

EFFECTS OF ENVIRONMENTAL CHARACTERISTICS ON THE FISH
ASSEMBLAGES OF HIGH LATITUDE KELP FORESTS IN SOUTH-CENTRAL
ALASKA

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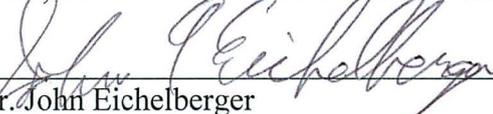
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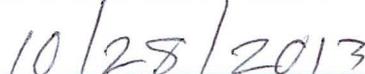
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ALASKA

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By

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Abstract

Alaskan kelp forests are patchy habitats, varying greatly in size, physical complexity, and biotic and abiotic characteristics, and are important to fish communities. Patchy habitats often support different communities on patch edges versus interiors, while patch size and physical complexity are typically correlated to the resident community structure. This study quantified the biological and physical heterogeneity within different sized kelp forests and identified which factors are important in structuring the associated fish communities. Fish and habitat surveys were conducted at ten kelp forests of varying sizes. Significantly different fish communities were found at edge compared to interior locations. The relative abundance of seven species explained 91.4% of the variability in the fish community. Fish community structure was not correlated with kelp forest size or the species composition of canopy forming kelps. Instead, it related to the abundances of two understory kelps, bottom rugosity, and water depth. Together these benthic attributes correlated with 53.6% of the fish community variability. These findings suggest that within patchy systems that are spatially and structurally non-uniform, associated fish species composition and abundance may be more directly linked to location within the patch and year-round habitat complexity rather than habitat patch size or foundational species composition.

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Introduction

Studies examining patchy habitats and how they influence resident biodiversity and abundances have their roots in the theory of island biogeography. This theory attempts to explain patterns in community dynamics, such as species richness and distribution, in relation to environmental factors such as habitat area, structural composition and physical features (MacArthur and Wilson, 1967). Originally applied to true islands, the theory has grown to include any habitat patch surrounded by dissimilar habitats and has been applied to terrestrial systems such as grasslands, shrublands, deserts, and canopy forests (Bradford et al., 2003; Davis and Brittingham, 2004; Hoover et al., 1995; Phillips and Shure, 1990). This theory has shown, in part, that population densities, species diversity and species interactions of island or patch inhabitants can be influenced by two characteristics: patch size and within-patch location, i.e. edge or interior region of a given patch (Bender et al., 1998). Another important aspect to the inhabitants of patchy environments is the morphology of the foundation species, or the dominant primary producer in terms of abundance and influence in an ecosystem. For example, oak, oak-pine, and pine forests in the Missouri Ozarks differ in bird species composition depending on the forest type showing that species composition is correlated to dominant vegetation type (Briggs et al., 1982).

In the marine environment, kelp forests epitomize patchy habitats. These forests often have distinct edges and are variable in distribution, size, and foundation species. Kelp forest location and size can be influenced by various factors such as wave exposure, grazing pressure by herbivores, availability of light, availability and type of substrate, and nutrient concentration (Dayton, 1985). The foundation species of these forests are the

canopy forming kelps, which can differ greatly in morphology (Lindeberg and Lindstrom, 2010). Combinations of these factors frequently result in kelp forest patches with abrupt edges and gaps between forests.

The physical structure of kelp forests is dictated by the morphology of the dominant kelp species and is under the influence of many factors. For example, *Macrocystis pyrifera* (hereafter *Macrocystis*) and *Nereocystis luetkeana* (hereafter *Nereocystis*) are two morphologically dissimilar canopy forming kelps whose ranges overlap in California. Which of the two kelps dominate a given forest is structured by the presence of severe and persistent disturbances, such as continued exposure to large swells or heavy grazing pressure (Dayton et al., 1980). In Kachemak Bay, Alaska, kelp forests have shifted in their dominant canopy forming species over the last forty years. In the 1970s, *Eualaria fistulosa* (formerly *Alaria fistulosa* and hereafter *Eualaria*) dominated (Lees, 1976). From 2000 to 2006, *Nereocystis* dominated (Deiman et al., 2008) and in the summers of 2008 and 2009, *Eualaria* began to reestablish (pers obs.). Currently, the dominant canopy forming kelp is *Nereocystis*; however, isolated *Eualaria* patches are becoming more common. Like the kelps in the California example above, *Eualaria* and *Nereocystis* differ in their morphology. *Eualaria* consists of a hapterous holdfast, short stipe, many reproductive blade-like sporophylls, and a single blade emerging from the top of the stipe. This apical blade has a fistulated midrib of pneumatocysts that keeps the wide blade floating in the water column. *Eualaria* ranges from Japan and Russia in the Northwest Pacific throughout the Aleutian Islands and down to southern Southeast Alaska. *Nereocystis* is also comprised of a hapterous holdfast, but the similarities stop

there. Each individual has a thallus that has a long slender stipe that reaches through the water column to a single large pneumatocyst located at or near the water's surface. Many blades, which become reproductive, grow from the pneumatocyst, creating a surface canopy. It is distributed from Umnak Island, in the eastern Aleutian Islands, to San Luis Obispo County, California (Lindeberg and Lindstrom, 2010). Where these kelp species distributions overlap, the persistence of one over another can be temporally and spatially variable including: monospecific forests, forests with spatial segregation of the two species with one dominating the nearshore edge and the other offshore, a homogenous mix, or the occasional individual growing within an otherwise single species dominated forest.

Kelp forests are important for fish communities. They are used for spawning/mating (Adreani et al., 2004; Erisman and Allen, 2006), nurseries (Carr, 1989; Holbrook et al., 1990; Love et al., 1991), feeding (Norderhaug et al., 2005; Schmitt and Holbrook, 1985), predator avoidance (Carr, 1992; Shaffer, 2003), and shelter from currents (Jackson and Winant, 1983). Fish can benefit directly from the three-dimensional structure (i.e., cover and shelter) or indirectly (i.e., kelp associated prey). Much of the fish/kelp forest association is grounded in the structure provided by the kelp, as there are very few fish that consume kelps. Consequently, the differences in the biotic and abiotic structure of kelp forests influence the fishes living within them.

Several characteristic of patchy aquatic habitats can affect fish communities including; within patch location, overall habitat size, the physical structure of the habitat as dictated by the morphology of the foundation species, benthic characteristics, and

water mass qualities. Different locations within patchy aquatic macrophyte habitats affect fish abundance often due to species specific predator prey dynamics or life history traits. For example, blue rockfish (*Sebastes mystinus*) typically occupy the midwater of the seaward edge of kelp patches on rocky pinnacles (Jorgensen et al., 2006). Reduced current velocity inside the forest, due to the baffling effect of the canopy kelps, increases the feeding efficiency of these planktivorous fish while occupying the seaward edge provides first access to the prey with the additional benefit of increased cover from predators (Gaines and Roughgarden, 1987). In salt marshes resident fish communities from the family *Cyprinodontiformes* and genus *Palaemonetes* dominate the central portion of the patch, while the edge is used by both the resident species and their transient predators (Peterson and Turner, 1994). Furthermore, ontogenetic shifts of larval dispersing fishes can result in non-homogenous distribution of a species through a patch. Many rockfishes (*Sebastes* spp.) recruit to the physical structure of kelps resulting in high densities along the seaward edges of the forest (Love et al., 1991), whereas some gadids recruit to intertidal areas and move offshore as a cohort (Rangeley and Kramer, 1998).

