Interactions between fish communities and shellfish aquaculture in Baynes Sound, British Columbia

by

Robert Bourdon
Bachelor of Arts, St. Mary's College of Maryland, 2012

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Supervisory Committee

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Abstract

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Shellfish aquaculture is a developing industry along northeast Pacific coastlines and represents another potential stressor to already impacted nearshore ecosystems. The industry is particularly prominent in Baynes Sound, British Columbia (BC), Canada. The region hosts the operations which account for approximately 35% of all clams and 50% of all oysters produced in BC. Concurrently, it represents one of the most ecologically valuable areas in the northeast Pacific. In this study, I examined the interactions of benthic intertidal shellfish aquaculture with nearshore fish communities using abundance, biodiversity (species richness, diversity, and evenness), and functional diversity (Rao's quadratic entropy and functional evenness) metrics. Also, I measured habitat complexity, as defined by a contour distance:linear distance ratio, at all fish sampling sites because it has often been identified as a driver of community variation. Fish abundance, biodiversity, and functional diversity did not vary between aquaculture and non-aquaculture sites. Additionally, habitat complexity, while on average was 1.2x greater at aquaculture beaches compared to non-aquaculture reference beaches, was not a strong driver of these indicators. Fish communities in Baynes Sound are relatively homogenous on a small scale and are highly functionally redundant, meaning that there is considerable overlap of species' roles in the ecosystem. In summary, the presence of shellfish aquaculture in Baynes Sound is not associated with either a positive or negative response of fish communities. Furthermore, these communities are functionally redundant and therefore are likely resilient to ecosystem disturbances.

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Chapter 1 - Introduction

1.1 Thesis structure

Chapter 1 provides an overview of current anthropogenic impacts on nearshore ecosystems including shellfish aquaculture, the focal industry of this research. It also introduces Baynes Sound, British Columbia, Canada, as a model system to study anthropogenic impacts as it boasts a prevalent shellfish aquaculture industry while fostering crucial biodiversity.

Chapter 2 highlights the significance of biodiversity and its utility as a tool to monitor ecosystem health. In this chapter, the observed interactions between intertidal shellfish aquaculture and native fish communities in Baynes Sound are summarized. Abundance as well as species diversity, richness, and evenness were used to describe species assemblages at aquaculture and non-aquaculture sites. Furthermore, the relationship between these measures and structural complexity (a noted driver of biotic community patterns in many ecosystems), which was measured at each site, was determined.

Chapter 3 further explores fish community responses to shellfish aquaculture, using functional diversity analyses to advance the understanding of Baynes Sound fish assemblages. This fine-scale functional diversity analysis is the first of its kind in the British Columbia marine intertidal environment.

Chapter 4 integrates findings from chapters 2 and 3 and places them within the context of existing research on shellfish aquaculture and other nearshore ecosystem stressors. Here, I comment on the outlook for the shellfish industry and recommend future research that will aid in formulating the most effective industry management and conservation strategies.

1.2 Overview

1.2.1 Anthropogenic impacts on nearshore environments

Coastal regions are highly attractive sites for human settlement. Genetic evidence verifies that even during the early and nomadic times of human history, the bulk of populations were concentrated along coasts (Amos and Manica 2006). The abundance of subsistence resources, the ease of transport and trade opportunities, and even recreational options has resulted in the majority of infrastructure to be concentrated along the world's coastlines (Neumann et al. 2015). Based on year 2000 estimates, McGranahan et al. (2007) report that 10% of the world's population inhabit areas of the coast less than 10 meters above sea level. This zone, referred to as the Low Elevation Coastal Zone (LECZ), accounts for only 2% of earth's land area. Consequently, population densities here are much greater than inland areas (McGranahan et al. 2007, Neumann et al. 2015). Furthermore, 20 of the world's 31 megacities, metropolitan areas with populations over 8-million, are found within the LECZ (Brown et al. 2013). Migration rates to coastal regions are also quite high, largely due to demographic and economic factors (Hugo 2011).

Human land and water use is one of the largest drivers of nearshore aquatic ecosystem health. Given that the LECZ hosts such high human population densities, littoral systems, particularly those in estuaries, are undoubtedly some of the world's most modified environments. Anthropogenic alterations to these habitats come in many forms, but only the most prominent (shoreline armouring, poor land use practices, invasive species, climate change, and the fisheries and aquaculture industries) are discussed below.

Shoreline armouring converts natural coasts into hard, homogenous habitat with the addition of rip-rap, stones, and concrete barriers. The goal is usually to protect shoreline housing and infrastructure from wave action and destabilization, but their construction is associated with many negative impacts on beach ecology. In fact, armouring can exacerbate beach erosion by reflecting wave energy back onto the beach. Most armoured shorelines have little, if any, beach habitat. Furthermore, these hard structures severely limit terrestrial-aquatic connectivity, blocking natural particulate transport necessary to maintain beaches and provide suitable fine-grained habitat (Macdonald et al. 1994, Runyan and Griggs 2003). Finer grained sand and light gravel beaches are valued on the west coast of North America due to their unique infaunal community composition, the foraging opportunities those communities provide, and the provision of habitat for species of concern such as forage fishes and juvenile salmonids (Macdonald et al. 1994, Rice 2006, Martin 2015). Armoured shorelines harbour only a small fraction of the biological diversity present on natural, dynamic shorelines (Morley et al. 2012). Upland practices such as dams have similar consequences by blocking riverine transport of particulates to the marine environment, further starving beaches of valuable sediments (Willis and Griggs 2003).

Anthropogenic land cover changes have notable effects on aquatic systems as well. Of particular concern is the replacement of natural vegetation cover with impervious surfaces and industrial agriculture operations. Poor soil management strategies facilitate run-off of nutrient rich sediments into waterways, encouraging both eutrophication and siltation (Carpenter et al. 1998). Siltation is a major concern for sessile and photosynthetic species. Heavy loads of sediment can block respiration and feeding of ecologically-important yet non-mobile species including a variety of bivalves and corals. Additionally, fine sediment particles may be slow to settle out of the water column, decreasing light penetration and threatening aquatic macrophytes, and in tropical environments, corals; both groups are recognized as two of the most important sources of habitat in the world (Rogers 1990, Jones et al. 2001, Airoldi 2003, Fabricius 2005, Orth et al. 2006). Heavy loads of limiting nutrients such as nitrogen and phosphorus are also characteristic of agricultural and urban run-off. These excess nutrients encourage unnaturally dense microalgae growth, which can decrease light availability to benthic photosynthesizers and promote anoxia/hypoxia during decomposition of these massive blooms (Carpenter et al. 1998).

Another threat to nearshore aquatic systems is the introduction of non-indigenous species, which are now a common occurrence in part due to vectors promoted by trade and travel globalization (Bax et al. 2003). If an introduced species finds the environmental characteristics of its new home favourable, it can easily become a successful invader. Once established, they are almost impossible to remove (Thresher and Kuris 2004). Invasive species present a number of issues to shallow marine environments including food chain disruption, competitive exclusion, hybridization, and spreading of disease (Bax et al. 2003, Molnar et al. 2008, Crego-Prieto et al. 2015).

Climate change and the associated process of ocean acidification are emerging threats to nearshore ecosystem ecology. These processes stress organisms, potentially taking them to the edge of thermal, oxygen, and pH limits; making them more vulnerable to the threats described previously (Roessig and Woodley 2004, Koch et al. 2013, Okey et al. 2014). Some species are quite adaptable and may tolerate changes to oceanographic conditions. Others may be highly mobile or have wide-dispersing young, which could allow them to colonize new areas favourable to their thermoregulatory and chemoregulatory regimes. However, not all species are so adaptable and will likely be pushed to the brink of extinction in some or all areas of their range (Okey et al. 2014, Jones and Cheung 2015). The Strait of Georgia ecoregion, in which the focal area of this study falls, is recognized as highly sensitive to environmental deviations associated with climate change. Most notably, the basin is particularly susceptible to declines in pH and dissolved oxygen due to oceanographic characteristics of the region (Johannessen and Macdonald 2009, Okey et al. 2014).

Fisheries are another major threat to nearshore ecosystem health. Decades of poor resource management and declining water quality have led to the severe decline of wild seafood stocks, heavily impacting coastal ecosystems and economies (Pauly et al. 1998, Jennings et al. 2001, Worm et al. 2006, Pitcher and Cheung 2013). Overfishing leads to food chain disruptions and can impede normal ecosystem processes. Furthermore, many types of fishing gear such as gill nets and trawls are prone to bycatch and may physically damage valuable habitat (Jennings et al. 2001). Aquaculture, the industry of focus for this research, is often touted as a solution to failing or damaging fisheries; however, it is not without its own suite of nearshore implications. The aquaculture industry is discussed in further detail below.

1.2.2 Current status of world fisheries and aquaculture

Despite mixed success of modern fisheries management in developed countries, the overall picture of world fisheries status is still dismal (Pitcher and Cheung 2013, Hilborn and Ovando 2014). Catch per unit effort remains in an overall decline, even as we shift to harvesting new and traditionally less desirable, lower trophic level species (Pauly et al. 1998, Pitcher and Cheung 2013). As of 2011, 28.8% of assessed fish stocks were considered overfished, or fished at levels greater that maximum sustainable yield (MSY). Of the remaining stocks, 63.3% were fished at MSY, and 9.9% were underfished at levels less that MSY. The trend continues towards more overfished and fewer underfished stocks (FAO 2014). Confounding (and either unrelated or indirectly linked to fisheries) factors such as climate change, ocean acidification, pollutants, exotic species introductions, and food web collapses only complicate the situation and limit the abilities of fisheries management to accurately predict appropriate catch levels (Pitcher and Cheung 2013).

Aquaculture, the practice of farming of aquatic species primarily for the purpose of human consumption, is an expanding industry designed to alleviate pressure on wild populations and to provide an alternative means of income for fishery dependent economies. The Food and Agriculture Organization of the United Nations (FAO) publishes a yearly report of world fisheries and aquaculture production. In the most recent report, primarily summarizing data from 2012, aquaculture accounted for a record high of 42.2% of world fish harvests (fish in this context refers to all animal seafood harvests – finfish, shellfish, crustaceans, etc.), and despite a slowing growth rate compared to past decades (6.2% per year during 2000-2012 compared to 10.8% and 9.5% for 1980-1990 and 1990-2000 respectively), is still one of the fastest growing food production industries in the world. Aquatic-derived proteins were the primary animal protein source for 16.7% of the world's population in 2010. They also accounted for 6.5% of all protein consumed worldwide (FAO 2014).

A significant portion of capture fisheries are indirectly linked to aquaculture. Farming of higher trophic level species (traditionally the most desired for human consumption) usually uses fishmeal as feed; fishmeal is commonly sourced from wild captured fish (FAO 2014). Aquaculture is also a major employer; Valderrama et al. (2010) estimate (based on 2005 data) that 23.4 million people worldwide are employed full-time by the aquaculture industry, both directly (on-farm) and indirectly (off-farm jobs generated by direct jobs). Additionally, it is estimated that collectively, wild capture fisheries and aquaculture ensure the livelihoods of 10-12% of the world's population (FAO 2014). Aquaculture is also a culturally significant industry, maintaining the ability of some regions to produce seafood despite rampant overfishing of wild stocks (Costa-Pierce 2002). Many of these operations are often small-scale and artisanal, and while they don't contribute much on a global scale, are vital components to community health (Costa-Pierce 2002, Brummett et al. 2008).

1.2.3 Aquaculture in Canada

While the majority of the world is still seeing aquaculture growth, North America (not including Latin America or the Caribbean) has seen a recent drop-off in production. This is likely attributable to lower production costs in developing parts of the world and the willingness of North America to rely on foreign producers for much of their seafood demand (FAO 2014). Nguyen and Williams (2013) provide a thorough summary of aquaculture statistics in Canada: In 2011, Canada contributed only 162,000 metric tons, or 0.25%, to the total world aquaculture production of 63.6 million metric tons. While minimal, this production is a vital economic input to smaller communities. Addtionally, Canada is a globally significant producer of farmed Atlantic Salmon (*Salmo salar*), ranking fourth worldwide at 7% of total production in 2009. Although finfish are the dominant taxa cultured in Canada (more than 90% by weight), farmed shellfish are a significant industry as well, generating more than $74 million CAD in 2011 (Nguyen and Williams 2013). While aquaculture production in Canada is low compared to much of the world, an area of notably high farmed shellfish production and also the focus of this research is Baynes Sound, British Columbia, Canada (Paynter 2002).

1.2.4 Shellfish Aquaculture

Bivalves are by far the most commonly farmed variety of shellfish (Dumbauld et al. 2009, FAO 2014). As such, "shellfish aquaculture" as used in this document refers almost exclusively to the culture of bivalve species. Consistent with most other aquaculture types, shellfish aquaculture has experienced significant growth since the mid-1900s (Dumbauld et al. 2009, FAO 2014). However, most of this production is centered in Asia, where aquaculture has been an accepted practice for centuries (Kurokura 2004, FAO 2014). Shellfish aquaculture is often perceived in a positive light compared to the more common and controversial practice of finfish culture. First and foremost, farmed shellfish feed on detritus and natural populations of microalgae, which can improve water quality and decrease anthropogenic eutrophication (Rice 1999). This occurs through top-down control, by which shellfish feed heavily on phytoplankton and incorporate available nitrogen into their muscle biomass, effectively removing that nitrogen from the aquatic system and reducing its availability for further phytoplankton growth (Rice 1999). Enhanced water quality and nutrient deposition by suspension feeding bivalves has also been shown to improve the growth of submerged aquatic vegetation, a vital source of habitat that is declining worldwide (Reusch et al. 1994, Peterson and Heck 1999, 2001, Newell and Koch 2004, Wall et al. 2008). Additionally, non-burrowing bivalves provide a source of hard substrate that is often a limiting resource in some aquatic environments.

Therefore, these bivalves are a preferred site of settlement for epifaunal organisms and macroalgae (Gutiérrez et al. 2003). Artificial habitats created by longlines, racks, nets, and on-bottom culture mimic natural shellfish reefs that have disappeared from much of their former range (e.g. Olympia Oyster, *Ostrea lurida*, on the west coast and Eastern Oyster, *Crassostrea virginica*, on the east coast of North America). A variety of organisms including fish and aquatic invertebrates have been found using shellfish aquaculture areas as sources of refuge or foraging grounds (Gutiérrez et al. 2003, Dealteris et al. 2004, Coen et al. 2007, Tallman and Forrester 2007, D'Amours et al. 2008, Dumbauld et al. 2009, Marenghi and Ozbay 2010, Marenghi et al. 2010). Finally, cultured bivalves themselves often become a food source for native predators such as sea stars, sea ducks, crabs, river otters, and sea otters (Barbeau et al. 1998, Nash et al. 2000, Zydelis et al. 2006, 2008, Kirk et al. 2007).

While shellfish aquaculture is considered one of the less damaging forms of seafood production, farming practices still involve significant environmental modifications. Dumbauld et al. (2009) places these modifications into three main categories: 1) material processes by which bivalves process food and produce wastes; 2) the addition of physical structure potentially used by other species as a refuge or attachment site; 3) pulse disturbances associated with farm maintenance and harvest. In some regions, cultured bivalves and gear associated with their production can occupy vast areas of shoreline; localized changes to the environment are inevitable. Shellfish farming has been associated with both geochemical and geophysical alterations of substrate characteristics (Jamieson et al. 2001, Munroe and McKinley 2007, Dumbauld et al. 2009). Most notably, high bivalve stocking density on floating culture operations is associated with sedimentation, organic matter enrichment, and oxygen depletion in the substrate (particularly under areas of raft or longline cultured bivalves) (Dahlbäck and Gunnarsson 1981, Chamberlain et al. 2001, Christensen et al. 2003, Wilson and Vopel 2015). Anoxia encourages the activity of sulfate-reducing bacteria, creating a benthic environment unsuitable for most infaunal species and aquatic vegetation (Christensen et al. 2003, Rice 2008). However, in some cases the high densities of bivalves associated with benthic shellfish culture and tenure maintenance activities can increase sediment oxygen content through bioturbation (Gutiérrez et al. 2003, Murphy et al. 2015). Additionally, the industry has been identified as a vector for the introduction of non-native species, many of them being considered invasive (Bax et al. 2003, McKindsey et al. 2007, Minchin 2007, Dumbauld et al. 2009). In some cases, the farmed shellfish themselves are non-natives and are able to establish viable populations. Also, associated biota may be unintentionally introduced with worldwide trade of cultured bivalves and their larvae. Introductions along the west coast of North America linked to the shellfish industry include the Japanese oyster drill (*Ocenebra inornata*), Asian eelgrass (*Zostera japonica*), and several species of seaweeds (Naylor et al. 2001). In the following discussion of my model system, Baynes Sound, the dynamic interaction between the industry and the aquatic environment is explored.

