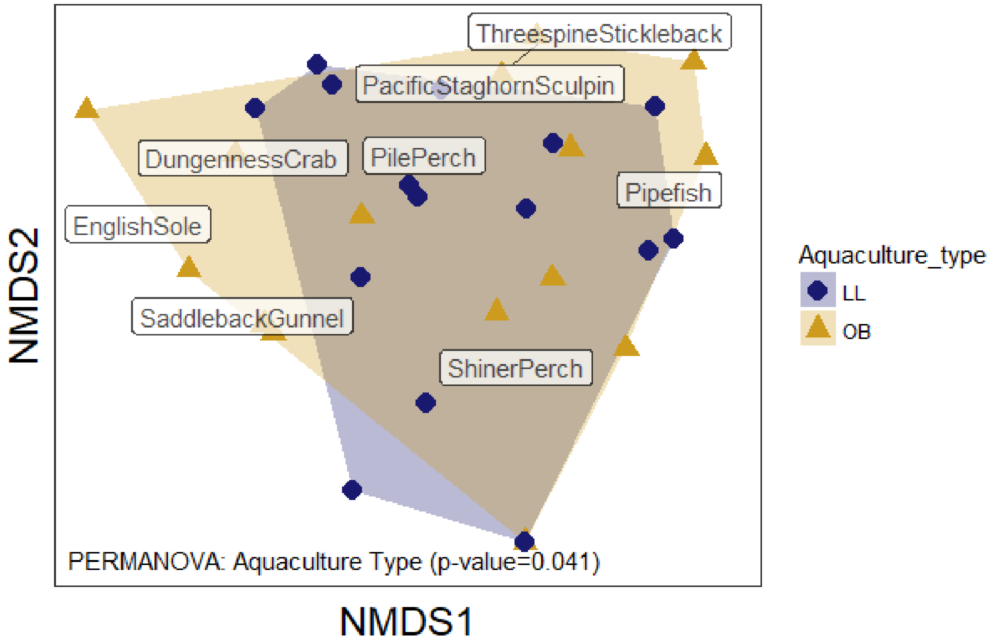

Figure 18. NMDS results of community data from videos. Polygons represent differences between aquaculture types. Labels correspond to the locations of the weighted average score for that species. Results of a PERMANOVA test between aquaculture types is noted.

CHAPTER 3: CONCLUSION

This work fills a unique gap within current scientific knowledge and emerging issues surrounding shellfish aquaculture and eelgrass. Results presented here directly compare nekton use of habitats created by on-bottom and long-line aquaculture to that provided by eelgrass at the seascape scale. At a basic level, this work offers evidence for a difference in habitat structure created by the two methods of aquaculture. This evidence could be used to formulate future regulations that permit certain types of aquaculture over others. So far, the shift in aquaculture methods has been largely driven by the industry and a desire to achieve a high-quality and more consistent product. This means that, in many cases, the ecological impacts are an afterthought. Nonetheless, it is important to understand how these various aquaculture techniques interact with the surrounding estuarine system. Aside from the comparison between the two aquaculture types, the design of this study also helped to elucidate the similarities between aquaculture and eelgrass as habitat. Specifically, the data suggests that long-line oyster aquaculture provides habitat that is similar to the habitat created by eelgrass. However, it must be noted that this study considered just one of many ecological functions of eelgrass and oysters within estuarine ecosystems. It cannot be said that long-line oyster aquaculture could replace eelgrass without a significant loss of ecosystem services (e.g. carbon sequestration, water quality improvement and mitigation of ocean acidification; Costanza et al. 1997, Hendriks et al. 2014). Thus, managers must take into account a wide breadth of information to make the most appropriate decisions. Consideration of aquaculture and eelgrass within the context of seascape ecology highlights the potential pitfalls of management by separate agencies. As human pressures continue to grow within coastal and marine systems, it is becoming increasingly difficult to view any activity in isolation.

Natural resource management has largely relied on sector-based approaches to regulate practices related to specific natural resources. Within estuarine systems, this means that fisheries have been managed separately from transportation and recreation and even aquaculture, among others. The regulatory conflict between shellfish aquaculture and eelgrass in Washington is just one example of how this sector-based management can become problematic. Because neither of these resource interests exists in isolation but is actually closely connected to the other in space, managing them separately can make the issue more complicated. In fact, within Washington State, there are at least five different federal, state, and local agencies that have established regulations concerning expansion of aquaculture near eelgrass beds. This means that groups seeking to obtain a permit for shellfish aquaculture must go through a tedious, bureaucratic process that can often be time-consuming, expensive, and confusing (Washington State Department of Ecology 2014). Recently, the US Army Corps of Engineers (USACE) revised and reissued Nationwide Permit 48 (NWP48) to help streamline the permitting process for commercial shellfish aquaculture (US Army Corps of Engineers 2017b). This is in line with NOAA's National Shellfish Initiative put forth in 2011. However, even with NWP48, aquaculture permittees must also comply with other policies at the federal level like the Clean Water Act and the Coastal Zone Management Act (*Clean Water Act* 1972, *Coastal Zone Management Act* 1972). At the state level, both the WA Department of Ecology and Department of Natural Resources have regulations surrounding establishment of shellfish aquaculture in the state's inland and coastal waters. This is further complicated in Washington because the Shoreline Management Act delegates authority to local counties to develop their own Shoreline Master Programs that regulate activities in their coastal zones (*Shoreline Management Act* 1971). Thus, there is separate regulation of shellfish aquaculture at all three levels of government (local, state, and federal) and these agencies have inconsistent regulations around the establishment of commercial aquaculture in or near eelgrass beds. For example, the USACE, in consultation with the NOAA National Marine Fisheries Service, decided on a 16-horizontal foot buffer between native eelgrass beds and new aquaculture activities (US Army Corps of Engineers 2017a). However, according to the Pacific Fishery Management Council, which designates "essential fish habitat" for fisheries along the West Coast, new aquaculture cannot occur within 25-30ft of existing eelgrass (Pacific Fishery Management Council 2014). This illustrates the complex regulatory environment surrounding shellfish aquaculture within Washington State, especially as it relates to eelgrass. To appropriately consider the myriad connections between aquaculture and eelgrass, a new type of management style may be necessary.

Ecosystem-based management (EBM) has received increasing attention in recent years as a way to account for the variety of human pressures that coexist in natural systems. In general, EBM is a strategy which strives to preserve the health, productivity, and resilience of an ecosystem for the benefit of services important to humans (COMPASS 2005). It recognizes the interconnectedness between different natural processes as well as between humans and the environment. By conducting shellfish aquaculture and conserving eelgrass beds within estuaries, humans become a part of the coupled socio-ecological system (McLeod and Leslie 2009). This designation recognizes that humans are not just external agents, but instead closely connected to the functioning of natural systems (Berkes 2012). Practicing EBM could thus provide a platform on which human interests like shellfish aquaculture and eelgrass preservation could support natural processes. Another key component of EBM that is of importance here is a focus on the particular location under management. The root of the issue between shellfish aquaculture and eelgrass is that they often overlap in spatial extent. By focusing on a specific place rather than a sector or industry, EBM inherently considers the connections that occur because of proximity. In the case of shellfish aquaculture and eelgrass, this would allow for a more explicit consideration of the trade-offs between the two interests. Both aquaculture and eelgrass provide ecologically, economically, and culturally important services but management of each resource individually does not give managers the ability to consider trade-offs. An EBM approach to estuarine management would allow for a more realistic perspective to be adopted, balancing the various stakeholder interests within the socio-ecological system.