In general, overall patch size can vary temporally and spatially. This variance has implications for the abundance and composition of associated species (Bender et al., 1998; Simberloff, 1974). Seasonality is one example of temporal variability that can impact habitat patch size and is especially pronounced in South-central Alaska where kelp forests are largely composed of annual kelp species. Kelp density and spatial extent is relatively high in summer compared to winter when annual kelps senesce and are removed by winter storms. Another factor impacting kelp forest size variability is

herbivore grazing, which may destroy kelp forests (Feehan et al., 2012; Konar, 2000; Konar and Estes, 2003; Sivertsen, 2006). In some areas around Alaska, large kelp forests have been diminished by sea urchin grazing so that only remnant forests remain (Estes et al., 2004; Konar, 2000).

Diminished patch size can affect fish community structure in many subtidal macrophyte systems. In Australia, large seagrass patches displayed two distinct fish communities based on their location within the patch (i.e., edge or interior) whereas small patches hosted an edge community (Jelbart et al., 2006). In another seagrass study, small patches hosted greater fish densities than medium or large patches (Jelbart et al., 2007). In kelp systems, little work has focused on forest size; however, many studies have shown the community level effects of kelp removals, which would take place as the forests diminish. Levin (1993) found that experimental kelp canopy removal in the Gulf of Maine increased the overall percent cover of the understory algal assemblages, which resulted in a significant increase in fish recruit density. In contrast, experimental kelp removals in California showed that adult midwater fish species, such as rockfish, significantly decreased in the absence of canopy kelp (Bodkin, 1988). In southeast Alaska, juvenile demersal fish abundances were twice as high in kelp canopy sites when compared to areas where the canopy had been cleared. Conversely mean total fish abundance in the no-canopy sites was six times greater, primarily driven by an increase in the abundance of schooling gadids (Siddon et al., 2008). The relationship between kelp canopy extent and fish community structure suggests that long-term success of some fishes may rely on large kelp forests.

Canopy kelp morphology can have an effect on kelp forest fish community structure. In central California kelp forests, where *Macrocystis* and *Nereocystis* forests both persist, fishes were more abundant within the more structurally complex *Macrocystis* forests. Differences in fish abundance occurred largely in the midwater rockfishes. However, three demersal species also showed significantly higher abundances within the *Macrocystis* forests, greenling (*Oxylebius pictus*), surfperch (*Embiotoca lateralis*) and rockfish (*Sebastes carnatus*) (Bodkin, 1986). Kelp forest fish assemblages in Kachemak Bay, where this study was conducted, are also likely to relate differently to structural dissimilarities in local canopy forming kelp species.

The benthic environment (including both biotic and abiotic attributes) as well as the water column within kelp forests exhibit high heterogeneity, including characteristics that affect fish communities. The grain size and cover of the seafloor dictates the abiotic habitat complexity, or rugosity, of a reef. This complexity structures fish communities in many regions, including tropical (Öhman and Rajasuriya, 1998), temperate (Connell and Jones, 1991), and subpolar (Hamilton and Konar, 2007). Across both terrestrial and marine systems, high environmental heterogeneity generally allows for greater niche diversification, which can lead to higher local faunal diversity (M.P. Johnson et al., 2003). Benthic communities of stipitate understory kelps, algal turf, and certain invertebrates can also add complexity to a substrate. In contrast, some invertebrate species and encrusting coralline algae grow prostrate on the surface of the substrate, not adding to the complexity of the habitat and, at times, excluding other individuals from colonizing. On temperate reefs, benthic fishes often recruit to and associate with

understory kelps (Carr, 1989). In Alaska, areas of high density understory had greater rock greenling (*Hexagrammos lagocephalus*) abundances than areas with sparse understory but a high cover of coralline algae (Reisewitz et al., 2006). Last of all, kelp forests also persist in a range of water conditions, with certain algal species better adapted to particular temperatures, salinities, and/or wave motion (Lindeberg and Lindstrom, 2010). These water characteristics are also well documented to affect fish distributions throughout the world's oceans (Abookire et al., 2000; Castillo et al., 1996; Corten and van de Kamp, 1996; Morita et al., 2010).

Recognizing the link between nearshore fish communities and kelp forest environmental parameters is important because the spatial and temporal variability in these patchy environments may affect the available habitat for fishes. In other patchy systems, patterns of resident species composition and abundance in relation to habitat characteristics are evident; however, the existence of these patterns has yet to be tested in high latitude kelp forests. In the face of diminishing habitat size and shifts of dominant foundational species, a study of how these communities relate to variation in their habitat is essential. South-central Alaska's Kachemak Bay hosts patchy forests of various sizes and has undergone changes in the dominant canopy forming kelp, while currently exhibiting forests of both species, making it an ideal location for this study.

The goal of this study was to identify which habitat factors correlate with kelp forest fish community structure, as defined by species composition and relative abundance. Specifically, the objectives were to determine 1) if fish community structure differed between kelp forest interiors and edges within a forest, 2) if fish community

structures were correlated to kelp forest size, and 3) if fish community structure differed depending on the relative abundances of *Eualaria* and *Nereocystis*. In addition to these three major kelp forest features, a variety of fine scale habitat characteristics were quantified to further elucidate the relationship of habitat and fish community structure.

Methods

Site Description:

This study was conducted in Kachemak Bay Alaska, on the southern tip of the Kenai Peninsula (N 59° 33.417' W 151° 35.833') (Figure 1). The region harbors both canopy kelps *Eualaria* and *Nereocystis*. Understory kelps include the annuals *Cymathære triplicata* and *Costaria costata*, in addition to the perennials *Agarum clathratum*, *Saccharina latissima*, *Laminaria yezoensis* and *Saccharina groenlandica* (Lindeberg and Lindstrom, 2010). Common fish families for the region are gadids, hexagrammids, sebastids, and cottids (Mecklenburg et al., 2002). In summer, adult fish abundance increases, which is particularly true of the gadids and sebastids (Hamilton and Konar, 2007; Markis, 2007). Within Kachemak Bay, ten sites with kelp forests of varying sizes were surveyed in the summer of 2009. Water depths of these beds varied from 5 to 10 m. Sites were chosen to represent the full distribution of kelp forest sizes in Kachemak Bay. Kelp forests surveyed in this study also had varying canopy, understory, and invertebrate species composition and abundances, and substrate type. Sampling where *Nereocystis* and *Eualaria* distribution overlapped made it possible to determine the influence that a given kelp species has on fish communities because both monospecific

and mixed beds were present. In addition, the large variation in kelp forest size was necessary to investigate the importance of habitat patch size and location within a patch.

Kelp Forest Surveys:

Community structure was assessed as a function of species richness and relative abundances of those species. To investigate how fish communities associate with kelp forest habitat, visual underwater survey techniques were conducted by divers using scuba. At each site, the kelp forest edge and interior locations were sampled. Edge surveys were conducted just inside the canopy along the offshore edge, while interior surveys targeted the center of the kelp forest so that no portion of the survey would be near the canopy edge. At each location, fish and habitat surveys were conducted along 2 m x 2 m x 50 m transects where all fish encountered were enumerated and visually identified to species. Fish surveys were conducted at two depths, along the benthos and in the midwater. Benthic transects were sampled from the seafloor to a height of 2 m off the bottom. The depth of the midwater transect varied as a function of bottom depth, and was centered 4 to 6 m above the bottom. By attaching two transect tapes to the start point and letting the tapes pay out behind the divers, the benthic and midwater transects were surveyed simultaneously. The benthic fish survey was conducted in a stepwise fashion. First, fast moving demersal fish above the understory were recorded along a 2 – 4 m long sub-section of the transect, depending on visibility. Second, the substrate and macroalgae were thoroughly searched, using a flashlight, to look for cryptic species along that same

section. The diver then swam to the end of the sub-section and the process was repeated along the length of the 50 m transect.