1.3 Baynes Sound

1.3.1 Geography and Oceanography

Baynes Sound is a narrow trough approximately 27km long and 3.5km wide at its widest point. Mid-sound depths generally range from 18-68m (Paynter 2002, Griffes 2004). It comprises approximately 8,700ha of aquatic habitat. Intertidal areas are a mosaic of habitat types including cobble beaches, salt marshes, and huge sand and mud flats that are ideal for shellfish culture (Paynter 2002). It is located along the eastern edge of Vancouver Island and is part of the larger Strait of Georgia ecosystem (Jamieson et al. 2001, Carswell et al. 2006). It exhibits a mixed semidiurnal tidal cycle with a maximum tidal amplitude of over 4m. Surface water currents are slow and generally run north to south, driven primarily by freshwater inflow from the Courtenay River near the north end of the sound (Waldie 1952). Deepwater currents are also generally north to south, but residence time is longer at approximately two months. Baynes Sound is bound on its eastern edge by Denman Island, which provides shelter from heavy wave action, and, in conjunction with freshwater inflows and lengthy deepwater exchange time, contributes to a stratified water column (Morris et al. 1979). Temperature, salinity, and dissolved oxygen vary seasonally, particularly due to pulses of freshwater from heavy rains or snowmelt and high summer temperatures which lead to more pronounced vertical stratification (Waldie 1952, Morris et al. 1979).

1.3.2 Ecological and Cultural Significance

Baynes Sound is widely recognized as one of the most ecologically important regions in British Columbia. It is a proposed worldwide Ecologically and Biologically Significant Area (EBSA). DFO (2012) outlines the core criteria for EBSA selection in Canada as: 1) uniqueness - unique, rare, distinct features; 2) aggregation, including areas where most individuals of a species aggregate for some part of the year; and 3) fitness consequences: defined as areas that are used by species for life history activity(ies) and that make a significant contribution to the fitness of individuals of those species. Baynes Sound meets these criteria primarily due to its attractiveness to marine birds, high densities of bivalves, provision of foraging and haul out areas for near threatened Steller sea lions (*Eumetopias jubatus*), and provision of critical spawning and rearing area for Pacific herring (*Clupea pallasii*) (DFO 2012). Additionally, it is certified as a globally Important Bird Area (IBA), and within British Columbia, supports abundances of waterbirds second only to the Fraser River Delta (IBA 2015). Finally, at least 23 rivers and creeks leading into the sound support prominent runs of one or more of the following salmonids: Chinook salmon (*Oncorhynchus tshawytscha),* Coho salmon (*O. kisutch*), Chum salmon (*O. keta*), Pink salmon (*O. gorbuscha*), Cutthroat trout (*O. clarkia*), and Steelhead (*O. mykiss*) (Jamieson et al. 2001).

Baynes Sound falls within the traditional territory of both the K'ómoks and Qualicum First Nations tribes and is recognized as an area of cultural significance due to the history of tribal usage of these waters. Native peoples harvested clams along these shorelines and continue to be involved in shellfish harvest practices, including shellfish aquaculture, to this day (Jamieson et al. 2001). The region is also a recreational hub, boasting a strong tourism industry in addition to recreational fishing opportunities. Nearshore habitat utilization is a frequent source of conflict between Baynes Sound residents and the shellfish industry (Jamieson et al. 2001, Paynter 2002, D'Anna and Murray 2015). Public opinion of shellfish farming in Baynes Sound varies widely. Many individuals hold a positive view of the industry, believing that the industry does not have strong negative impacts on the environment, enhances the local economy, and does not diminish their enjoyment of beaches or waterways. Many others are unsure or openly critical of shellfish farming and the extent to which it has developed in Baynes Sound (Murray and D'Anna 2015).

1.3.3 Shellfish aquaculture in British Columbia and Baynes Sound

Shellfish aquaculture in British Columbia arguably began approximately 5000 years ago; First Nations tribes modified portions of the coastline to make them favourable for bivalve settlement through the creation of clam gardens. Clam gardens create a terraced, level area of soft substrate bound behind a rock wall. Many of these historical clam gardens exist to this day (Cannon et al. 2008, Groesbeck et al. 2014). Modern shellfish aquaculture in British Columbia likely began in 1912 or 1913 with the intentional introduction of the Pacific oyster (*Crassostrea gigas*) to Ladysmith Harbour, although a major industry was not established until the 1920s (Lavoie 2005). Baynes Sound is the dominant producer in British Columbia. The region accounts for approximately 35% of clams and 50% of oysters cultured in British Columbia waters (Paynter 2002).

In Baynes Sound, the Pacific oyster and Manila clam (*Venerupis philippinarum*) are the most commonly produced species. Both are non-native Asian species introduced along the west coast of North America (Dumbauld et al. 2009). Prior to the construction of larvae producing facilities in North America in the 1980s, the bulk of oyster/clam seed (recently settled juveniles) and adults were being imported from Asia. This has been identified as the vector for the introduction of a number of now established non-native species. In fact, it is hypothesized that Manila clams were first introduced in oyster seed shipments (Quayle 1941). Pacific oysters were originally introduced following the decimation of native Olympia oyster (*Ostrea lurida*) and the unsuccessful introduction attempt of Eastern oysters (*Crassostrea virginica*) (Dumbauld et al. 2009).

While raft and longline culture of bivalves (primarily Pacific oysters) does occur in Baynes Sound, the most significant habitat modifications are concentrated along intertidal areas. Oyster aquaculture involves the spreading of oysters (either as individuals or as clusters referred to as "mother shell") in a layer across the intertidal substrate (Fig. 1). While this can provide some habitat for other organisms, it likely differs from native oyster reefs, which provide a more complex structure (Dumbauld et al. 2009). Also, the cobble substrate associated with the shoreline of many west coast estuaries may be altered to create a more level substrate. At the lower tidal heights, eelgrass may be damaged or removed to make room for more oysters (Quayle 1988, Jamieson et al. 2001, Dumbauld et al. 2009).

Figure 1. Beach culture of Pacific oysters (*Crassostrea gigas*) separated from a clam culture area (top left corner) by plastic fencing. Oysters in this photo are a mix of singles and 'mother' shell – oyster clusters formed by the settlement of multiple larvae on a shared parent shell. Photo courtesy of the Ecological Interactions Research Program of Vancouver Island University.

Modifications associated with manila clam culture include the addition of gravel to the substrate which can increase larval clam recruitment but consequently alters sediment characteristics and infaunal communities (Bendell-Young 2006, Munroe and McKinley

2007). Most clam aquaculture operations utilize plastic predator exclusion netting (PPEN) to minimize product loss to native predators such as sea ducks, crabs, and sea stars (Fig. 2). However, the effectiveness of these nets is contested and they (along with associated macroalgae) encourage sedimentation, entangle wildlife, and introduce a source of plastic pollution to the marine environment (Jamieson et al. 2001, Bendell 2015, Munroe et al. 2015). Bendell-Young (2006) reports that infaunal communities under PPEN in Baynes Sound had lower species richness, a lower abundance of rare species, and increased sediment organic matter and silt content. On the other hand, macroalgae commonly grows on the net surface and has been shown to be a valuable nursery habitat for juvenile fish and invertebrates (Powers et al. 2007). Finally, general increases in activity associated with tenure maintenance and harvest compromises substrate integrity through increases in digging and motor vehicle use (Jamieson et al. 2001, Dumbauld et al. 2009).

Figure 2. Plastic anti-predator netting placed over clam beds. Nets exhibit varying degrees of macroalgal fouling. Nets in photo A are relatively clean while those in B are heavily fouled with a red alga, *Mastocarpus* sp.

1.4 Objectives and justification for research

1.4.1 Objectives

Given the prevalence of the shellfish industry in Baynes Sound, this study will investigate biotic community responses using intertidal fish assemblages as indicators of change. These assemblages are, in general, poorly studied and overlooked by some conservation measures that focus on iconic and economically valued species. However, they hold tremendous ecological value, play important functional roles, and are good indicators for ecosystem assessments (Harrison and Whitfield 2004, Lamb and Edgell 2010). The primary objectives of this study are as follows: 1) To determine if fish abundance, species richness, diversity, and evenness vary according to the presence of active shellfish aquaculture, 2) to determine if habitat complexity varies according to shellfish aquaculture presence and if this complexity is a driver of fish community patterns, and 3) to investigate potential functional differences of fish communities between aquaculture and non-aquaculture beaches.

1.4.2 The importance of Baynes Sound

Baynes Sound is an ideal model system to study human impacts on the marine environment. The complex interplay between vulnerable wildlife, industry, and climate change within Baynes Sound presents unique research opportunities that aim to accomplish conservation goals while maintaining economic viability. Furthermore, much of the British Columbia coast provides favourable habitat for shellfish aquaculture, and expansions of the industry are planned (Silver 2013, 2014). If ecological function is able to be maintained in Baynes Sound while supporting a thriving shellfish trade, it may be used as a blueprint for future development of the industry. Furthermore, techniques used in this study, particularly functional diversity analyses as discussed in chapter 3, are powerful tools for understanding marine community responses to disturbances. British Columbia is currently undergoing extensive shoreline development and faces threats from other potentially damaging industries (oil export and coal mining among others) to which functional diversity analyses could be applied.

Chapter 2 – The influence of intertidal shellfish aquaculture on fish community patterns

2.1 The Importance of Biodiversity

The current unprecedented rate of species extinction and associated biodiversity loss, which are consistently linked to anthropogenic disturbances, have been a primary focus of ecological research since the 1980s (Millenium Ecosystem Assessment 2005a, Cardinale et al. 2012). Most of these studies report detrimental effects to the studied ecosystem, especially in terms of functionality (Hooper et al. 2012). Cardinale et al. (2012) define ecosystem functions as ecological processes that control the fluxes of energy, nutrients, and organic matter through an environment. Biodiversity loss is viewed as one of the primary drivers of ecosystem change during the past century. Results of a meta-analysis by Hooper et al. (2012) reveal that the effects of intermediate levels of species loss (21-40%) rival that of the often-documented effects of climate warming and increasing ultraviolet radiation. A recent study by Lefcheck et al. (2015) indicates that we may even be underestimating the detrimental effects of biodiversity loss, primarily because most studies only examine impacts to a single ecosystem function. In reality, ecosystems perform several functions upon which many species depend. The intertwined "multifunctionality" of ecosystems shows a stronger negative response to biodiversity loss than when a single function or taxonomic group is examined alone.

Biodiversity is often viewed as a feature that supports ecosystem function (Naeem 2002, Hooper et al. 2012). This is primarily due to the inherent nature of species assemblages to partition their use of resources, which maximizes the use of niche space while reducing competition with other species or groups of species. This is referred to as species complementarity and leads to more complete extraction of resources from the environment, thereby facilitating the flow of energy and materials among trophic levels (Fridley 2001, Hooper et al. 2005, Isbell et al. 2011, Reich et al. 2012). This flow is a central tenet of ecosystem function (Cardinale et al. 2012). Losses of biodiversity are associated with less efficient resource extraction, and therefore are associated with decreased overall ecosystem function (Hooper et al. 2012). Also, while the loss of just one or a few species may not initially appear to negatively affect function (especially in highly diverse systems), it destabilizes ecosystems and makes them more vulnerable to future environmental change. Thus, biodiversity enhances stability and resilience of ecosystem function to disturbances (Schwartz et al. 2000, Hooper et al. 2005).

Biodiversity is not only beneficial for ecological purposes, but also for humanity. Ecosystem services to humans enhanced by biodiversity include food production, disease and pest control, climate regulation, seed dispersal, freshwater provision, and nutrient and waste management (Hilborn et al. 2003, Klein et al. 2003, Millenium Ecosystem Assessment 2005b). Direct negative effects to humans associated with biodiversity loss have been documented. Worm et al. (2006) report that decreased biodiversity leads to increased instances of marine fisheries collapse, decreased recovery potential, and decreased stability of populations. Decreases in crop yield have also been reported in response to decreased pollinator diversity (Rogers et al. 2014). Also, biodiversity loss has been identified as a potential cause of increased incidence of some diseases among humans and animals (Millenium Ecosystem Assessment 2005a). The loss of coral and mangrove species and overall cover has been linked to increased incidences of flooding and threatens the success of ecotourism operations (Millenium Ecosystem Assessment 2005a). Finally, both government and private expenditures for biodiversity loss research and restoration have been enormous, potentially diverting funds away from other worthy ecological research.

2.2 The interaction of fish communities and shellfish aquaculture

2.2.1 What do we know?

Fish responses to shellfish aquaculture disturbances are poorly studied compared to other aspects of the ecosystem, likely because fish are quite mobile and more labour intensive study subjects compared to other biotic communities (e.g. phytoplankton, zooplankton, and infaunal invertebrate communities) (Harrison and Whitfield 2004). A notable exception to this is the suspended culture of bivalves, particularly mussels. Suspended and other floating shellfish culture gear have proven to be attractive features to many fish species (Iglesias 1981, Erbland and Ozbay 2008, D'Amours et al. 2008, Marenghi and Ozbay 2010, Marenghi et al. 2010), although it is unclear whether or not these increases in fish density are indicative of increases in overall fish abundance or just a redistribution of existing biomass. Suspended culture operations are also frequently linked to organic matter enrichment of the benthos, encouraging anoxic conditions unfavourable to infaunal and epibenthic invertebrates, both of which are valuable components of many fish species' diets (Dahlbäck and Gunnarsson 1981, Chamberlain et al. 2001, Christensen et al. 2003, Wilson and Vopel 2015). In fact, López-Jamar et al. (1984) observed a shift in fish feeding strategies, from primarily infaunal feeding to epifaunal feeding off of suspended aquaculture gear after the introduction of a suspended mussel farm in north-western Spain. However, this likely represents an opportunistic response of fish to a new food resource. Finally, suspended culture operations can cause seston depletion, potentially limiting resources for larval fish (Ogilvie et al. 2000, Duarte et al. 2008, Grant et al. 2008), but the severity of depletion is quite variable by season and oceanographic conditions. Ogilvie et al. (2000) even documented a net increase of phytoplankton biomass during November in a New Zealand estuary, although depletions were observed during most other times of the year.

Studies examining fish responses to benthic shellfish farming, particularly those practices relevant to this study such as the beach culture of oysters and deployment of plastic anti-predator nets (PPEN) over clam beds, are much less common. Pinnix et al. (2005) and Hosack et al. (2006) found that intertidal areas devoted to the culture of Pacific oyster (*Crassostrea gigas*) were generally of equivalent value to fish communities compared to eelgrass (*Zostera marina*) beds. Oyster culture in North American west coast estuaries frequently occurs in the low intertidal where it may compete for space with eelgrass beds. A recent study by Dumbauld et al. (2015) took this finding a step further, stating that benthic habitat (oyster aquaculture vs. eelgrass vs. mudflat vs. channel) in North American west coast estuaries may not be as strongly linked to fish foraging and survival as previously thought; they observed few fish community differences among those habitat types. Powers et al. (2007) demonstrated that PPEN fouled with macroalgae were of similar fish habitat value as seagrass beds in a North Carolina, USA estuary. On, the negative side, PPEN can cover extensive areas of intertidal habitat and potentially reduce fish foraging habitat (Jamieson et al. 2001, Carswell et al. 2006). Modifications associated with the industry such as the addition of gravel, beach levelling, compaction by vehicle traffic, and siltation can homogenize fish prey communities (Bendell-Young 2006) and eliminate habitat for beach spawning forage fishes (Martin 2015).

2.2.2 The importance of habitat complexity

The relationship between habitat complexity and species diversity is one of the most frequently studied interactions in ecological research. Complexity is defined as the variability in topographic elevation of a substrate, and can be measured by assessing a number of surface features including scale, spatial arrangement, and size, among others (Wilson et al. 2007, Tokeshi and Arakaki 2012). Generally, increases in complexity are associated with a positive response from at least one part of the biological community in terms of abundance, species richness, or diversity. This relationship has been demonstrated for almost all taxa, from the smallest of invertebrates to large mammal communities (Gratwicke and Speight 2005). However, the underlying mechanisms for this phenomenon are a source of controversy. Macarthur & Macarthur (1961), one of the first papers to address this topic, proposed that greater habitat complexity provides more niches, promoting diversification of the community. This was demonstrated through the observation of greater bird species richness in forests with greater foliage height diversity. Their niche hypothesis is still widely accepted today, but may be less applicable in systems with smaller scale changes in topography (St. Pierre and Kovalenko 2014). A number of other hypotheses exist. Heck & Wetstone (1977) proposed that complex habitats provide greater habitable surface area and thus attract a greater abundance of organisms. Though this may be the case in some systems, it is possible for complexity to vary significantly while maintaining the same surface area (Kovalenko et al. 2012). Complex habitats can also modulate predator-prey interactions by providing refuge and preventing over-exploitation of a prey species (Kovalenko et al. 2012). This promotes both diversity and stability of communities (Almany 2004, Warfe and Barmuta 2004, Grabowski et al. 2008, Kovalenko et al. 2012).