Because of the potential for aquaculture practices to impact eelgrass, current sector-based management positions aquaculture in opposition to eelgrass. This research suggests that one type of shellfish aquaculture (long-line oyster culture) could provide habitat similar to that provided by eelgrass. In addition, it considers the edge effects present when shellfish aquaculture occurs directly adjacent to eelgrass. A more complete characterization of the pervasiveness of these edge effects would help to inform the buffer zones defined by the various state and federal agencies mentioned above. All of this information would be necessary and pertinent to the development of an EBM framework for estuaries within Washington State or along the West Coast. Currently, the buffer zones prescribed by regulatory agencies recognize a connection between shellfish aquaculture and eelgrass but they inherently prioritize fisheries management (since it is through designation as “essential fish habitat” that eelgrass is protected) over aquaculture and do not recognize aquaculture itself as a habitat. With the conclusions presented here, managers could explicitly consider the impacts of expanding long-line oyster aquaculture into an area of tide flats in Willapa Bay that currently has sparse patches of eelgrass or historically had eelgrass meadows. Depending on the specific location within the bay and the dominant physical processes (e.g. frequent tidal flushing, high nutrient input), it may be advantageous to restore the eelgrass to its previous extent to preserve productive habitat and relocate the aquaculture to another location. The trade-off could also be between different methods of aquaculture; it may be more appropriate to use long-line aquaculture rather than on-bottom aquaculture near eelgrass beds to provide a similar habitat and less-destructive harvest methods (Wisehart et al. 2007, Dumbauld et al. 2009). Incorporating understanding of these connections into an ecosystem-based approach to management would give managers the ability to make decisions most suitable for specific locations and explicitly consider the trade-offs between establishing aquaculture or conserving eelgrass. Applying EBM to this issue could alleviate some of the bureaucratic burdens and encourage a more sustainable use of estuarine tidelands.

Estuaries are highly complex systems and there is no correct answer for how to manage the various human activities and interests that occur within them. However, the research presented here contributes to the best available science used by managers and policy-makers who make decisions about how to use these areas. In addition, adoption of a management style founded in EBM would allow for a more cooperative and realistic approach to these complex and interconnected systems. Ultimately, there will be trade-offs between expanding shellfish aquaculture and protecting eelgrass beds within coastal estuaries. The complexities of the issue only necessitate further work and collaboration to ensure that the most appropriate decisions are made.

REFERENCES

Bartlett, D., and R. W. G. Carter. 1991. Seascape ecology: the landscape ecology of the coastal zone. EKOLOGIA(CSFR)/ECOLOGY(CSFR). 10:43–53.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Beck, M. W., J. Heck Kenneth 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, and M. P. Weinstein. 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. BioScience 51:633.

Bell, S. S., R. A. Brooks, B. D. Robbins, M. S. Fonseca, and M. O. Hall. 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biological Conservation 100:115–123.

Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat Loss and Population Decline: A Meta-Analysis of the Patch Size Effect. Ecology 79:517–533.

Berkes, F. 2012. Implementing ecosystem-based management: evolution or revolution?: Implementing ecosystem-based management. Fish and Fisheries 13:465–476.

Bogaert, J., D. S.-V. Eysenrode, I. Impens, and P. V. Hecke. 2001. The Interior-to-Edge Breakpoint Distance as a Guideline for Nature Conservation Policy. Environmental Management 27:493–500.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Bologna, P. A. X., and K. L. Heck. 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25:1033–1044.

Boström, C., E. L. Jackson, and C. A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science 68:383–403.

Boström, C., S. Pittman, C. Simenstad, and R. Kneib. 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Marine Ecology Progress Series 427:191–217.

Bowden, D. A., A. A. Rowden, and M. J. Attrill. 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of Zostera marina seagrass beds. Journal of Experimental Marine Biology and Ecology 259:133–154.

Bush Act/Callow Act Lands. 2002. . Page RCW.

Carroll, J. M., and B. J. Peterson. 2013. Ecological trade-offs in seascape ecology: bay scallop survival and growth across a seagrass seascape. Landscape Ecology 28:1401–1413.

Castel, J., P.-J. Labourg, V. Escaravage, I. Auby, and M. E. Garcia. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuarine, Coastal and Shelf Science 28:71–85.

Clarke, L. 2017. Functional comparison of longline oyster aquaculture and eelgrass (Zostera marina L.) habitats among Pacific Northwest estuaries, USA. Oregon State University, Corvallis, OR.

Clean Water Act. 1972. . Page U.S.C.

Coastal Zone Management Act. 1972. . Page U.S.C.

Coen, L. D., M. W. Luckenbach, and D. L. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. Pages 438–454American Fisheries Society Symposium.

Costanza, R., R. d'Arge, R. de Groot, S. Faber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital.

Crawford, C. M., C. K. A. Macleod, and I. M. Mitchell. 2003. Effects of shellfish farming on the benthic environment. Aquaculture 224:117–140.

Cullen-Unsworth, L., and R. Unsworth. 2013. Seagrass Meadows, Ecosystem Services, and Sustainability. Environment 55:14–28.

Dealtris, J. T., B. D. Kilpatrick, and R. B. Rheault. 2004. A comparative evaluation of the habitat value of shellfish aquaculture gear, submerged aquatic vegetation and a non-vegetated seabed. Journal of Shellfish Research 23:867–874.

Debinski, D., and R. Holt. 2000. A Survey and Overview of Habitat Fragmentation Experiments. Conservation Biology 14:342–355.

Duffy, J. E., S. L. Ziegler, J. E. Campbell, P. M. Bippus, and J. S. Lefcheck. 2015. Squidpops: A Simple Tool to Crowdsource a Global Map of Marine Predation Intensity. PLOS ONE 10:e0142994.

Dumbauld, B., and L. McCoy. 2015. Effect of oyster aquaculture on seagrass Zostera marina at the estuarine landscape scale in Willapa Bay, Washington (USA). Aquaculture Environment Interactions 7:29–47.

Dumbauld, B. R., G. R. Hosack, and K. M. Bosley. 2015. Association of Juvenile Salmon and Estuarine Fish with Intertidal Seagrass and Oyster Aquaculture Habitats in a Northeast Pacific Estuary. Transactions of the American Fisheries Society 144:1091–1110.