After completion of the fish surveys, the midwater diver moved to the benthos and together the two divers completed a habitat survey moving back along the benthic transect. Habitat variables surveyed at each site included kelp forest size, canopy forming species composition and density, understory algal composition and density, percent cover of substrate occupying organisms, substrate composition and percent cover, rugosity, temperature, and salinity. Habitat surveys were conducted using five techniques: canopy forming algal swaths, understory/substrate quadrats, rugosity measurements, measuring seawater attributes, and kelp forest size measurements. To estimate species composition and density of canopy forming kelp species, all individuals > 2 m tall were identified to species and recorded along the 50 m x 2 m swath transect. Understory algal species, including canopy species < 2 m occur at much higher densities and were surveyed using a 0.25 m² quadrat placed every 10 m along each 50 m benthic transect, totaling 6 per transect. Also within these quadrats, percent cover of sessile and colonial organisms were estimated, as individual counts for these organisms are not an appropriate metric of abundance due their morphology or life history. These organisms include encrusting coralline algae, foliose red algae, green algae, *Desmarestia* spp. (a genus of highly branching brown algae), and sessile invertebrates. Additionally, percent cover of substrate type was approximated within the quadrats by using a modified Wentworth scale (Wentworth, 1922) where substrate was visually categorizing into sand (<2 mm), gravel (2 – 6 mm), cobble (6 – 100 mm), boulder (10 cm – 1 m), and bedrock (>1 m), and

the percent cover of each was estimated. Rugosity, a substrate complexity measure, is a ratio of the topographical distance compared to a straight line distance. Rugosity was measured adjacent to each quadrat using the chain and bar method where the topographical distance is measured using a 3 m length of chain (5 mm links) and is compared to straight line distance measured with a 1 m PVC bar (Hamilton and Konar, 2007). Sea water attributes included bottom water salinity and temperature. Salinity was measured using an Atago ATC-S/Mill-E hand-held refractometer with water samples collected along each benthic transect. Salinity measurements were made to the nearest 1 unit. Water temperature was recorded to the nearest degree F° using an Oceanic Versa Pro dive computer once during each transect survey, and then converted to degrees C° for analysis. To determine kelp forest area, all kelp forests were mapped from the surface with a small boat and portable Garmin Oregon 300c GPS at slack low tide to ensure that all possible canopy forming kelp adults were at the surface. The GPS track line data were uploaded into ArcGIS software (ESRI Software Inc., Redland, CA) and the area of the projected polygons was calculated. In all, 28 environmental measurable variables were collected to describe the kelp forest at each site, including forest size, abundance of two species of canopy forming kelps, abundance of nine species of understory algae, six substrate occupying organism categories, six substrate categories, depth, rugosity, salinity, and temperature.

Analysis:

Before formal statistical analysis, all of the environmental data were examined for any univariate correlations among the variables using draftsman plots (Clarke and Gorley, 2006). This procedure also assisted in choosing the appropriate transformations. Before being normalized, kelp forest area was log transformed, and all other environmental variables and fish abundances were square-root transformed to meet the assumptions of the multivariate tests. To combine the data for site-level comparisons, edge and interior abundance values (both fish and algae) were summed while site mean values were used for comparisons of percent cover, rugosity and sea water attributes.

Kelp forests ecosystems, including fish communities and habitat variability, are complex, and as such, a multivariate analytical approach was used (PRIMER-e v.6 software). The basis for this multivariate analysis is the creation and comparison of resemblance matrices based on the similarity between all sample pairs in a data set (Clarke and Gorley, 2006). In this study, resemblance matrices were created by applying one of two indices, Bray-Curtis similarity index or the Euclidian distance, to the transformed and normalized data (Clarke and Warwick, 2001). These indices are measures of similarity between two sites based upon all the measured variables and result in a matrix of all possible site pairs. Bray-Curtis measures are most appropriate for biological community analysis and were used on all fish assemblage data, while, Euclidian distance is most appropriate for environmental data and were used to analyze kelp forest habitat characteristics (Clarke and Warwick, 2001).

Three multivariate operations were used to examine how the observed fish communities related to their location within the forest or the surveyed habitat variables. A single factor Analysis of Similarity (ANOSIM) analysis was used to test for differences in the assemblages between levels of a single factor. In this case, it tested for differences in fish communities observed at two locations within a kelp forest. RELATE was used to measure how closely two sets of multivariate data were, for a matching set of samples, by calculating a rank correlation coefficient between all the elements of their respective resemblance matrices. Here, it tested for correlations between the fish assemblage resemblance matrix, based on fish diversity and abundance at each site, and matrices based on kelp forest size and canopy forming kelp species. The BEST-BIOENV test was used to search for high rank correlations between a secondary, fixed sample matrix and resemblance matrices generated from a different variable subset of a primary matrix. In doing this test, the best match between the multivariate among-sample patterns of an assemblage and that from the environment variables associated with those samples is identified. In this study, the BEST-BIOENV test was used to 1) identify the fishes that drove the differences between edge and interior fish communities and 2) identify the environmental variables (both biotic and abiotic) that correlated best with fish assemblage variability. Principal Component Analysis (PCA) and Multi-Dimensional Scaling (MDS) are two ordination techniques that were used to present the results of the ANOSIM and RELATE analyses. These are commonly used tools in the analysis of ecological data that reduce the effective dimensionality of multivariate datasets (Clarke

and Gorley, 2006; Peres-Neto et al., 2003). This allows for data visualization of these types of complex datasets.

Results

Fifteen fish species from eight families were observed (Table 1) in Kachemak Bay (Figure 1), with 98% of those observations occurring along the benthic transect. Fish communities differed significantly between kelp forest edges and interiors (Figure 2; ANISOM $R=0.137$, $p=0.028$). Of those fishes, the relative abundances of padded sculpin (*Artedius fenestralis*), Pacific sand lance (*Ammodytes hexapterus*), silverspotted sculpin (*Blepsias cirrhosus*), Pacific cod (*Gadus macrocephalus*), whitespotted greenling (*Hexagrammos stelleri*), crescent gunnel (*Pholis laeta*) and black rockfish (*Sebastes melanops*) explained 91.4% (BEST analysis) of the observed differences between edge and interior fish communities of the kelp forests. Pacific sand lance, silverspotted sculpin, whitespotted greenling, crescent gunnel and black rockfish showed an affinity for kelp forest interiors while Pacific cod and padded sculpin showed a distinct affinity for forest edges (Figure 3).

No linear relationships were found among the environmental characteristics across all sites. As such, all habitat variables were used in the analyses to identify correlations among the fish communities and their habitat. The resulting environmental matrices did not differ significantly between edge and interior regions (Table 2, Figure 4; ANISOM $R=-0.021$, $p=0.651$) suggesting that fish community differences were not correlated to habitat variability between the two locations.