Human activities are often associated with a homogenization or outright destruction of structural components of an ecosystem (Millenium Ecosystem Assessment 2005a, St. Pierre and Kovalenko 2014). Based on extensive empirical evidence and the hypotheses proposed above, structural homogenization is usually accompanied by decreases in species abundance, richness, or diversity. However, human interference may also take the form of the addition of habitat complexity. The phenomenon is quite notable in the marine environment where positive responses of the biotic community have been observed in response to features such as oil rigs (Seaman et al. 1989, Jørgensen et al. 2002, Fabi et al. 2004) and wind farms (Wilhelmsson et al. 2006) placed offshore in areas of relatively low complexity. Shellfish aquaculture is another disturbance that may actually represent a net increase in habitat complexity of the seafloor. In chapter 1, I discussed how the shellfish industry has been associated with the removal of complexity generating features, such as eelgrass and cobble, from the environment (Jamieson et al. 2001, Dumbauld et al. 2009). Unfortunately, there is little historical information regarding beach characteristics of Baynes Sound before the rise of the shellfish aquaculture industry in the mid-1900s. Most beaches, even those not currently host to aquaculture operations, have been farmed in the past and may have previously offered a more complex habitat than they do at present. Currently, intertidal shellfish culture areas are likely more complex than many non-aquaculture areas of seafloor due to the addition of Pacific oysters and PPEN (which often exhibits a high degree of macroalgal fouling). The goal of this project is to assess how benthic shellfish aquaculture influences habitat complexity and biotic communities (using fish as model organisms). My hypotheses are as follows: 1) Intertidal areas of shoreline under active shellfish culture tenure will be more structurally complex than non-aquaculture areas. 2) Fish communities will respond positively to the presence of shellfish aquaculture as evidenced through increased species abundance, richness, and diversity.

2.3 Fish as model organisms for ecosystem health assessments

Ecosystem health assessment is a frequent focus of ecological research. While some aspects of ecosystem health are apparent through measurements of abiotic components of the environment (e.g. physical or chemical), biological community status is also an important part of such assessments, especially when considering the variety of habitat variables they may reflect (Harrison and Whitfield 2004, Jørgensen et al. 2010). Due to economic and time-based constraints, it usually isn't feasible to effectively survey all biotic aspects of an ecosystem. Therefore, a certain group of taxa are selected to be representative of the whole biotic community (Harrison and Whitfield 2004). Intertidal fish communities were used for this study because they are poorly researched compared to other more economically valued fish groups in British Columbia, yet hold tremendous ecological significance. Furthermore, fish are excellent candidates to monitor ecosystem disturbances given their mobility (enabling them to respond quickly to poor environmental conditions), presence at most consumer trophic levels (thereby providing useful information about local food web structure), relatively long life span, presence in most aquatic systems, and diverse ontogeny which exposes them to a wide range of habitat variables (Whitfield and Elliott 2002, Harrison and Whitfield 2004). It is important to note that there are challenges to using fish for ecosystem assessments. Particularly, given their mobility and migration potential (either diel or seasonal), results can be biased depending on sampling design. Also, sampling is labour intensive and gear is often biased towards the capture of specific life histories. Fish communities may be altered by activities separate from study variables, such as stocking, angling, and commercial fisheries (Whitfield and Elliott 2002, Harrison and Whitfield 2004). The design of this study works to counteract most of these disadvantages, rendering fish communities worthy study subjects.

2.4 Methods

2.4.1 Site selection

I selected three pairs of active-aquaculture/non-aquaculture sites along the southwestern portion of Baynes Sound (Fig. 3). Pairs are grouped for concurrent sampling as follows: A1 and NA1, A2 and NA2, A3 and NA3. Sites named with “A” refer to active aquaculture sites and those named “NA” refer to comparative non-aquaculture sites. A2 and A3 were dominated by Manila clam culture with heavy implementation of PPEN. A1 also hosted PPEN clam culture but also a significant amount of beach cultured Pacific oysters. All sites had minimal slope, but total intertidal area was variable. A2, A3, NA2, and NA3 were more exposed and subject to greater wave action while A1, and particularly NA1, were more sheltered. The dominant substrate was variable both between and within sites. All sites except NA1 exhibited more compact substrates usually ranging from sand to small cobble. Base substrate at NA1 was considerably finer and dominated by mud. Beach surface characteristics are further described in Table 3. NA2 and NA3 have been farmed in the past, but current evidence of the industry is almost non-existent, though aquaculture-associated alterations of sediment characteristics are likely still present. NA1 is located near the Deep Bay marina and in the past was likely host to industrial infrastructure potentially associated with the logging trade. NA1 is currently held under tenure by the Deep Bay Marine Field Station, and while never intensively farmed like commercial tenures, is likely influenced by small-scale aquaculture research activities located approximately 100m southwest of the chosen sampling location. Infrequent low intensity digging is conducted at all non-aquaculture sites as part of small-scale harvests. Non-aquaculture sites still support high densities of infaunal bivalves, but are no longer intentionally seeded.

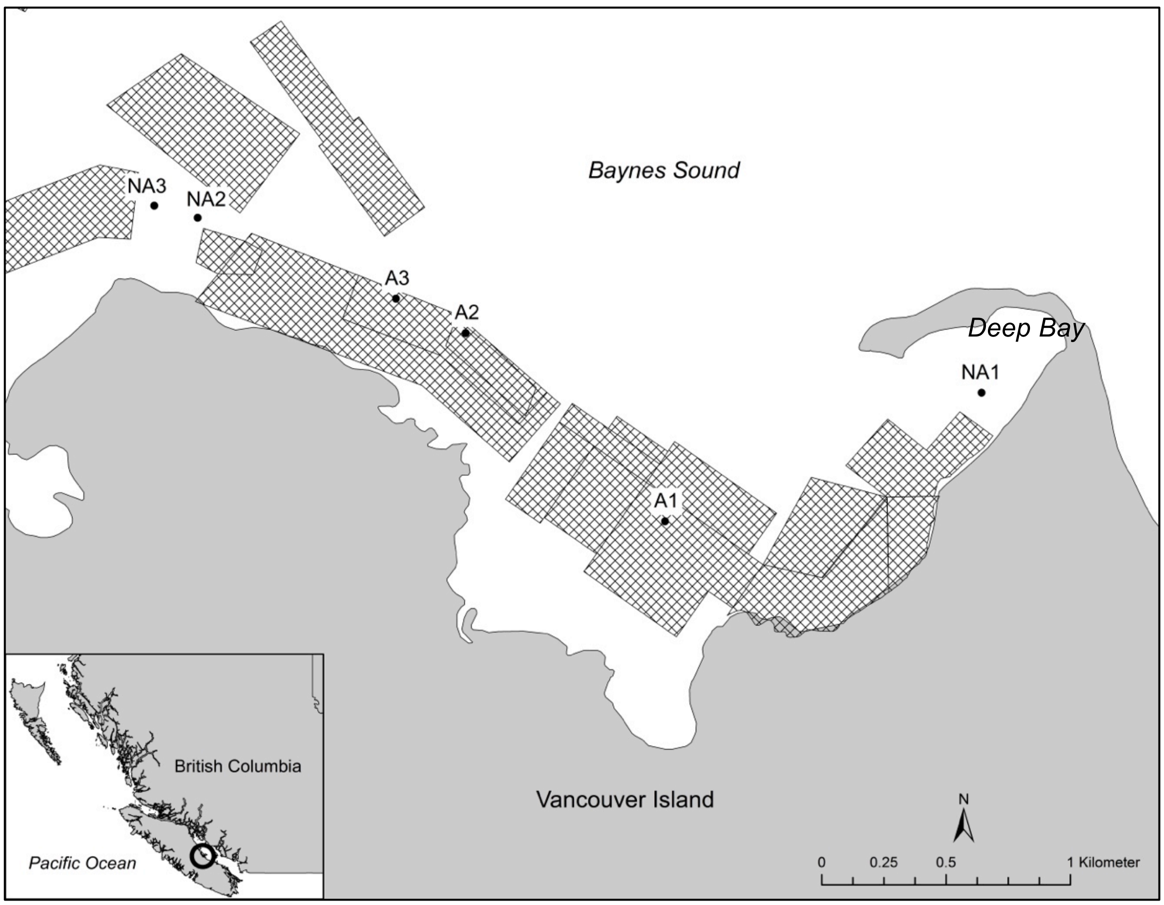

Figure 3. Map of fish sampling locations in the southern portion of Baynes Sound, BC. Markers labeled "A" are active shellfish aquaculture sites, and those labeled "NA" are non-aquaculture sites. The hashed polygons represent active shellfish tenures. Shared numbers denote site pairs.

2.4.2 Fish collection

Fish were collected from site pairs using two self-designed and constructed fyke nets modified from the designs of Pinnix et al. (2005) and Hosack et al. (2006) (Fig. 4). The dimensions of each net are as follows. The two outer wings were each 10m x 1m and angled approximately 40° from the 15m x 1m leader. Outer wings were constructed of 0.6cm (on stretch) knotless dark-green nylon netting. The leader was constructed using 1cm (on stretch) black nylon netting. The trap consisted of a 1.37m long x 0.63m high x 0.88m wide, 2.5cm diameter PVC frame lined with the 0.6cm knotless dark-green nylon netting. A section of 2.5cm (on stretch) knotless white nylon netting was incorporated into the trap to provide size gradation and reduce within trap predation. The trap opening was approximately 20cm x 15cm and located at the base of the trap.

Figure 4. Fyke nets exposed at low tide and submerged during a receding tide.

Fish were collected from each site pair four times throughout July and August 2014. Nets were placed at 1.0m above the mean low low water (MLLW) with the wings oriented directly upshore. Nets were anchored during a low tide event and then left for approximately 24 hours. Fish were collected alive from the trap the next day before water had completely receded. All captured individuals were identified to species and the total length of up to 15 individuals per species was taken. Small subsets of most species were euthanized using MS-222 and retained for diet analyses that will be described in chapter 3. All other fish were released alive post measurement.

2.4.3 Complexity measurements

Structural complexity at each net deployment site was quantified during July 2015 when intertidal macroalgae communities were similar to 2014 conditions. During low tide, a 20m wide area at each site was assessed from approximately 1.0m to 3.0m above MLLW. Each site was visually assessed and divided into zones based on surface features and characteristics (Table 1). In many cases, a single surface feature could not define zones. On those occasions, multiple features were included in the naming of a zone. For example, if a distinct zone was predominately gravel, but also contained significant sand and shell cover, it was named gravel-sand-shell, with the order of terms indicating prevalence of that component (in this case, gravel was most abundant, sand was second, and shell was third). Sites had anywhere from 2 - 4 zones. Total dimensions of each zone were recorded. At least three, but no more than five 0.5m x 0.5m quadrats were randomly placed in each zone. In each quadrat, three measurements of complexity were performed using a profile gauge modified from McCormick (1994). The profile gauge produces similar results to the classic chain and tape method (Risk 1972). According to Tokeshi & Arakaki (2012), there are at least 5 facets used to describe structural complexity in aquatic systems: 1) spatial scale, 2) the diversity of complexity-generating structural elements, 3) the spatial arrangement of complexity-generating structural elements, 4) the size of structural elements, 5) abundance or density of structural elements. Structural complexity is difficult to measure in-situ, and most metrics are only successful in addressing one of the five facets listed above. I utilized a contour length:linear length ratio (CR), which is successful in determining the size of structural elements. While this metric admittedly overlooks many facets of complexity, it provides an informative and rapid method of quantification (McCormick 1994) and correlates well with community variables such as species abundance, richness, and diversity (Risk 1972, Wilson et al. 2007). Furthermore, it is easy implemented across a range of habitats, a particularly attractive feature for this study given the mosaic nature of aquaculture beaches (Wilson et al. 2007). A notable shortcoming of the CR in Baynes Sound is its inability to address the abundance of refuges created by shells, between rocks, and within macroalgae mats. Many intertidal fish are small and cryptic and would likely be attracted to areas that provide increased refuge from predators (Hart 1973, Lamb and Edgell 2010).

For each estimate, the profile gauge was gently placed onto the substrate, levelled to account for any possible effect of beach slope, and a photo of the apparatus was taken (Fig. 5). To account for complexity generated by unstructured macroalgae (those species that only stand upright when submerged, i.e. *Ulva sp.*, *Gracilaria sp.*), as was often the case in PPEN zones, any peg that encountered the basal attachment of a macroalgae stem was noted and a measurement of algae height was recorded. Photos were processed using ImageJ and calibrated using a known distance (the 0.5m span of pegs from end to end). Macroalgae influence was incorporated by adding the recorded heights above their respective pegs and marking points to create a visual simulation of submerged complexity. A grid of 1cm^2 blocks was overlaid to aid proper marking of algae heights. The CR was determined by dragging a line across the top of all pegs (or points in the events that a macroalgae measurement was incorporated) and dividing that distance (the contour distance) by 0.5m (the linear distance). A total site weighted mean CR was formulated using the sum of products of each zone area (m^2 of beach surface covered) and respective mean zone CR (mean of all quadrat means for each zone).

Table 1. Criteria for beach zone partitioning. Mud, sand, gravel, and cobble size ranges were taken from the Wentworth scale (Kenny and Sotheran 2013).

Substrate Feature	Explanation
Mud	< 0.06mm grain size
Sand	0.06 – 2mm grain size
Gravel	0.2 – 6.5cm grain size
Cobble	6.5 – 25cm grain size
Oyster	Primarily singular and live oysters
PPEN	Plastic predator exclusion netting over clam culture. Mixed degree of macroalgal fouling
Barnacle	Live or deceased barnacle clusters
Shell	Largely intact clam shell halves, oyster shell halves, or sand dollar skeletons

Figure 5. Profile gauge deployed on low complexity (A) and high complexity (B) surfaces.

2.4.4 Indices and statistics

Fish abundance as well as species richness, diversity (Gini-Simpson index), and evenness (Pielou's evenness index) were used to compare fish communities between all sites and between site types. Results of the biodiversity indices (species richness, diversity, and evenness) were compared among all sites using one-way ANOVA. In the event that the null hypothesis was rejected, a Tukey post-hoc test was employed to determine which groups differed. Abundance data were highly non-parametric and unable to be transformed to normality. Thus, abundance among sites was analyzed using a Kruskal-Wallis rank sum test. For plotting purposes, square root of abundance is presented to increase the visibility of sites with low catch, but data were not transformed for analysis. I also selected five species that were present at both aquaculture and non-aquaculture sites and had suitable sample sizes for analysis (Plainfin Midshipman, Saddleback Gunnel, Shiner Perch, Pacific Staghorn Sculpin, and Tidepool Sculpin) to test for affinities to either a particular site or site type. Abundances of these species were unable to be transformed to normal distributions and were compared using Kruskal-Wallis rank sum tests. A Jaccard dissimilarity analysis visualized by non-metric multidimensional scaling (NMDS) was employed to visualize site and sampling replicate groupings, and a permutational multivariate analysis of variance (PERMANOVA) was undertaken to see if dissimilarities between groups were significantly greater than within groups (i.e. to see if community composition based on Jaccard dissimilarity is significantly different among sites). Finally, linear regressions were implemented to investigate whether changes in habitat complexity had an effect on biodiversity indices. All community analyses were conducted using the vegan package in R (Oksanen et al. 2013, R Core Team 2015).

2.5 Results

2.5.1 Biodiversity indices

A total of 3,158 fish were captured over the full sampling period. 2,112 were captured at aquaculture sites, and 1,047 were captured at non-aquaculture sites (Table 2). However, capture numbers were highly variable between replicates. Most notably, the aquaculture capture total is highly inflated by a particularly high catch of Plainfin Midshipman (abbrev. PLMI, *Porichthys notatus*) juveniles (approximately 1,200 individuals) at A2 during the third sampling replicate. Some species were only caught at specific sites, but only those of very low capture numbers were found at only one site type. Plainfin Midshipman, Saddleback Gunnel, Shiner Perch, Pacific Staghorn Sculpin, and Tidepool Sculpin, were selected for further analysis based on their suitable sample size and presence at both site types. No differences in the abundance of any of these species were observed between sites or according to site type (Kruskal-Wallis $p>0.05$). Three truly pelagic species were captured while the rest were primarily benthic. However, pelagic catch was almost entirely composed of Shiner Perch, which showed no site fidelity (Kruskal-Wallis $p=0.1276$).

Table 2. Combined aquaculture and non-aquaculture total fish catch by species throughout July and August 2014.