Dumbauld, B. R., B. E. Kauffman, A. C. Trimble, and J. L. Ruesink. 2011. The Willapa Bay Oyster Reserves in Washington State: Fishery Collapse, Creating a Sustainable Replacement, and the Potential for Habitat Conservation and Restoration. Journal of Shellfish Research 30:71–83.

Dumbauld, B. R., J. L. Ruesink, and S. S. Rumrill. 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in West Coast (USA) estuaries. Aquaculture 290:196–223.

Eggleston, D. B., L. L. Etherington, and W. E. Elis. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. Journal of Experimental Marine Biology and Ecology 223:111–132.

Erbland, P. J., and G. Ozbay. 2008. A comparison of the macrofaunal communities inhabiting a Crassostrea virginica oyster reef and oyster aquaculture gear in Indian River Bay, Delaware. Journal of Shellfish Research 27:757–768.

Everett, R., G. Ruiz, and J. Carlton. 1995. Effect of oyster mariculture on submerged aquatic vegetation: an experimental test in a Pacific Northwest estuary. Marine Ecology Progress Series 125:205–217.

Ewers, R. M., and R. K. Didham. 2007. The Effect of Fragment Shape and Species’ Sensitivity to Habitat Edges on Animal Population Size. Conservation Biology 21:926–936.

Ewers, R. M., S. Thorpe, and R. K. Didham. 2007. Synergistic Interactions Between Edge and Area Effects in a Heavily Fragmented Landscape. Ecology 88:96–106.

FAO. 2014. The state of world fisheries and aquaculture: opportunities and challenges. Food and Agriculture Organization of the United Nations, Rome.

Ferraro, S. P., and F. A. Cole. 2007. Benthic macrofauna–habitat associations in Willapa Bay, Washington, USA. Estuarine, Coastal and Shelf Science 71:491–507.

Ferraro, S. P., and F. A. Cole. 2010. Ecological periodic tables for nekton usage of four US Pacific Northwest estuarine habitats. Canadian Journal of Fisheries & Aquatic Sciences 67:1957–1967.

Ferrell, D. J., and J. D. Bell. 1991. Differences among assemblages of fish associated with Zostera capricorni and bare sand over a large spatial scale. Marine Ecology Progress Series:15–24.

Forman, R. T. ., and M. Godron. 1986. Landscape Ecology. John Wiley & Sons, New York.

Forrest, B. M., and R. G. Creese. 2006. Benthic Impacts of Intertidal Oyster Culture, with Consideration of Taxonomic Sufficiency. Environmental Monitoring and Assessment 112:159–176.

Forrest, B. M., N. B. Keeley, G. A. Hopkins, S. C. Webb, and D. M. Clement. 2009. Bivalve aquaculture in estuaries: Review and synthesis of oyster cultivation effects. Aquaculture 298:1–15.

Friard, O., and M. Gamba. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7:1325–1330.

Gain, I. E., R. A. Brewton, M. M. Reese Robillard, K. D. Johnson, D. L. Smee, and G. W. Stunz. 2017. Macrofauna using intertidal oyster reef varies in relation to position within the estuarine habitat mosaic. Marine Biology 164.

Gates, J. E., and J. A. Mosher. 1981. A Functional Approach to Estimating Habitat Edge Width for Birds. The American Midland Naturalist 105:189–192.

Gross, C., C. Donoghue, C. Pruitt, A. C. Trimble, and J. L. Ruesink. 2017. Taxonomic and functional assessment of mesopredator diversity across an estuarine habitat mosaic. Ecosphere 8.

den Hartog, C. 1970. The seagrasses of the world. North Holland, Amsterdam.

Harwell, H. D., M. H. Posey, and T. D. Alphin. 2011. Landscape aspects of oyster reefs: Effects of fragmentation on habitat utilization. Journal of Experimental Marine Biology and Ecology 409:30–41.

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

Hedgpeth, J. W., and S. Obrebski. 1981. Willapa Bay: A Historical Perspective and a Rationale for Research. Office of Biological Services, U.S. Fish and Wildlife Service, Washington, D.C.

Hendriks, I. E., Y. S. Olsen, L. Ramajo, L. Basso, A. Steckbauer, T. S. Moore, J. Howard, and C. M. Duarte. 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. Biogeosciences 11:333–346.

Hinchey, E. K., M. C. Nicholson, R. N. Zajac, and E. A. Irlandi. 2008. Preface: Marine and coastal applications in landscape ecology. Landscape Ecology 23:1–5.

Holsman, K. K., P. S. McDonald, and D. A. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab Cancer magister in a NE Pacific estuary. Marine Ecology Progress Series 308:183–195.

Hosack, G. R., B. R. Dumbauld, J. L. Ruesink, and 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.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous Inference in General Parametric Models. Biometrical Journal 50:346–363.

Hovel, K. A., and R. N. Lipcius. 2001. Habitat Fragmentation in a Seagrass Landscape: Patch Size and Complexity Control Blue Crab Survival. Ecology 82:1814–1829.

Jelbart, J. E., P. M. Ross, and R. M. Connolly. 2006. Edge effects and patch size in seagrass landscapes: an experimental test using fish. Marine Ecology Progress Series 319:93–102.

Jenkins, G. P., H. M. A. May, M. J. Wheatley, and M. G. Holloway. 1997. Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. Estuarine, Coastal and Shelf Science 44:569–588.

Jernakoff, P., A. Brearley, and J. Nielsen. 1996. Factors affecting grazer-epiphyte interactions in temperate seagrass meadows. Oceanography and Marine Biology: An Annual Review 34:109–162.

Johnson, R. W., C. Goepple, D. Jansen, and R. Paschal. 1991. The Public Trust Doctrine and Coastal Zone Management in Washington State. Washington Department of Ecology, Olympia.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as Ecosystem Engineers. Oikos 69:373.

Keenleyside, M. H. A. 1955. Some Aspects of the Schooling Behaviour of Fish. Behaviour 8:183–248.

Leslie, T., N. C. James, W. M. Potts, and A. Rajkaran. 2017. The relationship between habitat complexity and nursery provision for an estuarine-dependent fish species in a permanently open South African Estuary. Estuarine, Coastal and Shelf Science 198:183–192.

Long, M. H., J. E. Rheuban, P. Berg, and J. C. Zieman. 2012. A comparison and correction of light intensity loggers to photosynthetically active radiation sensors. Limnology and Oceanography 10:416–424.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. Science 312:1806–1809.

Macreadie, P., N. Geraldi, and C. Peterson. 2012. Preference for feeding at habitat edges declines among juvenile blue crabs as oyster reef patchiness increases and predation risk grows. Marine Ecology Progress Series 466:145–153.

Macreadie, P. I., J. S. Hindell, M. J. Keough, G. P. Jenkins, and R. M. Connolly. 2010. Resource distribution influences positive edge effects in a seagrass fish. Ecology 91:2013–2021.

Magnuson-Stevens Fishery Conservation and Management Act. 1976. . Page U.S.C.

Mahoney, R. D., M. D. Kenworthy, J. K. Geyer, K. A. Hovel, and F. Joel Fodrie. 2018. Distribution and relative predation risk of nekton reveal complex edge effects within temperate seagrass habitat. Journal of Experimental Marine Biology and Ecology 503:52–59.

Mallet, A. L., C. E. Carver, and T. Landry. 2006. Impact of suspended and off-bottom Eastern oyster culture on the benthic environment in eastern Canada. Aquaculture 255:362–373.

Matias, M. G., R. A. Coleman, D. F. Hochuli, and A. J. Underwood. 2013. Macrofaunal Responses to Edges Are Independent of Habitat-Heterogeneity in Experimental Landscapes. PLoS ONE 8:1–8.

Mattila, J., K. L. Heck, E. Millstein, E. Miller, C. Gustafsson, S. Williams, and D. Byron. 2008. Increased habitat structure does not always provide increased refuge from predation. Marine Ecology Progress Series 361:15–20.

McCune, B., and J. Grace. 2002. Analysis of Ecological Communities. Second edition. mjm Software Design, Gleneden Beach, Oregon.

McKindsey, C. W., M. R. Anderson, P. Barnes, S. Courtenay, T. Landry, and M. Skinner. 2006. Effects of shellfish aquaculture on fish habitat. Fisheries and Oceans.

Motley, J. 2017. Local and Regional Patterns in Eelgrass (Zostera marina L.) Communities Along an Upwelling-Productivity Gradient in Oregon Estuaries, USA. Oregon State University, Corvallis, OR.

Nagelkerken, I., M. Sheaves, R. Baker, and R. M. Connolly. 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish and Fisheries 16:362–371.

Neckles, H. A., F. T. Short, S. Barker, and B. S. Kopp. 2005. Disturbance of eelgrass Zostera marina by commercial mussel Mytilus edulis harvesting in Maine: dragging impacts and habitat recovery. Marine Ecology Progress Series 285:57–73.

Newell, R. I. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve mollucs: a review. Journal of Shellfish Research 23:51–61.

NMFS. 2016. Anuual Commercial Landings Statistics. https://www.st.nmfs.noaa.gov/pls/webpls/MF_ANNUAL_LANDINGS.RESULTS.

NOAA. 2011. Marine Aquaculture Policy. National Oceanic and Atmospheric Administration.

NOAA. 2016. Washington Shellfish Initiative. http://www.westcoast.fisheries.noaa.gov/aquaculture/washington_shellfish_initiative.html.

NOAA. 2017, October 10. What percentage of the American population lives near the coast? https://oceanservice.noaa.gov/facts/population.html.

NOAA. 2018. National Shellfish Initiative Fact Sheet.

Oksanen, J., F. Guillaume Blanchet, M. Friendly, R. Kindt, D. McGlinn, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. vegan: Community Ecology Package.

Orth, R. J., T. J. B. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S. L. Williams. 2006. A Global Crisis for Seagrass Ecosystems. BioScience 56:987–996.

Orth, R. J., K. L. Heck, and J. van Montfrans. 1984. Faunal Communities in Seagrass Beds: A Review of the Influence of Plant Structure and Prey Characteristics on Predator-Prey Relationships. Estuaries 7:339–350.

Orth, R. J., and K. A. Moore. 1986. Seasonal and year-to-year variations in growth of Zostera marina L. (eelgrass) in the lower Chesapeake Bay. Aquatic Botany 24:335–341.

Pacific Fishery Management Council. 2014. Appendix A to the Pacific Coast Salmon Fishery Management Plan: Identification and Description of Essential Fish Habitat, Adverse Impacts, and Recommended Conservation Measures for Salmon. PFMC, Portland, OR.

Pacific Fishery Management Council. 2016. Pacific Coast Salmon Fishery Management Plan for Commercial and Recreational Salmon Fisheries off the Coasts of Washington, Oregon, and California as Amended through Amendment 19. PFMC, Portland, OR.

Pinna, S., N. Sechi, and G. Ceccherelli. 2013. Canopy structure at the edge of seagrass affects sea urchin distribution. Marine Ecology Progress Series 485:47–55.

Pinnix, W. D., T. A. Shaw, K. C. Acker, and N. J. Hetrick. 2005. Fish communities in eelgrass, oyster culture and mudflat habitats of north Humboldt Bay, California, Final Report. US Fish and Wildlife Service, Arcata, CaliforniaTechnical Report 2.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasheed, M. A. 2004. Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. Journal of Experimental Marine Biology and Ecology 310:13–45.

Reynolds, P. L., J. J. Stachowicz, K. Hovel, C. Boström, K. Boyer, M. Cusson, J. S. Eklöf, F. G. Engel, A. H. Engelen, B. K. Eriksson, F. J. Fodrie, J. N. Griffin, C. M. Hereu, M. Hori, T. C. Hanley, M. Ivanov, P. Jorgensen, C. Kruschel, K.-S. Lee, K. McGlathery, P.-O. Moksnes, M. Nakaoka, M. I. O’Connor, N. E. O’Connor, R. J. Orth, F. Rossi, J. Ruesink, E. E. Sotka, J. Thormar, F. Tomas, R. K. F. Unsworth, M. A. Whalen, and J. E. Duffy. 2018. Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. Ecology 99:29–35.

Roberts, D. W. 2016. labdsv: Ordination and Multivariate Analysis for Ecology.

Rooper, C. N., D. R. Gunderson, and D. A. Armstrong. 2003. Patterns in Use of Estuarine Habitat by Juvenile English Sole (Pleuronectes vetulus) in Four Eastern North Pacific Estuaries. Estuaries 26:1142–1154.

Ruesink, J. L., B. E. Feist, C. J. Harvey, J. S. Hong, A. C. Trimble, and L. M. Wisehart. 2006. Changes in productivity associated with four introduced species: ecosystem transformation of a “pristine”estuary. Marine Ecology Progress Series 311:203–216.

Ruesink, J. L., J.-S. Hong, L. Wisehart, S. D. Hacker, B. R. Dumbauld, M. Hessing-Lewis, and A. C. Trimble. 2010. Congener comparison of native (Zostera marina) and introduced (Z. japonica) eelgrass at multiple scales within a Pacific Northwest estuary. Biological Invasions 12:1773–1789.

Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of Non-Native Oysters: Ecosystem Effects and Restoration Implications. Annual Review of Ecology, Evolution, and Systematics 36:643–689.

Salita, J. T., W. Ekau, and U. Saint-Paul. 2003. Field evidence on the influence of seagrass landscapes on fish abundance in Bolinao, northern Philippines. Marine Ecology Progress Series 247:183–195.

Schaalje, G. B., J. B. McBride, and G. W. Fellingham. 2002. Adequacy of approximations to distributions of test statistics in complex mixed linear models. Journal of Agricultural, Biological, and Environmental Statistics 7:512.

Schindelin, J., C. T. Rueden, M. C. Hiner, and K. W. Eliceiri. 2015. The ImageJ ecosystem: An open platform for biomedical image analysis. Molecular Reproduction and Development 82:518–529.

Selgrath, J. C., K. A. Hovel, and R. A. Wahle. 2007. Effects of habitat edges on American lobster abundance and survival. Journal of Experimental Marine Biology and Ecology 353:253–264.

Semmens, B. X. 2008. Acoustically derived fine-scale behaviors of juvenile Chinook salmon (Oncorhynchus tshawytscha) associated with intertidal benthic habitats in an estuary. Canadian Journal of Fisheries & Aquatic Sciences 65:2053–2062.

Sheaves, M., R. Baker, I. Nagelkerken, and R. M. Connolly. 2015. True Value of Estuarine and Coastal Nurseries for Fish: Incorporating Complexity and Dynamics. Estuaries and Coasts 38:401–414.

Shoreline Management Act. 1971. . Page RCW.

Short, F. T., and D. M. Burdick. 1996. Quantifying Eelgrass Habitat Loss in Relation to Housing Development and Nitrogen Loading in Waquoit Bay, Massachusetts. Estuaries 19:730–739.

Simenstad, C. A., and K. L. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: Scales of disturbance. Estuaries 18:43–70.

Simenstad, C. A., K. L. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343–364Estuarine Comparisons. Elsevier.

Sisk, T. D., and N. M. Haddad. 2002. Incorporating the effects of habitat edges into landscape models: Effective area models for cross-boundary management. Pages 208–240Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge, UK.

Skinner, M., S. Courtenay, and C. McKindsey. 2013. Reductions in distribution, photosynthesis, and productivity of eelgrass Zostera marina associated with oyster Crassostrea virginica aquaculture. Marine Ecology Progress Series 486:105–119.

Smith, T., J. Hindell, G. Jenkins, and R. Connolly. 2008. Edge effects on fish associated with seagrass and sand patches. Marine Ecology Progress Series 359:203–213.

Smith, T. M., J. S. Hindell, G. P. Jenkins, and R. M. Connolly. 2010. Seagrass patch size affects fish responses to edges. Journal of Animal Ecology 79:275–281.

Smith, T. M., J. S. Hindell, G. P. Jenkins, R. M. Connolly, and M. J. Keough. 2011. Edge effects in patchy seagrass landscapes: The role of predation in determining fish distribution. Journal of Experimental Marine Biology and Ecology 399:8–16.

State-owned tidelands, shorelands, and waterways. 1971. . Page RCW.

Sund, D. M. 2015. Utilization of the Non-Native Seagrass, Zostera japonica, by Crab and Fish in Pacific Northwest Estuaries. Oregon State University, Corvallis, OR.

Tallis, H. M., J. L. Ruesink, B. Dumbauld, S. Hacker, and L. M. Wisehart. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. Journal of Shellfish Research 28:251–261.

Tanner, J. E. 2005. Edge effects on fauna in fragmented seagrass meadows. Austral Ecology 30:210–218.

Terrados, J., and F. J. M. Pons. 2008. Epiphyte load on the seagrass Posidonia oceanica (L.) Delile does not indicate anthropogenic nutrient loading in Cabrera Archipelago National Park (Balearic Islands, Western Mediterranean). Scientia Marina 72:503–510.

Thom, R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (Zostera marina L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. Estuaries 26:1117–1129.

Townsend, C. H. 1896. The transplanting of eastern oysters to Willapa Bay, Washington with notes on the native oyster industry. U.S. Fisheries Commission.

Turner, M. G. 1989. Landscape Ecology: The Effect of Pattern on Process. Annual Review of Ecology and Systematics 20:171–197.

US Army Corps of Engineers. 2017a. Chapter IX: Aquaculture. http://www.nws.usace.army.mil/Missions/Civil-Works/Regulatory/Permit-Guidebook/.

US Army Corps of Engineers. 2017b. Nationwide Permits. Page 62.

Wagner, E., B. Dumbauld, S. Hacker, A. Trimble, L. Wisehart, and J. Ruesink. 2012. Density-dependent effects of an introduced oyster, Crassostrea gigas, on a native intertidal seagrass, Zostera marina. Marine Ecology Progress Series 468:149–160.

Walton, W. C., J. E. Davis, G. I. Chaplin, F. S. Rikard, T. R. Hanson, P. J. Waters, and D. L. Swann. 2012. Off-bottom oyster farming. Agriculture and Natural Resources Timely Information: Fisheries and Aquaculture Series. Alabama Cooperative Extension System. 8pp.

Washington Sea Grant. 2015. Shellfish aquaculture in Washington State. Final Report to the Washington State Legislature.

Washington State Department of Ecology. 2014. Existing Permitting Processes.

Washington State Department of Ecology. 2015. Aquaculture. Page 56Shoreline Master Programs Handbook.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short, and S. L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences 106:12377–12381.

Wedding, L., C. Lepczyk, S. Pittman, A. Friedlander, and S. Jorgensen. 2011. Quantifying seascape structure: extending terrestrial spatial pattern metrics to the marine realm. Marine Ecology Progress Series 427:219–232.

Wiens, J. A., and B. T. Milne. 1989. Scaling of “landscapes” in landscape ecology, or, landscape ecology from a beetle’s perspective. Landscape Ecology 3:87–96.

Wisehart, L., B. Dumbauld, J. Ruesink, and S. Hacker. 2007. Importance of eelgrass early life history stages in response to oyster aquaculture disturbance. Marine Ecology Progress Series 344:71–80.

Wright, J. T., J. E. Byers, J. L. Devore, and E. E. Sotka. 2014. Engineering or food? mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology 95:2699–2706.

Zhang, P. D., Y. S. Liu, D. Guo, W. T. Li, and Q. Zhang. 2016. Seasonal Variation in Growth, Morphology, and Reproduction of Eelgrass Zostera marina on the Eastern Coast of the Shandong Peninsula, China. Journal of Coastal Research 32:315–322.

Žydelis, R., D. Esler, M. Kirk, and W. Sean Boyd. 2009. Effects of off-bottom shellfish aquaculture on winter habitat use by molluscivorous sea ducks. Aquatic Conservation: Marine and Freshwater Ecosystems 19:34–42.

APPENDIX

Table A.1. Generalized linear mixed model results for percent cover of Z. marina. Data was fit to a Gaussian distribution. Reference is Transect Position A in long-line aquaculture (intercept).

Fixed Effect	Estimate	Std. Error	*t*
Intercept	4.862	5.212	0.933
Transect Position B	13.571	7.363	1.843
Transect Position C	22.286	7.363	3.027
Transect Position D	56.095	7.363	7.618
Transect Position E	47.048	7.363	6.389
Aquaculture Type (OB)	-2.476	7.363	-0.336
Transect Position B: Aquaculture Type (OB)	-15.714	10.413	-1.509
Transect Position C: Aquaculture Type (OB)	-1.095	10.413	-0.105
Transect Position D: Aquaculture Type (OB)	10.571	10.413	1.015
Transect Position E: Aquaculture Type (OB)	19.619	10.413	1.884

Table A.2. Results of post-hoc simultaneous pairwise comparisons for percent cover of Z. marina. Significant comparisons of interest (those between the edge (C) and other habitats as well as between aquaculture types at a given habitat location) are indicated in Figure 5.