Kelp forests surveyed in this study ranged from 2,522 m² to 1.8 km². Kelp patches smaller than 2,500 m² in Kachemak Bay were rare, consisted of only a few plants and were excluded in this study as two 50 m x 2 m transects could not be surveyed without the risk of overlap and double sampling an area. Fish community assemblages did not correlate with kelp forest size (Figure 5; RELATE $\rho=0.034$, $p=0.428$). In addition, none of the 15 fish species were individually correlated with kelp forest size. Forest size did relate to the environmental characteristics of the forest. A total of 60.8% of the kelp forest size variability correlated with the percent cover of encrusting coralline algae, and boulder substrate, as well as the abundance of *Saccharina latissima* and *Nereocystis* (BEST). However, none of these habitat characteristics were independently correlated to kelp forest size using draftsman plot linear regression analysis.

Kelp forests varied in their canopy kelp species composition and density (Table 2). The relative abundance of *Nereocystis* ranged from 100% at four sites to 2% at the least abundant site. The converse was found for *Eualaria* ranging from 98% of the canopy forming kelps to 0% at four of the sites. When present in the forest, *Eualaria* was much more dense (74.4 ± 43.2 individuals/100 m², mean \pm SE) while *Nereocystis* occurred at lower densities (17.9 ± 7.0 individuals/100 m², mean \pm SE). Despite these stark differences in the relative abundance and species densities, differences in the fish community were not correlated with the differences in canopy forming kelp (Figure 6; RELATE $\rho=-0.223$, $p=0.883$).

Four environmental characteristics best correlated with differences in fish community structure at each site. BEST analysis showed that 53.6% of the fish

community variability was described by the abundances of *Agarum clathratum* and *Saccharina latissima*, site rugosity, and depth. The two perennial understory species *A. clathratum* and *S. latissima* varied in their density across sites, ranging from absent to maximums of 29 individuals/0.25 m² and 110 individuals/0.25 m², respectively. Site rugosity varied from nearly flat (1.01) sandy bottoms to highly complex (1.87) bedrock and boulder substrate.

Discussion

Habitat preferences strongly influence fish distribution patterns throughout the world's oceans. In nearshore temperate and subpolar regions, many fishes favor kelp forest habitats, but within this general association, finer scale environmental characteristics influence habitat use patterns, and therefore fish abundance and diversity. All the environmental factors surveyed in this study have been shown to influence or correlate with fish habitat use in a variety of patchy systems (Carr, 1994; Hamilton and Konar, 2007; Lowe et al., 2003; Tupper and Boutilier, 1997). The purpose of this study was to identify which habitat characteristics are important in structuring kelp forest communities in south-central Alaska.

Location within the Forest:

There were significant differences in the fish communities between edge and interior locations within Kachemak Bay kelp forests. This pattern was driven by seven species; however, only two of the seven species were unique to a single location. The

other five were observed in both locations with differing relative abundances. While single species studies describing kelp forest edge or interior habitat preferences have been done before (Jorgensen et al., 2006), community level edge effects within kelp forests such as these have not been described. Studies in other patchy habitats, such as seagrass meadows, where fish communities exhibit such location-specific patterns often cite fine-scale habitat differences between the locations within the patch as the driving force (Smith et al., 2008; Vonk et al., 2010). However, that is not likely the case in the kelp forests in Kachemak Bay, as fine-scale environmental factors did not differ between locations within the forests. Due to the broad-scale approach of this research, community level patterns can be detected and correlations between community patterns can be made, but assertions of causal relationships between the observed fishes and their environment are inappropriate. Yet, similar patterns of fish abundance and diversity within other patchy environments suggest that prey availability, predation risk, and ontogenetic shifts are likely explanations for the observed distribution.

Prey availability is one of the most commonly cited mechanisms underlying patterns in fish abundances (see review by Lima and Dill, 1990). Species inhabiting the kelp forest edges may be dependent on prey resources derived from outside the forest, such as planktonic or pelagic organisms. While in nearshore waters, young-of-the-year Pacific cod, such as those seen in this study, feed primarily on calanoid copepods, mysids, and gammarid amphipods (Abookire et al., 2007). Amphipods are common within vegetated benthic areas, while pelagic copepods and mysids are likely delivered to the offshore edge of kelp forests by currents. Similarly, juvenile rockfish in central

California inhabiting offshore kelp forest edges prey upon planktonic larvae of intertidal species (Gaines and Roughgarden, 1987). Canopy kelps slow water movement through the forest (Gaylord et al., 2007), increasing the foraging efficiency of planktivorous fishes (Bray, 1980). Fishes occupying the edges of a kelp forest would have access to both planktonic and kelp associated prey while benefiting from the baffling and cover provided by the kelp forest.

In Kachemak Bay, interior dwelling species may be more dependent on prey resources derived from the interior of the kelp forests. Black rockfish feed on a wide variety of fishes and invertebrates (Love et al., 2002). The principal food of whitespotted greenling consists of crustaceans and fish, and secondary food items are mollusks, polychaetes, and echiurids (Napazakov, 2010). Worms and small crustaceans make up the diet of crescent gunnels (Armstrong, 1996), while calanoid copepods represent >90% of the summer diet of Pacific sand lance (Blackburn and Anderson, 1997). Although no formal diet study has been performed on silverspotted sculpin, these fish are thought to feed generally on crustaceans found within algal cover (Jared Guthridge, Alaska SeaLife Center, pers comm.). Studies in Kachemak Bay kelp forests have shown these prey types to be abundant within kelp forests (Daly and Konar, 2008; Hondolero, 2011; Markis, 2007; Schuster, unpublished data). An interior distribution of the predatory fish species found in this study would maximize the spatial overlap with their prey.

Predation risk may also be an important determinant of habitat use in these kelp forests. Those species found in the interior of the forest may be avoiding mobile piscivorous predators such as lingcod (*Ophioden elongatus*) and Steller sea lions

(*Eumetopias jubatus*). Both of these predators, which forage over large areas capable of encompassing multiple reefs (Greenley, 2009; Hegwer, 2003), were present in the study area. In other subtidal macrophyte systems, large predators roaming from patch to patch result in higher predation rates at patch edges than patch interiors (Smith et al., 2011).

Ontogenetic shifts may also play a role in the differences in abundance between edge and interior habitats of at least one of the influential fish species. Pacific cod, typically found offshore as eggs and larvae until early summer, move into nearshore and intertidal habitats as recruits. Throughout the summer, cod spend much of their juvenile stage in shallow rocky habitats (Hamilton and Konar, 2007; Hegwer, 2003; Markis, 2007). Once they are large enough, they move offshore to the pelagic domain (Rangeley and Kramer, 1998; Scott and Scott, 1988). Pacific cod were more abundant along the offshore edge of the kelp forest, possibly providing these individuals with a transitional habitat with ready access to open water for trial excursions while still providing access to cover (Dill, 1990).

Kelp Canopy Forming Species:

The concept that increased structural complexity influences community assemblages has been demonstrated for a number of habitats and animal groups (MacArthur, 1965). For example, bird diversity and abundance may be positively influenced by more complex tree structures (Graham and Blake, 2001). In Indonesian seagrass meadows, fishes were more abundant in areas where shoot biomass, density, length, and epiphyte abundance was greater (Vonk et al., 2010). In California kelp

forests, fish species were more abundant in the more structurally complex *Macrocystis* forests than in *Nereocystis* forests (Bodkin, 1986). Similarly, *Eualaria* has greater structural complexity than *Nereocystis*. This habitat difference created by these two species was anticipated to correspond with differing fish communities. However, this study showed no differences in fish community structure with respect to the canopy forming kelp species composition and abundance. The reason for the fish community similarities between forest types may be because nearly all fish encountered during these surveys were observed along the benthic transect, while the structural differences between the two kelp species are most pronounced in the midwater. Unlike kelp forests along the west coast of the United States, Alaskan kelp forests do not support many midwater fishes (Hamilton and Konar, 2007; S.W. Johnson et al., 2003). Midwater fish species that are found in lower latitude kelp forests do not extend their distributions into most of Alaska. For example, many surf perches (family Embiotocidae) spend time in midwater kelp habitats; however, their distribution only extends into southeast Alaska (Mecklenburg et al., 2002). Furthermore, lower latitude kelp forest rockfish that occur in both the midwater and along the benthos, such as *Sebastes flavidus* and *Sebastes melanops* (Love et al., 2002), adopt a more demersal behavior in Alaskan forests (S.W. Johnson et al., 2003). With benthic kelp forest fishes, benthic environmental factors would likely more closely correlate to fish abundance, which was the case in this study (see *Environmental characteristics* below).

Kelp Forest Size:

Terrestrial and marine research of patchy systems that support different within-patch communities have shown that faunal assemblages correlate with patch size (Bender et al., 1998; Smith et al., 2010). However, for forests surveyed in this study, canopy size did not correlate to fish community structure. In an attempt to explain this result it was found that other research directly relating kelp forest size to resident fish community structure is rare. More frequently found in the literature are clearing experiments where all canopy kelps are removed to test for the community structuring effects. These studies have shown that the fish communities in newly cleared areas are affected. For example, with *Macrocystis* kelp removals, associated fish communities shifted to a more benthic associated community (Bodkin, 1988). In Southeast Alaska, *Nereocystis* removals resulted in six times greater schooling gadids and hosted half as many juvenile benthic fish as before the removal of the canopy kelp (Siddon et al., 2008). When the outcomes of these clearing experiments are combined with the results of this study, shrinking forests should host a community similar that of the pre-diminished forest. However, the existence of edge and interior communities would not fit that assumption.

The relationship between the ratio of edge to interior area across different size forests would explain these results. Shrinking or fragmentation of kelp forests should result in a decrease in the edge to interior area ratio and therefore the available habitat for the two distinct communities. The largest kelp forest in this study had a perimeter (edge) to area ratio of 1 m: 7534 m², while the smallest was 1 m: 7 m². This drastic contrast in habitat availability between large and small forests may adversely affect interior dwelling

species if beds were to shrink to the smaller sizes such as those sampled in this study. In fact, this reaction to habitat loss occurs in other patchy habitats that support edge and interior communities (Fahrig, 2003; Opdam and Wascher, 2004). For interior communities, the decline in population sizes associated with habitat fragmentation per se will be greater than that predicted from pure habitat loss alone and for edge species (Bender et al., 1998). Clearly, further research into the patch dynamics of these communities is needed to resolve how fish communities may respond to habitat size reduction or fragmentation given the findings of this study.

Other Environmental Characteristics:

Although the fish communities did not change with kelp forest size, the abundances of *Nereocystis* and *Saccharina latissima*, the percent cover of encrusting coralline algae, and the boulder habitat all correlated to kelp forest size. Suitable substrate obviously plays a major role in algal success, especially canopy forming species that employ pneumatocysts to float the thallus. Boulder habitat serves as a more suitable substrate for large canopy forming kelp species, as there is a greater cover of suitable habitat with less kelp loss due to removal from hydrodynamic forces. As juvenile sporophytes, the drag and lift that water exerts on kelp is minimal, but as an individual grows, the alga is likely to be lifted away if it is attached to small substrate material (i.e., gravel, cobble or shell debris). The increased survivorship of canopy kelps growing on boulder substrate has an effect on the benthic algal assemblage. Density of understory kelps, such as *S. latissima*, is reduced in large stands of canopy kelp (Holbrook et al.,

1990) because as a forest grows larger and the adult canopy reaches the surface, the amount of light reaching the sea floor is greatly reduced. This, in turn, reduces growth and survival of smaller algae or younger canopy species (Dean et al., 1989). However, encrusting coralline algae are shade adapted, persisting not only in low light areas but even surviving overgrowth by ephemeral sessile invertebrates and other algae (Dethier and Steneck, 2001). Considering these relationships, high boulder cover can support a large canopy area that consists of less dense, but presumably larger, *Nereocystis* individuals than in a smaller area. Large *Nereocystis* decrease light to the benthos where foliose algal density declines in favor of the more shade adapted coralline algae. The present data do not have the resolution to elicit linear correlations between kelp forest size and each of these identified characteristics individually. However, kelp forest size did correlate with the combination of the *Nereocystis* and *Saccharina latissima* abundance, the percent cover of encrusting coralline algae, and the boulder habitat, which is consistent with reduced light availability and appropriate substrate.

Together, depth, rugosity, and the abundance of *Agarum clathratum* and *Saccharina latissima* play a role in structuring the fish assemblage in south-central Alaskan kelp forests. However, individually none of these characteristics could be solely attributed to differences in the fish assemblage. When the environmental data were analyzed as a matrix, these aforementioned characteristics correlated with fish community variability. Three of these four habitat variables relate to habitat complexity. In studies conducted on coral reefs, high rugosity positively affected fish settlement, post-recruitment survival, growth, predation avoidance, and survival (Connell and Jones,

1991; Tupper and Boutilier, 1997). Accordingly, higher reef fish abundances can occur in areas of greater rugosity (Andrews and Anderson, 2004). These effects are frequently attributed to predator-prey mechanisms, with more complex habitats containing a greater number of prey refuges (Hixon and Beets, 1993) and predators foraging less efficiently in more complex habitats (Beukers and Jones, 1998). Abundances of *Agarum clathratum*, *Saccharina latissima* and other understory kelps are also positively correlated to high rugosity, further amplifying the cover available to fishes (Hamilton and Konar, 2007). Understory kelps in southern California can greatly reduce predation potential on young fishes, promoting higher abundances on reefs with dense understory stands (Ebeling and Laur, 1985). Additionally, the enduring nature of these perennial species would also provide year round cover in a highly seasonal environment (Markis, 2007). Most understory kelps surveyed in this study were annuals and therefore much more ephemeral and probably not as important in structuring the year round kelp forest fish community. The final characteristic related to fish community structure was site depth. Average site depths varied little across sites. Surveys were performed in a relatively narrow depth range but did not approach the published depth ranges for any of the observed fish species. The offshore edge transects were frequently slightly deeper than those within the interior of the forests. As such, differences in fish abundance across depths are likely the result of the community differences between these two forest locations.

Conclusions:

This study applied patch dynamic concepts commonly associated with other habitats to kelp forests in south-central Alaska. Surveys of patchy kelp forest habitats showed different fish assemblages between forest edges and interiors. Among forest sizes, fish assemblage structure also varied but differences were not linked to size. However, it was revealed that kelp forest size related to differences in habitat characteristics. The species composition of the canopy forming kelp, and therefore foundational species morphology, did not correlate with differences in fish assemblages either. Instead, seafloor habitat characteristics such as benthic habitat complexity and water depth, were highly correlated to the fish assemblage structure. This study highlights the importance of habitat characteristics and the variability of these characteristics on fish communities. This study allows for future research to narrow its scope to determine causal relationships for the patterns observed in this study by carrying out experimental and species specific research. In a broader sense, within patchy systems that are spatially and structurally non-uniform, associated fish species composition and abundance may be more directly linked to location within the patch and year-round habitat complexity than habitat patch size or foundational species composition.

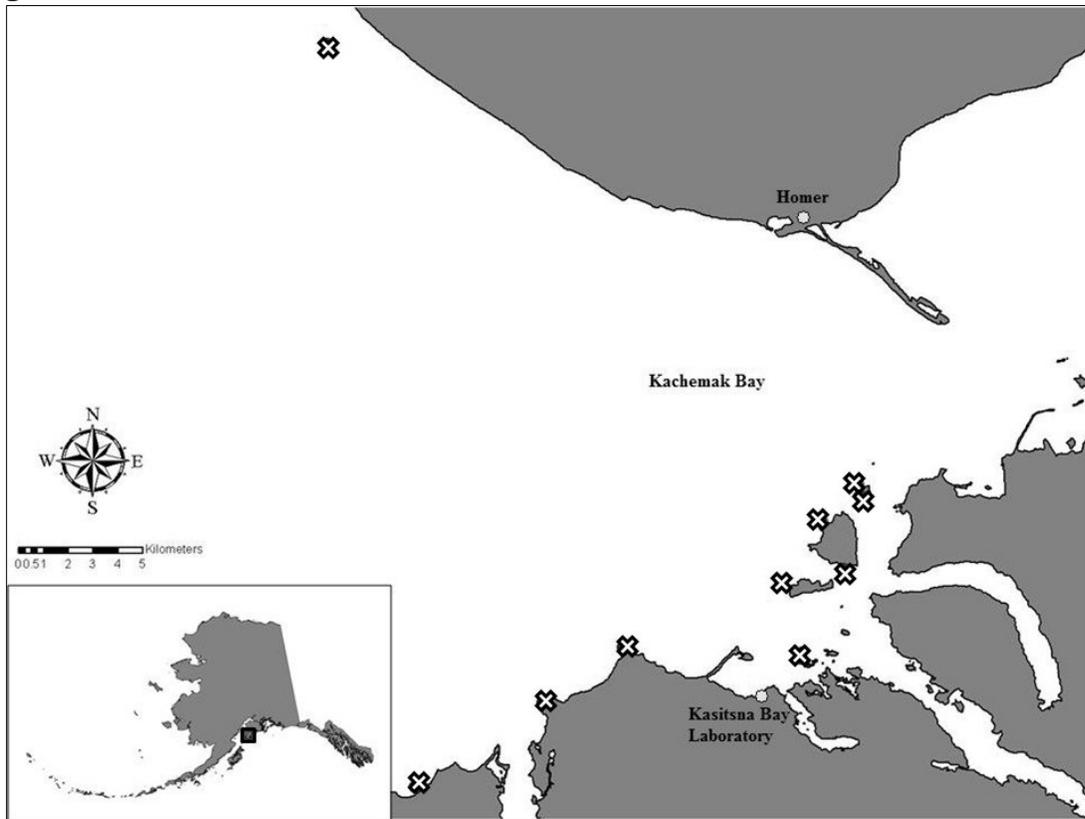
Figures and Tables:

Figure 1. Map of southern Kachemak Bay (N 59° 33.417' W 151° 35.833'). X's indicate the ten sites surveyed in the summer of 2009.

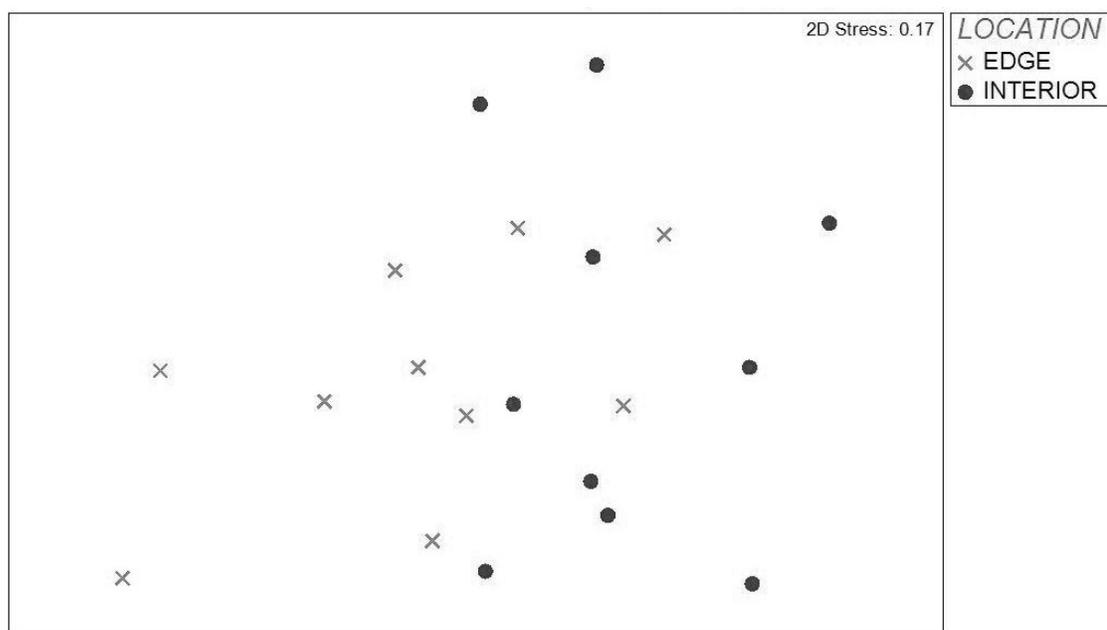


Figure 2. MDS plot of fish assemblages at edge and interior habitats. Assemblages were based on fish abundances. ANOSIM $R=0.137$, $p=0.028$

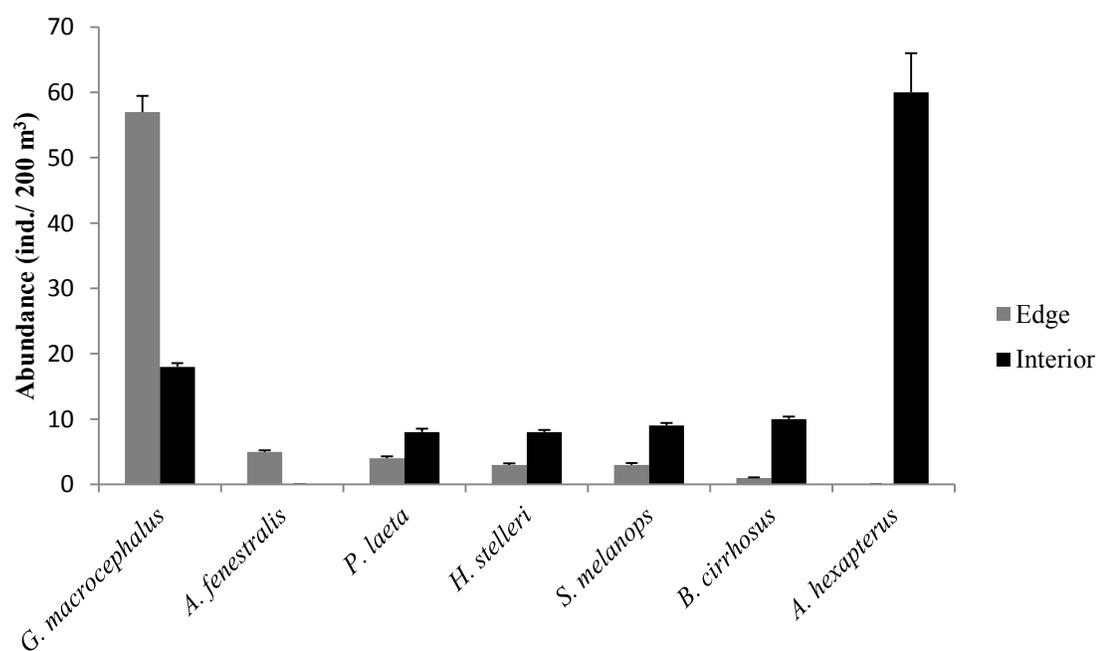


Figure 3. Abundance of seven fish species by location in all surveys combined. Bars are standard error of the means.

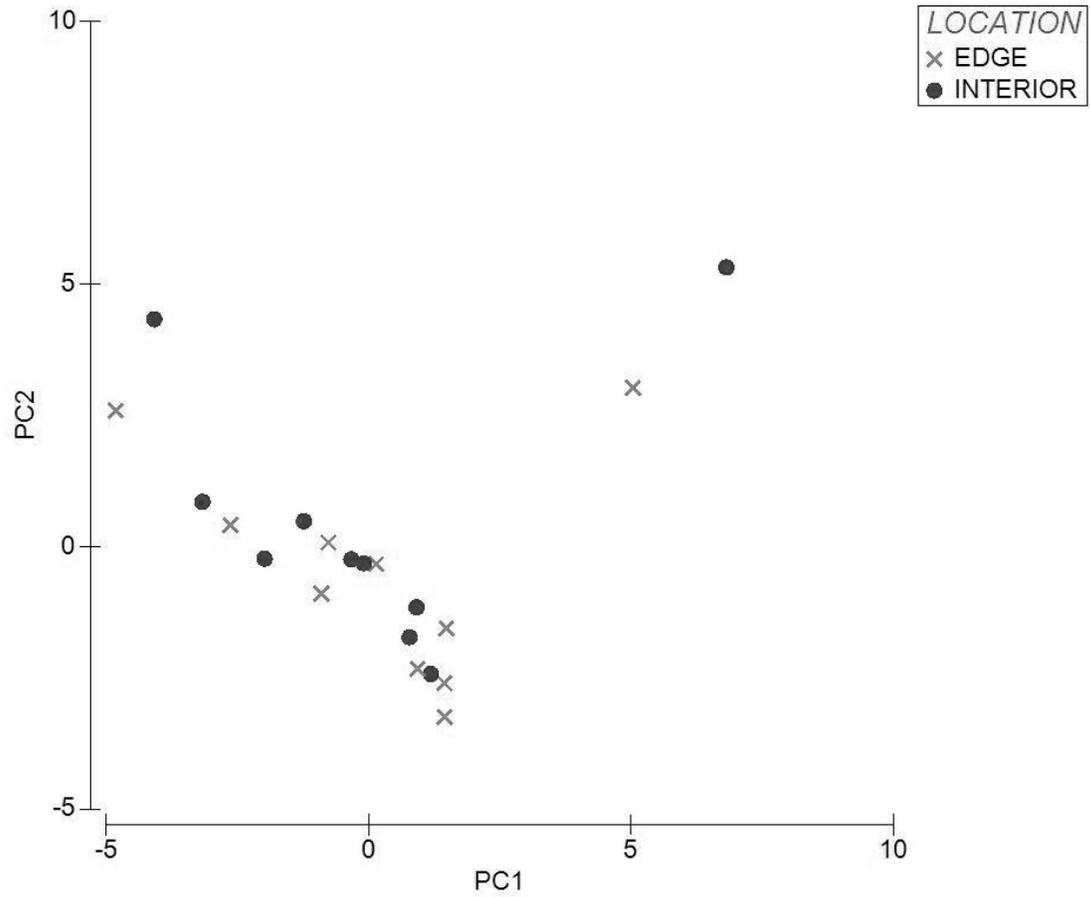


Figure 4. PCA ordination of environmental characteristics by location. ANISOM $R=-0.021$, $p=0.651$

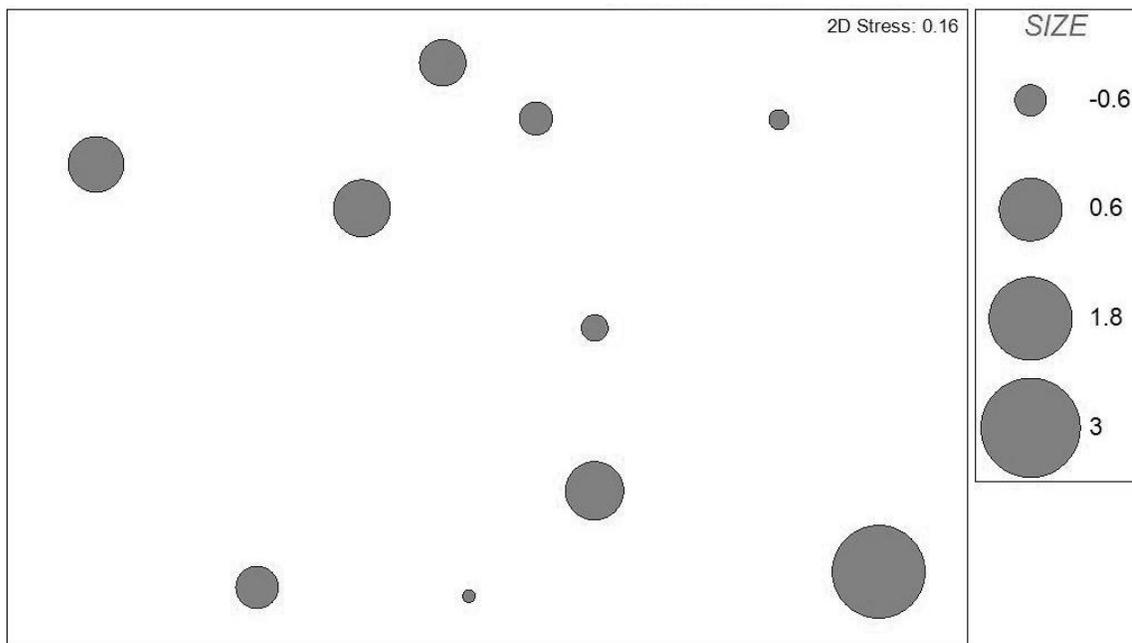


Figure 5. MDS plot of fish assemblages in relation to kelp forest size. Assemblages based on fish abundance. Bubble size corresponds to kelp forest size (log transformed and normalized). RELATE $\rho=0.034$, $p=0.428$.

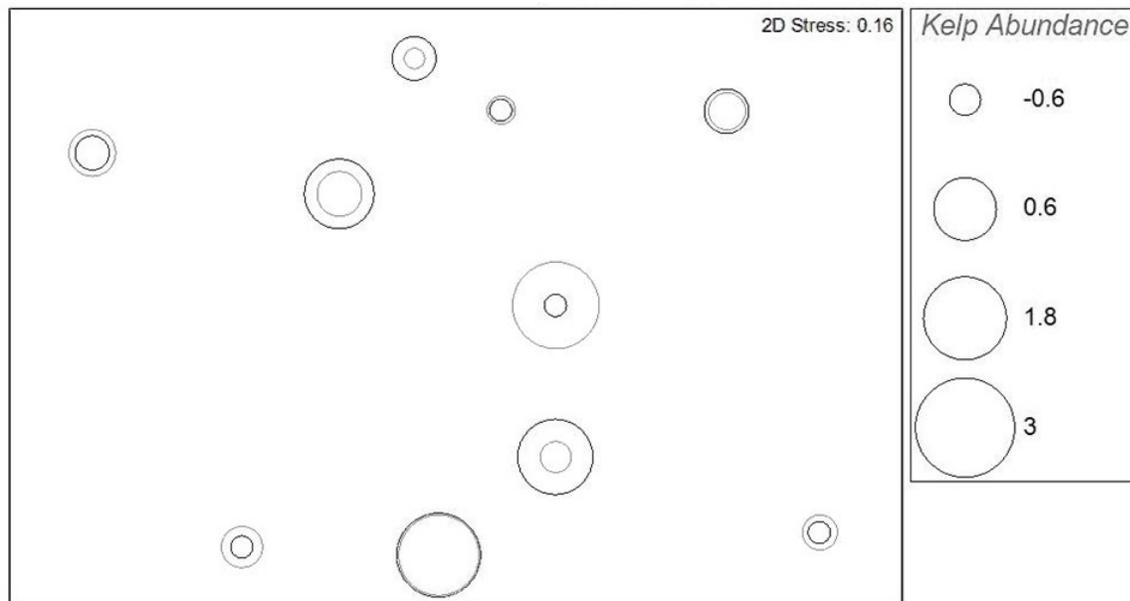


Figure 6. MDS of fish assemblages in relation to abundance of canopy forming algae. Black and gray bubbles distinguish abundance (transformed and normalized) of *Eualaria* and *Nereocystis*, respectively. When a point has two bubbles, both kelps were present at the site; likewise, if there is only one bubble, then only one species was found at that site. RELATE $\rho=-0.223$, $p=0.883$

Table 1. Mean \pm SD and percent occurrence of fish individuals observed across sites.

Family	Species	Common Name	Mean (individuals)	% Occurrence
Ammodytidae	<i>Ammodytes hexapterus</i>	Pacific sandlance	6.0 \pm 19.0	27.8%
Cottidae	<i>Artedius fenestralis</i>	Padded sculpin	0.5 \pm 0.7	2.3%
Cottidae	<i>Artedius sp. (Juvenile)</i>	Juvenile sculpin	0.4 \pm 0.7	1.9%
Cottidae	<i>Blepsias cirrhosus</i>	Silverspotted sculpin	1.1 \pm 1.2	5.1%
Cottidae	<i>Enophrys bison</i>	Buffalo sculpin	0.1 \pm 0.3	0.5%
Cottidae	<i>Hemilepidotus hemilepidotus</i>	Red Irish lord	0.5 \pm 0.9	2.3%
Cottidae	<i>Synchirus gilli</i>	Manacled sculpin	1.2 \pm 2.2	5.6%
Gadidae	<i>Gadus macrocephalus</i>	Pacific cod	7.5 \pm 9.1	34.7%
Hexagrammidae	<i>Hexagrammos decagrammus</i>	Kelp greenling	0.5 \pm 0.7	2.3%
Hexagrammidae	<i>Hexagrammos lagocephalus</i>	Rock greenling	0.2 \pm 0.4	0.9%
Hexagrammidae	<i>Hexagrammos stelleri</i>	Whitespotted greenling	1.1 \pm 1.6	5.1%
Liparidae	<i>Liparis florae</i>	Tidepool snailfish	1.2 \pm 2.0	5.6%
Pholidae	<i>Pholis laeta</i>	Crescent gunnel	0.5 \pm 1.0	2.3%
Sebastidae	<i>Sebastes melanops</i>	Black rockfish	0.1 \pm 0.3	0.5%
Stichaeidae	<i>Stichaeus punctatus punctatus</i>	Arctic shanny	0.7 \pm 1.0	3.2%

Table 2. Mean \pm SD and maximum of environmental variables across all sites. n=10.

		Edge (Indiv./0.25 m ²)		Interior (Indiv./0.25 m ²)	
		Mean	Maximum	Mean	Maximum
Understory species density	<i>Agarum clathratum</i>	2.0 \pm 1.6	9	0.5 \pm 0.5	6
	<i>Alaria marginata</i>	0.1 \pm 0.3	6	0.2 \pm 0.7	13
	<i>Costaria costata</i>	0.0	0	0.0 \pm 0.1	2
	<i>Cymathaere triplicata</i>	0.9 \pm 1.9	15	1.0 \pm 1.9	15
	<i>Eualaria</i> (Juvenile)	0.2 \pm 0.4	8	0.1 \pm 0.3	10
	<i>Laminaria yezoensis</i>	0.3 \pm 0.7	4	0.3 \pm 0.5	5
	<i>Nereocystis</i> (Juvenile)	0.1 \pm 0.2	3	0.1 \pm 0.3	4
	<i>Saccharina latissima</i>	5.5 \pm 5.2	35	4.3 \pm 3.3	21
	<i>Saccharina groenlandica</i>	2.6 \pm 2.2	23	2.1 \pm 2.6	18
		Edge (% Cover/0.25 m ²)		Interior (% Cover/0.25 m ²)	
		Mean	Maximum	Mean	Maximum
Primary % cover	<i>Desmarestia</i> spp.	3.5 \pm 8.3	100	1.7 \pm 4.2	80
	Red algal turf	30.1 \pm 30.3	60	25.2 \pm 18.5	90
	Bare	5.6 \pm 4.8	100	14.6 \pm 16.8	93
	Sessile Invertebrates	0.3 \pm 1.1	96	0.3 \pm 0.6	98
	Green algae	42.5 \pm 32.7	15	33.7 \pm 25.8	5
	Encrusting Coralline	21.9 \pm 25.1	95	32.1 \pm 26.0	90
Percent cover of substrate type	Bedrock	48.5 \pm 47.4	100	41.5 \pm 37.8	100
	Boulder	6.3 \pm 9.6	80	17.4 \pm 20.7	100
	Cobble	21.8 \pm 29.9	100	12.1 \pm 17.3	100
	Gravel	3.6 \pm 7.6	30	13.0 \pm 19.1	100
	Sand	10.0 \pm 22.5	95	6.6 \pm 13.6	75
	Shell	3.2 \pm 10.0	15	1.1 \pm 3.4	20
		Edge		Interior	
		Mean	Maximum	Mean	Maximum
<i>Nereocystis</i> adults (indiv./site)		8.3 \pm 7.2	22	22.1 \pm 39.0	108
<i>Eualaria</i> adults (indiv./site)		28.2 \pm 47.6	143	92.2 \pm 148.6	408
Depth (m)		7.9 \pm 1.7	11.5	6.5 \pm 2.1	10.6
Temperature (°C)		7.3 \pm 0.9	7.8	7.7 \pm 1.6	10.0
Salinity		34.1 \pm 1.1	35	33.7 \pm 1.1	35
Rugosity		131.6 \pm 10.2	187	126.4 \pm 9.5	182

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