Species	Common Name	Species Code	Aqua	Non-Aqua
Syngnathus leptorhynchus	Bay Pipefish	BAPI	46	42
Rhinogobiops nicholsii	Blackeye Goby	BLGO	1	0
Xiphister atropurpureus	Black Prickleback	BLPR	4	3
Enophrys bison	Buffalo Sculpin	BUSC	12	1
Scorpaenichthys marmoratus	Cabezon	CABE	2	0
Pleuronichthys coenosus	C-O Sole	COSO	1	2
Pholis laeta	Crescent Gunnel	CRGU	7	0
Ophiodon elongates	Lingcod	LING	3	0
Artedius fenestralis	Padded Sculpin	PASC	7	2
Apodichthys flavidus	Penpoint Gunnel	PEGU	7	4
Porichthys notatus	Plainfin Midshipman	PLMI	1413	704
Pholis ornata	Saddleback Gunnel	SAGU	28	5
Cymatogaster aggregata	Shiner Perch	SHPE	366	170

Clinocottus acuticeps	Sharpnose Sculpin	SHSC	16	9
Artedius lateralis	Smoothhead Sculpin	SMSC	1	0
Lumpenus sagitta	Snake Prickleback	SNPR	0	1
Sebastes diploproa	Splitnose Rockfish	SPRO	2	0
Citharichthys stigmaeus	Speckled Sanddab	SPSA	0	2
Leptocottus armatus	Pacific Staghorn Sculpin	STSC	130	90
Gasterosteus aculeatus	Threespine Stickleback	THST	2	0
Oligocottus maculosus	Tidepool Sculpin	TISC	54	7
Hexagrammos stelleri	Whitespotted Greenling	WHGR	10	5

Despite disparate total capture numbers, mean abundance did not vary among sampling sites (Fig. 6A; Kruskal-Wallis $p = 0.0816$, $df = 5$). Mean species diversity (Fig. 6B; ANOVA $p = 0.458$, $F = 0.977$, $df = 5$) and mean species evenness (Fig. 6C; ANOVA $p = 0.127$, $F = 2.001$, $df = 5$) also did not vary among sites. However, mean species richness did vary significantly, and differences were observed between site A2 and NA1 (Fig. 6D; ANOVA $p = 0.0318$, $F = 3.167$, $df = 5$; Tukey $p = 0.0118$). These indices responded similarly when sites were combined according to site type. Abundance (Fig. 7A; Kruskal-Wallis $p = 0.3122$, $df = 1$), species diversity (Fig. 7B; ANOVA $p = 0.185$, $F = 1.871$, $df = 1$), species evenness (Fig. 7C; ANOVA $p = 0.671$, $F = 0.185$, $df = 1$), and species richness (Fig. 7D; ANOVA $p = 0.0515$, $F = 4.241$, $df = 1$) all did not vary significantly according to a $p<0.05$ significance level. However, species richness was significant at the $p<0.1$ level.

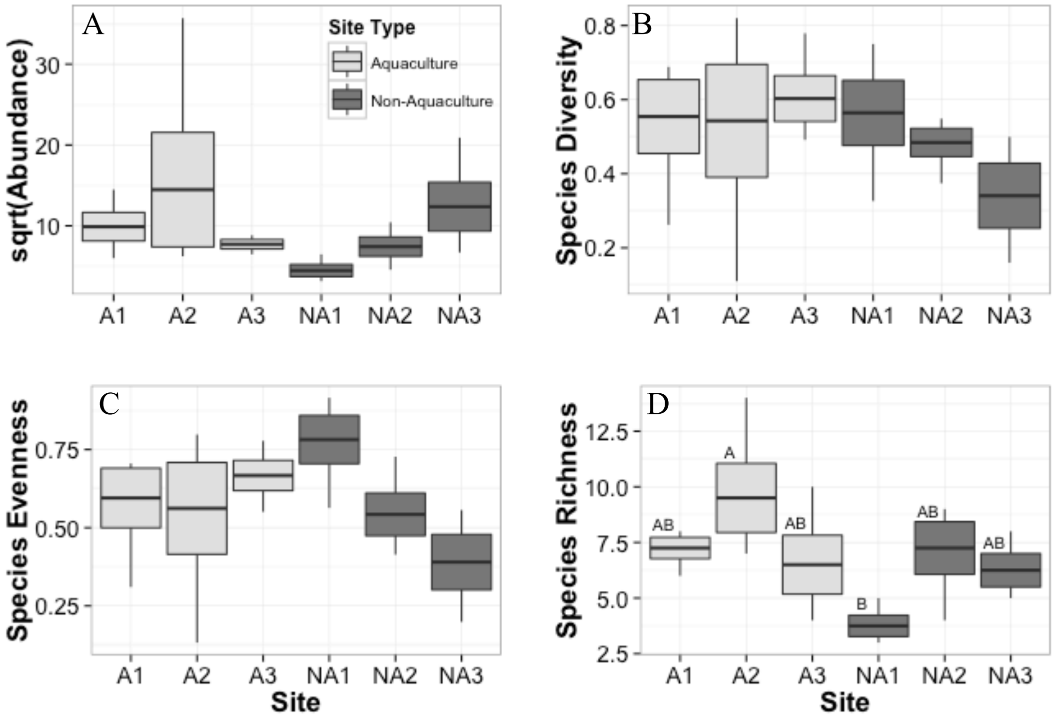

Figure 6. Mean total fish abundance (square root transformed to increase plot visibility) (A), species diversity (Gini-Simpson index) (B), species evenness (Pielou's) (C), and species richness (D), of fish captured at aquaculture and non-aquaculture sites. Boxes represent mean ± SEM and whiskers extend to data maximum and minimum. Species richness varied significantly between sites A2 and NA1 (ANOVA $p<0.05$, Tukey $p<0.05$). There were no significant differences observed in terms of abundance (Kruskal-Wallis $p>0.05$), species diversity (ANOVA $p>0.05$), or species evenness (ANOVA $p>0.05$).

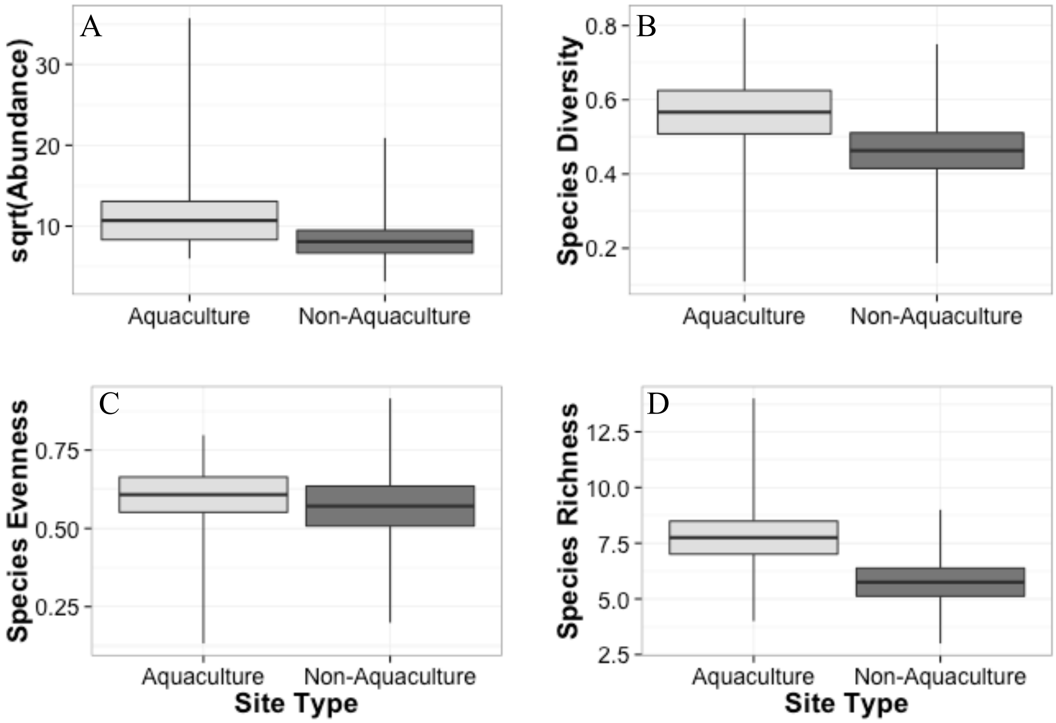

Figure 7. Mean total fish abundance (square root transformed to increase plot visibility) (A), species diversity (Gini-Simpson index) (B), species evenness (Pielou's) (C), and species richness (D), of fish captured at aquaculture and non-aquaculture habitats. Boxes represent mean ± SEM and whiskers extend to data maximum and minimum. Species richness approached significance at the $p<0.05$ level (ANOVA $p=0.0515$). There were no significant differences observed in terms of abundance (Kruskal-Wallis $p>0.05$), species diversity (ANOVA $p>0.05$), or species evenness (ANOVA $p>0.05$).

In the event that the anomalously high catch of PLMI for the third replicate of A2 was masking underlying patterns in the data, the data point was replaced with an average of previous catches at that site. The potentially affected indices (abundance, species diversity, and species evenness) were recalculated. No difference between sites was observed for revised mean abundance, but appeared to approach significance (Kruskal-Wallis $p = 0.05964$, $df = 5$). Revised mean species diversity also did not vary among sites (ANOVA $p = 0.14$, $F = 1.926$, $df = 5$). However, mean species evenness of the revised dataset did vary; significantly greater evenness was observed at NA1 relative to NA3 (Fig. 8; ANOVA $p = 0.0206$, $F = 3.559$, $df = 5$; Tukey $p = 0.0128$). This relationship was near the threshold for significance prior to the removal of the PLMI outlier at A2. Therefore, there appears to be a slight masking effect.

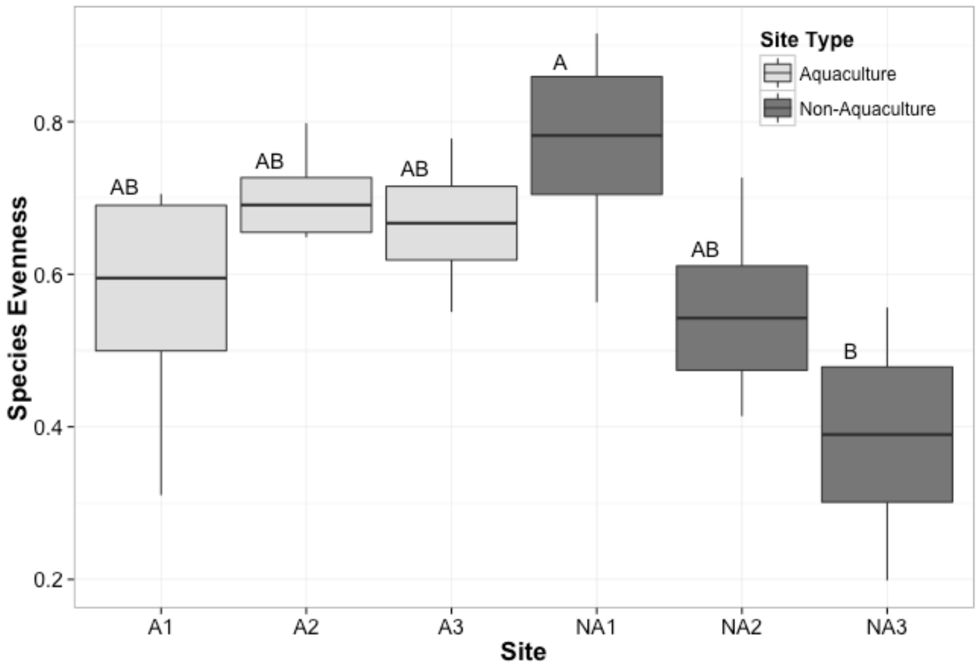

Figure 8. Mean fish species evenness (Pielou's) ± SEM of a modified dataset with a significant outlier removed from site A2. There was a significant difference between the means (ANOVA $p<0.05$). Groups that do not share a letter are significantly different (Tukey $p<0.05$).

2.5.2 NMDS and PERMANOVA

Some distinct site by replicate groupings were formed by NMDS plots of Jaccard dissimilarity matrix distances. NA1 displayed the tightest grouping and exhibited the least amount of overlap with other clusters. However, sites did not group according to site type (aquaculture or non-aquaculture). Furthermore, plotting stress was apparent and near the upper threshold of acceptable levels for an accurate representation in reduced dimensions, so the plot arrangement may not be entirely representative of site relationships (Fig. 9; NMDS stress = 0.2089434) (Oksanen et al. 2013). Even though NMDS identified partitions among sites, they were not statistically significant because community composition did not vary among sites (PERMANOVA $p = 0.341$, $F = 1.096$, $df = 5$).

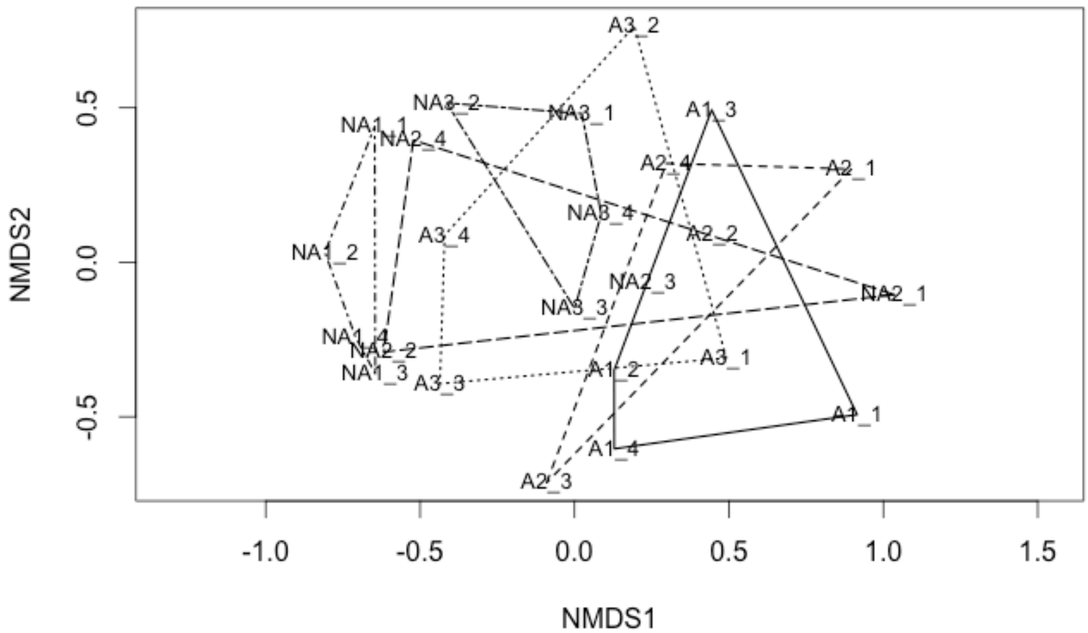

Figure 9. NMDS ordination plot of fish sampling events (site_replicate). Polygons connect all 4 sampling replicates of a single site. Plotting stress was apparent (NMDS stress = 0.2089434) (Oksanen et al. 2013).

2.5.3 Habitat complexity

Habitat structural complexity, defined by contour length ratio (contour distance:linear distance), was on average 1.2x greater at aquaculture sites compared to non-aquaculture sites (Table 3). However, fish community taxonomic indices did not vary according to these changes in complexity; species abundance (Fig. 10A; Linear regression - Adj. $R^2 = -0.0431$, $p = 0.8258$), species diversity (Fig. 10B; Linear regression - Adj. $R^2 = 0.0596$, $p = 0.1313$), species evenness (Fig. 10C; Linear regression - Adj. $R^2 = -0.0176$, $p = 0.4461$), and species richness (Fig. 10D; Linear regression - Adj. $R^2 = 0.0674$, $p = 0.1170$), were all unaffected.

Table 3. Habitat type and complexity descriptions (as contour length, CL, ratio) for each sampling site. Explanations of habitat type naming criteria can be found in Table 1. Habitat area is the total area covered by various habitat types within the 20m wide sampling area and between 1.0 – 3.0m tidal height. Percent beach identifies the percentage of the survey area covered by various habitat types and was used for weighting Site CL Ratio. Site CL ratio is a weighted average of CL ratios for each habitat at that site.

Site	Habitat Type	Habitat Area (m^2)	Percent Beach	Mean Habitat CL Ratio	Site CL Ratio
NA1	Mud-Gravel	991	55.06	1.06	54.06
	Mud-Shell	600	33.33	1.11	
	Oyster-Mud	194	10.78	1.09	
	Cobble-Mud	15	0.83	1.12	
A1	Oyster-Gravel-Shell	2140	58.47	1.27	60.07
	PPEN	853	23.31	1.10	
	Gravel-Sand-Barnacle	667	18.22	1.11	
NA2	Gravel-Mud-Shell	2412	67	1.22	59.19
	Mud-Shell	1060	29.44	1.11	
	Barnacle-Cobble-Mud	128	3.56	1.16	
A2	PPEN	1770	50.57	1.48	64.93
	Gravel-Sand-Shell	1560	44.57	1.11	
	Cobble	170	4.86	1.21	
NA3	Gravel-Barnacle-Shell	2000	64.52	1.03	51.79
	Gravel-Shell	1100	35.48	1.04	
A3	PPEN	2140	69.03	1.57	71.49
	Gravel-Sand	700	22.58	1.04	
	Cobble	260	8.39	1.29	

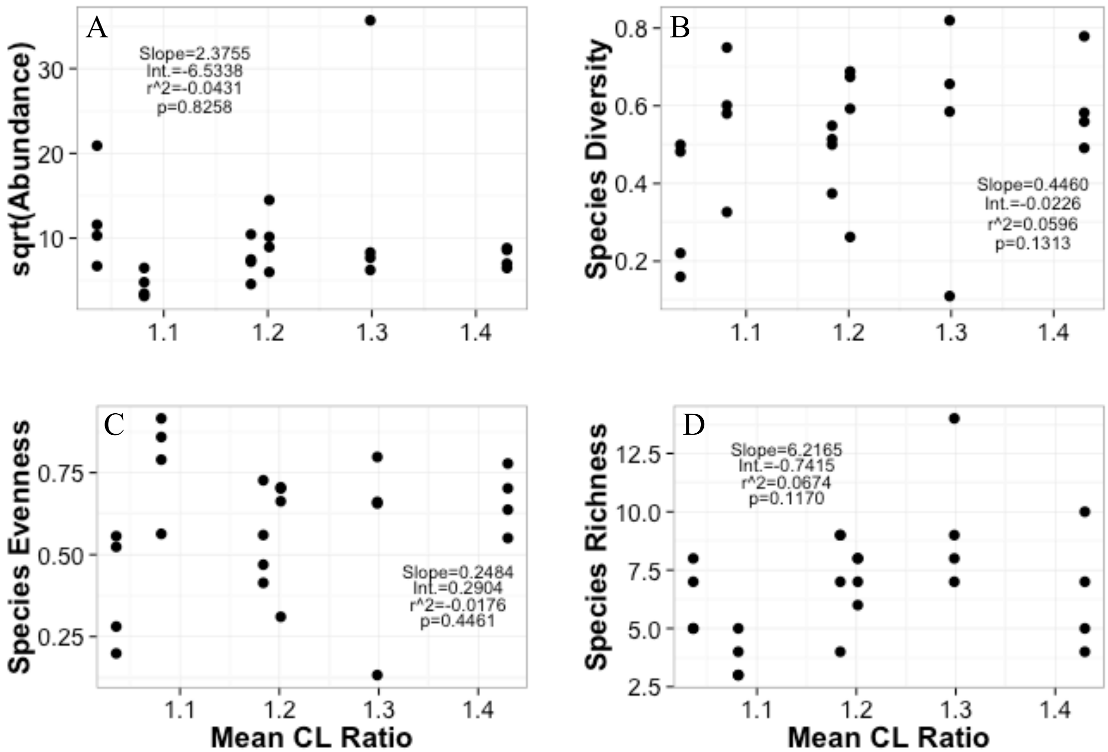

Figure 10. Scatterplot of square root transformed fish abundance (A), species richness (B), species diversity (Gini-Simpson Index) (C), and species evenness (Pielou's) (D) according to habitat structural complexity as defined by mean contour length ratio. Linear regressions showed no significant relationships between the variable pairs.

2.6 Discussion

In this study, I described the interactions of the shellfish aquaculture industry with the biotic community using intertidal fish communities as indicators of ecosystem change. I hypothesized that structural complexity, which is widely recognized as a strong driver of community patterns (Macarthur and Macarthur 1961, Risk 1972, Heck and Wetstone 1977, Tokeshi and Arakaki 2012), would be a relevant mechanism to facilitate biological variation in this system. As anticipated, structural complexity was higher in areas under active shellfish aquaculture tenure relative to non-farmed beaches. However, contrary to my hypothesis, fish communities varied little according to site type or habitat complexity.

Despite the challenges of working on active shellfish farms, I was able to evaluate entire fish communities from areas of intensive shellfish culture using fyke nets. I captured fish of a range of sizes (from as small as 1.6cm to as large as 24.4cm) and of both pelagic and benthic lifestyles. However, in this application, fyke nets were biased against the capture of pelagic species during high tide events when water levels rose above the maximum wing height. While more labour intensive than other nearshore sampling methods such as beach seining, which provides instantaneous measurements, fyke nets sampled fish for the entire tidal cycle, providing an integrated measure of abundance. By virtue of this feature, community information provided by fyke nets is able to account for transient species that are constrained by diel or tidal factors. I was also able to implement a novel application of the profile gauge method (McCormick 1994) to rapidly quantify structural complexity on heterogeneous intertidal beaches. While contour length ratios are commonly employed metrics that can be achieved using classical approaches such as the chain and tape method (Risk 1972), the profile gauge facilitates the incorporation of non-rigid features such as macroalgae. Macroalgae can significantly contribute to complexity and offer refuge and foraging opportunities for fish (Anderson 1994, Gee and Warwick 1994, Eriksson et al. 2006, Powers et al. 2007), but its contributions are difficult to quantify as most varieties are only upright when submerged.

Surprisingly, intertidal shellfish aquaculture infrastructure was not a strong driver of fish community patterns. While significantly lower species richness was observed at site NA1 compared to A2, richness among other sites was unaffected. Other indicators such as fish abundance, species diversity, and evenness did not vary at all according to site type (although species evenness did vary between NA3 and NA1 once a significant data outlier representing an anomalously high catch of Plainfin Midshipman was removed). When aquaculture habitats were compared to non-aquaculture habitats by combining all data for each site type (and therefore ignoring habitat variation within site types), similar results were found. Despite a small potential difference in species richness, there was not substantial evidence for meaningful variation in fish communities according to habitat. A PERMANOVA further corroborated these findings: it showed that communities did not vary significantly among sites. Pelagic and benthic fish groups also demonstrated a lack of response to these treatments. These findings represent a deviation from the results of both Pinnix et al. (2005) and Hosack et al. (2006), who observed differences in fish communities between benthic shellfish culture areas and unstructured mudflats (both concluding that aquaculture habitats should be considered to present greater habitat value to fish). They used similar assessment methods (Pinnix et al. (2005) – species richness and diversity, Hosack et al (2006) – species richness, diversity, and CCA) that should be comparable to this study. However, their aquaculture areas were comprised entirely beach cultured Pacific oysters while only one of my aquaculture sites (A1) had substantial oyster coverage. Additionally, the disparity between their findings and my own could be linked to differences in complexity at non-aquaculture beaches. Hosack et al. (2006) identify habitat complexity as a likely driver of fish community patterns (but they did not quantify it), and while not addressed by Pinnix et al. (2005), the same likely holds true for their study. Considering that non-aquaculture habitats in both of those studies were referred to as mudflats, it is possible that they offered an even more homogenous habitat than the non-aquaculture sites of my study (which while relatively unstructured, still displayed a mosaic surface with various substrate components), making the habitat differences among their site types more distinct.

At first glance, my findings seem to more clearly align with those of Dumbauld et al. (2015) who report similar communities at oyster culture and mudflat areas, concluding that they provide similar habitat value to fish. However, their study used sampling gear biased towards the capture of pelagic species, most notably juvenile salmon, which possibly explains why they did not observe a difference in communities at mudflat habitats. Benthic fish, which dominated catch in my study, are likely more influenced by benthic shellfish culture and may show different responses to alterations of the benthos than do pelagic species. If benthic species had been sampled more thoroughly by Dumbauld et al. (2015), their findings may have been more consistent with both Pinnix et al. (2005) and Hosack et al. (2006). However, when I grouped species according to benthic or pelagic lifestyles, there was no indication that benthic species responded differently to shellfish aquaculture than pelagic species. But, as previously noted, bias against the capture of pelagic species does exist when using fyke nets.

It is important to note that Pinnix et al. (2005), Hosack et al. (2006), and Dumbauld et al. (2015) did not investigate the effects of clam culture with PPEN (with varying degrees of macroalgae fouling). Two of my aquaculture sites, A2 and A3, were primarily PPEN clam culture areas while A1 was a multi-species site with both oyster culture and PPEN clam culture. While PPEN represents a similar increase in complexity over non-aquaculture sites as does oyster culture, it presents a different type of complexity with fluid structures as opposed to the hard stationary features offered by oysters. Powers et al. (2007) present evidence for the habitat value of macroalgae-fouled PPEN that is similar to those studies that investigate oyster culture; PPEN habitats were associated with positive responses of fish communities (as evidenced through abundance measures) and harboured communities more similar to those of complex habitats like seagrass than to unstructured seabed (as evidenced through NMDS). Despite the disparities between the results of these studies and my findings, I can conclude that there was minimal detectable community response to the presence of active shellfish aquaculture operations.

Beaches in North American west coast estuaries naturally vary from mud and sand flats to heavy cobble and boulders. What would be of most interest is examining the habitat value of shellfish aquaculture areas compared to the habitats they replace. However, the lack of this information is understandable as shellfish aquaculture has been a prominent industry here since the mid-1900s. In Baynes Sound in particular, most areas suitable for aquaculture either are currently farmed or have been in the past. Therefore, finding suitable sites to study the before and after effects of shellfish farming is difficult.

The lack of effect of increased structural complexity on fish community parameters is a notable exception to the generally accepted rule that greater complexity equates to greater faunal abundance (Orth et al. 1984, Heck Jr. et al. 1989, Fabi et al. 2004, Powers et al. 2007). Structurally complex habitats are recognized as hotspots for marine life due to their abundance of refuge and foraging opportunities. Additionally, structural complexity has been identified as a mediator of predator-prey relationships. As a consequence, small changes in the degree of complexity can have marked effects on the biological community. High levels of complexity can limit predator feeding efficiency while encouraging proliferation and competition between prey species (Crowder and Cooper 1982, Ryer 1988, Beukers and Jones 2009). Low levels of complexity are often associated with lower prey abundances and limited trophic breadth of predators. At intermediate levels, these phenomena balance each other, perpetuating a stable predator-prey relationship (Crowder and Cooper 1982, Ryer 1988). While I did measure greater levels of complexity at aquaculture sites, it is possible that this degree of increase was not high enough to differentiate them from non-aquaculture sites. However, most captured fish were small and likely exploited the complexity offered at aquaculture sites, even if they did not favour these areas over non-aquaculture sites. Only 6 of 22 species captured are known to favour habitats of lower complexity (Hart 1973, Lamb and Edgell 2010). Additionally, eelgrass beds were prevalent in lower intertidal and subtidal areas just below my net anchoring points. Eelgrass meadows are widely recognized as a valuable source of fish habitat (Pinnix et al. 2005, Hosack et al. 2006, Robinson et al. 2011, Robinson and Yakimishyn 2013). While not tested during this study, they undoubtedly offer more complex habitat than the intertidal areas I sampled. Most species I observed have been frequently observed in and around eelgrass beds (Hart 1973, Lamb and Edgell 2010). Although intertidal areas are also recognized as valuable foraging, spawning, and refuge habitat (Dumbauld et al. 2009; Martin 2015), it is possible that some fish favoured nearby eelgrass areas due to the high levels of complexity they provide.

Fish are highly mobile organisms that can utilize large areas of coastline (Harrison and Whitfield 2004). Given the small scale of my study area, it is possible that fish were frequently moving among habitat types and were captured during only a transient usage of the habitat. However, a number of the species I encountered, such as the Tidepool Sculpin, exhibit some degree of fidelity for their home beaches (Hart 1973, Lamb and Edgell 2010). It is possible that more pelagic species, such as the Shiner perch, were the only species that were frequently covering large areas and moving between both habitat types. Despite this, no species exhibited an affinity for particular sites or site types. Additionally, due to the prevalence of shellfish aquaculture in Baynes Sound, its effects, either positive or negative, extend beyond the boundaries of active leases. Non-aquaculture sites may have been influenced by aquaculture as an artifact of their proximity to active leases. Also, non-aquaculture sites were previously sites of active shellfish farming, although evidence of the industry at these locations is quite limited (no PPEN, lower densities of clams, essentially no oyster cover). In the future, one could build upon this study by repeating it at a larger spatial scale with high, medium, and low aquaculture prevalence areas. Baynes Sound would be an ideal high prevalence site. Furthermore, expanding the sampling timeframe would allow the study of migratory species such as various Pacific salmonids whose responses to the shellfish industry could be different from other species.

Chapter 3 – Interactions of fish and intertidal shellfish aquaculture: A functional diversity approach

3.1 An introduction to functional diversity

3.1.1 Functional diversity basics

Biodiversity assessment is a common method for examining impacts of ecosystem disturbance (Millenium Ecosystem Assessment 2005a). It is popular because biodiversity metrics, such as species richness, diversity, and evenness, are easy to calculate and are applicable to all ecosystems. Furthermore, biodiversity supports ecosystem functions (Hooper et al. 2012), or the processes that regulate the flow of energy, nutrients, and organic matter through an environment (Cardinale et al. 2012). Biodiversity also provides for numerous ecosystem services from which humans benefit (Hilborn et al. 2003, Klein et al. 2003, Millenium Ecosystem Assessment 2005b). Therefore, the ongoing extinction crisis is viewed as a major threat to both ecosystem and human health (Millenium Ecosystem Assessment 2005b). Detectable losses of biodiversity and overall lower levels of ecosystem functioning often accompany increased human presence in an environment (Millenium Ecosystem Assessment 2005a, Cardinale et al. 2012, Hooper et al. 2012). However, biodiversity indices are unable to directly address the role that species' identity plays in the maintenance of ecosystem function. As a consequence, each species is assumed to have a unique contribution to ecosystem functioning. In reality, all ecosystems exhibit at least some degree of overlap of species roles. This overlap, known as functional redundancy, is not detectable using taxonomic biodiversity indicators (Guillemot et al. 2011, Mason and Mouillot 2013). Consequently, functional diversity is now regarded as the favoured tool for monitoring the effects of ecosystem disturbance (Cadotte 2011).

The general definition of functional diversity is the diversity of species traits (e.g. diet, body size, behaviours, etc.) in an ecosystem that are linked to an organism's function (Schleuter et al. 2010, Mason and Mouillot 2013). While simple taxonomic indices, such as species richness, are still widely implemented for ecological research, and are used as indicators of ecosystem health, it is now recognized that ecosystem function depends much more on the maintenance of ecosystem processes (e.g. habitat and food provision, nutrient recycling, pest control, gene flow, etc.) rather than the preservation of the maximum number of species (Petchey and Gaston 2002, 2006, Petchey et al. 2004, Botta-Dukat 2005, Cadotte 2011). Where taxonomic biodiversity indicators tell us little about the relationship between species assemblages, environmental filters (environmental constraints on species composition), and ecosystem function, functional diversity methods group species according to their functional traits, thereby allowing users to predict how groups of species relate to specific ecosystem processes (Mason and Mouillot 2013). Given that metrics such as species richness treat all species as functionally similar, taxonomic and functional diversity indices may even produce contradictory results. For example, high species richness does not maintain a high level of ecosystem function unless it is accompanied by sufficient levels of functional variation among species (Cadotte 2011, Cadotte et al. 2011). Few, if any, ecosystems exhibit equivalent functional diversity and species diversity; functional redundancy is present at least at a small level and can only be detected using a functional diversity approach (Rosenfeld 2013). Thus, functional diversity is a far superior tool for monitoring ecosystems and for setting conservation goals.

3.1.2 How is functional diversity calculated?

Functional diversity encompasses a number of very informative indices that describe what functional groupings exist and how species are distributed amongst them. Commonly employed indices, including functional richness and evenness of Villéger et al. (2008), functional dispersion of Laliberté & Legendre (2010), and Rao's Quadratic Entropy (Rao's Q) of Botta-Dukat (2005), rely on the combination of biological trait information and community composition data (species and their abundances found in a specified habitat) in multidimensional space. This space is constructed by creating an axis for each functional trait used to partition a community. Subsequently, each species is orientated in this space based how they correspond to each trait, represented by axes. The multidimensional area encompassed by a community is referred to as functional trait space. The above listed indices describe various attributes of functional trait space and how abundance is distributed amongst species. The quality of trait information and relevance of traits to the studied ecosystem are critical to accomplish proper separation of species into functional groupings (Petchey and Gaston 2006, Cadotte et al. 2011). Further explanation of Rao's Q and functional evenness calculations are provided in the appendix of this document.

3.1.3 Functional diversity in Baynes Sound

As mentioned in chapter 2, intertidal shellfish aquaculture increases the structural complexity of beaches in Baynes Sound. While increases in complexity are often associated with biotic responses such as changes in abundance and biodiversity indices, these measures tell us little about the functional composition of the community. Contrary to many other reports investigating fish responses to increases in complexity, I found little evidence that shellfish aquaculture was a driver of taxonomic indicators such as abundance, species richness, diversity, or evenness. However, this does not rule out community functional variation between aquaculture and non-aquaculture areas. First and foremost, complexity is a major driver of predator-prey dynamics and diversity. Low levels of complexity are usually associated with less speciose and functionally similar communities that offer little refuge for prey species. In contrast, high levels of complexity reduce the capacity of predators to regulate prey communities by limiting feeding efficiency, potentially inhibiting the functional diversification of predatory species (Crowder and Cooper 1982, Ryer 1988, Beukers and Jones 2009). Therefore, both low and high complexity extremes likely only facilitate the success of few groups of functionally similar species. Stable trophic relationships conducive to the functional proliferation of both predator and prey species are more likely to be found in areas of intermediate complexity that offer refuge for prey, but not to the extent that the complexity impedes predation (Crowder and Cooper 1982, Ryer 1988). Increases in structural complexity are associated with both increases in available niche space (Macarthur and Macarthur 1961) and greater habitable surface area (Heck and Wetstone 1977).

Besides aquaculture beaches, other benthic nearshore habitats available to fish in Baynes Sound include non-aquaculture beaches and eelgrass beds. As demonstrated in chapter 2, complexity at aquaculture beaches is greater than those without aquaculture, but is certainly less than in eelgrass beds, whose dense foliage presents a highly complex habitat. I suggest that intertidal shellfish culture represents a source of intermediate habitat complexity (relative to other nearshore habitats available to fish) that supports the diversification of both predator and prey assemblages. Furthermore, as demonstrated in chapter 2, aquaculture beaches are mosaic environments and usually displayed greater variation in complexity between component habitat types than those observed on non-aquaculture beaches. In Baynes Sound, oyster and clam culture occur on shared beaches and are interspersed with areas of cobble, gravel, sand, mud, fences, and shell. Each of these 'micro-habitats' should increase the appeal of these locations to fish of various life history types. Based on this, my hypotheses are as follows: 1) Functional diversity (as defined by the index Rao's Q) will be higher at aquaculture sites due to their mosaic of structural features and the overall intermediate levels of structural complexity associated with those locations. Furthermore, low-complexity habitats characteristically offer fewer niches and foraging opportunities, limiting the functional groups that can inhabit such habitats. 2) Functional evenness (as defined by Villéger et al. (2008)) will be greater at aquaculture sites because intermediate levels of habitat complexity contribute to stable communities that encourage success of multiple functional groups rather than the dominance of few.

3.2 Methods

For information concerning the collection of fish for this study, see sections 2.3.1 and 2.3.2 in the previous chapter.

3.2.1 Trait selection and diet analyses

Functional diversity indices were calculated using the FD package for the data analysis software R (Laliberté and Legendre 2010, Laliberté and Shipley 2011, R Core Team 2015). The package requires the combination of a community dataset (at least presence/absence data, but abundances are required for the calculation of some indices) with a biological trait matrix. Traits chosen for this study system included average body length, body form, mobility, intertidal residence time, preferred habitat complexity, and trophic group (Table 4). These traits were specifically chosen for fish that live in intertidal environments and are effective descriptors of the functional role of species. Trait information was a combination of observed and literature data. British Columbia intertidal fishes are poorly studied overall, so only well-supported literature information was incorporated to maintain the integrity of analysis. Still intraspecific variability is possible, so literature accounts may not be entirely reflective of the Baynes Sound community. Nevertheless, most functional diversity studies rely heavily on literature information.

Diet information is an important part of functional diversity analyses. However, most species encountered during this investigation are poorly studied and detailed diet information is lacking (likely because these species are not economically valued). Therefore, a small-scale study was undertaken to gather this information. During fish community sampling in July and August 2014, small subsets of fish were euthanized with an MS-222 solution. Fish from most species encountered were taken (collection permit restrictions limited my ability to lethally sample all species). Within a maximum of six hours of capture, the entire gut length was excised and preserved in 10% buffered formalin. Gut contents were examined using an Olympus SZX16 stereo microscope and generally identified to the order level whenever possible. These findings were supplemented with diet information from scientific literature. Sample sizes analyzed were variable (from 1 – 56 individuals per species) and literature information was often sparse and varied widely. Variability between my findings and literature reports (and even within literature reports) is understandable given that my sampling period was limited to two months and that fish diet likely varies by season. Diet information was incorporated into functional diversity trait information as trophic group (e.g. herbivore, invertivore, piscivore). If more than one taxon was identified as a major food source, multiple groups were incorporated in hyphenated form (e.g. invertivore-piscivore). Higher resolution diet data may have been useful for functional diversity analyses and could have been incorporated as a more informative trait (e.g. percent reliance of a species on identified prey groups), but many species captured are reported as generalists. It is likely that they would consume almost any organism within their gape limit that they encountered and were able to capture.

Table 4. Details of biological traits used to characterize fish species for a functional diversity analysis.

Trait	Justification	Data Type	Explanation
Average body length	Energy of individuals & trophic influence	Interval	Average body length observed during field collection
Body Form	Hydrodynamic ability & water column position	Categorical	Filiform, Globiform, Taeniform, Fusiform, Depressed, Compressed, Elongated
Mobility	Range & Site Fidelity	Ordinal	1 = Low mobility; incapable of rapid swimming 2 = Frequently sedentary but capable of short bursts of speed 3 = Generally sedentary but capable of strong, sustained swimming 4 = Constantly moving, pelagic species
Intertidal residence time	Overlap time with aquaculture & availability to terrestrial predators	Ordinal	0 = Only observed intertidally during high tide events 1 = Occasionally observed intertidally during low tide events 2 = Frequent or permanent intertidal resident during low tide events

Preferred habitat complexity	Attractiveness of complex habitat features	Ordinal	0 = Virtually no complexity 1 = Low complexity 2 = Medium complexity 3 = High complexity
Trophic group	Preferred forage	Categorical	Primary trophic grouping. Two groups were included if 2 major food types were identified (e.g. invertivore-piscivore)

3.2.2 Rao's Quadratic Entropy and Functional Evenness

Functional diversity encompasses numerous indices that describe various aspects of functional trait space. Functional trait space is the area in which species are grouped according to their functional traits. It is most often multidimensional (because usually more than one trait is required to effectively describe species), with each trait representing a different dimension. Two of these indices, Rao's Quadratic Entropy (Rao's Q) (Rao 1982, Botta-Dukat 2005) and evenness (Villéger et al. 2008) were chosen to characterize Baynes Sound fish communities. Rao's Q represents the sum of the products of pairwise distances between species and their relative abundances. Rao's Q corrects for shortfalls of functional richness (the volume of functional trait space occupied by a group of species) as described by Villéger et al. (2008). Most notably, it can take into account abundances where functional richness cannot, thereby preventing overestimation of the influence of uncommon species. Functional evenness is a measure of how evenly distributed abundance is amongst points in multidimensional space and also takes into account relative abundances of species. A Cailliez correction was applied to both Rao's Q and functional evenness calculations to correct for negative eigenvalues as they correspond to axes that cannot be represented in Euclidean space (Cailliez 1983). The indices were compared among aquaculture and non-aquaculture sites using one-way ANOVA.

3.2.3 Functional groupings and redundancy analysis

Functional groups were determined using a kmeans cluster analysis with the Caliński - Harabasz (1974) criterion. The Caliński - Harabasz criterion aids in identifying the optimum number of clusters by formulating an F-statistic based on the ratio of sum of squares between and within clusters. The number of clusters with the highest F-statistic indicates the optimal number of clusters. These clusters represent functional groups. When more than one species is found per functional group, functional redundancy, which represents the degree to which species' functions overlap, is present. A quantitative method to define functional redundancy is to calculate the amount of species diversity that is not explained by functional diversity (de Bello et al. 2007). I used the Gini-Simpson Index and Rao's Q as the representative metrics for species diversity and functional diversity respectively. These indices were chosen based on their complementarity. Both range from 0 - 1 and Botta-Dukat (2005) identified the intrinsic relationship between the two. If each species is functionally different, then Rao's Q will equal the Gini-Simpson diversity and functional redundancy is zero. If each species performs the same function, then Rao's Q will be zero and functional redundancy will be equivalent to the Gini-Simpson diversity. Functional redundancy was compared between all sites using a one-way ANOVA. Functional redundancy patterns were also observed based on the plotted relationship between functional diversity and species diversity. The slope from linear regressions was used to describe the relationship between the two variables.

3.2.4 Biodiversity/Functional diversity relationships

Given the history of usage of biodiversity indices such as species richness, diversity (most commonly Shannon, Simpson, and Gini-Simpson indices), and evenness as proxies for functional diversity, the relationships between these variables and the functional diversity indices, Rao's Q and functional evenness, were explored. Scatterplots comparing these variables were created and linear regressions were performed to analyze the relationships.

3.3 Results

3.3.1 Rao's Quadratic Entropy and Functional Evenness

Rao's Q of fish communities did not vary based on the presence of active shellfish aquaculture (Fig. 11A; ANOVA p = 0.633, F = 0.685, df = 5). Similarly, functional evenness did not vary according to the presence of active shellfish aquaculture (Fig. 11B; ANOVA p = 0.628, F = 0.107, df = 5).

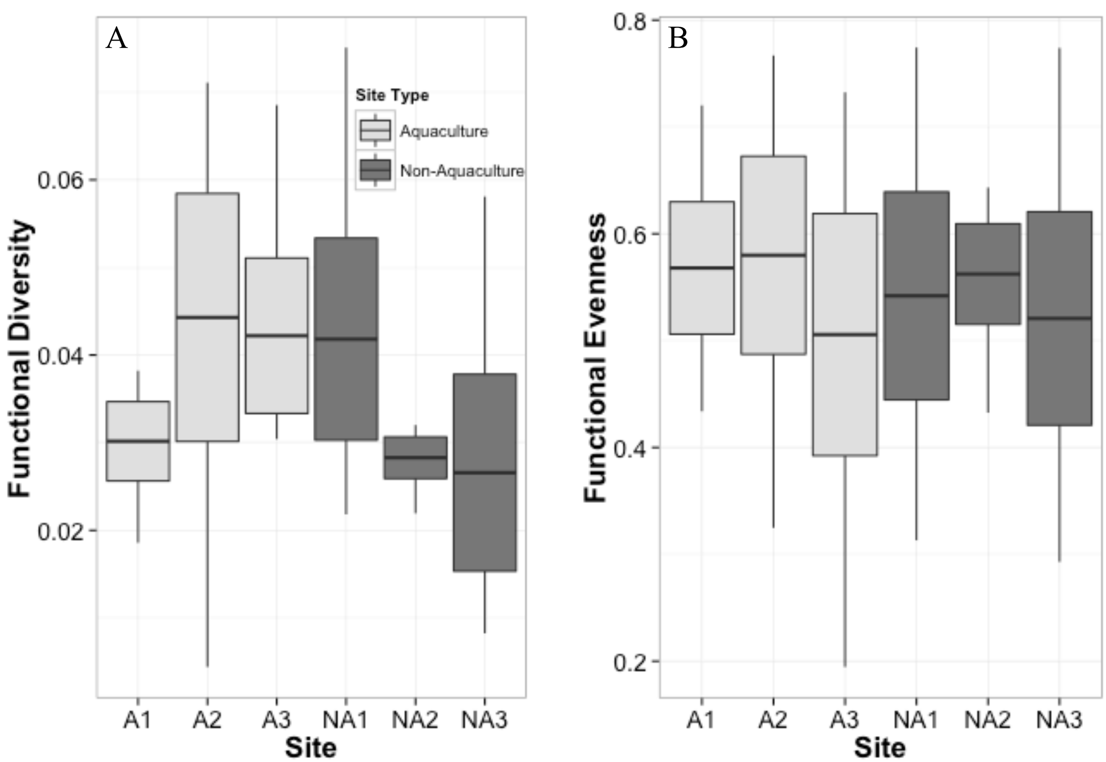

Figure 11. Mean functional diversity (A) as defined by Rao's Q and functional evenness (B) of fish communities captured at aquaculture and non-aquaculture sites. Boxes represent mean ± SEM and whiskers extend to data maximum and minimum. There were no differences between means (ANOVA p>0.05).

3.3.2 Clustering analysis and functional redundancy

Seven functional groups were identified via the kmeans clustering method with the Caliński-Harabasz criterion. The identified functional groups were arranged into a dendrogram (Fig. 12). Number of species per functional group varied between 1 and 6, and life histories ranged from large benthic generalists to pelagic invertivores. Some functional groups were not observed at all sampling locations, although this only occurred for groups with very low catch overall. Furthermore, no functional groups were specific to either aquaculture or non-aquaculture sites (Table 5).

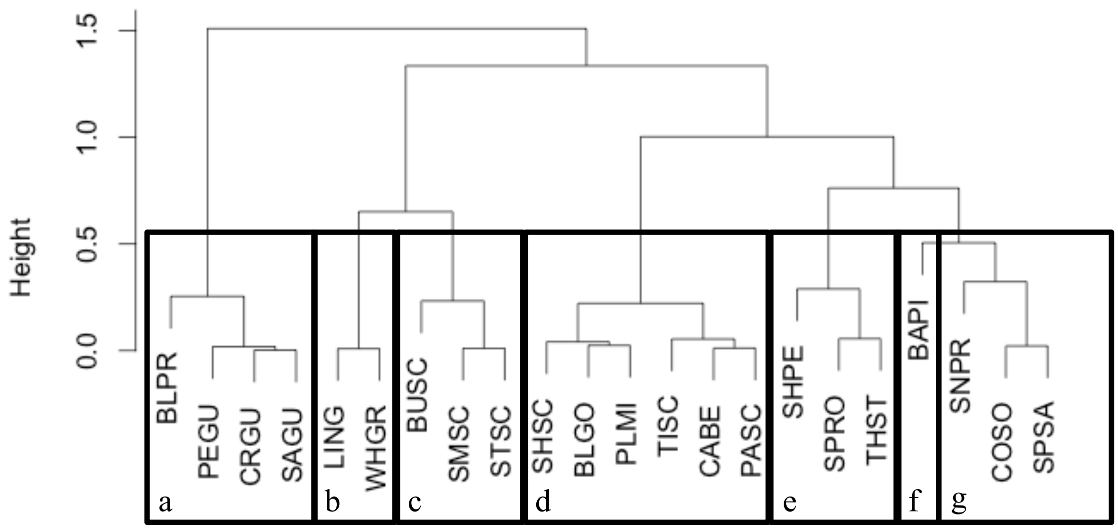

Figure 12. Dendrogram of species arranged by functional group. Functional groups were named as follows: a) eel-like intertidal invertivores, b) benthopelagic predators, c) large benthic generalists, d) small benthic invertivores, e) pelagic invertivores, f) cryptic high complexity invertivores, g) low complexity favouring benthic invertivores. Explanations of species codes can be found in Table 2 of section 2.4.1.

Table 5. Total catch number of fish falling within seven functional groups (A-G) by site and sampling replicate. Functional groups were named as follows: a) eel-like intertidal invertivores, b) benthopelagic predators, c) large benthic generalists, d) small benthic invertivores, e) pelagic invertivores, f) cryptic high complexity invertivores, g) low complexity favouring benthic invertivores.

Site & Replicate	A	B	C	D	E	F	G
NA1_1	0	0	4	1	3	3	1
NA1_2	0	0	5	4	0	1	0
NA1_3	0	0	0	14	5	4	0
NA1_4	0	0	0	34	4	4	0
A1_1	11	4	38	27	0	0	0
A1_2	1	1	9	20	3	2	0
A1_3	2	0	7	22	179	0	0
A1_4	12	0	0	77	10	4	0
NA2_1	4	1	44	6	0	0	1
NA2_2	0	0	0	14	5	2	0
NA2_3	3	0	0	77	24	5	0
NA2_4	1	0	1	35	7	6	2
A2_1	3	5	24	7	8	12	0
A2_2	4	0	36	16	10	3	0
A2_3	1	2	4	1222	41	2	1
A2_4	4	0	6	4	24	1	0
NA3_1	1	4	30	0	70	1	0
NA3_2	0	0	1	13	29	1	1
NA3_3	2	0	3	405	18	9	0
NA3_4	1	0	3	119	5	6	0
A3_1	6	1	5	4	12	14	0
A3_2	1	0	5	8	34	1	0
A3_3	1	0	0	40	27	6	0
A3_4	0	0	9	46	22	1	0

Multiple species within functional groups was recognized as a preliminary indicator of functional redundancy within the community. A full functional redundancy comparison using the method of de Bello et al. (2007) demonstrated that functional redundancy of fish communities was high (i.e. large portions of species diversity were unexplained by functional diversity), but did not vary among sites (Fig. 13; ANOVA p = 0.426, F = 1.038, df = 5). Mean functional redundancy among all groups, ignoring the influence of aquaculture, was 0.479, equating to approximately 93% of species diversity going unexplained by functional diversity. Further evidence for redundancy was observed based on the plotted relationship between functional diversity and species diversity. Incremental increases in species diversity were approximately 12x greater than those of functional diversity. (Fig. 14A; Linear regression – slope = 0.0835, $p<0.05$).

