

## Structure of nearshore fish assemblages in relation to varying levels of habitat complexity

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### ABSTRACT

In temperate regions kelp can dominate hard-bottom nearshore communities, providing structure at the substrate and throughout the water column, which can be used by many invertebrates and fishes. