Seagrass meadows as seascape nurseries for rockfish (*Sebastes* spp.)

by

Angeleen Olson
Bachelor of Science (Honours), Simon Fraser University, 2013

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Dr. Francis Juanes, Department of Biology
Supervisor

Dr. Margot Hessing-Lewis, Hakai Institute
Co-Supervisor

Dr. Rana El-Sabaawi, Department of Biology
Departmental Member

Abstract

Nearshore marine habitats provide critical nursery grounds for juvenile fishes, but their functional role requires the consideration of the impacts of spatial connectivity. This thesis examines nursery function in seagrass habitats through a marine landscape ("seascape") lens, focusing on the spatial interactions between habitats, and their effects on population and trophic dynamics associated with nursery function to rockfish (*Sebastes* spp.). In the temperate Pacific Ocean, rockfish depend on nearshore habitats after an open-ocean, pelagic larval period. I investigate the role of two important spatial attributes, habitat adjacency and complexity, on rockfish recruitment to seagrass meadows, and the provision of subsidies to rockfish food webs. To test for these effects, underwater visual surveys and collections of young-of-the-year (YOY) Copper Rockfish recruitment (summer 2015) were compared across adjacent seagrass, kelp forest, and sand habitats within a nearshore seascape on the Central Coast of British Columbia. Recruitment was positively influenced by the structural complexity of seagrass and adjacency to kelp forest sites, however a negative interaction between seagrass complexity and kelp forest adjacency suggests that predation modifies Copper Rockfish recruitment densities. In addition, using $\delta^{13}C$ and $\delta^{15}N$ isotopes to determine the basal contributions to seagrass food webs, kelp-derived nutrients were on average 47% ± 0.4 of YOY Copper Rockfish diets, which was 3x and 67x greater than the contribution of autochthonous seagrass production (seagrass epiphyte and seagrass blades, respectively). YOY Copper Rockfish diets in seagrass adjacent to sand habitats had the greatest amounts of kelp-derived nutrients and harpacticoid copepods, and concurrently had lower body condition compared to rockfish in the seagrass kelp edges and interior, feeding predominantly on seagrass epiphytes and calanoid copepods. This thesis provides further evidence that temperate seagrasses are nurseries for rockfish and that spatial elements of seascapes, including connectivity via habitat adjacency and variability in habitat structure, alter the recruitment and diets of rockfish in seagrass habitats. These seascape nursery effects are important considerations for marine planning, especially given the global decline of nearshore habitats.

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Chapter 1: Introduction

1.1 The coastal seascape

Nearshore habitats are among the most threatened ecosystems in the world (Halpern et al., 2008), despite playing a fundamental role in structuring ecological communities and the economy of coastal populations (Barbier et al., 2011). Today, no marine ecosystems remain untouched by human activity (Jackson, 2001), leaving them vulnerable to habitat loss. Ecosystem habitat loss, along with its associated biodiversity and ecosystem functions, is increasing globally from destructive anthropogenic activities (Balmford & Bond, 2005). Direct impacts like habitat degradation, overfishing and pollution (Blaber et al., 2000; Shahidul Islam & Tanaka, 2004), and indirect processes such as climate change (Hoegh-Guldberg & Bruno 2010) are dramatically altering coastal areas. Approximately 29% of seagrass meadows, 30% of coral reefs, 35% of mangroves, and 50% of salt marshes have disappeared or have dramatically degraded worldwide (Waycott et al., 2009, Lotze et al., 2006). These rates of decline are increasing, as seen in a 7-fold increase in seagrass meadow loss since the 1940's (Waycott et al., 2009). Many of these nearshore habitats play an important role in supporting juvenile stages of the ocean's species.

Nearshore ecosystems are highly connected, with these linkages having profound impacts on ecosystem function and productivity (Polis, Anderson, & Holt, 1997). Nearshore marine habitats are tightly connected with other habitats in a larger ecosystem mosaic, herein referred to as a "seascape" (Appendix A). Seascapes are linked passively by spatial arrangement, and dynamically, through biological and physical movements (Loreau 2003). The spatial arrangement, and connectivity of habitats determined by distance, within seascapes is thought to have important consequences to marine populations by: (1) adding habitat heterogeneity to areas, which in turn influences community assemblages and their persistence (Baguette, Blanchet, Legrand, Stevens, & Turlure, 2013; Kool, Moilanen, & Treml, 2013; Olds, Connolly, Pitt, & Maxwell, 2012), (2) facilitating ontogenetic movements from juvenile to adult habitats (Able, 2005; Gillanders, Able, Brown, Eggleston, & Sheridan, 2003), and (3) altering resources available to food webs of adjacent habitats (Davis, Pitt, Fry, Olds, & Connolly, 2014;

Igulu, Nagelkerken, van der Velde, & Mgaya, 2013). Because nearshore habitats are commonly used by juvenile fishes, seascape connectivity may augment the nursery value of these habitats to fisheries by increasing optimal areas of foraging and refugia (Sheaves, Baker, Nagelkerken, & Connolly, 2014). While the concept of connectivity remains a classic theory in ecology, its application to the nursery functions of coastal habitats has only recently been explored (Nagelkerken, Sheaves, Baker, & Connolly, 2015).

1.2 Connectivity of nursery habitats

Many coastal nursery habitats are situated within a complex seascape, bordering terrestrial ecosystems, adult habitats, and other nursery habitats, among others. Nursery areas are important for promoting a composite of higher juvenile growth, survival rates, densities, and/or movement to adult populations (Beck, Heck, Able, & Childers, 2001). Though it is well established that the structural complexity of nursery habitats is a fundamental criteria for nursery function by providing substrate for recruitment, shelter from predators, and food sources at sensitive juvenile stages (Gratwicke & Speight, 2005; Heck, Hays, & Orth, 2003; Nagelkerken, 2009), these processes can vary greatly across a habitat based on the broader seascape and result in seascape-level biotic responses (Levin 1997, Bostrom 2006). To fully capture both the internal and, importantly, the external factors that regulate nursery functions, a seascape level approach has been identified to study nearshore nurseries at a larger scale (Nagelkerken et al., 2015; Sheaves et al., 2014).

The various types of connectivity occurring in nearshore seascapes can produce spatially variable processes occurring within nursery habitats. The spatial connectivity of habitats, such as habitat adjacency or edge effects, can alter fish densities and diets between edges and interiors (Macreadie, Hindell, Jenkins, Connolly, & Keough, 2009; Nagelkerken et al., 2001; Smith, Hindell, Jenkins, Connolly, & Keough, 2011). The flow of carbon and nitrogen through detrital pathways can link nearshore habitats within a seascape through trophic dynamics (Hyndes et al., 2014; Igulu et al., 2013; Kelly, Krumhansl, & Scheibling, 2012). Further, the movement of fish results in biological connectivity when they use multiple habitats during juvenile stages (Kamimura & Shoji, 2013). Although evidence for a “seascape nursery” paradigm is growing via the illumination of these linkages among nursery habitats, the clear majority of studies remain among tropical systems (e.g.: seagrass, mangrove, and coral reef connections) and little focus has been given to temperate nurseries, including seagrass habitats.

1.3 The importance of seagrass meadows

Seagrasses are a marine angiosperm that grow in shallow coastal waters, with various species occurring globally (Hemminga, & Duarte 2000, Larkum 2006). Seagrass ecosystems are highly productive and resource rich (Mateo et al. 2006, Orth et al., 2006) resulting in one of the most productive autotrophic communities in the world (Duarte & Chiscano, 2000). Although continuously debated, current consensus suggests that live seagrass itself only plays a minor role as a food source within seagrass meadows because much of its in-situ productivity remains within the sediment (Hemminga and Duarte 2008, Moncreiff & Sullivan, 2001, Jaschinski et al., 2008, Doropoulos et al. 2009, Lebreton et al. 2011). While seagrass can provide large amounts of subsidies to near and distant habitats through animals, plant detritus, and detached live plants (Heck et al., 2008), the main drivers of secondary production within a meadow are epiphytic algae, periphyton, and detritus produced by mesograzers in which further support consumers (Orth & van Montfrans, 1984; Jernakoff et al., 1996). This production of prey is a contributing factor to the nursery function of seagrasses (Nagelkerken, 2009).

A diverse range of marine fishes use seagrass beds as nursery habitats during their juvenile stages (Heck & Thoman, 1984, Heck et al., 2003). Greater juvenile fish densities have been demonstrated in seagrass beds compared to unvegetated habitats (Orth & van Montfrans 1987, Heck et al., 1997) and relative to adult habitats like coral reefs (Nagelkerken et al., 2000, de la Morinière et al., 2002). As the evidence for a nursery effect of seagrass on juvenile fish is mounting, not only are most studies focusing on seagrass ecosystems in insolation (Nagelkerken et al., 2015), the majority of nursery studies confine comparisons between seagrass and unstructured areas, rarely including comparisons to other structured habitats (McDevitt-Irwin, Iacarella, & Baum, 2016). However, multiple habitats, including those dominated by macroalgae, persist adjacent to seagrass beds along the temperate exposed and complex shorelines.

The connectivity of temperate seagrasses (*Zostera marina*) and kelp forests (*Nereocystis luetkeana* and *Macrocystis* spp.), dominant canopy forming algae, and their effects on community dynamics is emerging to justify a seascape-level approach to studying nearshore nurseries. Seagrass and kelp forest habitats are linked through detrital pathways, such that seagrass invertebrate consumers can uptake kelp-derived nutrients (Doropoulos, Hyndes, & Lavery, 2009; Hyndes, Lavery, & Doropoulos, 2012). Ontogenetic movement of young-of-the-year (YOY) rockfishes from seagrass to kelp forest (Kamimura & Shoji, 2013), or vice versa (Haldorson & Richards, 1987) can connect these habitats biologically. And lastly, speculation of spatial adjacency effects have been noted where densities of YOY rockfish in seagrass may be higher when near kelp forests due to the dampening of wave energy (Jeffery, 2008). Because commercially and biologically relevant fish, like rockfish (*Sebastes* spp.), depend on both these habitats as nurseries (Carr, 1991; Love, Carr, & Haldorson, 1991), examining the connectivity of seagrass and kelp forests may reveal seascape level nursery effects.

1.4 Rockfish

Rockfish are a type of groundfish that occur in coastal areas of the temperate Pacific Ocean (Love, Yoklavich, & Thorsteinson, 2002). Of more than 100 species of rockfish in existence, approximately 37 species occur in British Columbia (BC), Canada (Love et al., 2002). Rockfish undergo a complex life history, such that larvae are born alive in the nearshore, but are swept off-shore for weeks to several months in the pelagic zone. Many rockfish species spend most of their non-larval lives in nearshore waters (vs. in deeper, offshore waters). Generally, the young-of-the year (YOY) of these rockfishes return to nearshore waters in early spring to settle into habitats like kelp forests, rocky reefs, and seagrasses. This settlement process into nearshore habitats for an undetermined amount of time is herein defined as their “recruitment” stage (Appendix A). As they grow in size and age, rockfish undergo an ontogenetic movement towards more benthic and deeper adult habitats (Carr, 1991; Love et al., 1991). Aside from established ontogenetic movements, juvenile and adult rockfish can show high site-fidelity and small home ranges, often <10m^2 (Hoelzer, 1988; K. R. Matthews, 1990). They are characterized by long life spans, late maturity, and slow growth; due to these traits, among others, rockfish are vulnerable to overfishing (Leaman, 1991; Parker et al., 2011). As such, populations in the northeast Pacific are on decline (Love et al., 2002; Yamanaka et al., 2004).

In BC's in-shore rockfish fisheries, Quillback (*S. maliger*), Yelloweye (*S. ruberrimus*), Copper (*S. caurinus*), Tiger (*S. nigrocintus*), China (*S. nebulosus*), and Black (*S. melanops*) rockfishes are mainly targeted (Yamanaka & Logan, 2010). Non-targeted bycatch of rockfishes in other fisheries is another source of mortality attributed to population declines (Favaro, Rutherford, Duff, & Côté, 2010). Of the species affected by fisheries, Quillback, Copper, and Black rockfishes are known to use seagrass ecosystems during juvenile stages (Buckley, 1997; Haldorson & Richards, 1987; Kamimura & Shoji, 2013; Kamimura, Kasai, & Shoji, 2011; West, Buckley, & Doty, 1994). However, there are unknown consequences to rockfish when seagrass ecosystems, and other nearshore habitats they are connected to, undergo major changes in habitat, structure, and, function from top-down and bottom-up factors.

A decline in both nearshore habitats and fisheries has led to increased marine conservation efforts, such as the establishment of marine reserves (Foley et al., 2010; Lotze et al., 2006), including those for rockfishes (Yamanaka & Logan, 2010). The incorporation of habitat connectivity is increasingly recognized as a part of marine spatial planning, however is rarely implemented (Engelhard et al., 2016). Albeit when spatial connectivity is protected for, it can lead to improved conservation efficacy (Martin et al., 2015; Olds, Albert, Maxwell, Pitt, & Connolly, 2013; Olds et al., 2014) and nursery function (Mumby, 2006). Because of the unknown consequences to ecosystem function and structure from the loss of foundational species, such as seagrasses and kelp forests (Ellison et al., 2005), understanding how the influence of their spatial connectivity affects their role as nursery habitats is of the upmost importance for marine conservation.

1.5 Thesis objectives

This thesis aims to enhance our empirical understanding of seascape linkages in temperate nearshore nurseries. Specifically, I investigate how spatial connectivity of adjacent habitats alters seagrasses' nursery functions for rockfish species. I hypothesized that the structural complexity of seagrass, and their adjacent habitats, would be primary contributors to nursery effects. To test these hypotheses, I compared the role of adjacent bull kelp forests (*Nereocystis luetkeana*) and sandy habitats as comparative structured vs. unstructured adjacent habitats, respectively. Chapter 2 establishes that seagrass meadows on the Central Coast of BC may act as nurseries for rockfish. I demonstrate this through a comparison of rockfish recruitment, defined as the settlement of YOYs to nearshore habitats, across multiple adjacent nearshore habitats. Chapter 3 investigates the contributions of allochthonous and autochthonous sources of primary production to seagrass food webs using the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). To determine seascape-wide patterns in source uptake by seagrass-associated food webs, I compared the contributions of primary production to YOY rockfish residing at seagrass sites adjacent to both kelp forest and sand habitats, and within the interior of the seagrass meadow. Moreover, I used YOY rockfish diets for further resolution of trophic dynamics in the seascape. Finally, chapter 4 concludes with a summary of the ecological and conservation significance of the thesis findings.

I conducted this research on the Central Coast of British Columbia (BC), which is characterized as a heterogeneous and pristine landscape. The Central Coast, while occupied for thousands of years by First Nations, remains relatively untouched by large-scale development, pollution, and recreational and commercial activity. The coastline is particularly complex compared to the southern coastlines of California, where most rockfish habitat studies have taken place. In BC, the coastline is scattered with many small islands, large watersheds, and fjords creating a dynamic and unique nearshore seascape. It is common for sub-tidal seagrass meadows to be sheltered behind outer islands, but occupy space next to exposed canopy-forming kelp forests like *Nereocystis luetkeana* and *Macrocystis pyrifera*, and in similar depths. Likewise, it is common for soft-sediment substrate, which is seagrass-associated, and rocky boulders or reefs, kelp-associated, to be adjacency at these exposed island groups. This study focuses on influences by the canopy-forming kelp *N. luetkeana* explicitly, which may not be transferrable to influences by *M. pyrifera* because of their differences in life history and structural complexity.

Chapter 2: Context-dependent influence of kelp forest adjacency on rockfish recruitment to seagrass meadows

2.1 Introduction

2.1.1 Habitat-associated recruitment shapes population dynamics

The recruitment of juveniles to nearshore habitats can determine the success of fish populations (Connell & Jones, 1991; Doherty, 2002; Schmitt & Holbrook, 1999). While it is widely recognized that pre-recruitment patterns, such as climatic and oceanographic processes, influence populations (Platt, Fuentes-Yaco, & Frank, 2003; Swearer, Caselle, Lea, & Warner, 1999; Victor, 1986), there is mounting evidence for the importance of post-recruitment influences on populations (Aburto-Oropeza, Sala, Paredes, Mendoza, & Ballesteros, 2007; Juanes, 2007; Levin, 1993; Levin, Petrik, & Malone, 1997). Spatial habitat variability has been highlighted as a key factor in post-recruitment success (Johnson, 2007; Shima, Osenberg, & Mary, 2008) because it can augment juvenile mortality and survival (Hixon & Beets, 1993; Walters & Juanes, 2011). However, there is a lack of understanding of the spatial drivers, at a landscape level, of post-recruitment processes that can improve management and conservation for important fish species (Gaines, White, Carr, & Palumbi, 2010; Man, Law, & Polunin, 1995) .

2.1.2 Habitat complexity of nearshore nurseries

Habitat complexity, defined as the 3-dimensional structure of a habitat in the water column (Appendix A), can greatly influence the recruitment, abundance, and diversity of fish settling in nearshore habitats (Gratwicke & Speight, 2005). Many fish recruit to and reside in nursery habitats of high structural complexity for post-recruitment growth and survival periods (Cocheret de la Morinière, Pollux, Nagelkerken, & van der

Velde, 2002; Smith & Sinerchia, 2004). Nursery habitats are those that contribute to increasing the growth, density, and/or survival of juveniles, and their movement to adult populations (Beck et al., 2001). Habitat structure created by these habitats can control community and population dynamics (Ellison et al., 2005). The provision of refuge for juveniles can decrease predation by reducing encounters with predators and predator foraging efficiency (Beukers & Jones, 1998; Greenberg, Paszkowski, & Tonn, 1995) and thus mediate mortality (Connell & Jones, 1991; Juanes, 2007). Thus, areas of high structural complexity are important areas for juvenile fishes.

Most studies demonstrate the impact of a single habitat on fish populations, but rarely incorporate the entire potential nursery area, even though fish often use multiple habitats during early life stages (Boström, Pittman, Simenstad, & Kneib, 2011; Nagelkerken, 2007). For instance, recent tagging evidence reveals short and long term seascape-level movement across nurseries of structurally complex habitats (Verweij, Nagelkerken, Hol, van den Beld, & van der Velde, 2007). Alternatively, there can be landscape effects to fish communities, such that adjacent habitats can influences fish densities and/or assemblages (Pittman, Caldow, Hile, & Monaco, 2007). Because growth and survival in nursery habitats can ultimately influence adult fish abundances and fisheries yield (Aburto-Oropeza et al., 2008; Beck et al., 2001; Mumby, 2006), studying the spatial connectivity of habitats can give rise to better understanding of population dynamics. As such, the "seascape nursery hypothesis" suggests that a landscape level approach can better assess nearshore habitats as nurseries because migration hot spots and optimal foraging or refuge grounds can be revealed at larger spatial scales (Nagelkerken et al., 2015; Sheaves et al., 2014).

Seagrass meadows are known as nursery habitats for many marine fishes (Heck et al., 2003) and serve as important habitats for newly recruited juvenile fishes (Levin et al., 1997). However, within a single seagrass meadow, the distribution of fish can vary greatly based on the seascape configuration (Macreadie et al., 2009; Smith, Hindell, Jenkins, & Connolly, 2008). The structural complexity of adjacent habitats is a main driver of these distributions, by altering areas for refuge and prey availability (Macreadie, Hindell, Keough, Jenkins, & Connolly, 2010; Smith, Hindell, Jenkins, Connolly, & Keough, 2011b). The direction and magnitude of adjacent habitat effects on fish abundances in seagrass meadows remains context and species dependent, and primarily focused on comparative adjacent un-structured habitats (Connolly & Hindell, 2006). In temperate coastal areas, commercially important nearshore rockfishes (*Sebastes* spp.) use seagrass habitats as nurseries when recruiting to the nearshore after a larval-pelagic stage (Love et al., 1991; Pastén, Katayama, & Omori, 2003). Because seagrasses are often surrounded by a mosaic of other nearshore habitats, recent work suggests adjacent kelp forests may influence seagrass habitats for rockfish (Jeffery, 2008).