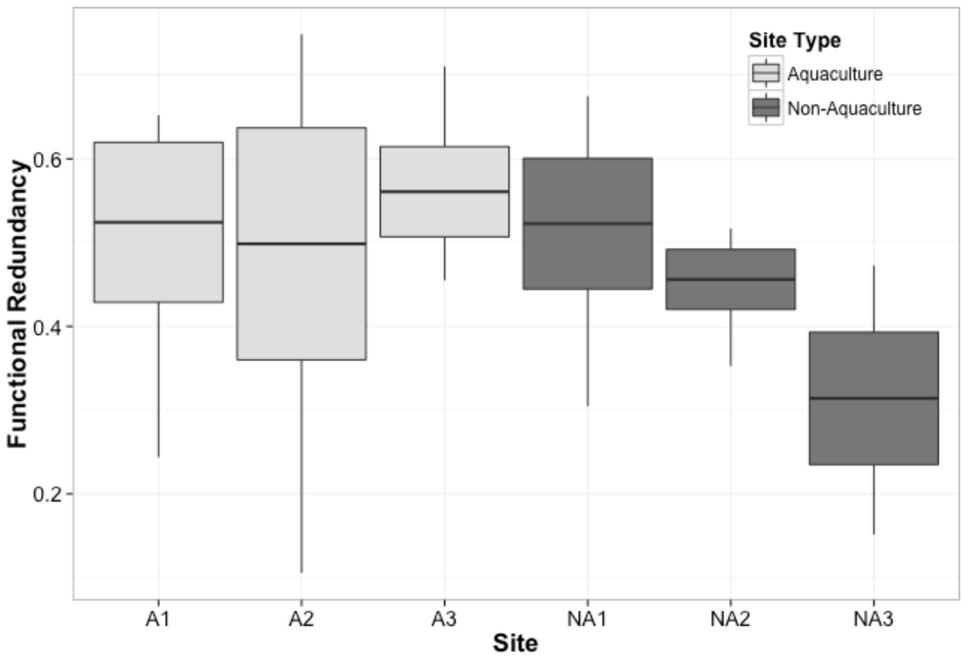

Figure 13. Mean functional redundancy of fish communities captured at aquaculture and non-aquaculture sites. Boxes represent mean ± SEM and whiskers extend to data maximum and minimum. There was no difference between means (ANOVA $p>0.05$).

3.3.3 Biodiversity/Functional diversity relationships

Strong relationships were observed between most functional diversity and biodiversity indices. Functional diversity (Rao's Q) was positively correlated with species diversity (Gini-Simpson) and species evenness; functional evenness was positively correlated with species diversity and species evenness (Fig. 14 A, B, C, D; linear regression $p < 0.05$). There was no relationship observed between functional diversity and species richness or functional evenness and species richness (Fig. 14 E, F; linear regression $p > 0.05$). It is also worth noting that while the relationship of functional diversity to both species diversity and evenness is significant and positive, the increases of functional diversity compared to those variables are small. A 0.1 increase in species diversity or evenness is only accompanied by a 0.0083 (Fig. 14A; linear regression – slope = 0.0835) and 0.0069 (Fig. 14B; linear regression – slope = 0.0689) increase in functional diversity respectively.

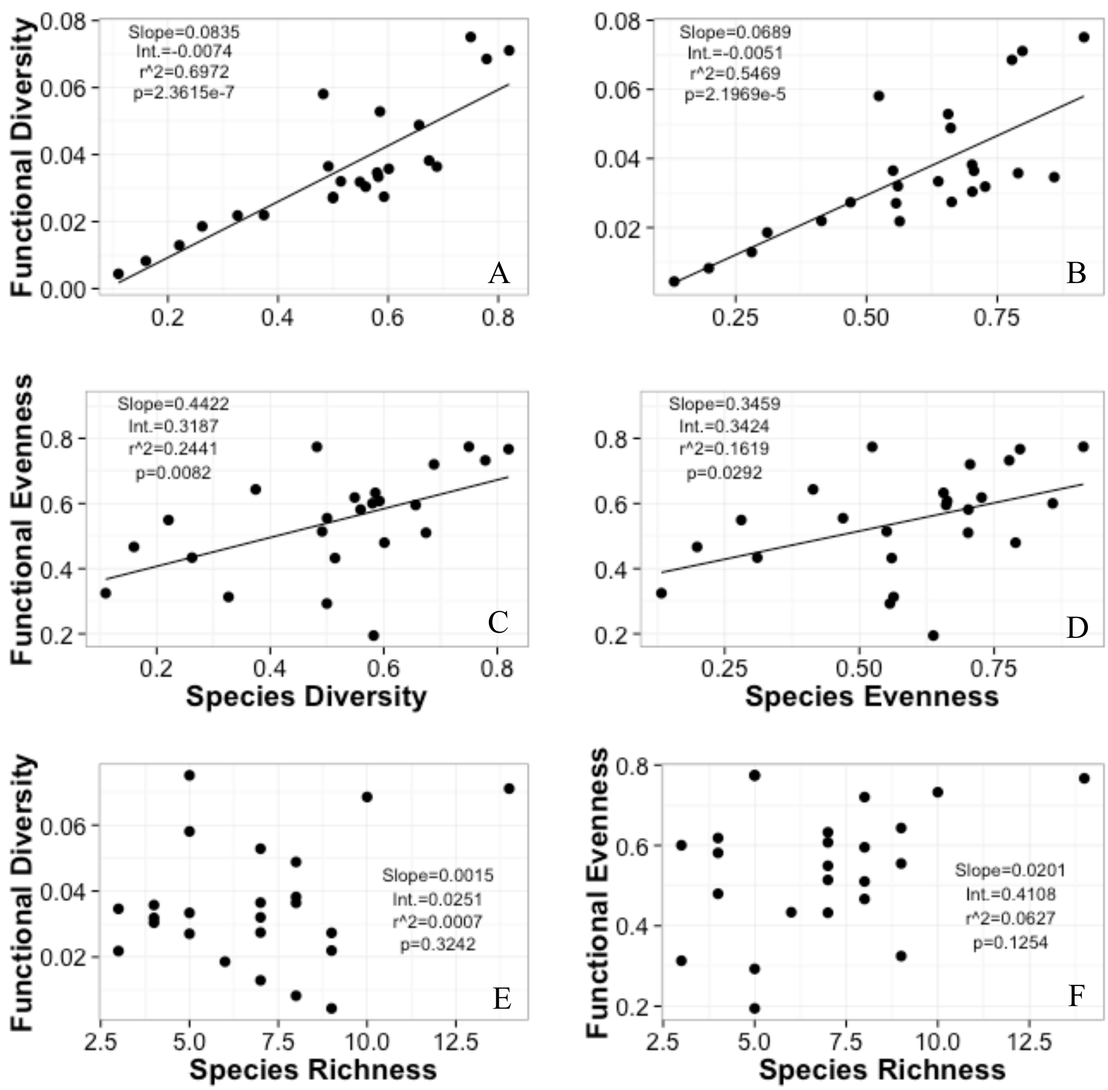

Figure 14. Scatterplots of various functional indices vs. biodiversity indices. Slope, intercept, r^2, and p-values present results from linear regressions. There were significant positive relationships (Linear regression $p<0.05$) between functional diversity (Rao's Q) and species diversity (Gini-Simpson Index) (A), functional diversity and species evenness (B), functional evenness and species diversity (C), and functional evenness and species evenness (D). There was no significant relationship (Linear regression $p>0.05$) between functional diversity and species richness (E) or functional evenness and species richness (F).

3.4 Discussion

In this study, I analyzed the interactions of the intertidal shellfish aquaculture industry with poorly-studied, yet ecologically-significant fish communities, using functional diversity as a tool to increase understanding of the functional organization of these assemblages. Given that aquaculture beaches were more complex than non-aquaculture beaches, I hypothesized that this increase in complexity would be an attractive feature to fish of diverse life history strategies that fulfill a variety of functional roles. Surprisingly, the addition of aquaculture infrastructure does not appear to be a strong driver of fish community functional diversity parameters. There was no observed effect on either Rao's Q, an abundance weighted measure of functional diversity, or functional evenness.

In the nearshore environment of Baynes Sound, there are three main habitat types available for fish: non-aquaculture beaches, aquaculture beaches, and eelgrass beds. A number of studies have compared the fish habitat value of shellfish culture areas to eelgrass beds and unstructured areas of shoreline (Pinnix et al. 2005, Hosack et al. 2006, Dumbauld et al. 2015). In general, they found these habitats to be of similar value to fish. However, they only used biodiversity indicators to support this finding and were therefore unable to determine how these habitats were organized functionally. I predicted that a driving factor of the functional organization of these communities was habitat complexity. Many non-aquaculture beaches are flat and lack high abundances of complexity generating epibionts such as macroalgae (though this is likely an artifact of there being less suitable substrate for epibiont settlement at these locations) and are proven areas of low complexity. On the opposite end of the spectrum, eelgrass beds are present along the majority of Baynes Sound coastlines and represent one of the most complex aquatic habitats available (BCMCA 2011). Therefore, of the three available habitats, shellfish aquaculture habitats likely represent areas of intermediate complexity in the context of Baynes Sound. Thus, I predicted greater functional diversity on aquaculture beaches for the following reasons: 1) Intermediate levels of complexity (high enough to offer suitable refuge for prey, but not so high that it would prevent most predation) support stable communities and predator-prey relationships, facilitating the proliferation of a variety of functional groups (Crowder and Cooper 1982, Ryer 1988), 2) Complex habitats increase available niche space (Macarthur and Macarthur 1961), and 3) Complex habitats afford greater habitable surface area (Heck and Wetstone 1977). Furthermore, I hypothesized that the homogenous habitat present at non-aquaculture sites would act as an environmental filter, excluding species with a known affinity for complex habitats and result in lower functional evenness through the dominance of few very specific functional groups. However, functional diversity and evenness, like biodiversity indices in chapter 2, did not vary according to the presence of shellfish aquaculture.

I captured 22 species of fish that were arranged into 7 main functional groups. The cryptic high-complexity invertivores group was the least speciose, represented only by the Bay Pipefish *(Syngnathus leptorhynchus*), while the small benthic invertivore group was populated by six species. While this seems to indicate that cryptic high-complexity invertivores group is functionally unique, this method of strict partitioning of species is losing favour to more recently developed techniques. In reality, functional groups and their component species exhibit varying degrees of overlap when analyzed using more advanced methods in multidimensional space (Pillar et al. 2013). Given that the number of species per functional group is no longer considered a good indicator of functional redundancy, I quantified it as the difference between species diversity and functional diversity (de Bello et al. 2007). This measure reports the amount of species diversity that functional diversity fails to explain. Highly redundant communities exhibit high disparities between the two variables while those with low redundancy display similar functional and species diversity. Functional redundancy did not vary based on the aquaculture status of beaches, but was quite high overall. Mean functional redundancy including both aquaculture and non-aquaculture groups was 0.479. Functional redundancy ranges on a scale of 0 to 1 where higher values equate to higher redundancy. Based on this, I determined that approximately 93% of species diversity went unexplained by functional diversity. It is apparent that despite the identification of seven distinct functional groups, overlap in the functional role of these groups does exist.

Functional redundancy is often linked to community resilience. In theory, losses or decreases of abundances of species from redundant ecosystems have less impact on overall ecosystem function compared to ecosystems with low redundancy. This theory is only valid if another functionally similar species increases its own abundance to fill the functional gap created (Guillemot et al. 2011, Cadotte 2011). Given the high degree of functional redundancy observed at all sampling locations, and therefore in the community as a whole, one might expect the above theory to hold true for Baynes Sound. The redundancy, and therefore resilience, of these fish communities may explain why no effects of habitat changes associated with shellfish aquaculture on functional diversity and evenness were observed. However, given the long history of shellfish aquaculture in Baynes Sound, it is possible that community homogenization has already occurred and only the most resilient functional groups remain and are present regardless of small-scale variation in shoreline use. Furthermore, even in a comparable pristine temperate system, functional diversity of nearshore fish communities is likely low, especially relative to tropical regions (Stuart-Smith et al. 2013). A study of temperate estuarine fish by Baptista et al. (2015) also reported low overall functional diversity (defined by Rao's Q) of approximately 0.1 over a 24 year period. Functional diversity estimates of this study were lower still, but likely because of a much shorter sampling period that was unable to incorporate all life histories that are only present seasonally.

Not all functional groups were present at all sampling sites. However, none were entirely absent from either all aquaculture or non-aquaculture sites. Furthermore, absences usually only occurred for functional groups that were very infrequently captured. One exception is the absence of eel-like invertivores [eg. Black Prickleback (*Xiphister atropurpureus*), Crescent Gunnel (*Pholis laeta*), Penpoint Gunnel (*Apodichthys flavidus*), and Saddleback Gunnel (*Pholis ornata*)] from sampling site NA1. 58 individuals of this functional group were captured from the other sites, and nearly half of these were captured at A1. Most of these pricklebacks and gunnels were juveniles and are known to favour high complexity environments and at times will reside almost entirely intertidally, hiding out among rocks and under vegetation (Hart 1973, Lamb and Edgell 2010). NA1 had the second lowest complexity of all non-aquaculture beaches and had an overall muddier substrate than all other sites with low abundances of intertidal vegetation. These features may explain this group's absence. High catch at A1 could be linked to proximity and high stocking density of the floating oyster aquaculture operation, located just offshore from my sampling site. In past experiments, I have observed these species residing in and around the suspended oyster cages. The abundance of both intertidal and floating aquaculture infrastructure may increase the appeal of A1 to these complexity-dependent invertivores. This absence was not reflected by any other metrics such as functional diversity or evenness.

Strong interactions were observed between some functional diversity indices and their biodiversity counterparts. Both functional diversity and functional evenness were positively correlated with both species diversity and species evenness. There has been much interest in the relationship between functional and biodiversity indices, as functional diversity metrics can be quite laborious to calculate and are conceptually complex. Biodiversity is viewed as a phenomenon that supports ecosystem function (Hooper et al. 2012) and its representative indices, most commonly species richness and diversity, have been shown to be good proxies for functional diversity in some environments (Petchey et al. 2004, Micheli and Halpern 2005, Petchey and Gaston 2006, Pomerleau et al. 2015). However, in Baynes Sound, species richness and functional diversity do not demonstrate a significant interaction, indicating functional redundancy. Species richness is not a suitable proxy for functional diversity in this system. Also, while I demonstrated a strong relationship between functional diversity and species diversity, it must be noted that the increase of functional diversity is approximately 12x slower than species diversity. Again, this is reflective of high redundancy in the community. Therefore, I urge caution when using biodiversity metrics as proxies for functional diversity. Unless the relationship between the two types of variables is well established in the environment and using the taxa of interest (i.e. unless the slope of the plotted relationship between the two variables has been verified), functional diversity must be strictly measured.

Shellfish aquaculture infrastructure offers ecologically valuable features to fish that favour structurally complex environments (Dealteris et al. 2004, Pinnix et al. 2005, Hosack et al. 2006, Powers et al. 2007, Erbland and Ozbay 2008, Marenghi et al. 2010, Dumbauld et al. 2015). Many captured species are known to inhabit complex habitats or at least frequent them for foraging. However, my diet analyses demonstrated that the most frequently consumed foods were crustacean invertebrates, which were present in stomachs of fish from all sampling sites. While formal analyses of prey communities at aquaculture and non-aquaculture sites should be conducted, fish stomach contents from this research provide preliminary evidence that the complexity generated at aquaculture beaches may not be a driving factor of invertebrate prey communities. Bendell-Young (2006) did observe differences in epifaunal and infaunal invertebrate communities between aquaculture and non-aquaculture sites in Baynes Sound, but they did not link these to diets of fish in those areas. Therefore, the lack of functional variability of fish communities may be an artifact of homogenous prey communities among sampling sites.

Many studies have linked increased human presence in an ecosystem with decreases in ecosystem function or functional diversity (Micheli and Halpern 2005, Millenium Ecosystem Assessment 2005a, Bulleri and Chapman 2010, Keck et al. 2014, Allan et al. 2015, Teresa et al. 2015). However, shellfish aquaculture follows the opposite trend of most human disturbances. It represents an addition of complexity whereas in most other systems, human activity is associated with a homogenization of habitat (Millenium Ecosystem Assessment 2005a). Despite this, the addition of complexity may not appear attractive to fish relative to unstructured areas of shoreline due to high levels of activity associated with shellfish farming. Practices such as substrate disturbance for harvesting and bed maintenance, substrate compaction by vehicle traffic, and increased boat traffic may all reduce the appeal of these complex habitats to fish of diverse life history strategies (Jamieson et al. 2001, Dumbauld et al. 2009).