Comparison	Estimate	Std. Error	*z*	Pr (>|z|)
LL B - LL A	13.571	7.363	1.843	0.708
LL C - LL A	22.286	7.363	3.027	0.074
LL D - LL A	56.095	7.363	7.618	**<0.001**
LL E - LL A	47.048	7.363	6.389	**<0.001**
OB A - LL A	-2.476	7.363	-0.336	1.000
OB B - LL A	-4.619	7.363	-0.627	1.000
OB C - LL A	18.714	7.363	2.542	0.246
OB D - LL A	64.190	7.363	8.718	**<0.001**
OB E - LL A	64.190	7.363	8.718	**<0.001**
LL C - LL B	8.714	7.363	1.183	0.975
LL D - LL B	42.524	7.363	5.775	**<0.001**
LL E - LL B	33.476	7.363	4.546	**<0.001**
OB A - LL B	-16.048	7.363	-2.179	0.470
OB B - LL B	-18.190	7.363	-2.470	0.285
OB C - LL B	5.143	7.363	0.698	1.000
OB D - LL B	50.619	7.363	6.874	**<0.001**
OB E - LL B	50.619	7.363	6.874	**<0.001**

LL D - LL C	33.810	7.363	4.592	**<0.001**
LL E - LL C	24.762	7.363	3.363	**0.027**
OB A - LL C	-24.762	7.363	-3.363	**0.027**
OB B - LL C	-26.905	7.363	-3.654	**0.010**
OB C - LL C	-3.571	7.363	-0.485	1.000
OB D - LL C	41.905	7.363	5.691	**<0.001**
OB E - LL C	41.905	7.363	5.691	**<0.001**
LL E - LL D	-9.048	7.363	-1.229	0.968
OB A - LL D	-58.571	7.363	-7.954	**<0.001**
OB B - LL D	-60.714	7.363	-8.245	**<0.001**
OB C - LL D	-37.381	7.363	-5.077	**<0.001**
OB D - LL D	8.095	7.363	1.099	0.985
OB E - LL D	8.095	7.363	1.099	0.985
OB A - LL E	-49.524	7.363	-6.726	**<0.001**
OB B - LL E	-51.667	7.363	-7.017	**<0.001**
OB C - LL E	-28.333	7.363	-3.848	**0.005**
OB D - LL E	17.143	7.363	2.328	0.370
OB E - LL E	17.143	7.363	2.328	0.370
OB B - OB A	-2.143	7.363	-0.291	1.000
OB C - OB A	21.190	7.363	2.878	0.112
OB D - OB A	66.667	7.363	9.054	**<0.001**
OB E - OB A	66.667	7.363	9.054	**<0.001**
OB C - OB B	23.333	7.363	3.169	**0.049**
OB D - OB B	68.810	7.363	9.345	**<0.001**
OB E - OB B	68.810	7.363	9.345	**<0.001**
OB D - OB C	45.476	7.363	6.176	**<0.001**
OB E - OB C	45.476	7.363	6.176	**<0.001**
OB E - OB D	0.000	7.363	0.000	1.000

Table A.3. Generalized linear mixed model results for shoot density of Z. marina. Data was fit to a Gaussian distribution. Reference is Transect Position A in long-line aquaculture (intercept)

Fixed Effect	Estimate	Std. Error	*t*
Intercept	0.381	0.384	0.992
Transect Position B	0.762	0.543	1.403
Transect Position C	1.952	0.543	3.595
Transect Position D	1.714	0.543	3.157
Transect Position E	2.333	0.543	4.297

Aquaculture Type (OB)	-0.381	0.543	-0.701
Transect Position B: Aquaculture Type (OB)	-0.714	0.768	-0.93
Transect Position C: Aquaculture Type (OB)	-0.524	0.768	-0.682
Transect Position D: Aquaculture Type (OB)	2.524	0.768	3.286
Transect Position E: Aquaculture Type (OB)	1.238	0.768	1.612

Table A.4. Results of post-hoc simultaneous pairwise comparisons for shoot density of Z. marina. Significant comparisons of interest (those between the edge (C) and other habitats as well as between aquaculture types at a given habitat location) are indicated in Figure 6.

Comparison	Estimate	Std. Error	*z*	Pr (>|z|)
LL B - LL A	12.190	8.689	1.403	0.927
LL C - LL A	31.238	8.689	3.595	**0.012**
LL D - LL A	27.429	8.689	3.157	0.051
LL E - LL A	37.333	8.689	4.297	**<0.001**
OB A - LL A	-6.095	8.689	-0.701	1.000
OB B - LL A	-5.333	8.689	-0.614	1.000
OB C - LL A	16.762	8.689	1.929	0.649
OB D - LL A	61.714	8.689	7.103	**<0.001**
OB E - LL A	51.048	8.689	5.875	**<0.001**
LL C - LL B	19.048	8.689	2.192	0.463
LL D - LL B	15.238	8.689	1.754	0.764
LL E - LL B	25.143	8.689	2.894	0.108
OB A - LL B	-18.286	8.689	-2.104	0.524
OB B - LL B	-17.524	8.689	-2.017	0.587
OB C - LL B	4.571	8.689	0.526	1.000
OB D - LL B	49.524	8.689	5.700	**<0.001**
OB E - LL B	38.857	8.689	4.472	**<0.001**
LL D - LL C	-3.810	8.689	-0.438	1.000
LL E - LL C	6.095	8.689	0.701	1.000
OB A - LL C	-37.333	8.689	-4.297	**<0.001**
OB B - LL C	-36.571	8.689	-4.209	**0.001**
OB C - LL C	-14.476	8.689	-1.666	0.815
OB D - LL C	30.476	8.689	3.507	**0.016**
OB E - LL C	19.810	8.689	2.280	0.402
LL E - LL D	9.905	8.689	1.140	0.981
OB A - LL D	-33.524	8.689	-3.858	**0.004**
OB B - LL D	-32.762	8.689	-3.770	**0.006**

OB C - LL D	-10.667	8.689	-1.228	0.968
OB D - LL D	34.286	8.689	3.946	**0.003**
OB E - LL D	23.619	8.689	2.718	0.167
OB A - LL E	-43.429	8.689	-4.998	**<0.001**
OB B - LL E	-42.667	8.689	-4.910	**<0.001**
OB C - LL E	-20.571	8.689	-2.368	0.346
OB D - LL E	24.381	8.689	2.806	0.134
OB E - LL E	13.714	8.689	1.578	0.859
OB B - OB A	0.762	8.689	0.088	1.000
OB C - OB A	22.857	8.689	2.631	0.203
OB D - OB A	67.810	8.689	7.804	**<0.001**
OB E - OB A	57.143	8.689	6.576	**<0.001**
OB C - OB B	22.095	8.689	2.543	0.246
OB D - OB B	67.048	8.689	7.716	**<0.001**
OB E - OB B	56.381	8.689	6.489	**<0.001**
OB D - OB C	44.952	8.689	5.173	**<0.001**
OB E - OB C	34.286	8.689	3.946	**0.003**
OB E - OB D	-10.667	8.689	-1.228	0.968

Table A.5. Generalized linear model results for total abundance in minnow traps. Data was fit to a Poisson distribution. Reference is Transect Position A in long-line aquaculture (intercept).