Kelp forests are canopy-forming macrophyte communities extending through the entire water column (Dayton, 1985). Kelp forests promote high densities and biomass of reef-associated fish (E. C. Siddon, Siddon, & Stekoll, 2008; Trebilco, Dulvy, Stewart, & Salomon, 2015). Kelp forests, particularly of *M. pyrifera*, serve as critical juvenile habitat for young-of-the year (YOY) rockfish, influencing temporal and spatial recruitment (Carr, 1991; 1994). Ontogenetic habitat shifts by YOY rockfish based on seasonal availability of kelp forests and seagrass reveal biotic connectivity of these habitats from rockfish movement (Kamimura & Shoji, 2013; Haldorson & Richards, 1987). For example, the dominant kelp forests of *N. luetkeana* are annuals, relative to perennial *M. pyrifera*, and may only provide habitat during the summer months. Additionally, detrital connectivity between kelp forests and seagrasses can lead to the incorporation of kelp-derived nutrient subsidies into gastropod diets of seagrass meadows (Doropoulos et al., 2009; Hyndes et al., 2012). In studies of YOY rockfish recruitment off Vancouver Island, B.C. the structural presence of kelp forests may enhance the recruitment to seagrass nursery habitats by YOY rockfishes (Haldorson & Richards, 1987; Jeffery, 2008). However, little is known about the habitat adjacency of kelp forests and seagrass meadows, with respect to influences on habitat complexity at ecosystem boundaries and/or prey availability and their effects on rockfish recruitment.

2.1.3 Objectives

In this chapter, I examined the nursery effects of seagrass meadows in a seascape context, examining the role of seagrass habitat complexity and prey availability, and their adjacency to common habitats in nearshore temperate ecosystems: kelp forests and sandy substrates. A main difference in these adjacent habitats is the dramatic difference in their provision of structural complexity, from towering and complex kelp forests to unvegetated sandy substrates. My goal is to understand the role of adjacency of structured vs. unstructured habitats in promoting YOY rockfish recruitment (Appendix A) to seagrass meadows, and their interactions with other primary factors contributing to the nursery role of seagrass habitats. My specific questions were:

a. What are the spatial and temporal recruitment patterns of YOY rockfish to the nearshore environment?

b. What seagrass factors (habitat & prey availability) influence rockfish recruitment?

c. How does the adjacency to other habitats in the seascape affect recruitment to seagrass meadows?

I hypothesized that the vertical structure of kelp forests would increase rockfish densities and potential prey availability, leading to spillover effects into the adjacent seagrass habitats.

2.2 Methods

2.2.1 Study area

From May-September 2015, I monitored rockfish recruitment in a seagrass bed on the exposed outer coast of Calvert Island, B.C. in Choked Passage (Fig. 2.1, Appendix B). Choked Passage is characterized by a narrow waterway between Calvert Island and a string of rocky islets to the west, which creates high current during tidal exchanges. The *Zostera marina* meadow in the passage is estimated to be 367,300 m^2 in size (Fig. 2.1C) and characterized as subtidal and near-contiguous, with patchy areas, on sandy substrate. It is bordered by canopy-forming *Nereocystis luetkeana* beds propagating from the rocky bordering islets, and sandy, soft-bottomed, unstructured habitats. The depths of these adjacent habitats were variable, either deeper or shallower, compared to the seagrass meadow. The depth range of the seagrass meadow itself was very broad, ranging from 3 – 23ft (chart datum).

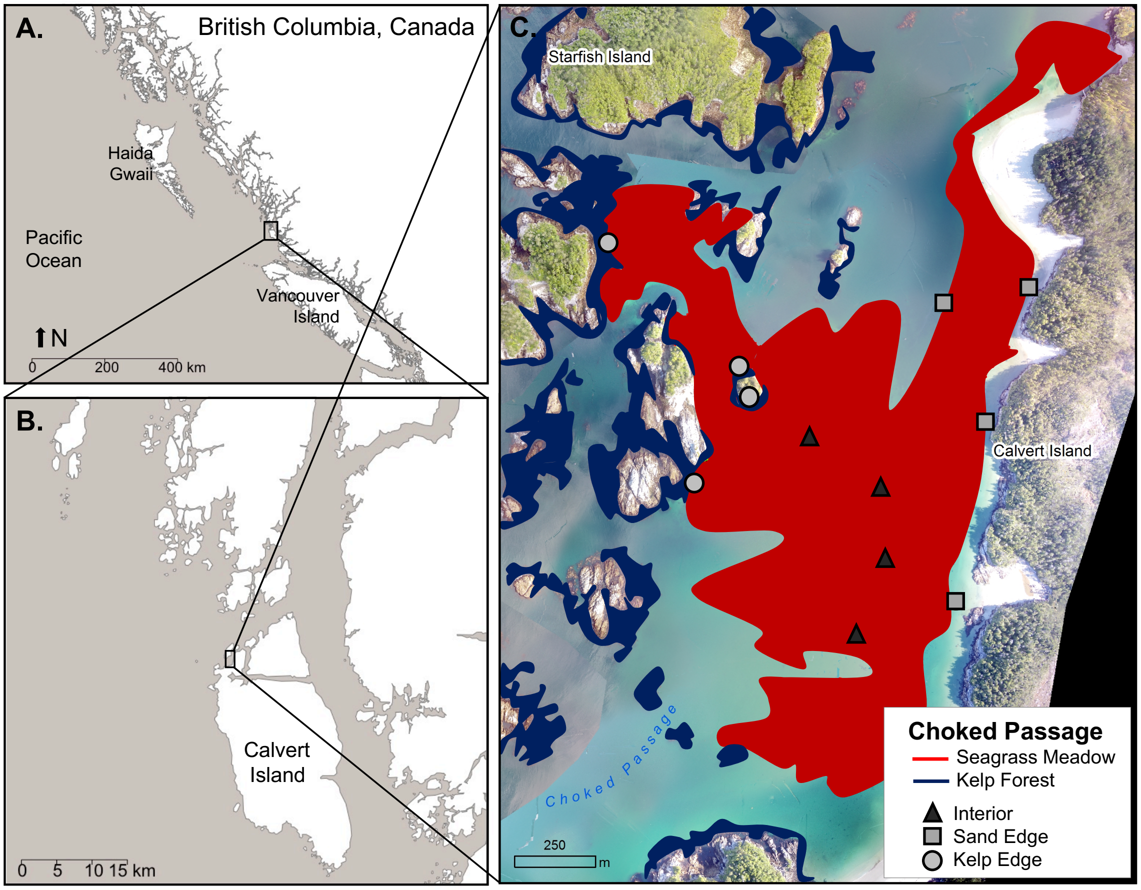

Figure 2.1 Map of the study area in A) and B) Central Coast of British Columbia, Canada and C) the focal seagrass meadow (red), approximately 367,000m^2 in area, located in Choked Passage northwest of Calvert Island. The meadow bordered *N. luetkeana* kelp forests (dark blue) and sand habitats. Study sites include *Interior* (triangle, dark grey), and *Edge* (light grey) sites bordering either *Kelp* forests (circles) and *Sand* habitats (squares). At all *Edge* sites, surveys were also conducted directly in the adjacent habitat.

To select sites of varying habitat adjacency, the seagrass bed perimeter was classified by adjacent habitat type (kelp or sand) and then further segregated into 50m sections. From the available selection of 50m sections of each habitat, sites were randomly chosen along the perimeter with a minimum 50m distance from any another established site. Thus, seagrass edge sites consisted of spatially explicit sites adjacent to either bull kelp forest “Kelp Edge” (n=4) or sandy habitat “Sand Edge” (n=4) (Appendix B1). Interior seagrass bed sites were randomly selected from a set of 50m sections with minimum distances of 200m from the edge and again at least 50m from another site. Once established, seagrass sites were all >100m apart from one another. Another 8 sites were established in the adjacent sand habitat (n=4) and kelp forest (n=4) (Appendix B2). At each of these 12 sites, I established a permanent 40m transect; at the edge sites, the transect was set in the seagrass bed 2m from the bordering habitat. Transects were marked with a permanent lead line and small submerged floats attached to rebard stakes at each 10m interval. I repeatedly monitored these sites during three temporal intervals throughout the 2015 summer: May 27 - June 15 (early), July 1 -July 15 (mid), July 30 - August 15 (late).

2.2.2 Seagrass habitat characterization & biomass collections

At the beginning of each sampling period, metrics of seagrass habitat complexity (Appendix A) and food availability in the seagrass meadow were characterized along the permanent transects, using SCUBA. The number of shoots per quadrat ($0.06m^2$) were counted as a measure of shoot density, with quadrats placed every 5m (n=9 quadrats/transect). A transect tape was used to measure the maximum height of blades as a metric of canopy height (cm). Within each 5m interval, patchiness and substrates were also characterized. Patchiness was estimated by the size of the sand patch (<1m, <5m, <10m, >10m), recorded on an ordinal scale from 0–3, indicating increasing patchiness, respectively. Non-seagrass characteristics, including primary and secondary substrate type (sand, gravel, cobble, boulder) and adjacent habitat vegetation (macroalgae species, if present) and dominant substrates, were also recorded along the transect. Lastly, seagrass edge sites further classified ecotone type, having either a distinct boundary, with clear separation of habitats, or a mixed boundary, where habitats overlapped in space (Appendix B2).

In addition, SCUBA divers collected seagrass shoot samples at 10m intervals along the transects to estimate seagrass biomass and characterize their epifaunal and epiphytic communities per shoot. Shoots were carefully covered with a Ziploc (TM) bag, and detached from the rhizome, to ensure seagrass invertebrates (herein, ‘mesograzers’) were captured in association with the shoot sample. In the laboratory, the entire contents of the bag, including seawater, seagrass, and epifauna, were filtered through a 500µm sieve and rinsed with filtered seawater. Microscope slides were used to gently scrape all epifauna and epiphytes from individual seagrass blades and combined with any free-floating mesograzers and epiphyte material. For each shoot, epifaunal mesograzers were identified to functional group (Appendix C), enumerated and weighed (mg). Epiphytic algae (e.g. *Smithora naiadum*, *Ulva* sp., and *Punctaria* sp.) were also sorted and weighed by group. *Z. marina* shoot length (cm), width (mm), and wet weight (g) were also recorded. All samples were placed in an oven for 48 hours at 60°C for a measure of dry weight which was used as our measure of biomass.

2.2.3 Fish surveys: underwater visual observations

Underwater visual observations of fish abundance and size were conducted at all sites along the 40m long transects, 2m on either side. Repeated surveys were conducted for a longitudinal analysis of habitat-specific recruitment over the duration of the YOY rockfish recruitment phase during early, mid, and late summer. When YOY rockfish recruit to nearshore habitats, they exhibit ontogenetic shifts from initial preference for high water column to benthic waters with age and size (Carr, 1991). Both SCUBA and snorkel observations were used to include observations of the full water column: snorkeler effort focused on the water column, while SCUBA effort focused on benthic observations within the seagrass canopy. During each observation period (early, mid, and late summer), sites was visited 3-4 times, with each visit consisting of one set of snorkel surveys (ie: n=2) and SCUBA surveys (n=2). Within each observation mode (SCUBA vs. snorkel), a repeat survey immediately followed the first to capture variability of observer effort. Snorkel and SCUBA observations were not concurrent, rather the same sites were observed by SCUBA ~1-2 days after snorkel surveys were completed. Survey durations were standardized to 5 minutes each. In addition to seagrass transects, the same observations were made directly into the adjacent habitat sites along a 40m transect. Observers recorded a categorical measure of perceived current, from none to very strong (0-6). When not recorded, the category was estimated based on tidal data. Tide height was haphazardly randomized for the observations. Over the course of the summer, at all sites, 794 unique surveys took place.

YOY rockfish morphological characteristics are not well defined during the recruitment phase to nearshore environments (Love et al., 2002). As such, species identification is difficult based on visual observation alone, and genetic analyses are often needed for species confirmation (Li, Nishimoto, Love, & Gharrett, 2006). For identification purposes, I used visual underwater identification, retrospective underwater photography of fish, and expert opinions. Copper (*S. caurinus*) and Quillback (*S. maliger*) rockfish exhibited similar morphological characteristics in the field and were difficult to differentiate. I assumed, *post-hoc,* that these were predominantly Copper Rockfish based on identifying characteristics, and use “Copper Rockfish” generally, recognizing that Quillback Rockfish may also be mixed among these recruits. Moreover, Black (*S. melanops*) and Yellowtail (*S. flavidus*) were equally difficult to differentiate underwater.

2.2.4 Modelling habitat effects on recruitment and predator density

To determine the nursery effects of seagrass on rockfish recruitment, I used separate generalized linear mixed-effects models (GLMMs) to assess relationships between each seagrass nursery habitat factor (e.g., *Z. marina* canopy height, biomass, density, and patchiness) and each prey biomass (gammarid, caprellid, and polychaete biomass) on YOY Copper Rockfish densities. The subset of key prey mesograzers were chosen from the invertebrate inventory found on the shoots (Appendix C) based on known rockfish diets (Haldorson & Richards, 1987; Studebaker & Mulligan, 2009). Model structures reflected the hierarchical nature of observations (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Multiple random effects were included: *Observer* nested within ordinal *Date* to account for repeated daily surveys that occurred over the summer; *Current* category to account for behavioral effects of water velocity on fish density; and chart datum *Depth* (ft), *Ecotone type*, and *Mesograzer Biomass* to capture variability among sites. A Poisson distribution was assigned to the models because the response variable had discrete, positive values inherent to count data.

To determine the relative role of seagrass nursery vs. landscape-level influence, I used GLMMs including these multiple predictor variables on YOY Copper Rockfish densities. To compress properties of seagrass habitat (density, biomass, and canopy height), a Principal Component Analysis (PCA) was used to obtain a singular "*Zostera complexity*" metric (Appendix D). PC1 accounted for the highest amount of variation

(60%); thus, was used in the GLMM as an explanatory variable of seagrass habitat complexity. Gammarid amphipod biomass was used to represent prey biomass, as they were most consistently found in the diets of YOY Copper Rockfish relative to other mesograzers (Chapter 3). Because a positive correlation between *Zostera complexity* and *gammarid biomass* was found (Appendix E), collinearity of these fixed effects was controlled for by using sequential regression (Dormann et al., 2012; Graham, 2003), whereby the residual gammarid biomass from the linear regression was used. A set of models was built using different combinations of fixed effects: *Zostera complexity*, *prey biomass*, and *site adjacency*. All models had the same random effects (see above; *ecotone type* was not included as it is akin to *site adjacency*). Model fits were compared using Akaike's Information Criterion (AIC) values measured by model parsimony and maximum likelihood (Zuur et al., 2009). The lowest relative AIC value (ΔAIC) and highest relative model weight (W_i) were used to choose the best model in predicting YOY Copper Rockfish densities. All continuous variables were standardized by subtracting the mean and dividing by standard deviation for direct comparison of scaled parameter estimates (Gelman, 2008).

The abundance and sizes of potential predators of YOY rockfishes were also recorded on the same underwater visual surveys at all nearshore sites. These included predatory reef fishes that are known to eat juvenile rockfish: adult rockfish (Hallacher & Roberts, 1985), greenlings (*Hexagrammos* spp.) (Hobson, Chess, & Howard, 2001), and lingcod (*Ophiodon elongatus*) (Beaudreau & Essington, 2007; Frid, Marliave, & Heithaus, 2012). All species of adult rockfish (*S. caurinus* and *S. melanops*), classified as greater than 10 cm, observed on individual transects were grouped, as well as all species of greenling (*H. decagrammus*, *H. lagocephalus*, and *H. stelleri*). Mean predator densities were assessed across all sites and observation periods. The relationship between *Zostera complexity* (PCA metric) and *habitat adjacency* on each predator group was examined using a comparative model set of Poisson GLMMs. I used the same random effects as per the seagrass models, as well as model comparison techniques. All models were conducted using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in R statistical software (R Core Team, 2013).

2.3 Results

2.3.1 Recruitment patterns to the nearshore seascape

Across the sampling period of summer 2015, I detected a large recruitment of YOY Copper Rockfish (Table 2.1). YOY Copper Rockfish observed were on average 3.9cm, ranging in size from 1 – 10 cm, across all sampling periods. YOY Black, Yellowtail, and Bocaccio (*S. paucispinis*) rockfishes were also observed on surveys, but to a lesser extent than YOY Copper Rockfish (Table 2.1). YOY Copper Rockfish recruitment increased at all sites throughout the summer, with the highest recruitment occurring during the last observation period, July – August. Very few rockfishes were observed in the first observation period. Due to the consistently large recruitment of Copper Rockfish, the following analyses focused on this species.

Table 2.1 Young-of-the-year (YOY) rockfish recruitment to all nearshore sites across 3 sampling periods (in order: May-June, July, and July – Aug) over the summer of 2015 as measured by mean (± standard errors) densities. Mean densities represent the average number of YOY rockfish species observed per transect during an observation period. Note: Black (*S. melanops*) and Yellowtail (*S. flavidus*) rockfishes are morphologically similar at YOY stages and were grouped together for identification purposes.

YOY Rockfish Species	**Mean ± SE Densities (Abundance/ Transect) by Observation Period**		
	May- June (n=190)	**July** (n=328)	**July - Aug** (n=273)
Copper (*S. caurinus*)	0.5 ± 0.3	5.4 ± 1.1	34.7 ± 4.9
Black (*S. melanops*) & Yellowtail (*S. flavidus*)	0	2.2 ± 1.0	20 ± 4.9
Boccacio (*S. paucispinis*)	0	0.2 ± 0.6	0.1 ± 0.1

2.3.2 Seagrass nursery influences on rockfish recruitment

Habitat Complexity - Multiple metrics of seagrass structural complexity were related to rockfish recruitment across the Choked Passage seagrass meadow. Across all sites, *Z. marina* shoot density was relatively low, but variable, with very tall shoots covered in high epiphyte biomass (Table 2.2). *Smithora naiadum* biomass contributed the most to epiphyte load while *Punctaria* sp. and *Ulva* sp. epiphyte biomasses were low (<0.05 mg biomass per shoot). Low patchiness (sand patches <1m) dominated sites across the entire meadow. For most seagrass habitat metrics, there were positive relationships with YOY Copper Rockfish densities (Fig. 2.2 A-C). *Z. marina* canopy height, shoot biomass, and density all had positive effects on rockfish densities. In contrast, patchiness had no effect on YOY rockfish densities.

Table 2.2 Site-level variation of seagrass nursery metrics from May – August, 2015: mean and standard error (SE) of habitat complexity (shoot density, canopy height, and shoot biomass) and prey availability (mesograzer and gammarid biomass) at seagrass sites in the interior of meadow and varying in habitat adjacency.

Seagrass Nursery Parameter (Mean ± SE)		**Habitat Adjacency**		
		Interior	**Sand Edge**	**Kelp Edge**
Habitat	Shoot Density (#/ Quadrat)	8.1 ± 0.3	9.6 ± 0.5	10.4 ± 0.3
	Canopy Height (cm)	141.2 ± 1.8	127.0 ± 3.3	162.5 ± 3.1
	Shoot Biomass (g)	2.4 ± 0.1	1.8 ± 0.1	2.7 ± 0.1
Prey Availability	Mesograzer Biomass (mg)	288.6 ± 54.9	374.1 ± 48.5	491.8 ± 57.8
	Gammarid Biomass (mg)	4.5 ± 1.6	43.6 ± 17.1	69.1 ± 27.7
	Caprellid Biomass (mg)	4.4 ± 1.9	14.4 ± 3.6	87.9 ± 42.2
	Polychaete Biomass (mg)	10.2 ± 3.0	15.2 ± 5.2	9.4 ± 4.2

Seagrass prey provision - Mesograzer abundance was high within the seagrass meadow with a diverse array of grazer groups (Table 2.2, Appendix C). The biomass of potential seagrass-associated prey items, gammarid amphipods, polychaetes, and caprellid amphipods, had varying influences on YOY Copper Rockfish densities. Only gammarid amphipods exhibited significant positive effects on YOY Copper Rockfish densities (Fig. 2.2D), while polychaetes and caprellids showed no relationships.