Functional diversity is a rapidly developing tool for ecological research, and most ecosystems lack sufficient research utilizing this very powerful technique. This study likely represents the first attempt at a fine-scale functional diversity analysis in northeast Pacific waters. Stuart-Smith et al. (2013) performed a worldwide analysis of functional diversity in nearshore environments, but had a low resolution that made the drawing of conclusions within smaller-scale geographic regions impossible. Given that my analysis only incorporates data from a two-month period (published reports often include years of data), this report should be regarded as a pilot study for future functional diversity analyses in the region. To better assess impacts of shellfish aquaculture, functional diversity analyses should be carried out along a more pronounced gradient of industry influence (e.g. identify distinct high, medium, and low impact areas). This study took place in an area highly modified by the shellfish industry, and it is quite possible that some effects of the practice extended beyond the farms themselves. A longer sampling period would likely also facilitate the incorporation of new functional groups of fish that are only present in the region seasonally (most notably, both adult and juvenile salmon).

In summary, shellfish aquaculture is not a strong driver of functional diversity indices. However, I was able to determine that the nearshore fish communities in Baynes Sound exhibit a high degree of functional redundancy, and may be quite resilient to ecosystem disturbances. It is possible that even the complete loss of a species from this environment would have minimal effect on overall ecosystem function. However, this would only occur if a functionally similar species increased its abundance accordingly to fill in the functional gap. This should not downplay the significance of biodiversity loss. Even loss of species from highly redundant niches can come with repercussions as redundancy plays a strong role in structuring species assemblages and trophic interactions (Guillemot et al. 2011, Philpott et al. 2012, Reich et al. 2012). Furthermore, understanding redundancy in a community may present ethical dilemmas when creating conservation goals. While seeking to maintain ecological processes and requisite species, we may find ourselves overlooking other species in need of conservation action because they are ‘less valuable’ to overall ecosystem function. All threatened species in their native environment are considered worthy of conservation, but in highly impacted systems this may not be possible. Therefore, formulating intuitive conservation measures that benefit multiple species, not just those deemed functionally or commercially valuable, is the most ethical option. Additionally, such conservation strategies may increase redundancy of communities, thereby promoting stability of ecosystem processes and services (Philpott et al. 2012, Reich et al. 2012, Rosenfeld 2013).

Chapter 4 – The future of shellfish aquaculture and nearshore conservation

Given that the majority of human population is concentrated in coastal regions, nearshore ecosystems have been disproportionately impacted relative to other marine environments (McGranahan et al. 2007, Neumann et al. 2015). A variety of stressors, including shoreline armouring, poor land use, invasive species introductions, fisheries, and climate change have been cited as the most damaging practices impacting nearshore systems and are discussed in detail in chapter 1. Aquaculture is a rapidly developing industry that represents another potential source of disturbance in already threatened coastal waters (FAO 2014). In this study, I have presented Baynes Sound as a model system to study the impacts of shellfish aquaculture on nearshore systems, using intertidal fish communities as a biotic indicator. The sound plays a dual role by providing some of the most critical wildlife habitat in the northeast Pacific region while supporting an aquaculture industry that accounts for nearly 50% of shellfish production in British Columbia (Paynter 2002).

Shellfish aquaculture, while a much less common practice than finfish culture, is practiced at locally high intensities along the northeast Pacific coast (Dumbauld et al. 2009, Nguyen and Williams 2013, FAO 2014). Most research on the industry focuses on suspended raft culture of bivalves, which does provide habitat for a variety of organisms (López-Jamar et al. 1984, Gutiérrez et al. 2003, D'Amours et al. 2008, Dumbauld et al. 2009), but can also alter both geochemical and geophysical properties of nearby areas of the benthos (Dahlbäck and Gunnarsson 1981, Chamberlain et al. 2001, Christensen et al. 2003, Wilson and Vopel 2015). This study addresses intertidal shellfish culture, which is less-comprehensively studied, but still represents a notable alteration of the environment.

In Baynes Sound, this practice has been linked to changes in sediment characteristics and accompanying homogenization of infaunal and epifaunal communities relative to unfarmed beaches (Bendell-Young 2006, Munroe and McKinley 2007). However, based on evidence from this study, disparities in benthic composition do not seem to be replicating themselves at higher trophic levels. I found that fish communities were essentially equivalent at both aquaculture and non-aquaculture beaches using both traditional biodiversity and more informative functional diversity approaches. This is surprising, not only because fish are not responding to the increase in complexity associated with aquaculture sites, but also because potential homogenization of one of their primary prey sources (benthic invertebrates) does not seem to negatively affect them. Many of the fish encountered in this study were invertivores with low diet specificity. This diet plasticity may render them quite adaptable in disturbed environments. Since intertidal fish communities seem to respond neither positively nor negatively to the presence of shellfish aquaculture in an industry dominated environment, changes to communities even higher up the food chain that depend on these fish for forage (large predatory fish, birds, marine mammals, and aquatic-foraging terrestrial predators) are unlikely.

Given the long history of industrial usage in Baynes Sound, it is possible that the present day status of fish communities may be an artifact of past alterations to their composition and ecology. Levitz & Willott (1997) provide a detailed summary of the history of the Deep Bay region of Baynes Sound (largely the focus of this study). Before the boom of shellfish aquaculture in the mid-1900s, Deep Bay was subject to heavy industrial use. Log booms were prevalent, railways to deliver timber ran all the way to the beach, and adjacent lands were heavily logged and stripped of vital vegetation buffers. Additionally, the area supported large harvests of wild clam and fish stocks; a number of canneries and fish processing facilities dotted the shoreline. Presently, Deep Bay and outlying regions are likely experiencing fewer impacts from industrial use than they were throughout the 1900s. However, in addition to present day industrial use, the area is likely still under the influence of historical activities such as timber production. Benthic environments may be slow to recover from the influences of log booms, which litter the seafloor with stray logs and bark, causing anoxia and decreasing aquatic vegetation cover (Picard et al. 2003). While fish community disparities between my sites were either non-existent or minimal, we did observe overall lower species richness at NA1. This site was closest to Deep Bay, which was likely the hub of industrial activities throughout the 1900s. This presents potential evidence for lingering effects of historical development.

Compared to other disturbances, impacts of shellfish aquaculture appear to be localized and of less concern than the other primary drivers of nearshore ecosystem change. However, shellfish aquaculture is practiced on a very small scale globally relative to other coastal stressors (FAO 2014). There is still a substantial amount of research to be done before a conclusive decision on the sustainability of shellfish aquaculture can be made. While the intertidal fish communities used in this study are acceptable proxies for overall ecosystem health, there are many other aspects of the interaction between the industry and the environment worthy of scientific investigation. Previous studies in other parts of the world have linked suspended shellfish culture to seston depletion in the water column, potentially reducing the prey base of native planktivores (Ogilvie et al. 2000, Duarte et al. 2008, Grant et al. 2008). I suggest that similar studies should be conducted in Baynes Sound, as plankton communities represent the base of the food chain and are highly influential to the energy dynamics of all consumer trophic levels (Ware and Thomson 2005). Another notable concern worthy of investigation is impacts to spawning habitat used by forage fishes. The Strait of Georgia, which includes Baynes Sound, provides some of the most valuable intertidal and nearshore spawning habitat for ecologically-valuable forage fishes such as Pacific Herring (*Clupea pallasii*), Pacific Sand Lance (*Ammodytes hexapterus*), and Surf Smelt (*Hypomesus pretiosus*) in the northeast Pacific (Martin 2015). As mentioned above, shellfish culture in all forms alters substrate characteristics. The forage fishes mentioned previously, particularly the Pacific Sand Lance and Surf Smelt, only spawn in areas with very particular grain size and are therefore very sensitive to changes in benthic composition (Martin 2015). Finally, shellfish aquaculture introduces large amounts of plastic to the marine environment, primarily in the form of predator exclusion nets, PVC piping, ropes, floats, and cages. These materials are frequent sources of marine debris on Baynes Sound beaches. Plastics in the marine environment present a variety of challenges to marine organisms ranging from entanglement to ingestion of macro and microplastic particles (Derraik 2002, Gregory 2009, Barnes et al. 2009, Andrady 2011). Research that investigates the source, extent, impacts, and potential mitigation strategies of plastic pollution in Baynes Sound should be undertaken. I'm hopeful that this research will promote sustainable aquaculture practices as the industry continues to develop along British Columbia coastlines.

Given the extent of the current biodiversity crisis, it is critical that monitoring and management strategies take into account the most current and informative metrics. Even though no functional differences among habitat types were observed in this study, we still gained valuable insight into the functional organization of Baynes Sound fish communities and discovered the high degree of functional redundancy among species. While conceptually complex and at times difficult to implement, I believe functional diversity strategies should be more frequently implemented in biodiversity and conservation research. Once the laborious process of building a framework of functional characteristics of species is created for the area of interest, it is easy to monitor functional changes within communities over time. Furthermore, the knowledge attained is far more informative and more useful for formulating conservation strategies that benefit the most number of species that fulfill the widest variety of functional roles. This form of integrated management that simultaneously addresses multiple species and facets of the ecosystem is our best hope to preserve biodiversity and maintain ecosystem goods and services for future generations.

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Appendix

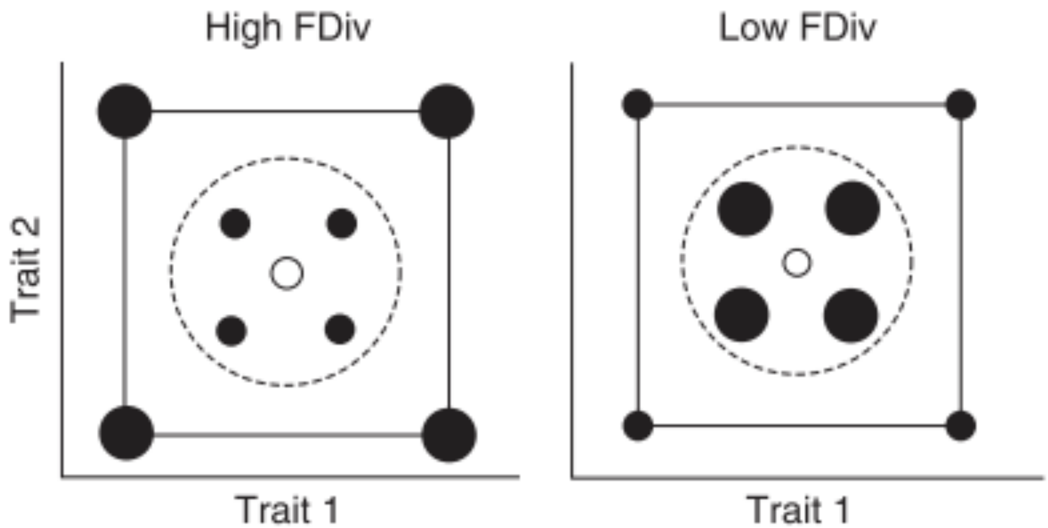

Figure 15. Illustration describing how functional diversity varies according to species abundance distribution in multidimensional trait space (reduced to only two dimensions for ease of visualization). Black dots represent species and their size is proportional to their abundance. The small, central, open circle represents the unweighted centroid point of all species. The dashed circle represents the unweighted mean distance of species from the centroid. The solid square represents the convex hull containing all species. Functional diversity is lower in the right figure because the abundance is biased close to the centroid point. Figure was borrowed from Mason and Mouillot (2013).

Calculation explanation for Rao's Quadratic Entropy (Rao's Q) and Functional evenness:

Rao's Q (Botta-Dukat 2005) -
Rao's Q (FD_Q) is determined by

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_i$$

where S is the number of species in the community, d_{ij} refers to the Euclidean distance in functional trait space between the two species (i and j), and p_i represents the relative abundances of the species.

Functional evenness (Villéger et al. 2008) -
Calculation of functional evenness begins by constructing a minimum spanning tree between all species in functional trait space. From this, weighted evenness (EW) of individual branches of the tree (l) (sometimes referred to edges) is determined by

$$\mathrm{EW}_l = \frac{\mathrm{dist}(i,j)}{w_i + w_j}$$

where dist(i,j) refers to the Euclidean distance between the two species (i and j) the branch connects and w_i and w_j refer to the relative abundances of the species. From this, partial weighted evenness (PEW) of branch l is determined by

$$\mathrm{PEW}_l = \frac{\mathrm{EW}_l}{\sum_{l=1}^{S-1} \mathrm{EW}_l}$$

and represents the proportion of total tree evenness that branch l represents. S is equivalent to the number of species in the community. From this, total functional evenness (FEve) of the community is determined by

$$\mathrm{FEve} = \frac{\sum_{l=1}^{S-1} \min\left(\mathrm{PEW}_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}.$$

Table 6. Biological trait matrix used for functional diversity calculations. Mobility was inferred from body form, caudal fin shape, and habitat preferences, field observations of behaviour, and information from Lamb and Edgell (2010): 1 = Low mobility, 2 = Generally sedentary but capable of bursts of speed, 3 = Generally sedentary but capable of strong sustained swimming, 4 = Constantly moving, pelagic species. Intertidal residence time: 0 = Only found intertidally during high tide events, 1 = Occasionally found intertidally during low tide events, 2 = Frequent or permanent intertidal resident during low tide events. Preferred habitat complexity: 0 = Virtually no complexity, 2 = Low complexity, 3 = Medium Complexity, 4 = High Complexity. Trophic groupings are based on a combination of field data and literature data, and dashed names indicate that more than one prey group was a common feature of a species' diet. Ordering of diet terms relates to the prevalence of that type of feeding.

Species	Body Form	Mobility	Intertidal residence time	Average length (cm)	Preferred habitat complexity	Trophic group
Bay Pipefish	Filiform	1	0[1,2,3]	13.1	3[1,2,3]	Invertivore[1]
Blackeye Goby	Globiform	2	0[2,4]	7.7	1[2,4]	Invertivore[8]
Black Prickleback	Taeniform	2	2[1,2,5]	6.6	2[1,2,5]	Herbivore-Invertivore[1,2]
Buffalo Sculpin	Globiform	2	1[2,5]	10.5	2[2,5]	Invertivore-Herbivore[1,9]
Cabezon	Globiform	2	1[2,6]	4.3	2[2,6]	Invertivore[1,10]
C-O Sole	Depressed	2	0[2,5]	14.6	1[2,5]	Invertivore[11]
Crescent Gunnel	Taeniform	2	2[1,2,5]	5.9	2[1,2,5]	Invertivore[12]
Lingcod	Elongated	3	0[1,2,5]	12.3	2[1,2,5]	Invertivore-Piscivore[1]
Padded Sculpin	Globiform	2	1[1,7]	5.8	2[1,7]	Invertivore[6]
Penpoint Gunnel	Taeniform	2	2[2,5]	7.9	2[2,5]	Invertivore[1,10]
Plainfin Midshipman	Globiform	2	0[1,2]	4.5	1[1,2]	Invertivore[1,10]
Saddleback Gunnel	Taeniform	2	2[2,5]	6.2	2[2,5]	Invertivore[5]
Shiner Perch	Compressed	4	0[2,5]	6.9	2[2,5]	Invertivore[13]
Sharpnose Sculpin	Globiform	2	0[2,5,18]	2.3	2[2,5,18]	Invertivore[1]
Smoothhead Sculpin	Globiform	2	1[2,7]	11.6	2[2,7]	Invertivore-Piscivore[14]
Snake Prickleback	Taeniform	2	0[2]	23.7	1[2]	Invertivore[1]
Splitnose Rockfish	Fusiform	3	0[2,5,15]	2.2	2[2,5,15]	Invertivore[15]
Speckled Sanddab	Depressed	2	0[1,15]	12.8	0[1,5]	Invertivore[11,16]
Pacific Staghorn Sculpin	Globiform	2	1[1,2,5]	11.2	1[1,2,5]	Invertivore-Piscivore[13]
Threespine Stickleback	Fusiform	4	0[1,2]	2.1	2[1,2]	Invertivore[1]
Tidepool Sculpin	Globiform	2	2[1,2]	3.0	2[1,2]	Invertivore[17]
Whitespotted Greenling	Elongated	3	0[1,2,5]	11.1	2[1,2,5]	Invertivore-Piscivore[1]

[1] Hart (1973) [2] Lamb and Edgell (2010) [3]Dawson (1985) [4] Moser (1996) [5]Eschmeyer and Herald (1983) [6]Clemens and Wilby (1961) [7]Jensen (2015) [8]Fitch and Lavenberg (1975) [9]Johnson (1968) [10]Yoshiyama and Darling (1982) [11]Hobson and Chess (1986) [12]Armstrong (1996) [13]Morrow (1980) [14]Boyle and Horn (2006) [15]Gomez-Buckley (2001) [16]Cross et al. (1985) [17]Nakamura (1971) [18]Martin (2015)