Fixed Effect	Estimate	Std. Error	*z*	Pr (>|z|)
Intercept	2.197	0.136	16.146	**<0.001**
Transect Position C	0.216	0.183	1.18	0.238
Transect Position E	0.054	0.19	0.285	0.775
Aquaculture Type (OB)	-0.275	0.207	-1.33	0.184
Transect Position C: Aquaculture Type (OB)	-1.627	0.508	-3.204	**0.001**
Transect Position E: Aquaculture Type (OB)	0.083	0.286	0.289	0.773

Table A.6. Results of post-hoc simultaneous pairwise comparisons for total abundance in minnow traps. Significant comparisons of interest (those between the edge (C) and other habitats as well as between aquaculture types at a given habitat location) are indicated in Figure 11.

Comparison	Estimate	Std. Error	*z*	Pr (>|z|)
LL C - LL A	0.216	0.183	1.180	0.835
LL E - LL A	0.054	0.190	0.285	1.000
OB A - LL A	-0.275	0.207	-1.330	0.753
OB C - LL A	-1.686	0.467	-3.608	**0.004**
OB E - LL A	-0.139	0.199	-0.696	0.981
LL E - LL C	-0.162	0.180	-0.897	0.942
OB A - LL C	-0.491	0.198	-2.477	0.119
OB C - LL C	-1.902	0.464	-4.103	**<0.001**
OB E - LL C	-0.355	0.190	-1.863	**0.403**
OB A - LL E	-0.329	0.205	-1.609	0.571
OB C - LL E	-1.740	0.466	-3.732	**0.002**
OB E - LL E	-0.193	0.197	-0.979	0.918
OB C - OB A	-1.411	0.474	-2.979	**0.031**
OB E - OB A	0.137	0.214	0.639	0.987
OB E - OB C	1.548	0.470	3.290	**0.011**

Table A.7. Generalized linear model results for total video sightings. Data was fit to a Poisson distribution. Reference is Transect Position A in long-line aquaculture (intercept).

Variable	Estimate	Std. Error	*z*	Pr (>|z|)
Intercept	4.072	0.075	54.019	**<0.001**
Transect Position B	-0.114	0.11	-1.041	0.298
Transect Position C	-0.596	0.126	-4.711	**<0.001**
Transect Position D	-0.417	0.12	-3.486	**<0.001**
Transect Position E	-0.065	0.108	-0.596	0.551
Aquaculture Type (OB)	-0.705	0.131	-5.376	**<0.001**
Transect Position B: Aquaculture Type (OB)	-0.362	0.205	1.768	0.077
Transect Position C: Aquaculture Type (OB)	0.607	0.197	3.081	**0.002**
Transect Position D: Aquaculture Type (OB)	0.669	0.186	3.593	**<0.001**
Transect Position E: Aquaculture Type (OB)	0.326	0.179	1.82	0.069

Table A.8. Results of post-hoc simultaneous pairwise comparisons for total video sightings. Significant comparisons of interest (those between the edge (C) and other habitats as well as between aquaculture types at a given habitat location) are indicated in Figure 12.

Comparison	Estimate	Std. Error	*z*	Pr (>|z|)
LL B - LL A	-0.114	0.110	-1.041	0.989
LL C - LL A	-0.596	0.126	-4.711	**<0.001**
LL D - LL A	-0.417	0.120	-3.486	**0.017**
LL E - LL A	-0.065	0.108	-0.596	1.000
OB A - LL A	-0.705	0.131	-5.376	**<0.001**
OB B - LL A	-1.181	0.156	-7.595	**<0.001**
OB C - LL A	-0.693	0.131	-5.309	**<0.001**
OB D - LL A	-0.452	0.121	-3.739	**0.007**
OB E - LL A	-0.443	0.121	-3.676	**0.009**
LL C - LL B	-0.482	0.129	-3.729	**0.007**
LL D - LL B	-0.303	0.122	-2.472	0.277
LL E - LL B	0.050	0.111	0.446	1.000
OB A - LL B	-0.590	0.134	-4.417	**<0.001**
OB B - LL B	-1.067	0.158	-6.765	**<0.001**
OB C - LL B	-0.579	0.133	-4.347	**<0.001**
OB D - LL B	-0.338	0.124	-2.731	0.157
OB E - LL B	-0.329	0.123	-2.666	0.184
LL D - LL C	0.179	0.138	1.300	0.952
LL E - LL C	0.531	0.128	4.152	**0.001**
OB A - LL C	-0.109	0.148	-0.737	0.999
OB B - LL C	-0.586	0.170	-3.450	**0.020**
OB C - LL C	-0.097	0.147	-0.661	1.000
OB D - LL C	0.144	0.139	1.037	0.990
OB E - LL C	0.153	0.138	1.103	0.984
LL E - LL D	0.352	0.121	2.908	0.100
OB A - LL D	-0.288	0.142	-2.028	0.572
OB B - LL D	-0.765	0.165	-4.641	**<0.001**
OB C - LL D	-0.276	0.141	-1.954	0.624
OB D - LL D	-0.035	0.132	-0.265	1.000
OB E - LL D	-0.026	0.132	-0.198	1.000
OB A - LL E	-0.640	0.132	-4.831	**<0.001**
OB B - LL E	-1.117	0.157	-7.125	**<0.001**
OB C - LL E	-0.629	0.132	-4.762	**<0.001**
OB D - LL E	-0.387	0.122	-3.165	**0.049**
OB E - LL E	-0.379	0.122	-3.100	0.059
OB B - OB A	-0.477	0.173	-2.753	0.150

OB C - OB A	0.011	0.151	0.076	1.000
OB D - OB A	0.253	0.143	1.768	0.750
OB E - OB A	0.261	0.143	1.833	0.708
OB C - OB B	0.488	0.173	2.825	0.124
OB D - OB B	0.730	0.166	4.403	**<0.001**
OB E - OB B	0.738	0.165	4.463	**<0.001**
OB D - OB C	0.241	0.142	1.693	0.795
OB E - OB C	0.250	0.142	1.759	0.756
OB E - OB D	0.009	0.133	0.067	1.000