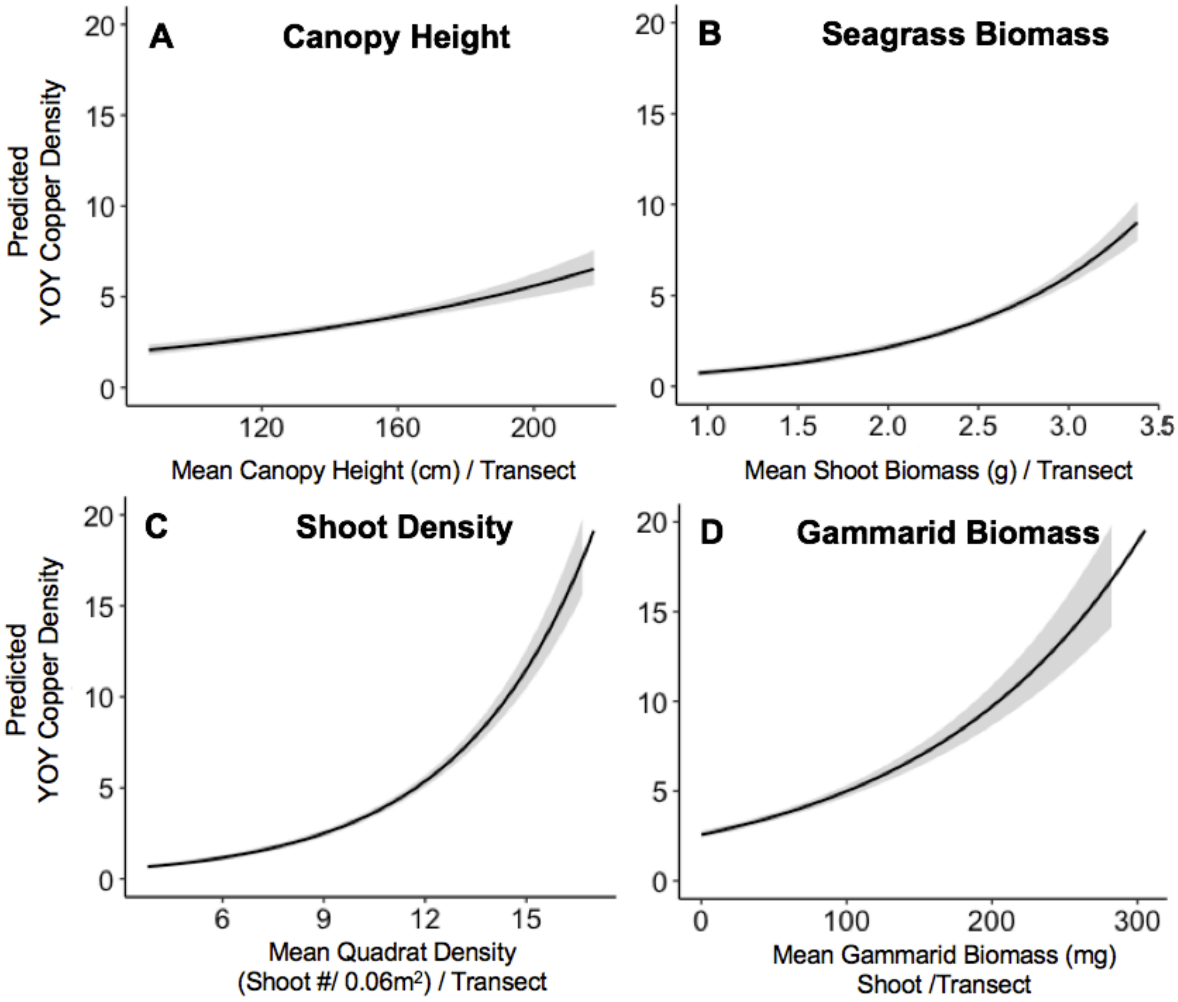

Figure 2.2 Predicted YOY Copper Rockfish densities related to seagrass habitat metrics A) mean canopy height (cm) per transect (*b* = 0.08, p = 0.02), B) mean shoot biomass per transect (*b* = 4.72, p = 0.003), C) mean shoot density per quadrat per transect (*b* = 1.00, p = <0.001), and prey availability D) gammarid amphipod biomass (mg) per transect (*b* = 0.03, p = 0.003). Only seagrass sites were used in this analysis.

2.3.3 Seascape variability in recruitment patterns

Across the seascape, YOY Copper Rockfish recruitment varied based on habitat adjacency, with higher rockfish recruitment densities at seagrass sites and kelp forest sites compared to unstructured sand sites throughout the summer (Fig. 2.3A-C). Recruitment to sand habitats was near negligible across the summer. The first large recruitment pulse occurred in mid-summer (early July) at the seagrass kelp edge, with a small increase in abundance at the sand edge (Fig. 2.3B). The highest recruitment numbers were observed during the last summer observation period, where the highest densities of rockfish occurred in the kelp forests, followed by seagrass sites (in order of decreasing densities): kelp edges, sand edge, and interior sites (Fig. 2.3C). Habitat-associated patterns in YOY rockfish sizes did not support any size-specific movement from seagrass beds to kelp forests (e.g., an ontogenetic shift) (Fig. 2.3D-F). Sizes of YOY Copper Rockfish increased at all sites in late summer relative to the previous mid-summer observation period, and showed little site-site variability once noticeable recruitment began (Fig. 2.3E-F).

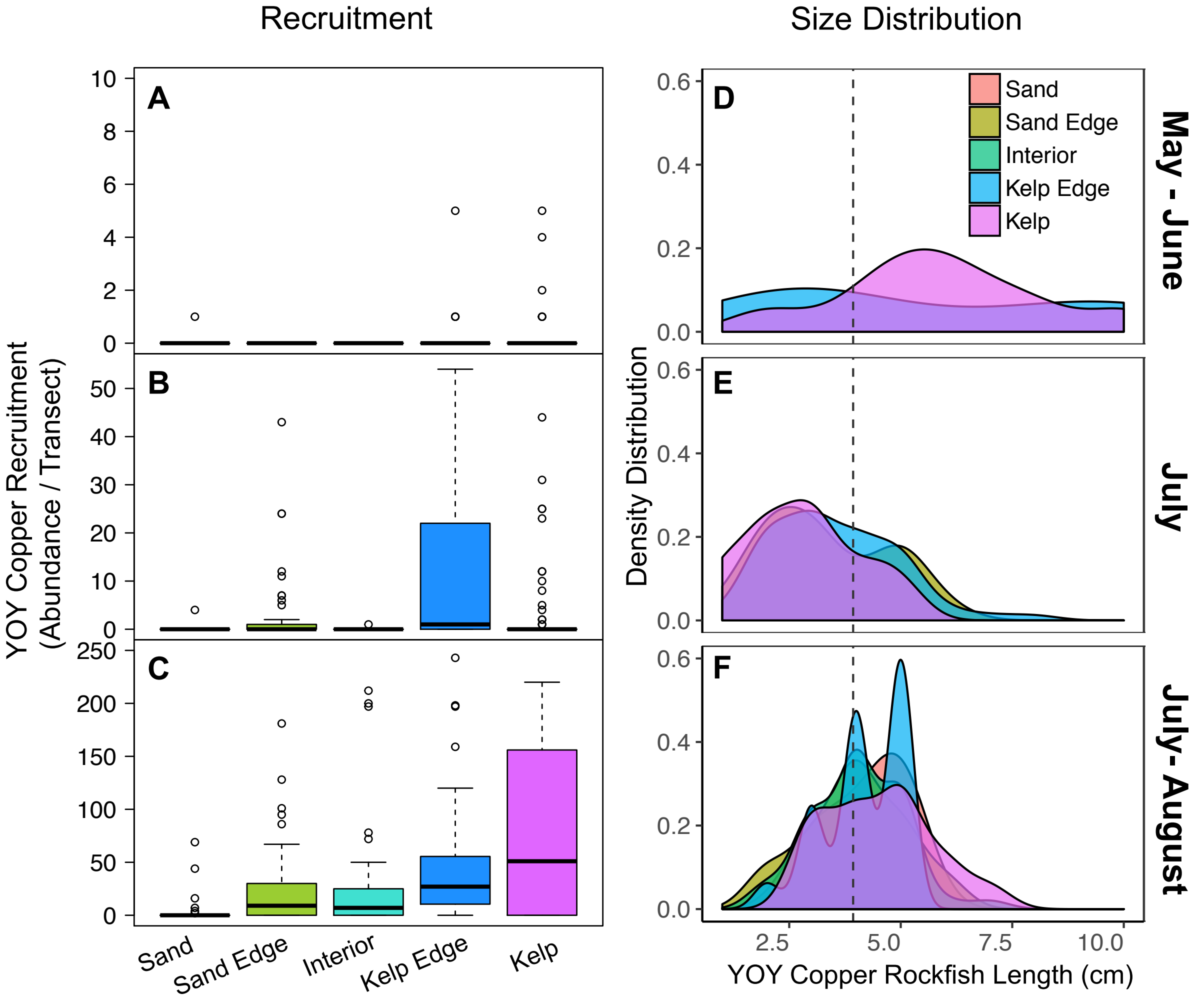

Figure 2.3 YOY Copper Rockfish recruitment (A-C) and size distribution (D-F) to nearshore sites in Choked Passage, BC over observation periods in the summer of 2015: May – June (A, D), July (B,E), and C) July-August (C,F). *Sand* sites (light pink) were categorized as having no structurally complexity, *Sand Edges* (green) were sites within the seagrass bed adjacent to contiguous sand habitat, sites in the *Interior* (cyan) of the seagrass bed were 200m away from any edge, *Kelp Edges* (blue) were seagrass sites adjacent to *N. luetkeana* kelp forests categorized as structurally complex, and *Kelp* (purple) sites were directly in the adjacent *N. luetkeana* kelp forest. YOY Copper Rockfish densities were measured as abundance over a 160m^2 transect. Size distributions are kernel density plots, where the dashed line is the mean YOY Copper Rockfish length over all sites and all time periods (3.93 cm ± 1.41 SD**).**

2.3.4 Seascape impacts on rockfish recruitment to seagrasses

Of the model set tested, the top model indicated that the interaction between *Zostera complexity* with *adjacent habitats* and *prey provision* by seagrass, best predicted the observed patterns in YOY Copper Rockfish recruitment (Table 2.3). Comparing the relative influences of these factors in the top model, *Zostera complexity* had the largest effect on Copper Rockfish recruitment to seagrass beds (*b* = 10.4, p<0.001), which was eight times greater than prey provision (*b* = 1.29, p<0.001) (Fig. 2.4). Adjacency to *N. luetkeana* kelp forests positively influenced Copper rockfish densities (*b* = 5.11, p<0.01). This was four times greater than seagrass *prey availability*, but not as large as *Zostera complexity* (Fig. 2.4). Important, but negative effects of *habitat adjacency* interacting with *Zostera complexity* were also found for both adjacent kelp forests (*b* = -10.7, p <0.001) and sand habitats (*b* = - 8.77, p < 0.001). The positive effect on Copper Rockfish densities conferred by spatial adjacency was thus highest at low values of seagrass structural complexity.

Table 2.3 Strength of evidence for alternative models explaining YOY Copper Rockfish densities by *habitat adjacency*, *Zostera complexity*, and seagrass *prey biomass*. Models are ranked by differences in Akaike Information Criterion (ΔAIC) and normalized Akaike weights (W_i), obtained from the balance between model likelihood (Log(L)) and parsimony indicated by degrees of freedom (DF). Model with interactions (*) are denoted in short form: factors involved in the interaction were included as separate terms in the model. Model in bold was chosen as the top model.

Response: YOY Copper Rockfish Density

Explanatory Parameters	Log (L)	AIC	ΔAIC	DF	W_i
Zostera Complexity * Adjacent Habitat + Gammarid Biomass	**-3694**	**7410**	**0**	**11**	**1**
Zostera Complexity + Adjacent Habitat	-4268	8552	1142	8	<0.001
Zostera Complexity	-4383	8779	1368	6	<0.001
Zostera Complexity + Prey Biomass	-4383	8780	1370	7	<0.001
Adjacent Habitat	-4614	9242	1832	7	<0.001
Prey Biomass	-4934	9880	2470	6	<0.001
Null	-5232	10474	3064	5	<0.001

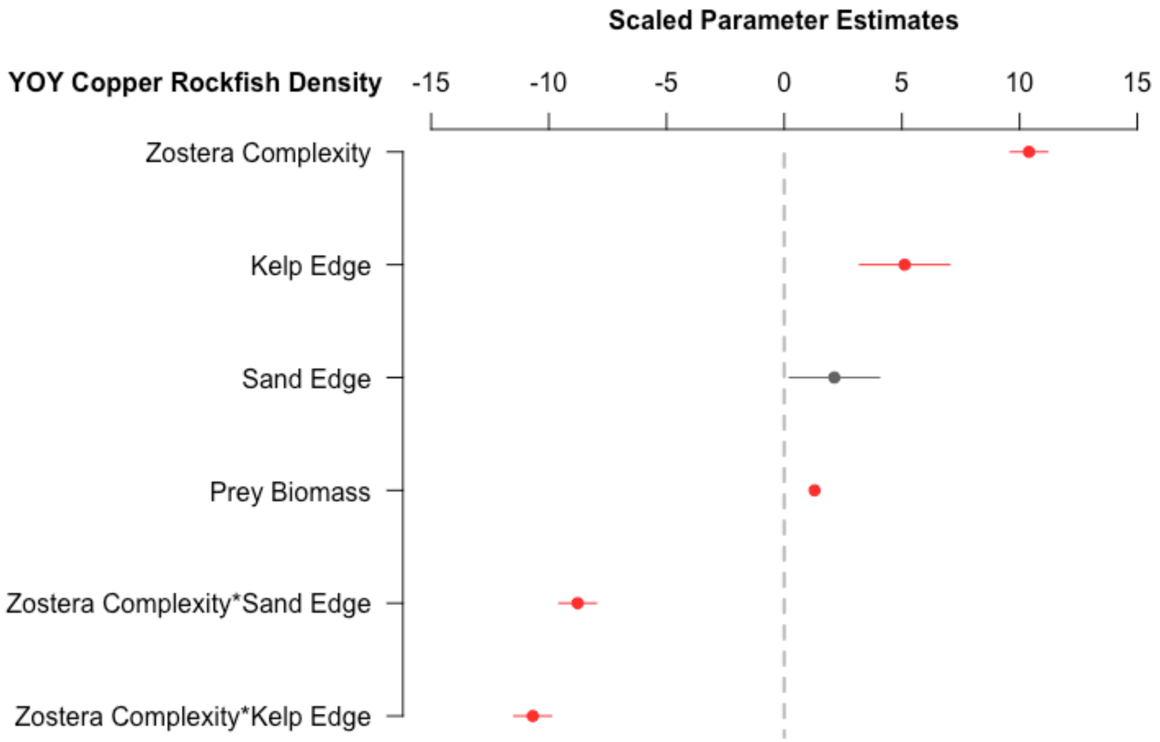

Figure 2.4 Scaled parameter estimates and 95% confidence interval from the top model explaining YOY Copper Rockfish densities in the seagrass meadow. Parameters include: seagrass nursery attributes (*Zostera complexity* and *prey biomass*) and *habitat adjacency* to either structurally complex kelp forests (*Kelp Edge*) and unstructured sand habitats (*Sand Edge*) as set to a reference of interior sites. Estimates greater than 0 (dashed line) indicate a positive influence on rockfish densities, and vice versa. Interaction terms between *Zostera complexity* and levels of habitat adjacency are denoted with an asterisk (*). Significant parameter estimates, that do not cross 0, are shown in red.

2.3.5 Predator densities across the seascape

Predator abundances were variable among habitat types. Adult rockfishes were observed in kelp forests and both edge types of seagrass, but never at the seagrass interior or sand habitats (Fig. 2.5A). Within the seagrass meadow, adult rockfish mean density was at least 24 times greater at kelp edges than other areas, whereas densities at the sand edge were 1.9 times greater than the interior. Overall, the densities of adult rockfishes were highest in the kelp forests. Species of adult rockfish, greater than 10cm, observed on transects were Black Rockfish that ranged in total length from 11 – 36cm, and Copper

Rockfish, ranging in total lengths from 11 – 42cm. Patterns in greenling density by habitat were similar to rockfish, being higher at seagrass edges and kelp forests, and never occurring in the seagrass interior; however, means were consistently less than one on all surveys (Fig. 2.5B). Concurrently, lingcod were rare on fish surveys.

Rockfish predator densities were affected by both *Zostera complexity* and *habitat adjacency* ($W_i = 1.0$, $\Delta AIC = 0$, Appendix F). Both these effects were positive, however habitat adjacency to kelp forests had a greater overall positive effect (Fig. 2.6, $b = 2.34$, $p = 0.035$) than the complexity of seagrass habitat ($b = 1.05$, $p < 0.001$). Adjacency to sand habitats had no effect on adult rockfish densities.

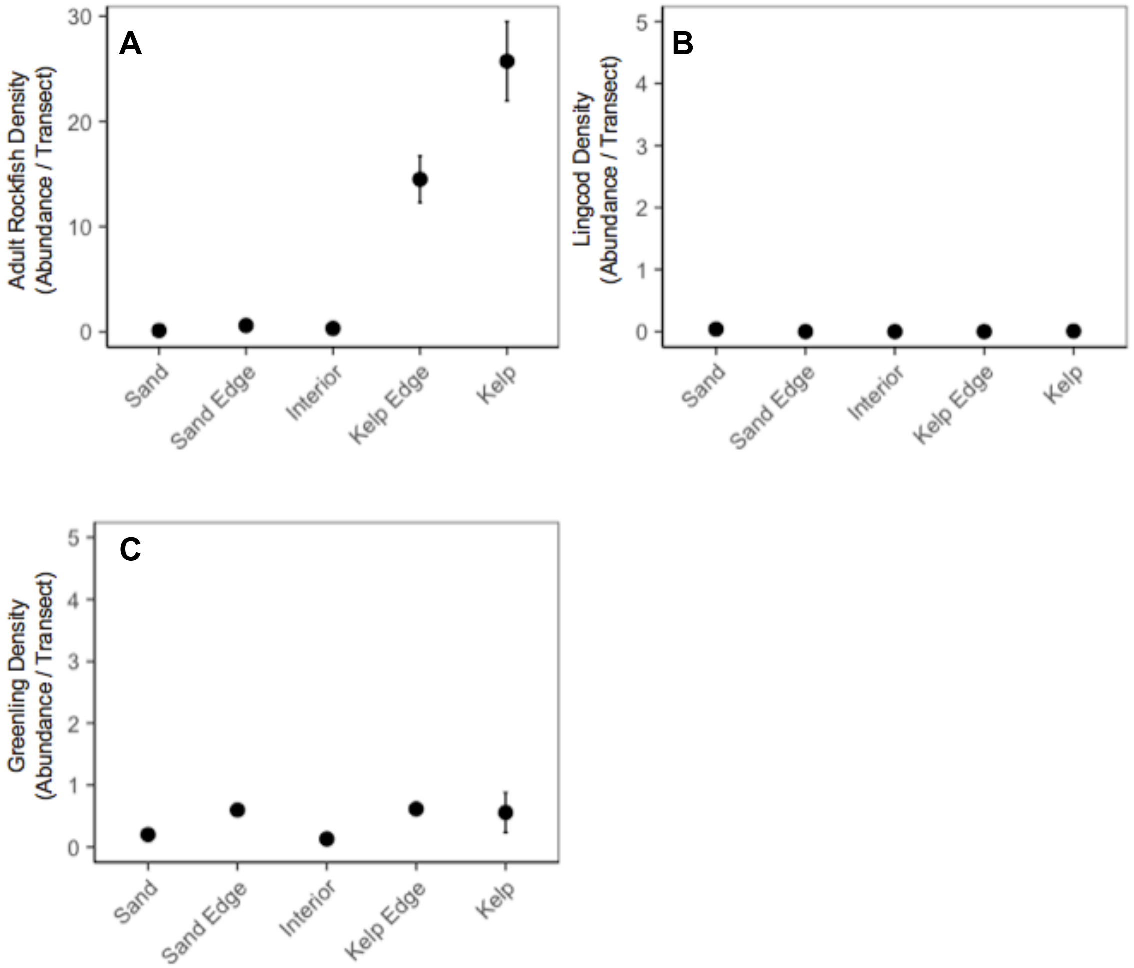

Figure 2.5 Mean (± standard error) densities (abundance/ 160m^2 transect) of potential YOY Copper Rockfish predators A) adult rockfish >10cm (*S. melanops* and *S. caurinus*), B) Lingcod (*O. elongatus*), and C) greenlings (*H. decagrammus*, *H. lagocephalus*, and *H. stelleri* species) observed on the same underwater observation surveys at nearshore sites. Densities were averaged over the entire observation period from May – August, 2015.

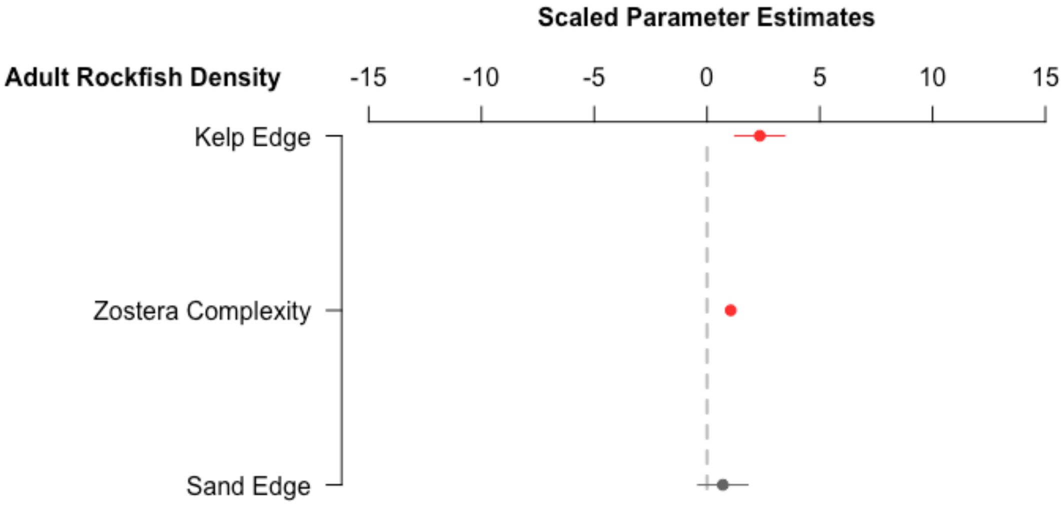

Figure 2.6 Scaled parameter estimates and 95% confidence intervals from the top model explaining adult rockfish densities in the seagrass meadow (Appendix F). The relative effect sizes of parameter estimates include seagrass habitat, *Zostera Complexity*, and habitat adjacency to either kelp forests (*Kelp Edge*) and unstructured sand habitats (*Sand Edge*) as set a reference of no connectivity at interior sites. Estimates greater than 0 (dashed line) indicate a positive influence on rockfish densities, and vice versa. Significant parameter estimates are colored red.

2.4 Discussion

Relationships between rockfish population dynamics and habitat complexity, during post-recruitment stages (Carr, 1991; Johnson, 2007), highlight the role of foundational habitats as key nurseries for juvenile rockfishes. However, the post-recruitment stage is one of the least studied aspects of rockfish life histories (Love et al., 1991). In a seagrass meadow on the Central Coast of BC, YOY Copper Rockfish recruited to structured vegetated habitats (seagrass and kelp forests) across the nearshore seascape (Fig. 2.3). As predicted, YOY Copper Rockfish recruitment patterns were positively influenced by seagrass habitat complexity and spatial adjacency to kelp forests (Fig. 2.2A-C, Fig. 2.4), whereas the direct provision of prey items by seagrass had only a small postive effect on recruitment (Fig. 2.2D, Fig. 2.4). Unexpectedly, a negative interaction was observed on YOY Copper Rockfish densities when habitat adjacency interacted with high complexity of seagrass habitat (Fig. 2.6). High rockfish predator densities spilling over from kelp forests may explain this negative interaction (Fig. 2.5A). Overall, these results provide further evidence that seagrass meadows may be a nursery habitat for rockfish at early life stages, and show that habitat adjacency within the seascape mosaic adds value, yet increase risk of predation, to seagrass as a nursery.

2.4.1 Recruitment dynamics to seagrass meadows

Contrary to other studies of rockfish recruitment to seagrass meadows in BC (Jeffery, 2008; Studebaker & Mulligan, 2009), YOY Copper Rockfish recruitment densities were high, yet temporally variable, compared to much lower YOY Black Rockfish densities (Table 2.1). Differences in species recruitment levels may be associated with climatic drivers of interannual recruitment patterns, such as the 2015 El Niño event (McCabe et al., 2016). Enhanced recruitment of benthic, solitary rockfish species (e.g., copper rockfish) over more pelagic, schooling species, like Black Rockfish has been demonstrated in El Niño years (Lenarz & Tresca, 1995; Markel, 2011). In this study, YOY Copper Rockfish recruitment peaked in the late summer months, with relatively low values across the seagrass bed prior to this. Copper Rockfish larvae are released from March–June and exhibit a short pelagic juvenile stage (Love et al., 2002), in keeping with the observed late summer recruitment patterns observed here. This study, and the few published papers of YOY Copper Rockfish in B.C., show later timing in recruitment of YOY Copper Rockfish relative to California (Haldorson & Richards, 1987; Jeffery, 2008; Love et al., 2002; Markel, 2011).

2.4.2 Habitat complexity drives seagrass nursery effect

Habitat complexity is known to influence fish population sizes by decreasing mortality (Beukers & Jones, 1998; Connell & Jones, 1991) and/or increasing growth (Quinn & Peterson 1996, Tupper & Boutilier 1997). Multiple metrics of seagrass structural complexity were positively associated with YOY Copper Rockfish recruitment (Fig. 2.2), including an overall complexity metric that had an eight times greater effect than prey provision (Fig. 2.4). Shoot density and height had positive effects on recruitment, consistent with studies of fish recruits in both tropical (Bell & Westoby, 1986; D Bell & Westoby, 1986) and temperate coastal areas (Gratwicke & Speight, 2005). There was no evidence for the patchiness of seagrass cover to influence densities of YOY rockfish. Seagrass patchiness effects on fish densities remain unclear in the literature, where it can be positive (Jelbart, Ross, & Connolly, 2007), negative (Salita, Ekau, & Saint-Paul, 2003), or as in this case, have no effect (Macreadie et al., 2009).

Prey provision also contributed to seagrass nursery effects, and was an important determinant of rockfish densities (Table 2.3, Fig. 2.4). The relative role of this factor may reflect the prey considered in these analyses: gammarid amphipod seagrass-associated mesograzers. Dietary studies of YOY Copper and Black Rockfishes feeding in seagrass meadows identify smaller zooplankton, like copepods, as dominant components to their diets relative to amphipod mesograzers (Kamimura et al., 2011; Studebaker & Mulligan, 2009). Thus, while structural complexity offered by seagrasses was clearly a primary contributor to rockfish densities, prey was also important, and its role may increase when considering the full assemblage of prey available to juvenile rockfishes within a seagrass meadow.

2.4.3 Importance of seascape scale for seagrass nursery value

There was evidence that habitat connectivity at the seascape-level influenced YOY Copper Rockfish recruitment in seagrass habitats. Kelp edges had the highest site values for rockfish density during the study period (Fig. 2.3-2.4), suggesting that this ecosystem boundary may be optimal nursery habitat for rockfish. Similar ecotone effects have been observed in tropical habitats, marshes, and riparian zones (Baltz, Rakocinski, & Fleeger, 1993; Dorenbosch, Grol, Nagelkerken, & van der Velde, 2005; Hammerschlag, Heithaus, & Serafy, 2010). However, for seagrass ecosystems, it is still debated if seascape effects contribute substantially to function (Boström, Jackson, & Simenstad, 2006; Connolly & Hindell, 2006; Smith et al., 2008). Edge effects associated with kelp forests have received little empirical attention, though have been described at the seascape-level to influence the foraging and migration of herbivorous consumers (Parnell, 2015). While the importance of detrital-based (Doropoulos et al., 2009; Hyndes et al., 2012), and temporal (Kamimura & Shoji, 2013) connectivity between seagrass habitats and kelp forests is growing, this study demonstrates the role of spatial and physical adjacency between kelp forests and seagrass on population-level dynamics.

Though seagrass complexity and kelp adjacency were important factors augmenting YOY Copper Rockfish densities, the interaction of seagrass complexity and habitat edges led to unexpected negative effects on YOY Copper Rockfish densities (Fig. 2.4, Table 2.3). Adjacency to other habitats can influence species abundances due to increased predation (Murcia, 1995; Ries & Sisk, 2004). In seagrass meadows adjacent to sand, predation at edges is known to be higher than interior areas (Bologna & Heck, 1999; Gorman, Gregory, & Schneider, 2009; Smith, Hindell, Jenkins, Connolly, &

Keough, 2011). Adult rockfish densities were slightly higher at sand edges than interior sites, which may have resulted in the small, yet negative interaction. More notably, adult rockfish densities were 24 times greater at kelp edges than the seagrass interior (Fig. 2.5A) and were positively influenced by seagrass complexity (Fig. 2.6), thereby increasing the likelihood of predation on YOY Copper Rockfish at kelp edges. Thus, the negative interaction of seagrass complexity and habitat adjacency on recruitment (Fig. 2.4) may be due to adult rockfish predators spilling over from kelp forests to seagrass areas that are structurally complex. In addition, high densities of YOY fish at seagrass-kelp sites may be attracting predators (Hobson et al., 2001).

Despite high predator density at seagrass edges, a trade-off between predation risk and foraging may be occurring. The distribution of resources at seagrass edges have been shown to positively influence fish densities (Macreadie et al., 2010). Evidence that the structural complexity of kelp forests alters basal communities is emerging (Clasen & Shurin, 2015; Pakhomov, Kaehler, & McQuaid, 2002). Due to potential changes in prey provision, the benefits of foraging success may outweigh predation risk, resulting in higher densities, especially if there is a minimum size for successful recruitment (Walters & Juanes, 1993; Tupper & Juanes, 2017). Further research is needed to elucidate mechanisms behind the negative interaction between kelp forests and seagrass habitat complexity, and the relationship between prey provision, refuge availability, and predation. Moreover, while this study used fish density to understand relationships to habitat, direct measurements of demographic rates could be used to fully understand the nursery role of habitats (Horne, 1983).

2.4.4 Conclusion

This study highlights the importance of subtidal seagrass meadows as rockfish nurseries, and how seascape connectivity plays a role in seagrasses' nursery function. Seagrass and kelp forest ecosystems are undergoing major changes in habitat, structure, and function from top-down and bottom-up factors (Krumhansl et al., 2016; Orth, Carruthers, Dennison, & Duarte, 2006; Waycott et al., 2009), thus these findings can have ramifications for seagrass conservation and restoration. The loss of nursery habitats, may have unknown influences on fish community structures and processes (Beck et al., 2001). Recognizing the full seascape-level processes of nurseries is of the utmost importance for conservation (Lindenmayer et al., 2008) and marine planning (Mumby, 2006; Nagelkerken et al., 2015; Sheaves et al., 2014). Efforts to conserve elements of seagrass complexity and habitat adjacency should be emphasized in marine planning, and fostered throughout restoration.

Chapter 3: Seagrass meadows as spatially subsidized nurseries in the coastal seascape

3.1 Introduction

3.1.1 Landscape influences on food webs

Food webs are a key theme in ecology, categorizing the assemblages and interactions of organisms in space and time (Paine, 1966; Polis, 1994; Polis & Strong, 1996). Increasingly, the structure and dynamics of food webs as influenced by their landscape context, including organismal and nutrient connectivity with adjacent ecosystems, has received focused research attention (Darimont, Paquet, & Reimchen, 2009; Doi, 2009; Finlay, Khandwala, & Power, 2002; Lamberti, Chaloner, & Hershey, 2010; Polis et al., 1997). The movement of animals and nutrients across landscapes can alter resources directly at ecosystem boundaries (Gaylord, Denny, & Koehl, 2008; Lastra, Page, Dugan, Hubbard, & Rodil, 2008; Paetzold, Yoshimura, & Tockner, 2008; Vander Zanden & Sanzone, 2004) or at distances far from these interfaces (Hyndes et al., 2013; Sanchez-Pinero & Polis, 2000; Vanderklift & Wernberg, 2008). These cross-boundary fluxes (herein “spatial subsidies”) have been shown to increase the abundances and growth of consumers in recipient systems (Callaway & Hastings, 2002; Marczak & Richardson, 2008; Tanentzap et al., 2014). The connectivity of landscapes in marine systems, known as ‘seascape connectivity’, has received comparatively little attention, but is likely to play a substantial role in marine foods webs, and trophic-level functions (Doi, 2009; Lamberti et al., 2010).

3.1.2 Seagrass nurseries in a seascape-level context

A seascape-level approach has recently been proposed to understand how the mosaic of habitats in nearshore environments contribute spatially to marine conservation, and the management of nurseries for productive fisheries (Nagelkerken et al., 2015; Sheaves et al., 2014). Seascape-level studies have revealed that habitat adjacency can increase population densities (Nagelkerken et al., 2001), alter consumer diets (Melville & Connolly, 2003; Nagelkerken & van der Velde, 2004) and provide optimal foraging areas for juvenile fish at ecosystem boundaries (Grober-Dunsmore, Pittman, Caldow, Kendall, & Frazer, 2009). A growing literature exists documenting how spatial adjacency can be a main driver of abiotic and biotic movement patterns across seascapes, and in example, between nursery habitats, (McMahon, Berumen, & Thorrold, 2012; Mumby, 2006; Olds et al., 2012; Verweij et al., 2007). However, patterns and processes associated with habitat adjacency at the scale of seascapes have not been applied across the wide array of habitats occupying marine systems.

Seagrasses, globally cosmopolitan constituents of nearshore seascapes, are known as a nursery habitat for a suite of marine organisms (Beck et al., 2001; Heck et al., 2003; Hughes, Stachowicz, & Williams, 2009; Larkum, Orth, & Duarte, 2006; McDevitt-Irwin et al., 2016). They are often viewed as sources of allochthonous subsidies to both marine and terrestrial consumers (Heck et al., 2008). Because seagrasses have high autochthonous productivity, from both seagrass and algal epiphytes (Larkum et al., 2006; Orth & vanMontfrans, 1984), few studies have examined subsidy inputs to seagrass beds (Jernakoff, Brearley, & Nielsen, 1996). Although it is expected that highly productive seagrass ecosystems incorporate little allochthonous energy, some evidence suggests that autochthonous productivity does not influence the amount of allochthonous nutrients incorporated by consumers (Marczak, Thompson, & Richardson, 2007). To test these ideas in temperate seagrass systems, an analysis of the role of adjacent habitats, such as kelp forests, is needed.

3.1.3 Influence of kelp forests on adjacent habitats

Kelp-derived nutrients from rocky reefs may play an important role in adjacent food webs (Duggins, Simenstad, & Estes, 1989). The accumulation of kelp detritus has been documented in many coastal regions (Krumhansl & Scheibling, 2011; Mann, 1986), subsidizing consumers in both high and low productivity recipient ecosystems (Adin & Riera, 2003; Kelly et al., 2012; Krumhansl & Scheibling, 2012; Orr, Zimmer, Jelinski, & Mews, 2005). The accumulation of detritus can decrease with distance from kelp beds (Kaehler, Pakhomov, & McQuaid, 2000) or remain widespread in the form of particulate organic matter (Kaehler, Pakhomov, Kalin, & Davis, 2006), affecting its role in subsidizing adjacent habitat. Moreover, kelp forests provide complex habitats, and can influence invertebrate communities available to higher level consumers (Barros, Underwood, & Lindegarth, 2001; Pakhomov et al., 2002). As such, spatial patterns of kelp forests may alter food webs in the coastal seascape, including inputs to nearby seagrass habitats.

Kelp detritus can accumulate in large quantities within seagrass meadows (Wernberg, Vanderklift, How, & Lavery, 2005). Recent experiments have determined that seagrass macrophytes and invertebrate consumers can uptake kelp-derived nutrients in their diets despite the availability of other autochthonous nutrients (Doropoulos et al., 2009; Hyndes et al., 2012). Evidence also suggests that kelp primary production supports top consumers, including fish, in nearshore food webs (Koenigs, Miller, & Page, 2015). The degree to which kelp forests affect spatial subsides to seagrass food webs, from lower level consumers to fish, has yet to be considered.

3.1.4 Objectives

The purpose of this study was to determine how allochthonous subsidies interact with habitat adjacency to influence fish consumers in seagrass food webs. In the temperate Pacific Ocean, rockfishes (*Sebastes* spp.), commercially valuable species of conservation concern, use nearshore habitats, including seagrass meadows and kelp forests, as nursery grounds during young-of-the-year (YOY) stages (Carr, 1991; Haldorson & Richards, 1987; Kamimura et al., 2011; Love et al., 2002). I asked the following questions, using YOY Copper Rockfish, and their food webs in seagrass ecosystems, to understand nursery effects in seagrass seascapes:

Sources of production

- *a.* How does the palatability (nutrient content) of autochthonous seagrass primary production (seagrass or algal epiphytes) compare to allochthonous kelp production?
- *b.* What is the relative contribution of seagrass-derived vs. kelp-derived inputs to seagrass habitats? How do these vary spatially across the seascape?
- *c.* Does seascape habitat adjacency drive variation across the seascape?

Prey contribution

- *d.* How does habitat adjacency alter the contribution of prey to YOY rockfish consumers?

e. Does adjacency influence the body condition (e.g. health) of rockfish using seagrass as a nursery?

I hypothesized that YOY rockfish in seagrass habitats uptake allochthonous kelp-derived nutrients into their diets. Further, I predicted that the proportion of kelp-derived nutrients would be influenced by habitat adjacency: rockfish adjacent to kelp forests would have the highest input of kelp-derived sources. I anticipated that these local effects would hold at the scale of the overall seagrass seascape, with high variation across the seascape based on differences in adjacent habitat. At the kelp-adjacent sites, I predicted that consumers would have higher body condition because of A) increased accessibility to highly palatable primary resources (kelp-derived nutrients) other than only autochthonous seagrass production and B) increased foraging area (structural complexity of kelp habitat offering predator refugia and alternative prey sources).

3.2 Methods

3.2.1 Study area

The study site was located on the Central Coast of B.C. in a subtidal seagrass meadow in Choked Passage, northwest of Calvert Island (Fig. 3.1). Choked Passage is a narrow waterway between a string of rocky islets and reefs and the mainland of Calvert Island. Due to its exposure to the Pacific Ocean, relatively shallow depths, and confined passageway, high currents are experienced in Choked Passage during tidal exchanges. A large *Zostera marina* seagrass meadow covers the center of the passage and is bordered by 2 dominant and contiguous habitats: sandy, soft-bottom habitats and kelp forests (propagating from fringing rocky-reef habitats). Together, this habitat mosaic creates a diverse and complex nearshore seascape. *Nereocystis luetkeana* (bull kelp) is the primary canopy-forming kelp forest in this area; an annual Laminaria algae, its rapid summer growth accrues into high kelp biomass in this nearshore ecosystem.

At the end of the summer, from August to September 2015, after visual transects were completed (Chapter 2), I examined how local seascape connectivity affected the seagrass food web, comparing consumers in isolated seagrass sites vs. seagrass sites adjacent to other habitats. Seagrass sites adjacent to the following habitats were chosen: highly structured, seagrass-to-kelp forests sites (n=3, "*Kelp Edge*") and unstructured seagrass-to-sand habitats (n=3, "*Sand Edge*"). Adjacent sites were compared to "*Interior*" seagrass sites (n=4), located in the middle of the meadow with no direct spatial connectivity to other habitats. All sites were chosen randomly (see section 2.2.1). For Interior sites, coordinates for potential sites were at least 200m from any dominant edge. For edge sites, coordinates were selected after an initial survey that categorized all adjacent edge habitats along the perimeter of the seagrass bed.