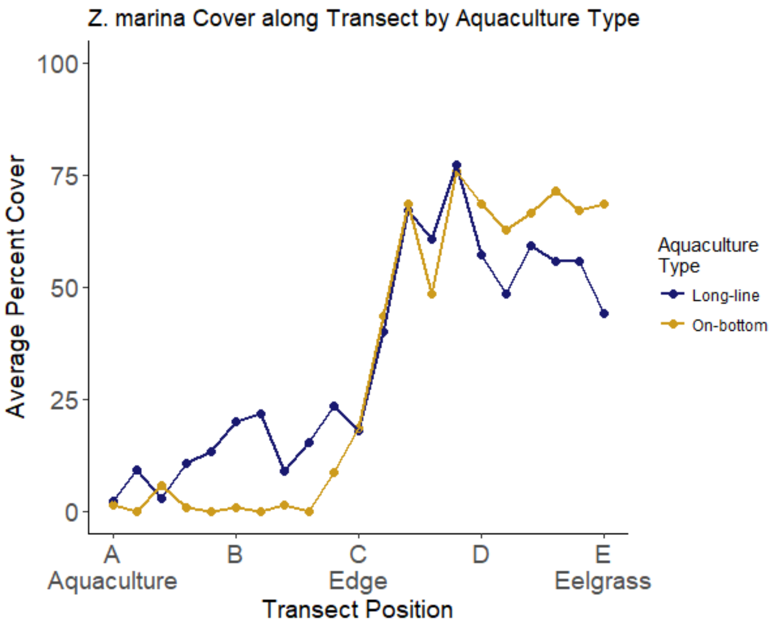

Figure A.1. Percent cover of Z. marina along the transects in each aquaculture type. Data was collected every three meters (N=6).

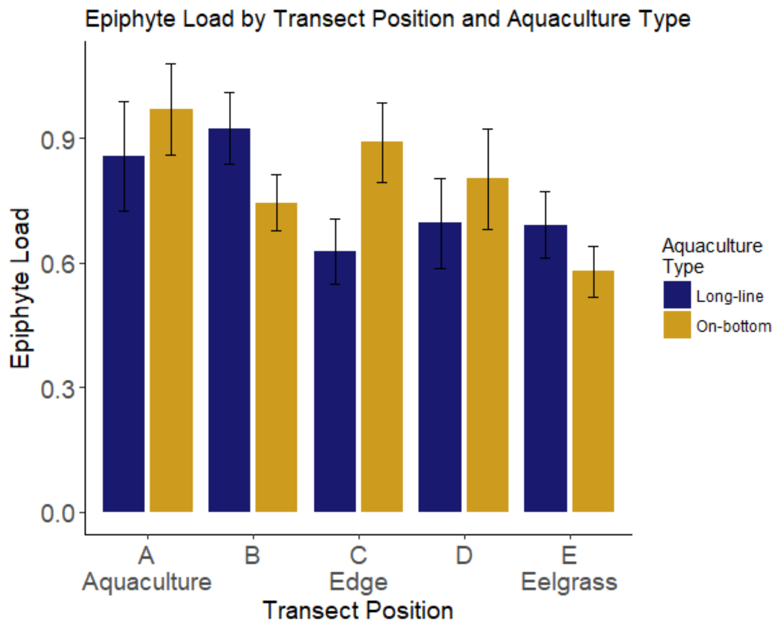

Figure A.2. Epiphyte load (dry mass of epiphytes/dry mass shoot) on Z. marina blades along the transect in each aquaculture type (N=6).

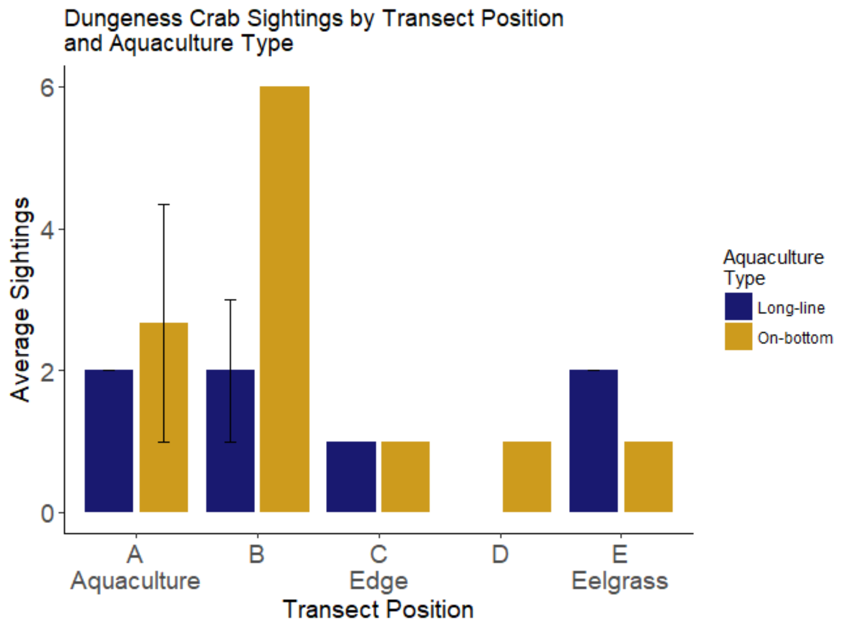

Figure A.3. Sightings of Dungeness crabs in video across the transect and between aquaculture types (N=3).

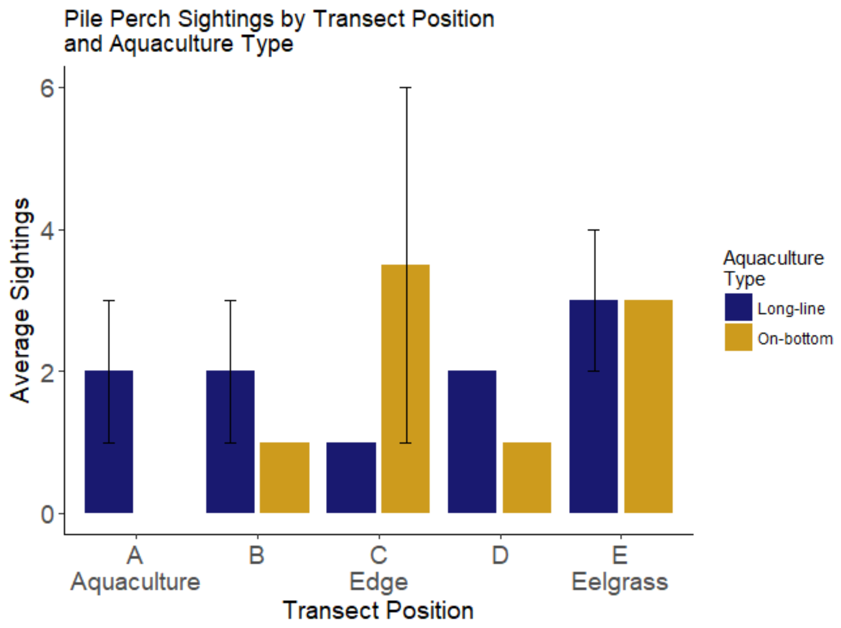

Figure A.4. Sightings of Pile perch in video across the transect and between aquaculture types (N=3).