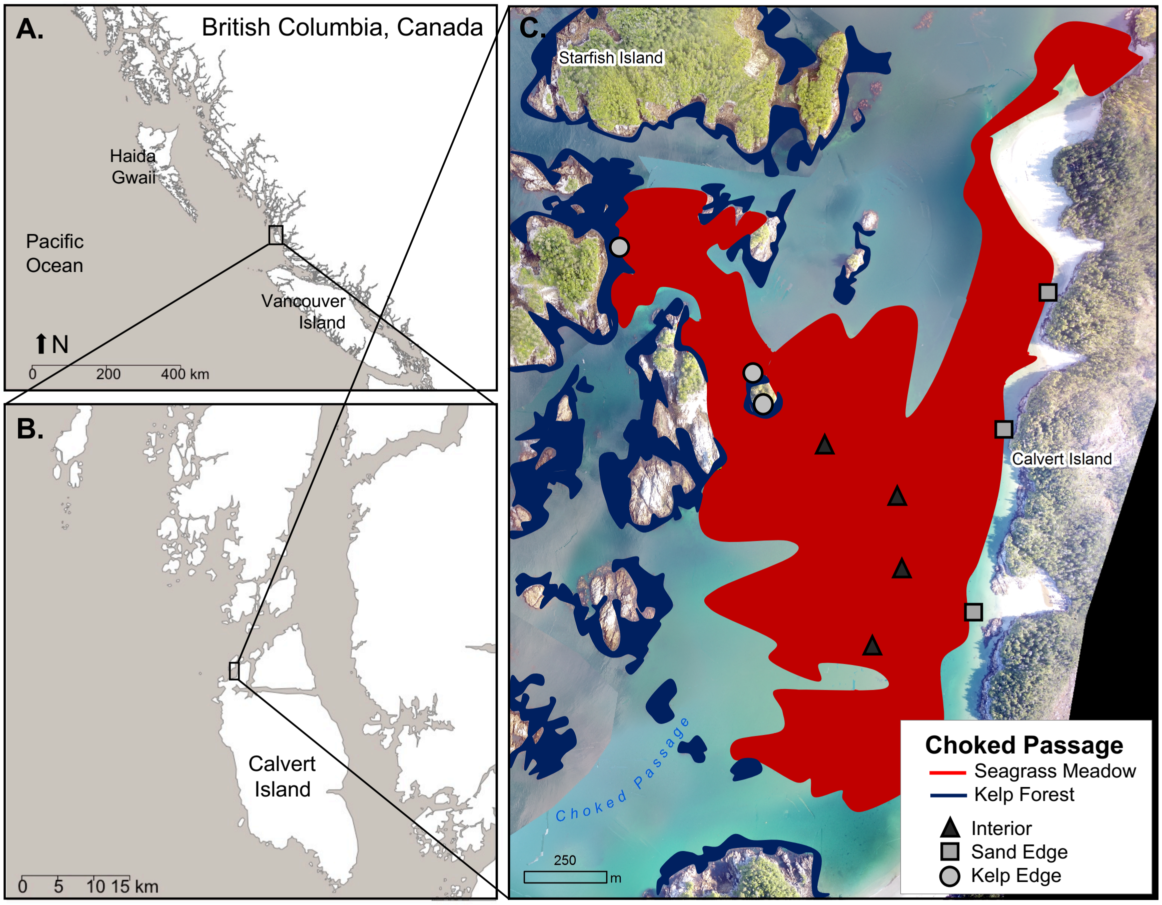

Figure 3.1 Map of study area in A) and B) Central Coast of British Columbia, Canada and C) the focal seagrass meadow (red) located in Choked Passage. The meadow bordered *N. luetkeana* kelp forests (dark blue) and sandy habitats. Study sites include *Interior* sites (triangle, closed), and *Edge* sites (open) bordering either *Kelp* forests (circles) or soft-bottom *Sand* habitats (squares).

3.2.2 Producer and consumer collections

Dominant vegetation types were collected haphazardly from all sites by SCUBA. To represent autochthonous production from the seagrass meadow, I collected *Zostera marina* shoots (n=25) and associated algal epiphytes, including the dominant epiphyte *Smithora naiadum* (n=17). For allochthonous kelp sources, I collected *N. luetkeana* blades from individuals in the surrounding kelp forests (n=5), as well as drift assemblage blades from dominant benthic algae *Cymathaere triplicata* and *Alaria marginata* (n=10 combined). Particulate organic matter (POM) was collected using plankton tows at 0m and 5m depth over the northern section of the seagrass bed and 2km outside of the seagrass bed, to represent oceanic conditions (n=8). All samples were collected over a three-week period to minimize confounding effects of temporal changes in isotopic signatures to consumers, and were kept frozen until laboratory processing.

I used a modified otter trawl net with 10mm mesh size to capture YOY rockfish (e.g., fish consumers) in the subtidal seagrass sites. From a small boat, trawls were set at sites and towed through the seagrass canopy for approximately 5 minutes. A maximum of 10 individuals were retained per site. YOY rockfish were immediately dissected to retrieve stomachs and measured for total length (mm), body depth (mm at the largest height), and weight (g). Stomach contents were placed in ethanol for later examination, while the remaining intact whole bodies were frozen for isotope analysis. All rockfish caught were visually identified as Copper Rockfish (*S. caurinus*). Due to close similarities in morphologies between Copper and Quillback (*S. maliger*) rockfish, samples may be comprised of both species, which are only truly differentiable by genetic analyses.

3.2.3 Isotope analysis and diet contribution modeling

In the laboratory, producer and consumer samples were defrosted and thoroughly cleaned of any contaminating carbonate materials using visual inspection and light scraping. The longest intact *Z. marina* blade from the shoot was used for analysis, representing a temporally integrated signature. The total epiphyte biomass per seagrass blade was used as a single sample to achieve sufficient weights for isotope analysis. For larger kelps, a subsample of algae tissue was taken from the outermost section of the blade. Due to the small sizes of YOY rockfish, the whole body was used for isotopic analysis. Samples were rinsed in two subsequent baths of deionized water. The samples were dried at 60°C for 48 hours and packed in tin capsules for isotopic measurement using a Delta IV Isotope Ratio Mass Spectrometer at the University of Victoria. $\delta^{15}N$ and $\delta^{13}C$ were calculated using the ratio of heavy to light isotope relative to a laboratory standard (Eq. 1) and are measured in per mille (‰):

Equation 1 $\delta^{15}N$ or $\delta^{13}C=[(R_{sample}/R_{standard})-1] \times 1000$

C:N ratios were calculated using the ratio between the percentage of carbon and nitrogen in the samples. Ratios were used as a measure of the relative nutritional value of potential sources of primary production (e.g., palatability). In general for primary producers, lower C:N ratios are indicative of higher palatability. I further grouped sources of primary production by isotopic nearness, relative palatability, and biological characteristics to improve the interpretation of the mixing model (Phillips et al., 2014).

From this assembled base of production, a simplified seagrass food web was modelled to determine the relative contribution of producer sources to rockfish consumers (Fig. 3.2). The diet source contribution model linked potential predator-prey interactions and included trophic fractionation of carbon and nitrogen. Primary (1°) consumers were defined as organisms foraging directly on primary sources by grazing, scraping, or filter feeding. Primary consumers were thus analogous to herbivorous prey of rockfish consumers, such as species of copepods or the suspension feeding *Caprellid alaskana*. Secondary (2°) consumers were classified as omnivorous organisms that consumed primary sources directly or 1° consumers. I conservatively assumed that 2° and

3° consumers ate 50% of each potential source (Reid, Quinn, Lake, & Reich, 2008). Rockfish consumers were assumed to be tertiary (3°) consumers at the top of the food web, foraging on 1° and 2° invertebrate consumers.

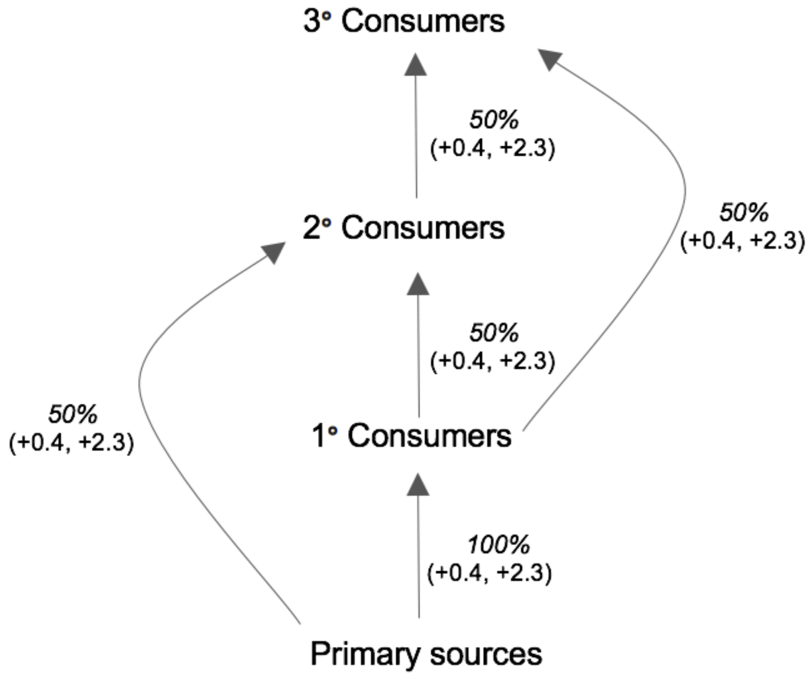

Figure 3.2 Simplified food web, and trophic transfers, of the seagrass ecosystem. 1° and 2° consumers represent herbivorous and omnivorous invertebrate prey items, respectively, of YOY Copper Rockfish (3° consumers). Trophic discrimination factors in parentheses represent fractionation of $\delta^{13}C$ and $\delta^{15}N$, respectively, between transfers, and are multiplied by the conservative estimates of dietary proportions. Discrimination factors were derived from averaged values of aquatic environments, poikilotherms, and whole tissue analysis, and lab methods (McCutchan, Lewis, Kendall, & McGrath, 2003).

Between each trophic transfer, or consumption of prey by a predator, stepwise changes in $\delta^{13}C$ and $\delta^{15}N$ stable isotopes occur by fractionation (DeNiro & Epstein, 1978; Minagawa & Wada, 1984). Isotopic mixing models use discrimination factors, based on field or experimental observations, to correct for these changes. However, models are highly sensitive to these factors, making their determination among the most important steps for modelling consumer diets (Bond & Diamond, 2011). I used values, averaged across consumer metabolic traits, aquatic environments, whole-body tissue analyses, and rinsing methods (McCutchan et al., 2003). For the total fractionation from primary sources to 3° consumers, values were multiplied by the number of trophic transfers and the relative proportion of prey consumed in our food web model (Reid et al., 2008). Lipids can also deplete the $\delta^{13}C$ signature of consumers during lipid synthesis (DeNiro & Epstein, 1977; Logan et al., 2008). I found the lipid content in YOY Copper Rockfish samples to be high (C:N > 5), such that the rockfish $\delta^{13}C$ estimates were likely negatively biased. Therefore, I employed a mathematical conversion (Eq. 2) on the $\delta^{13}C$ signatures of rockfish consumers (Post et al., 2007), prior to the subtraction of the discrimination factors from consumers (Appendix G).

Equation 2 $\delta^{13}C_{\text{normalized}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 * C{:}N$

I then used a Bayesian mixing model, commonly conducted for estimating the dietary proportions of predators (Moore & Semmens, 2008), to estimate the percent composition of five basal sources to YOY Copper Rockfish consumers in the seagrass meadow. The Bayesian statistical approach incorporates the variance of isotopic sources to produce estimates of uncertainty in dietary proportions, and allows for auxiliary *a priori* knowledge to be incorporated. I used the R package MixSIAR (Stock & Semmens, 2013) to estimate the proportion of source contribution attributed to rockfish isotope signatures, corrected for trophic enrichment and lipids, across the seagrass seascape. I pooled replicate habitat adjacency sites to account for naturally occurring spatial variance in diets. An uninformative prior was used to give an equal probability among basal sources of being consumed. To retrieve the posterior density estimates of source contribution, model iterations via Markov Chain Monte Carlo chain lengths were run 50,000 times, with the initial 25,000 estimations not used.

3.2.4 Stomach content analysis

The prey items of YOY rockfish were identified to the lowest taxonomic level possible using a dissecting microscope and grouped into taxonomically similar groups (Appendix H). Prey were counted and weighed to the nearest mg. If digestion affected the intactness of prey bodies, a conservative count of 1 was assigned as a group count. If a group weight was not heavy enough to register a weight, a conservative weight of 0.001mg was assigned. I then calculated the mean numerical abundance, gravimetric weight, and frequency of occurrence in a stomach by site. Proportional representation of a prey item was calculated based on the total sum of prey across each habitat-adjacency type (all sites) to estimate percent number (%N), gravimetrical weight (%W), and frequency of occurrence (%O) for each prey item. An index of relative importance (%IRI) (Eq. 3) was calculated to facilitate comparisons (Liao et al. 2001, Hart et al. 2002). To further assess the composition of prey items, prey diversity was calculated using the Shannon Index (H') based on %IRI (Eq. 4), where S is the total number of prey items. Evenness, defined as the similarity of prey items in %IRI in consumer diets, was calculated using Pielou's Evenness (J) metric (Eq. 5).

Equation 3 $$\%\mathrm{IRI} = \frac{\%\mathbf{N}+\%\mathbf{W}}{\%\mathbf{O}}$$

Equation 4 $$\boldsymbol{H' = -\sum_{i=1}^{S} p_i \log_b p_i}$$

Equation 5 $$\mathrm{J} = \boldsymbol{H'/\log(S)}$$

3.2.5 Estimating consumer body condition

To assess the potential impact of kelp subsidies on consumer nutritional and health status, I calculated YOY Copper Rockfish body condition using two metrics. First, I measured the overall body condition using a modified version of Fulton's length-weight relationship (Jones, Petrell, & Pauly, 1999), where the inclusion of body height accounts for another dimension of fish size related to weight (Eq. 6), and thereby increasing the accuracy of the model (Richter, Luckstadt, Focken, & Becker, 2000).

Equation 6 $B = \text{Weight} / \text{Length}^2 * \text{Height}$

The amount of lipids metabolized by consumers relative to their nitrogen concentrations is another proxy measurement for body condition (Matthews & Mazumder, 2005). Because lipids contain mostly carbon, and very little nitrogen, it is assumed that an increase in body tissue correlates with C:N ratio; thus, higher C:N ratios are used to predict better body condition in fish (Dempson, Braithwaite, Doherty, & Power, 2010; Sweeting, Polunin, & Jennings, 2006). Body condition was also measured using the C:N ratio of fish consumers grouped by habitat adjacency. Body conditions and size metrics were compared across regions using analysis of variance (ANOVA) and post-hoc Tukey's HSD testing.

3.3 Results

3.3.1 Palatability of sources

Among the basal resources in the seagrass ecosystem of Choked Passage, fast-growing primary producers (POM and the seagrass epiphyte *S. naiadum*) had the lowest C:N values, indicative of high palatability (Fig. 3.3, Table 3.1). Larger, slower growing species (*Z. marina* and benthic macroalgae: *A. marginata*, and *C. triplicata*) had relatively high C:N values indicating low palatability). *N. luetkeana* was intermediate in the scale of palatability, but was still relatively low in C:N value. Variations in the C:N ratios arose from small differences in mean percent concentrations of carbon and nitrogen among primary producers (Table 3.1). Furthermore, the $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures of the grouped primary sources showed no overlap in values.

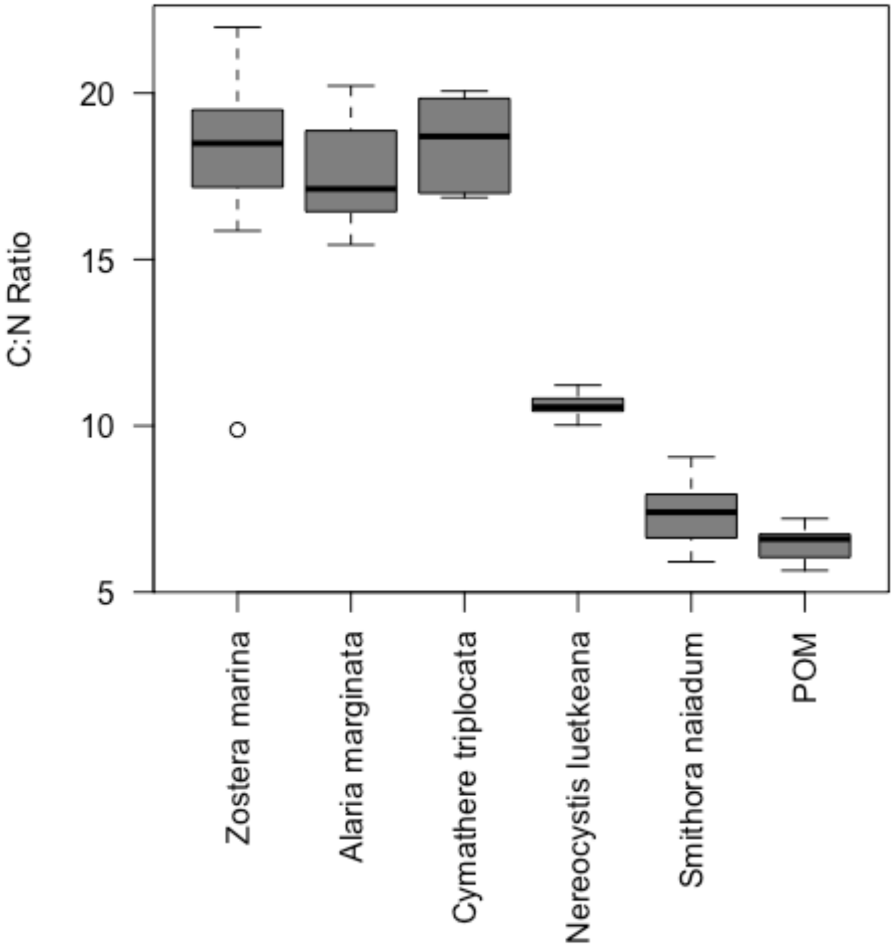

Figure 3.3 Relative palatability, estimated by C:N ratios, of basal sources in the seagrass meadow: *Z. marina* (n= 25), *A. marginata* (n=5), *C. triplicata* (n=5), *N. luetkeana* (n=5), *S. naiadum* (n=17), and POM (n=8). The boxplot is comprised of the median (horizontal black bars), first and third quantiles (box edges), and 95% confidence intervals (error bars) of the median.

Table 3.1 Summary of the basal sources, and specific primary producer species attributed to each source, contributing to the seagrass meadow food web. Mean and standard error (SE) of δ^{13}C signatures, δ^{15}N signatures, percentage carbon (C), percentage (N) concentrations, and sample sizes (N) are shown for each source.

Source Group	**Species**	**Percent C Mean ± SE**	**Percent N Mean ± SE**	**δ^{13}C (‰) Mean ± SE**	**δ^{15}N (‰) Mean ± SE**	**N**
Seagrass	*Zostera marina*	41.69 ± 0.66	2.40 ± 0.11	-11.10 ± 0.30	4.22 ± 0.19	25
Benthic macroalgae	*Alaria marginata*	34.65 ± 1.80	1.99 ± 0.15	-15.33 ± 0.92	6.05 ± 0.20	5
	Cymathaere triplicata	35.36 ± 1.74	1.93 ± 0.13	-15.32 ± 1.04	5.47 ± 0.39	5
Kelp forest	*Nereocystis luetkeana*	38.30 ± 0.77	3.61 ± 0.10	-18.60 ± 0.88	3.86 ± 0.93	5
Seagrass Epiphyte	*Smithora naiadum*	35.72 ± 1.28	4.94 ± 0.28	-22.37 ± 0.31	6.38 ± 0.15	17
Particulate Organic Matter (POM)	NA	NA	NA	-20.39 ± 0.40	6.30 ± 0.13	8

3.3.2 Isotopic seagrass food web

The range of mean δ^{15}N for basal producers was low (2.08 ‰), while a wider isotopic range was observed in mean δ^{13}C values (9.29 ‰) (Fig. 3.4, Table 3.2). The signatures of sources were distinct and varied, bounded by *Z. marina* (the most enriched δ^{13}C signature) and the dominant algal epiphyte, *S. naiadum,* (the most depleted δ^{13}C signature) (Fig. 3.4). *A. marginata* and *C. triplicata* macroalgal species had overlapping δ^{13}C signatures, and were combined for the mixing model for a mean value: δ^{13}C: -15.33 ± 2.08 SD, δ^{15}N: 5.76 ± 0.72 SD). The mean isotope signatures of *N. luetkeana* were also intermediate, being more enriched than *S. naiadum,* but depleted relative to benthic macroalgaes.

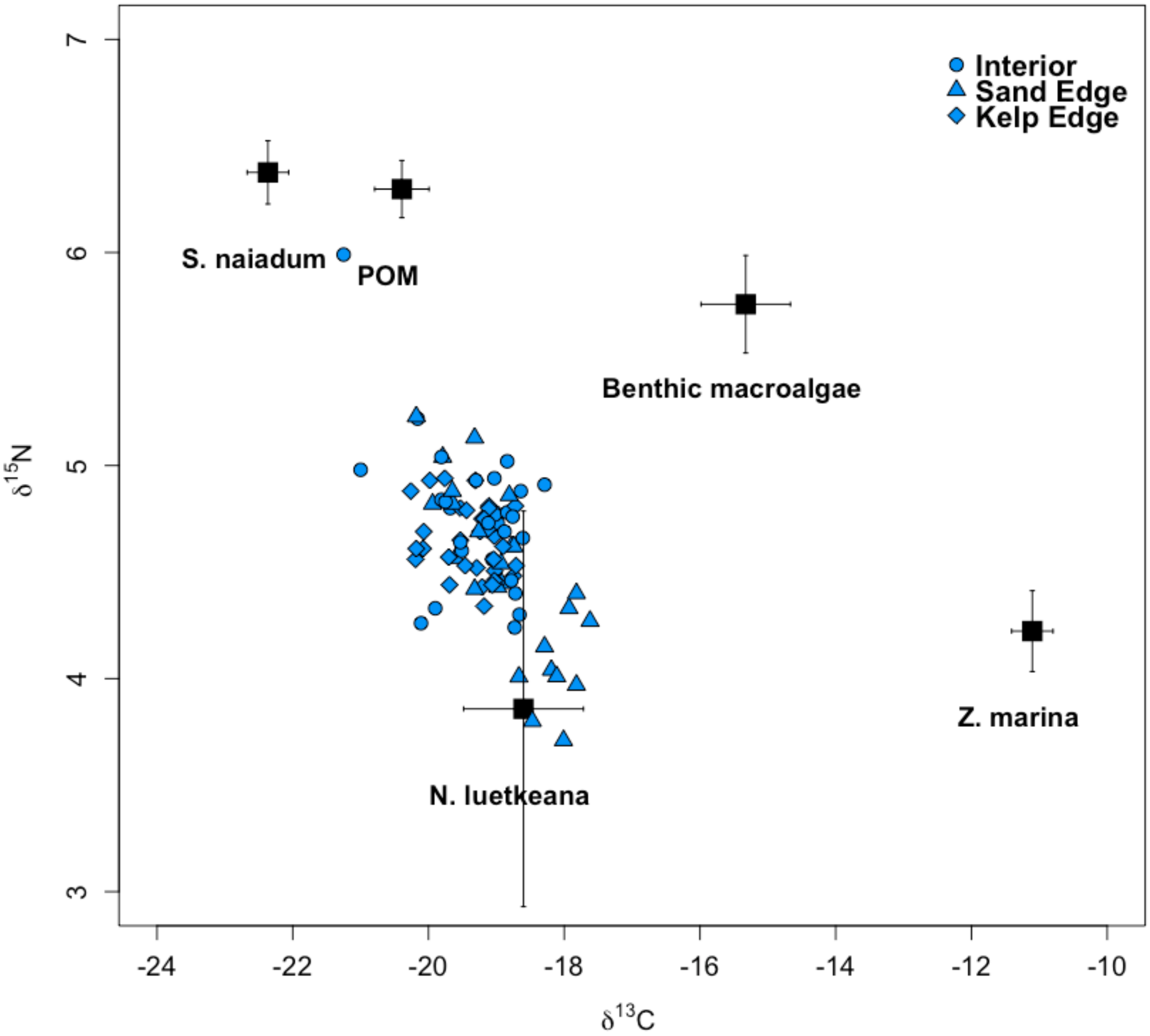

Figure 3.4 $\delta^{13}C$ and $\delta^{15}N$ biplot of the mean and standard error isotopic signatures of basal resources (black squares) in the seagrass food web and YOY Copper Rockfish individuals after subtraction of trophic enrichment corrections (blue) based on the simplified food web model in Fig. 3.2. Rockfish were sampled at seagrass sites varying in habitat adjacency: Interior (circles, n=29), Sand Edge (triangles, n=25), and Kelp Edge (diamonds, n=32). Appendix G shows the initial uncorrected isotope signatures of YOY Copper Rockfish.

Table 3.2 Summary of YOY Copper Rockfish mean and standard error (SE) body lengths (mm), weights (g), isotope signatures (δ^{13}C and δ^{15}N), and sample sizes (N) across sites within each seagrass habitat adjacency classification.

Habitat Adjacency	**Site**	**Length (mm) Mean ± SE**	**Weight (g) Mean ± SE**	**δ^{13}C (%) Mean ± SE**	**δ^{15}N (%) Mean ± SE**	**N**
Interior	Interior 1	43.19 ± 0.01	0.91 ± 0	-17.63 ± 0.19	11.73 ± 0.06	2
	Interior 2	41.06 ± 2.97	1.05 ± 0.22	-18.11 ± 0.25	11.65 ± 0.09	10
	Interior 3	40.21 ± 2.31	0.85 ± 0.13	-18.2 ± 0.27	11.75 ± 0.16	9
	Interior 4	41.4 ± 3.33	1.01 ± 0.3	-18.07 ± 0.19	11.57 ± 0.08	9
Kelp Edge	Lower	41.29 ± 1.7	1.03 ± 0.11	-18.15 ± 0.13	11.63 ± 0.03	12
	North Pigu	37.31 ± 1.88	0.64 ± 0.08	-18.4 ± 0.13	11.43 ± 0.03	10
	South Pigu	41.71 ± 1.34	0.79 ± 0.09	-17.97 ± 0.12	11.56 ± 0.06	11
Sand Edge	Inner Sand	47.7 ± 1.51	1.25 ± 0.12	-17.01 ± 0.18	11.05 ± 0.08	10
	Alcove	35.78 ± 1.39	0.58 ± 0.08	-17.81 ± 0.18	11.47 ± 0.15	7
	Wolf	34.2 ± 2.04	0.49 ± 0.11	-18.25 ± 0.16	11.7 ± 0.1	8

Consumer YOY Copper Rockfish (mean δ^{13}C: -17.99 ± 0.66 SD, mean δ^{15}N: 11.53 ± 0.33 SD) had small isotopic variations among sites within habitat-adjacency types (Table 3.2). Once corrected for trophic enrichment, consumers fell among the source mixture, and clustered by habitat-adjacency (Fig. 3.4). Overall, rockfish had the strongest isotopic overlap with *N. luetkeana* in δ^{13}C space, and were situated between *N. luetkeana*, *Z. marina* and benthic macroalgae in δ^{15}N space. Across regions, rockfish mean δ^{13}C was depleted at kelp edges and interior sites relative to sand edges and δ^{15}N enriched at interior sites relative to sand edges (Table 3.2). Lengths of YOY Copper Rockfish did not differ across habitat-adjacency and thus, ontogenetic dietary shifts reflecting fish movement between habitats with size, were not considered to be a factor influencing these trends.

3.3.3 Basal inputs to YOY Copper Rockfish

Allochthonous kelp-derived subsidies contributed the largest proportion to YOY Copper Rockfish diets: 43% to 53% of consumer diets was estimated by the mixing model (Fig. 3.5, Appendix I). Across the Choked Passage seascape, kelp-derived subsidies were 2.7 to 7.2 times greater than autochthonous seagrass production: seagrass (5-10%) and its algal epiphyte (10-26%). Basal contributions from POM were the second highest contribution to YOY Copper Rockfish diets, albeit half as much as *N. luetkeana* (14-24%). Allochthonous benthic macroalgae (*C. triplicata* and *A. marginata*) was relatively uncommon in diets, on par with seagrass (6-12%).

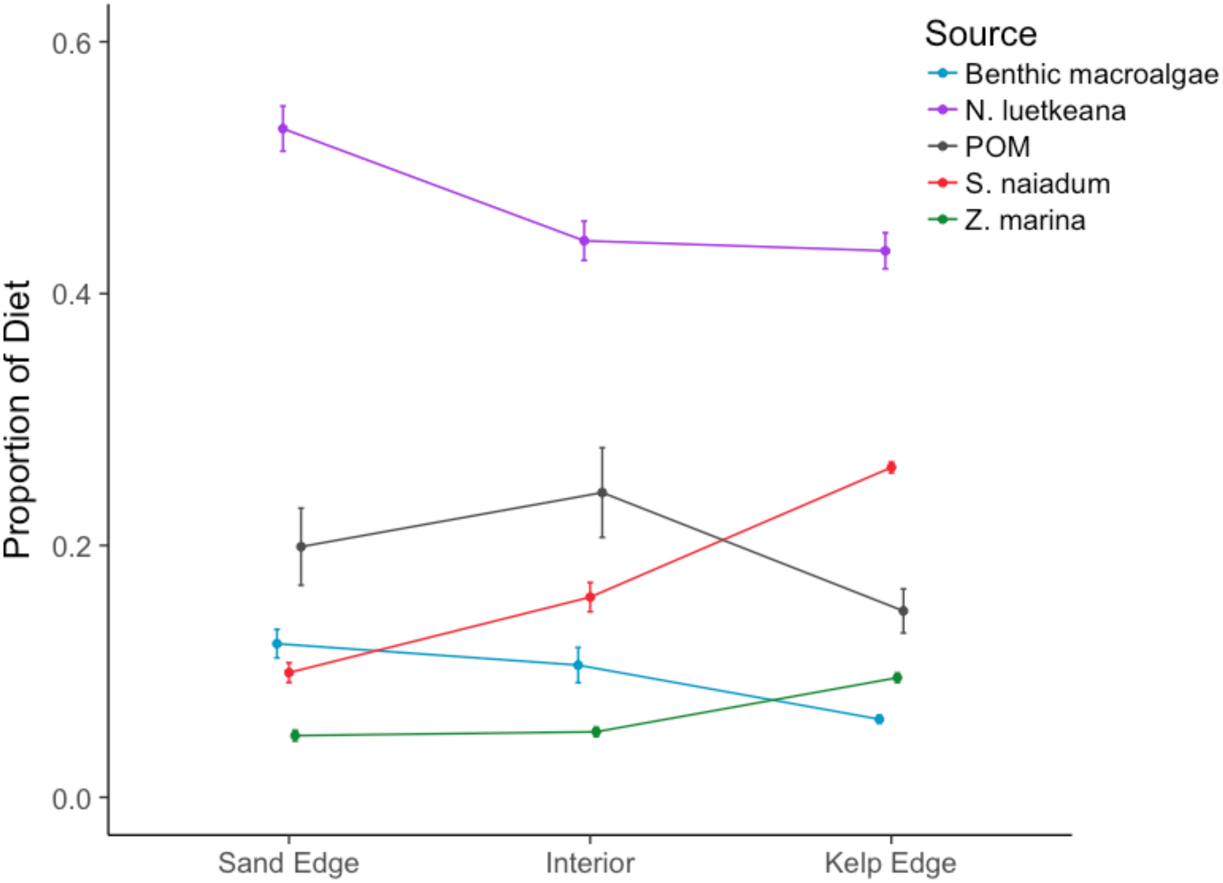

Figure 3.5 Isotopic mixing model results exhibiting the mean proportion of basal sources in the diet of YOY Copper Rockfish residing in the Choked Passage seagrass seascape. Sources include benthic macroalgae (blue), *Nereocystis luetkeana* (purple), POM (grey), *S. naiadum* (red), the dominant seagrass epiphyte, and *Z. marina* (green). YOY Copper Rockfish were caught in the seagrass meadow Sand Edge (n=25), Interior (n=29), and Kelp edge (n=32), reflecting potential differences in basal sources derived from seascape adjacency effects. Error bars represent the standard error around the mean proportion. Evenness of basal contribution is defined as the similarity of proportion contribution to the diet.

Within the seascape, differences in dietary contribution of sources were found between habitat-adjacency types. Kelp-derived contributions were 1.2 times higher at the sand edge relative to interior and kelp edge sites (Fig. 3.5). Conversely, the proportion of *S. naiadum*, the dominant seagrass epiphyte, in the diet at the sand edge was lowest, and increased in the interior and kelp edge (Fig. 3.5). The estimated POM contribution to diets was largest at the interior of the seagrass meadow, albeit the variance around POM contributions was high across all habitat groupings (Fig. 3.5). Similarly, estimated diet contributions for benthic macroalgae and seagrass were similar across adjacency groupings (Fig. 3.5). Evenness of primary producer contributions to diets, defined by the similarity in proportions, also varied by habitat adjacency. Diets at the sand edges were less evenly distributed (dominated by *N. luetkeana*), and diets at the kelp edge were the most evenly distributed (Fig. 3.5).

3.3.4 Prey consumed by YOY Copper Rockfish

Direct observations of YOY Copper Rockfish diets through stomach content analysis revealed a diverse diet, including epifaunal prey that have high affinity to both seagrass and macroalgal substrates (Fig. 3.6, Appendix J). To balance the large discrepancy in prey weight and abundance consumed (Appendix J1-3), %IRI was used to described prey importance. Copepods and amphipods generally dominated the diet of YOY Copper Rockfish, while larger prey (e.g. shrimp) were relatively unimportant (Fig. 3.6). Harpacticoid and calanoid copepods were the most dominant taxa in the stomachs, respectively, with means of 28% (± 24 SD) and 25% (± 24 SD). Shifts in dominant copepod taxa being consumed among sites explained the large differences in copepod %IRI (Fig. 3.6, Appendix JA). Among amphipod taxa, gammarids dominated (22% ± 0.15 SD) over *Caprellid alaskana* (0% + 0 SD) and corophids (0.5% ± 0.1 SD).

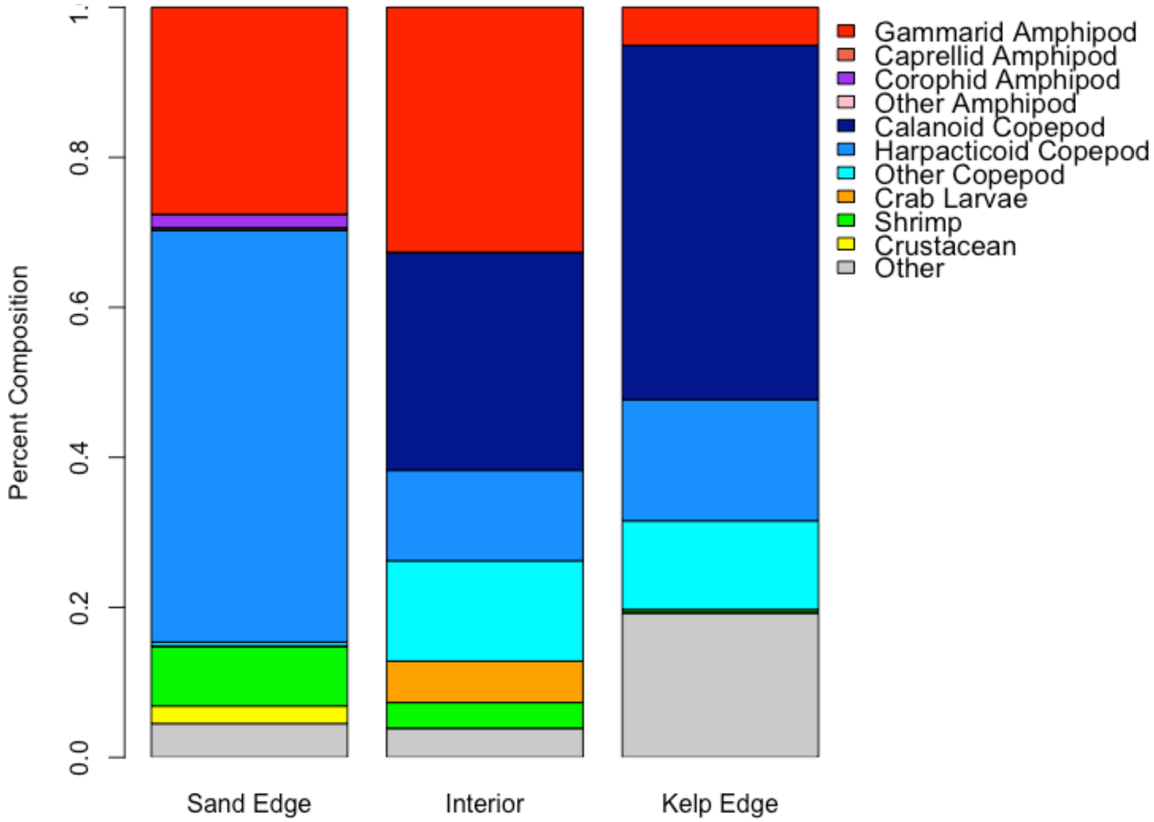

Figure 3.6 Percent composition of the index of relative importance (%IRI) of prey groups in YOY Copper Rockfish diets across seagrass sites: Sand Edges (n=29), Interiors (n=4), and Kelp Edges (n=19). %IRI was calculated using % numerical abundance, % gravimetrical weight, and % frequency of occurrence of prey items (Appendix J) to reflect the contribution of prey to a consumer based on both energetic value and consumer foraging selection.

The relative importance of taxa varied among habitat-adjacency types. Harpacticoid copepods were three and two times more important at the sand edge (55% of diet), than the interior (12%) and kelp edge (16%) sites (Fig. 3.6). Calanoid copepods, however, were the most important prey item, and copepod species, at the kelp edge sites (47% of diet). Prey composition was most diverse and even at the interior (H'=1.65, J = 0.85) as compared to kelp edge (H' =1.39, J=0.72) and sand edge (H' =1.24, J=0.52), respectively. Prey composition at the interior sites was an intermediate of both edge sites, consisting of similar species type and composition from both edges. The sample size at the interior sites, however, was low (n=4) relative to edge sites, and may be a less reliable representation of prey composition at these sites.

3.3.5 Body condition of YOY Copper Rockfish

I found differences in the health of YOY Copper Rockfish across habitat adjacencies in the seagrass meadow using elemental (carbon and nitrogen) metrics (Fig. 3.7). YOY rockfish body condition, based on C:N ratio of tissue, was significantly different among sites (ANOVA; p=0.004), with higher values at kelp edges and interior sites than sand edges (Fig. 3.7). Body condition using the modified Fulton's K index did not differ across sites, nor did length or weight. However, fish exhibited smaller body thickness (e.g. height) at the sand edges relative to interior (ANOVA; p <0.001) and kelp edges (ANOVA; p=0.03).

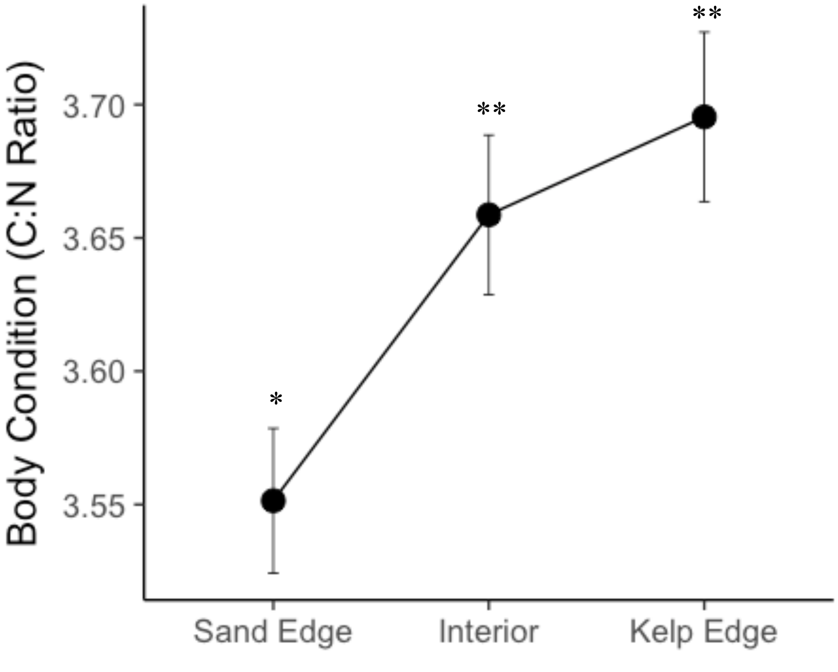

Figure 3.7 Mean (± SE) body condition of YOY Copper Rockfish, as calculated by C:N ratio. Rockfish were collected at sites in the seagrass meadow varying in habitat adjacency: sand edge (n=25), interior sites (n=29) and kelp edges (n=32). Differences in asterisk (*) number indicates significant differences among body conditions by Tukey's post-hoc testing.

3.4 Discussion

Seascape connectivity, particularly the adjacency of kelp forests, influenced seagrass nursery function for juvenile fish by providing broad and spatial detrital contributions to the base of the seagrass food web. Based on isotopic dietary analysis, allochthonous, kelp-derived nutrients were the most prevalent basal source to YOY Copper Rockfish consumers in the seagrass meadow (43-53% of diet, Fig. 3.5). Seagrass itself contributed the least to dietary sources across the seascape (5-10% of diet). Kelp occupied the mid-range of producer palatability, but the more palatable sources contributed less to diet (POM: 20%, seagrass epiphytes: 17% of diet). Basal inputs from *N. luetkeana* forests broadly subsidized seagrass food webs, at both interior and edge sites, despite high autochthonous seagrass and epiphyte biomass production (Chapter 2) and palatability (Fig. 3.3). Along with the ubiquity of kelp-derived nutrients in diets across the seascape, I also found that within a single seagrass meadow, there was spatial variation of basal sources and prey composition in juvenile rockfish diets, as well as higher body conditions, in association with adjacency to habitat structure. Kelp forests likely provided habitat complexity and associated sources for diverse, multi-trophic subsidies to the seagrass food web.

3.4.1 Spatial distribution of basal subsidies by habitat adjacency

While trophic subsidization operated across the spatial scale of the entire seagrass seascape, effects on nursery function were observed in association with local effects of habitat-adjacency. Contrary to our hypothesis, rockfish at the sand edges had the highest proportion of kelp-derived nutrients in their diets (e.g., higher than kelp edges) and the lowest proportion of seagrass epiphytes (Fig. 3.5). Previous studies have shown that despite declines in kelp-detritus away from kelp forests, broken-down suspended particulate kelp is widespread and easily integrated into food webs (vonBiela, Newsome, Bodkin, Kruse, & Zimmerman, 2016). Comparable to studies of other nearshore habitats (Kaehler et al., 2006; Ramshaw, 2012), the incorporation of kelp-derived nutrients throughout the Choked Pass seagrass bed was not limited by kelp bed proximity, but showed local scale effects on juvenile fish consumers depending on habitat adjacency. Local habitat-adjacency effects were also observed for POM, where the contribution of POM to YOY diets was significantly lower at the kelp edge. Physical shading from kelp forest canopies may limit POM productivity, altering availability of POM to the food web (Borchers & Field, 1981).

Aquatic habitat connectivity has been demonstrated to alter the diversity and evenness of prey items (e.g. species niche), thereby affecting trophic stability and function (Doi, 2009; Layman, Quattrochi, Peyer, & Allgeier, 2007; Polis et al., 1997). Diets of YOY Copper Rockfish at the edge sites were altered relative to interior sites (Fig. 3.5-3.6). Rockfish at sand edges consumed noticeably less calanoid copepods, relative to at interior and kelp edges (Fig. 3.6, Appendix J). Calanoid copepods are one of the most lipid-rich prey items in the nearshore environment (Falk-Petersen, Sargent, & Tande, 1987; Sargent & Falk-Petersen, 1988), supporting some of the largest marine consumers such as North Atlantic Right Whales (Baumgartner, Cole, Campbell, Teegarden, & Durbin, 2003). Improved rockfish body condition in structurally complex habitats may be a result of access to the high quality, lipid-rich calanoid copepods (Falk-Petersen et al., 1987) associated with kelp forests (Pakhomov et al., 2002).

Transport of allochthonous kelp detritus has been shown to subsidize a large suite of consumers in recipient ecosystems (Duggins et al., 1989; Hyndes et al., 2012; Kelly et al., 2012; Vanderklift & Wernberg, 2008). Kelp-derived nutrients were the dominant source of basal contribution to YOY rockfish, two times greater than the uptake of POM production, the secondarily dominant basal contribution to rockfish (Fig. 3.5). Analogous to other food webs, POM reflected low to intermediate isotopic contributions to consumers (Benstead, March, Fry, Ewel, & Pringle, 2006; Jaschinski, Brepohl, & Sommer, 2008). However, in most other studies of seagrass food webs, seagrass or its epiphytic algal production, best reflect consumer diets, despite the inclusion of allochthonous sources (Benstead et al., 2006; Jaschinski et al., 2008; Kharlamenko, Kiyashko, Imbs, & Vyshkvartzev, 2001; Moncreiff & Sullivan, 2001). This study demonstrates the opposite; allochthonous primary production fuels the diets of YOY rockfish in a seagrass meadow, with spatial variation based on the type of adjacent habitat. Autochthonous production within seagrass beds is an important contributor to rockfish diets, but does not appear to influence the uptake of allochthonous subsidies.

3.4.2 Variation in rockfish prey and consequences on body condition

In the food web models, I assumed that primary production propagated through the food web from primary sources to primary or secondary invertebrate consumers (i.e., fish prey). Direct isotopic measurements of invertebrate consumers were not available, but experimental evidence (Doropoulos et al., 2009; Hyndes et al., 2012), assumptions based on knowledge of predator (Studebaker & Mulligan, 2009) and prey feeding behaviors (Brown & Sibert, 2011; El-Sabaawi, Dower, Kainz, & Mazumder, 2009; Kleppel, 1993; Rieper, 1978), and stomach content data (Fig. 3.6), indicate strong trophic linkages between primary producers and YOY rockfish consumers (Fig. 3.2). Fish stomach contents revealed that harpacticoid copepods, a detritivorous and bottom-feeding zooplankton, were four to five times more important to diets at the sand edge, whereas pelagic calanoid copepods were most important in interior and kelp edge diets (Fig. 3.6), suggesting habitat availability influences prey distributions. Prey preference may reflect local invertebrate abundances, drift of invertebrates into the seagrass edge, or whether invertebrates foraged in the adjacent habitat. The modeled food web was robust to these potential variations in prey and basal input pathways because producer values used to model YOY rockfish diets were not constrained by site, rather the food web was open to the full seascape, with producer inputs spatially averaged.

Allochthonous kelp inputs can boost invertebrate consumer production (Bustamante et al., 1995b; Duggins & Eckman, 1997) and contribute to the diets of fish consumers (Koenigs et al., 2015). YOY rockfish demonstrated higher nutritional condition, as calculated by C:N ratio, associated with sites having high structural complexity, autochthonous seagrass epiphyte production, and diets comprised of calanoid copepods (Fig. 3.5 & 3.7). This can be in part due to the quality of primary producers available (Fig. 3.3). Their nutritional quality can propagate through trophic levels and impact juvenile fish condition (Boersma et al., 2008), as seen in larval herring (*Clupea pallasii*) (Malzahn, Aberle, Clemmesen, & Boersma, 2007). Not mutually exclusive to this, better fish condition could be due to better quality prey at sites in seagrass interiors and kelp forests (Fig. 3.6). These results suggest that higher body condition of YOY rockfish is mediated by habitat complexity and its interactions with prey communities. Thus, the spatial adjacency to structural kelp forests may be a component of seagrass' nursery role for YOY Copper Rockfish. While rockfish did not demonstrate differences in the modified Fulton’s measure of body condition, lipid content of YOY rockfish has been demonstrated to be a better assessor of nutritional condition than length-weight relationships (Norton, 2001).

3.4.3 Mechanistic effects of habitat adjacency on seagrass meadows

Multiple mechanisms may explain how the structural complexity of adjacent kelp forests affects subsidization of the seagrass food webs at the local scale. Due to high biomass and vertical structure, kelp forests can decrease water velocities and increase deposition of particulate matter (Eckman, Duggins, & Sewell, 1989; Gaylord, Rosman, Reed, & Koseff, 2007). Because kelp can be incorporated into the diets of grazers and suspension feeders through detrital pathways (Bustamante, Branch, & Eekhout, 1995a; Duggins et al., 1989; Dunton & Schell, 1987; Norderhaug, Fredriksen, & Nygaard, 2003), detrital production and retention in kelp forests may alter the relative availability and composition of basal sources to consumers (Duggins, Eckman, & Sewell, 1990; Eckman et al., 1989). This likely explains the high evenness of source inputs to kelp edges within the adjacent seagrass edge sites (Fig. 3.5).

Zooplankton availability may be optimized in kelp forests. Large detrital quantities in kelp forests can prime microbial activity and communities (Clasen & Shurin, 2015), augmenting zooplankton feeding rates (Delille, Marty, Cansemi-Soullard, & Frankignoulle, 1997). Kelp forests can also provide a prey refuge for zooplankton compared to the open ocean (Pakhomov et al., 2002); increasing their local densities and altering their distributions. Thus, mobile seagrass consumers may benefit from adjacency to kelp habitats, allowing proximate access to a diverse array of prey items (Fig. 3.5). Or, kelp-associated plankton may drift into seagrass beds as a subsidy for bottom consumers (Fig. 3.5-3.6).

Lastly, YOY fish foraging behaviours may be altered by structural complexity, at both interior and kelp edge sites. At the kelp sites, the added vertical growth of kelp through the adjacent water column may provide additional protection from predators and access to pelagic-associated lipid-rich calanoid copepod prey rather than harpacticoids. Our study design did not allow for an explicit distance-based examination of the propagation of adjacency effects into the seagrass meadow, but producer and prey trends at interior sites may reflect the influence of edge effects from both adjacent habitats. Interior sites appear to represent a transition zone in dominance of secondary sources of primary production (Fig. 3.5), and a mix of dominant invertebrate prey from both kelp and sand edges (Fig. 3.6).

3.4.4 Summary

While the concept of allochthonous subsidies from seagrass to recipient ecosystems is familiar (Heck et al., 2008), this study illustrates that reciprocal subsidies and habitat adjacency, demand equal research attention. Allochthonous kelp-derived nutrients were dominant constituents of seagrass food webs, and local effects of adjacent habitats were also important. Spatial adjacency to kelp forests provided both inputs to seagrass food webs, as well as the addition of structural complexity, which can alter proximate physical and biological conditions at the seagrass bed edge resulting in alterations to the food web. Together, these components of habitat adjacency affected the composition of basal sources and prey inputs across the seagrass seascape and ultimately, were also associated with differences in body condition, a key trait associated with survival, and thus nursery function (Beck et al., 2001). However, the robustness of these findings demand broader comparative studies. From a seascape perspective, additional understanding of the interaction between adjacent habitat, and distance from recipient habitat, could be further investigated through examination of alternative habitat configurations or experimental manipulations of the seascape. Moreover, understanding fish feeding behaviours and acquiring species-specific discrimination factors would refine the assumptions made in the simplified mixing model.

Coastal seascape configuration is complex. The Choked Passage seagrass bed is illustrative of this complexity, located within a matrix of different habitats types (some vegetated, and others un-vegetated), and with physical and biological processes operating at several spatial scales to affect ecosystem dynamics. This study adds to the growing consensus that marine food webs are dynamic and highly influenced by seascape connectivity. Because of the high connectivity between important nearshore habitats, the impacts of habitat loss and species declines, cannot be viewed in isolation. Rather, the conservation of nearshore nurseries and marine fisheries needs to be addressed through the lens of the seascape, including an understanding of habitat diversity, connectivity, and spatial scale.

Chapter 4: Conclusion

The nearshore seascape in Choked Passage, BC, exemplified by the large subtidal seagrass bed and adjacent habitats, demonstrate how habitat adjacency, and its structural complexity, can influence recruitment of juvenile rockfishes to seagrass nursery habitats. This study focused on determining how seagrass connectivity to adjacent habitats, either kelp forests or sand habitats, influenced both the recruitment and diets of YOY Copper Rockfish. Specifically, I documented spatial and seasonal patterns in YOY Copper Rockfish densities following a large recruitment likely associated with an El Nino event during the summer of 2015 (McCabe et al., 2016), thus may not be representative of recruitment in other years. Underwater observations of YOY Copper Rockfish recruitment densities were associated with prey availability, habitat complexity, and habitat adjacency. Food web analysis using stable isotopes, also suggested spatial variation in YOY Copper rockfish diets between seagrass sites that varied in habitat adjacency. However, the dominance of kelp-derived production fueled juvenile rockfish food webs across the seagrass seascape. These findings reinforce, and augment, our understanding of seagrass meadows as functional nursery grounds in temperate nearshore systems. Together, the results emphasize the overarching role of seascape (e.g. 'landscape') connectivity, including metrics of habitat complexity and adjacency, in determining nursery function.

4.1 Seagrass nurseries for rockfish

Seagrass meadows have been previously documented as important nursery habitats for Copper Rockfish, where broadly both habitat and prey provision contribute to nursery effects (Haldorson & Richards, 1987; Jeffery, 2008; Love et al., 1991;

Studebaker & Mulligan, 2009). Building on this work, this study found that seagrass habitat complexity was a major driver of YOY Copper Rockfish recruitment, such that higher complexity led to higher densities within different areas (e.g. edge vs. interior) of the seagrass meadow (Chapter 2). During initial, early summer observations, greater recruitment was found in the seagrass meadow compared to adjacent kelp forests, however this pattern reversed in the late-summer. The sizes of rockfish also increased at all sites in the last observational period relative to the previous observation period, thus this study was not able to detect seascape-specific movement of rockfish from seagrass beds to kelp forests. Extending the observation period into fall would aid in detecting such habitat transitions. Elsewhere, it has been observed that YOY rockfish transition to kelp forests after spending time in seagrass beds (Kamimura & Shoji, 2013; Love et al., 1991), however in the Strait of Georgia (BC), YOY Copper Rockfish had an opposite habitat transition due to the ephemeral summer availability of *N. luetkeana* (Haldorson & Richards, 1987). This study did not include observations beyond the summer months, thus full knowledge of habitat-mediated rockfish recruitment, throughout their life cycle, is lacking. Additional studies are encouraged that track rockfish movement and habitat usage from settlement to recruitment to the adult populations.

Study findings also demonstrated that seagrass-associated prey provided a positive influence on rockfish densities (Chapter 2). Only a single prey item from seagrass habitats, gammarid amphipods, was a positive predictor of rockfish density among a suite of invertebrates tested. This is likely due to the early life stage and small sizes of rockfish occupying the seagrass habitats and their dependence on smaller prey items (Love et al., 1991). Small zooplankton, such as harpacticoid and calanoid copepods, were the dominant prey items in Copper Rockfish diets, whereas gammarids were less so (Chapter 3). These results are comparable to other dietary studies of Copper Rockfish in seagrass (Haldorson & Richards, 1987; Studebaker & Mulligan, 2009). While both internal attributes influenced the nursery role of seagrass for rockfish, habitat adjacency demonstrated to be an equally important factor in its nursery role.

4.2 Seascape-level effects on nursery function

The connectivity of seagrass to both kelp forests and sand habitats via spatial adjacency revealed complex consequences on the recruitment and diets of YOY Copper Rockfish occupying seagrass. Adjacency to kelp forests positively affected recruitment densities, as expected (Chapter 2). However, this effect was interactive and dependent on seagrass habitat complexity, where increased seagrass complexity at kelp edges reduced recruitment (Chapter 2) despite the availability of high-quality prey and high YOY body condition at seagrass-kelp adjacent sites (Chapter 3). These results suggest that a trade-off may exist between habitat, food availability, and predation. The augmented densities of YOY Copper Rockfish and food web subsidies, predicted with the provision of adjacent kelp habitat structure, may also be modified by increased predation associated with kelp habitats and habitat complexity.

The ability of predators to modify the behavior of their prey and their use of the landscape is prevalent among marine organisms (Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009), including those inhabiting seagrass edges (Smith, Hindell, Jenkins, Connolly, & Keough, 2011), and rockfish, specifically (Frid, Marliave, & Heithaus, 2012). In this study, adult rockfish likely spilled over from kelp forests, enhancing predation at seagrass sites adjacent to kelp edges. In addition, these edge effects were likely amplified by complex seagrass habitat structure, which both YOY Copper Rockfish, and their predators, had affinity towards (Chapter 2). Together, these trends may explain the interactive results observed, where higher predation and/or predation risk may decrease recruitment to seagrass-kelp edges when seagrass habitat complexity is high, similar to other systems (Smith et al., 2008).

Across the seagrass landscape, *N. luetkeana* was consistently >40% of the total basal contributions to rockfish diets, based on isotopic analysis (Chapter 3), further demonstrating seagrass and kelp forests connectivity. This study highlights the importance of allochthonous kelp forest detritus at small and large scales in coastal ecosystems, as seen in other areas in BC (Ramshaw, 2012) and around the world (Kaehler et al., 2006). In seagrass systems specifically, studies in temperate Australia have demonstrated that seagrass invertebrate consumers can uptake kelp-derived sources of production (Doropoulos et al., 2009; Hyndes et al., 2012). We build on this work, demonstrating that kelp-derived contributions can resonate to higher trophic levels (Chapter 3).

Overall, seascape connectivity altered two of the four factors (e.g. density, growth, survival, and movement to adult populations) contributing to a habitat's nursery role, according to (Beck et al. 2001): juvenile growth and density. While growth was not measured directly, the nutritional condition and diets of YOY Copper Rockfish were measured as proxy for growth and survival probability (Norton, 2001), and were observed to be influenced by the adjacency of habitat types (Chapter 3). YOY Copper Rockfish in seagrass adjacent to unstructured sand habitats had lower quality diets and body condition relative to fish in seagrass interiors and kelp edges, while YOY Copper

Rockfish adjacent to kelp forests had the highest contributions of better quality prey. The influence of kelp forests on YOY rockfish densities can be attributed to greater prey availability and/or the physical, structural attributes kelp forests produce, including protection from wave energy (Madsen, Chambers, James, Koch, & Westlake, 2001). Another primary influence on densities is the provision of refuge from predators due to structural complexity. However, due to both the observed negative interaction with seagrass habitat complexity and the large abundances of predators at these sites, refugia at seagrass-kelp edges may be context-dependent. Kelp forests may provide some compensatory refugia when seagrass complexity is low, but the cost of predation outweighs the benefits of resources.

To disentangle the connectivity processes at play, future research should include both observational and experimental approaches investigating the effects of seascape habitat parameters on nursery function. Because a major role of habitat adjacency is a change in resource availability to consumers (Ries and Sisk 2004), comprehensive surveys of zooplankton communities across the nearshore seascape would enhance the findings of this study. Isotopic diet analysis of primary and secondary consumers in the seagrass meadow (e.g., zooplankton and seagrass mesograzers) at each site would give better resolution to the pathways of allochthonous and autochthonous nutrient transfer within the food web, and ultimately to YOY Copper Rockfish. Predation experiments at edges and interiors that vary in habitat complexity, would provide additional evidence towards predatory edge effects and habitat-mediated predator refugia. Lastly, the tagging of rockfish recruits would complement observations and provide increased resolution to studies of movement between habitats.

4.3 Implications for nearshore conservation

As seagrass ecosystems are under threat from increasing anthropogenic pressures globally, conservation is an utmost priority and should include seascape level considerations (Orth et al., 2006). Seascape-level conservation (e.g. conservation including connectivity to other habitats) for seagrasses may counteract habitat fragmentation, increase fish production, and protect areas of high biodiversity (Engelhard et al., 2016; Nagelkerken et al., 2015). Moreover, protecting seagrasses for direct contributions to nursery effects, but recognizing the spatial configuration of the nearshore seascape, especially adjacency to other nursery habitats, may enhance their nursery role. In tropical regions, for example, marine reserves can be more effective with the inclusion of seascape connectivity (Martin et al., 2015; Olds et al., 2013). For example, protected seagrass meadows adjacent to reefs contain higher juvenile fish than non-connected habitats (Olds et al., 2014). As such, incorporating seascape connectivity when identifying and implementing marine spatial planning should be prioritized (Engelhard et al., 2016).

Because kelp forests impact the nursery role of seagrass meadows, factors affecting their biomass, density and distribution are necessary considerations alongside seagrass conservation. Locally on the Central Coast, sea otters (*Enhydra lutris*) are returning to the area since their extirpation during the commercial fur trade in the 1700s (Gregr, Nichol, Watson, Ford, & Ellis, 2008; Kenyon, 1969; Nichol, Watson, Abernethy, Rechsteiner, & Towers, 2015; Rechsteiner & Olson, 2016). Effects on seagrass nursery function from an indirect alteration of *N. luetkeana* biomass via consumption by sea urchins by sea otters (Estes, Jameson, & Rhode, 1982) may positively influence the amount of kelp (habitat and resources) in the nearshore seascape available for rockfish (Markel & Shurin, 2015). Globally, kelp forest trends are variable, but demonstrate long term resiliency (Krumhansl & Scheibling, 2011). Kelp forest resiliency may spillover and have long term positive effects on seagrass ecosystems that are in more rapid decline (Waycott et al., 2009).

In BC, the declines of rockfish abundances (Yamanaka et al., 2004) have instigated the implementation of Rockfish Conservation Areas (RCAs) across the coast to recover rockfish populations (Yamanaka & Logan, 2010). RCAs have been focused on adult habitats, such as rocky-reef and kelp forest areas, due to rockfish's long-life span and increased fecundity with age. The protection of seagrasses may complement the actions of RCAs by fueling rockfish supply to adult habitats, via increased nursery area and/or aiding ontogenetic movements between habitats. The increasing evidence that rockfish species use seagrasses as nurseries should highlight the importance of seagrasses for commercially, biologically, and culturally significant fish, including rockfish and others.

Seagrass meadows and kelp forests have both been identified as critical habitats for conservation on the Central Coast (Marine Planning Partnership Initiative, 2015). This study provides empirical data on the importance of seagrass and kelp forests as nurseries, through the provision of both habitat and prey, to rockfish. Moreover, it suggests that conserving spatial connectivity between these habitats may enhance conservation efforts. While this thesis is a case study of one seascape on the Central Coast, BC, the matrix of structured seagrass and macroalgae habitats, and unstructured soft sediments are emblematic of nearshore seascapes throughout temperate coastlines, and provide guidance on ‘landscape’ consideration for marine planning.

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Appendix

Appendix A. Definitions of commonly used ecological terms.

Definitions
Settlement: The stage at which a larval or young-of-the-year fish transitions from a pelagic environment to nearshore, shallow habitats. **Recruitment:** The settlement and early use of nearshore habitats. **Habitat Complexity:** The physical, three-dimensional structure of a vegetative habitat (e.g. seagrass) created by blades in the water column. **Spatial Adjacency:** The distance between two different habitat patches. **Seascape Connectivity:** The movement of animals or materials between habitat patches and driven by mechanisms like animal mobility, hydrodynamic forces, and spatial adjacency. **Nursery Habitat (Beck et al. 2001)**: An area that promotes the successful transition from juvenile to adult life stages, by increasing juvenile density, growth, survival, and/or movement to adult populations on a per unit habitat basis. **Seascape Nursery (Nagelkerken et al. 2013):** A spatially explicit seascape consisting of multiple mosaics of habitat patches that are functionally connected.

Appendix B. Site descriptions in Choked Passage within the 1) seagrass meadow (n=12) and 2) adjacent habitats: kelp forests (n=4) and sand habitats (n=4). Depth (ft) is represented by chart datum (ft), Ecotone Type describes the seagrass in detail, and Number (#) of Surveys is the total observational surveys conducted by SCUBA and snorkel along the permanent 40m transects at each site.

1) Seagrass Meadow Sites

Site	**Coordinates**	**Survey**	**Depth**	**Ecotone Type**	**# of Surveys**
FI	51.67491251 N, 128.1239469 W	Kelp Edge	15	Distinct edge to structure	44
LW	51.67892563 N, 128.1260155 W	Kelp Edge	6.6	Mix edge to structure	49
NP	51.67682936 N, 128.1226902 W	Kelp Edge	4.9	Mix edge to structure	49
SP	51.67634048 N, 128.1228858 W	Kelp Edge	4.9	Mix edge to structure	53
IT	51.67495962 N, 128.1194509 W	Interior	14.1	None	22
ID	51.67456225 N, 128.1177582 W	Interior	13.1	None	50
IC	51.67354962 N, 128.1179672 W	Interior	13.1	None	43
IA	51.67244774 N, 128.1179417 W	Interior	11.2	None	47
WF	51.67277642 N, 128.1169345 W	Sand Edge	6.6	Distinct edge no structure	42
AL	51.67525108 N, 128.1160256 W	Sand Edge	6.6	Distinct edge no structure	52
IS	51.67824958 N, 128.1145984 W	Sand Edge	5	Mix edge no structure	43
OS	51.67784391 N, 128.1167723 W	Sand Edge	16.3	Mix edge no structure	22

2) Adjacent Habitat Sites

Site	**Depth** (ft)	**Survey**	**Canopy Structure** (Listed in order of dominance)	**Understory Structure** (Listed in order of dominance)	**# of Surveys**
FI	15	Kelp	*Nereocystis luetkeana,* *Pterygophora californica*	*Desmarestia ligulata*, *Costaria costata*, *Cymathaere triplocata*	21
LW	6.6	Kelp	*Nereocystis luetkeana,* *Pterygophora californica*	*Desmarestia ligulata*, *Cymathaere triplocata*	34
NP	4.9	Kelp	*Nereocystis luetkeana*	*Desmarestia ligulata*, *Cymathaere triplocata*	33
SP	4.9	Kelp	*Nereocystis luetkeana*	*Desmarestia ligulata*, *Cymathaere triplocata*	36
WF	3.3	Sand	none	none	41
AL	3.3	Sand	none	none	48
IS	3.3	Sand	none	none	41
OS	23.3	Sand	none	none	21

Appendix C. List of invertebrates (or "mesograzers") identified on *Zostera marina* blades collected across the seascape in Choked Passage from May – August 2015.

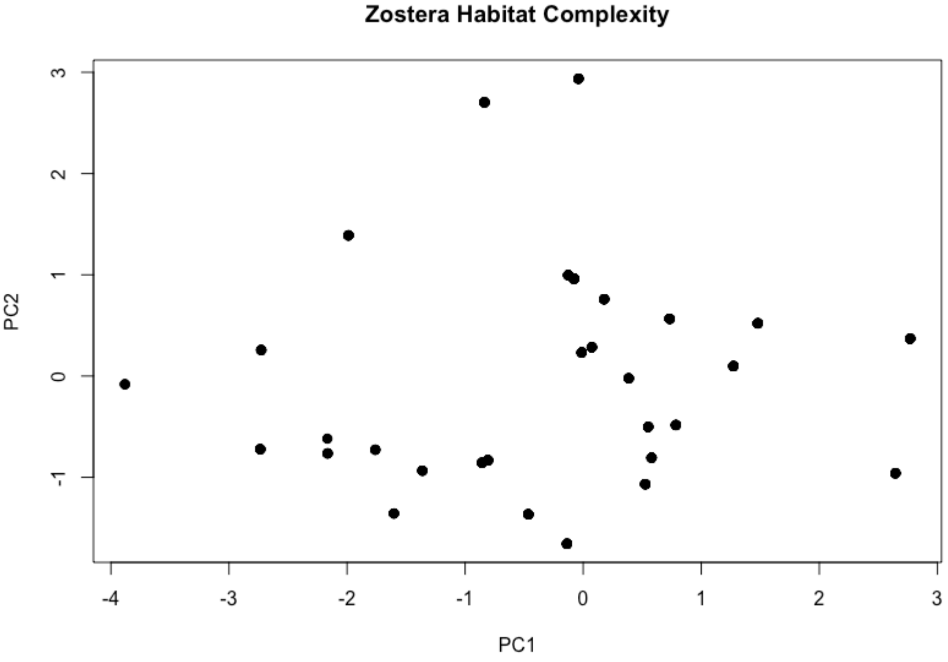
Broad Classification	**Prey Functional Group**	**Further identification (If applicable)**
Amphipod	Caprellid Amphipod	*Caprellid alaskana*
	Gammarid Amphipod	Gammaridae spp
Anemone	Anemone	Stalked Anemone, Brooding Anemone
Bryozoan	Bryozoan	
Echinoderm	Sea cucumber	*Parastichopus californicus*
Fish	Fish egg	*Aulorhynchus flavidus*
Hydroid	Hydroid	
Isopod	Isopod	*Idotea resecata*, Idotea spp
Medusozoa	Jelly Fish	
Mollusca	Bubble snail	
	Lacuna snail	
	Lacuna snail egg	
	Limpet	
	Mussel	
	Nudibranch	
	Crab	Magidae spp, Cancer spp
Worm	Worm	Polycheate spp, Annelidae spp, Platyhelminthes *spp*

Appendix D. Principal Components Analysis (PCA) results using mean *Z. marina* biomass (g), mean *Z. marina* shoot density (number of shoots/quadrat), and *Z. marina* canopy height (cm) per transect, to obtain a metric of *Zostera marina* habitat complexity. PC1 accounted for 60% of the variability among transect, whereas PC2) accounted for 29% and PC3 accounted for 11% variation (D1). Explaining the most variance of Zostera habitat complexity, PC1 was used as the metric of habitat complexity in GLMMs (shown in D2).

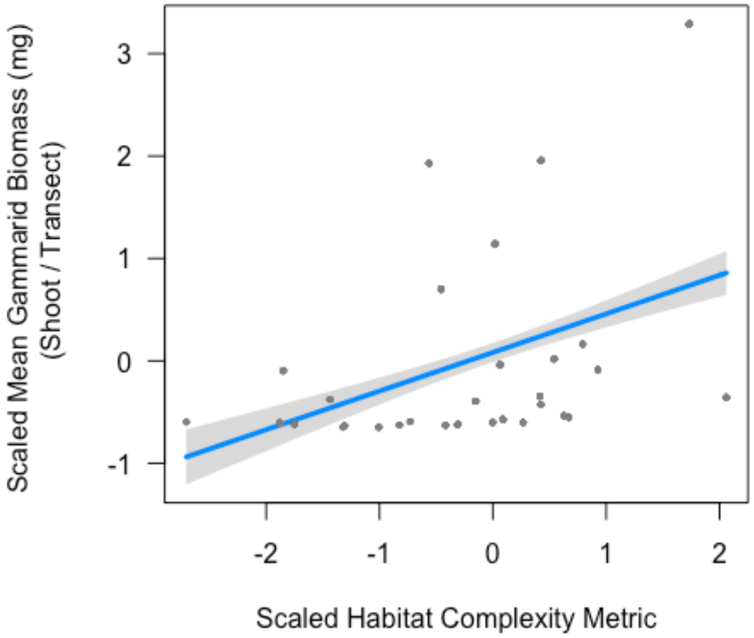
1) Table of Results

		PC1	**PC2**	**PC3**
Seagrass Habitat Measurement	Mean Canopy Height	0.66	-0.20	-0.72
	Mean Biomass	0.64	-0.33	0.68
	Mean Density	0.38	0.92	0.09
Principal Components Results	Standard Deviation	1.34	0.93	0.57
	Proportion of Variance	0.60	0.29	0.11
	Cumulative Proportion	0.60	0.89	1.0

2) Plot of PC1 and PC2.



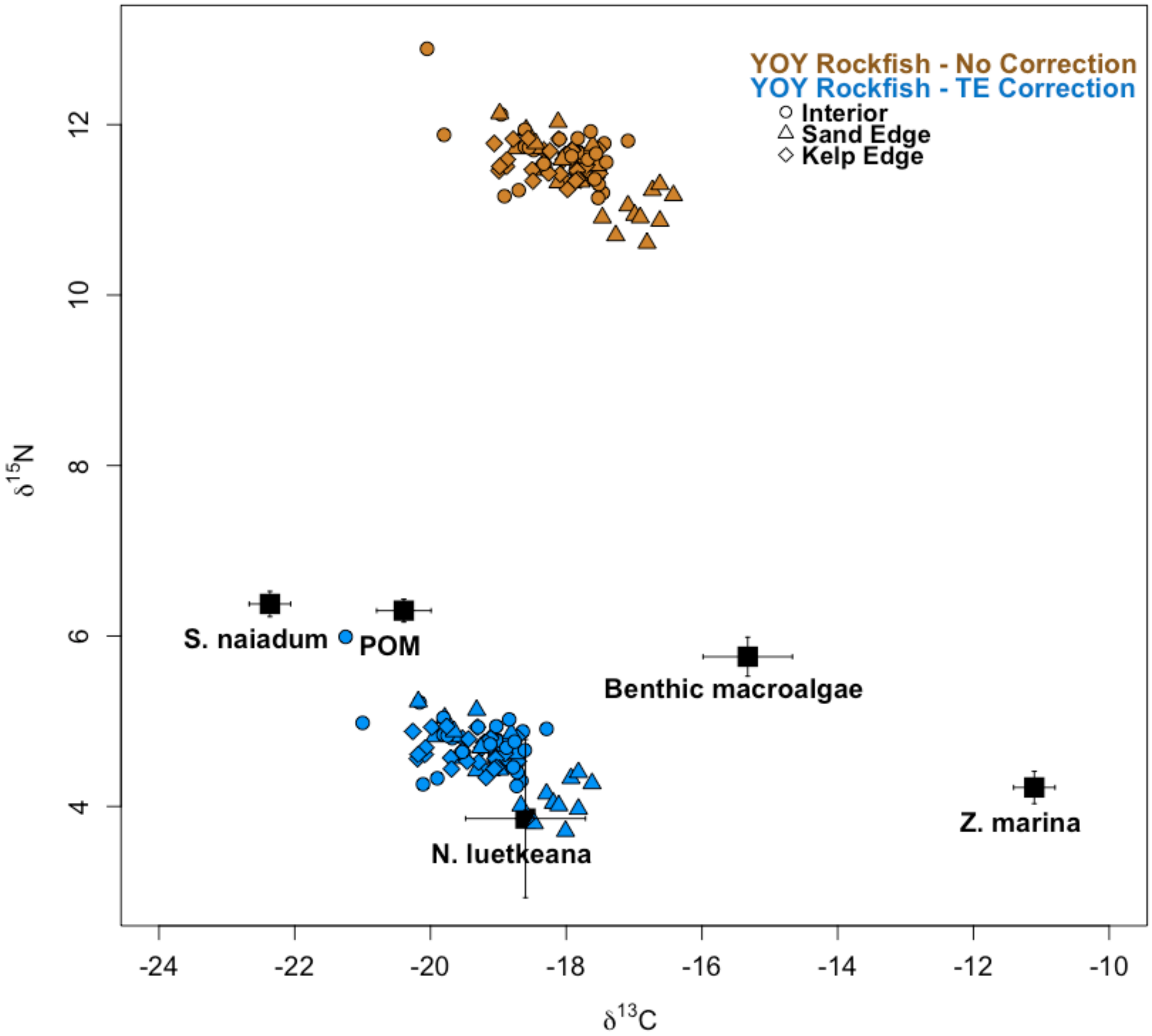
Appendix E. Positive linear relationship between *Zostera marina* complexity habitat metric from PCA 1 (Appendix D) and mean gammarid shoot biomass (mg) per transect (blue line, *b* = 0.38, p <0.001). Grey bars indicate the 95% confidence intervals around the predicted linear relationship.



Appendix F. Strength of evidence for alternative candidate models explaining adult rockfish densities in seagrass meadows by habitat features (Zostera complexity and habitat adjacency). Models are ranked by differences in Akaike Information Criterion (ΔAIC) and normalized Akaike weights (W_i), obtained through the balance between model likelihood (Log(L)) with model parsimony indicated by number of parameters (K).

Response: Adult Rockfish					
Explanatory Parameters	DF	Log (L)	AIC	ΔAIC	W_i
Zostera Complexity * Adjacent Habitat	**8**	**-896**	**1808**	**0**	**1**
Zostera Complexity	6	-940	1893	83.9	<0.001
Adjacent Habitat	7	-1213	2440	631.4	<0.001
Null	5	-1629	3270	1461.1	<0.001

Appendix G. $\delta^{13}C$ and $\delta^{15}N$ biplot of YOY Copper Rockfish values before (brown) and after (blue) trophic enrichment correction factors based on the simplified seagrass food web showing estimating trophic transfers (Fig. 2). Mean and standard errors of basal sources $\delta^{13}C$ and $\delta^{15}N$ signatures (black squares) based on the following sites in the seagrass meadow: Interior (circles), Sand Edge (triangles), and Kelp Edges (diamonds).



Appendix H. List of invertebrates found in the stomach contents of YOY Copper Rockfish within the seagrass meadow of Choked Pass: sand edge (n = 29), interior (n=4), and kelp edge (n = 19).

Broad Category	**Prey Grouping**	**Species**	**Foraging behaviours**
Amphipods	Caprellid amphipod	*Caprella alaskana*	Suspension feeder
	Corophid amphipod	-	Detritivore
	Gammarid amphipod	-	Carnivorous & Herbivorous
	Other amphipod	-	-
Copepods	Calanoid copepod	-	Omnivore
	Harpacticoid copepod	-	Detritivore
	Other copepod	Cyclopoid copepod	-
		Unknown copepod	-
Shrimp	Shrimp	Caridean spp.	Omnivore
		Pandalid spp	Omnivore
Crab	Crab larvae	Unknown larval crab, brachyuran pre-zoea	Plankton Plankton
Crustacean Other	Crustacean Unknown	Nauplius larvae	Plankton
Other	Other	Unknown eggs	-
		Unknown	-

Appendix I. Mean dietary proportions of each basal resource for rockfish consumers estimated by MIXSIAR mixing model, along with standard deviation (SD) and quantiles of posterior probability distributions. YOY rockfish were collected across the seagrass landscape at the interior of the bed, sand edges, and kelp edges. 5 potential basal resources were included: Benthic macroalgae (*C. triplicata* and *A. marginata*), *N. luetkeana*, POM, *S. naiadum*, and *Z. marina*).

Primary Source	**Site**	**Source Contribution**	**Source Contribution in Posterior Density Quantiles**				
		Mean (%) ± SD	**2.5**	**25**	**50**	**75**	**97.5**
Benthic macroalgae	Interior	0.105 ± 0.098	0.002	0.025	0.074	0.161	0.342
	Kelp Edge	0.062 ± 0.055	0.001	0.017	0.048	0.093	0.201
	Sand Edge	0.122 ± 0.119	0.001	0.019	0.081	0.202	0.395
N. luetkeana	Interior	0.442 ± 0.118	0.258	0.355	0.427	0.515	0.71
	Kelp Edge	0.434 ± 0.118	0.256	0.347	0.415	0.503	0.707
	Sand Edge	0.531 ± 0.139	0.312	0.429	0.513	0.618	0.839
POM	Interior	0.242 ± 0.151	0.01	0.118	0.237	0.357	0.533
	Kelp Edge	0.148 ± 0.105	0.007	0.063	0.132	0.21	0.39
	Sand Edge	0.199 ± 0.15	0.005	0.065	0.178	0.313	0.514
S. naiadum	Interior	0.159 ± 0.096	0.018	0.082	0.143	0.223	0.37
	Kelp Edge	0.262 ± 0.114	0.021	0.186	0.277	0.347	0.453
	Sand Edge	0.099 ± 0.082	0.005	0.035	0.075	0.144	0.305
Z. marina	Interior	0.052 ± 0.037	0.004	0.023	0.043	0.071	0.149
	Kelp Edge	0.095 ± 0.052	0.003	0.056	0.096	0.134	0.193
	Sand Edge	0.049 ± 0.045	0.001	0.013	0.035	0.072	0.159

Appendix J. Stacked bar plots showing the 1) numerical, 2) gravimetric, 3) frequency, and 4) Index of Relative Importance percent contributions of prey items (colours) consumed by YOY Copper Rockfish across seagrass Sand Edge (n=29), Interior (n=4), and Kelp Edge (n=19) sites in Choked Passage.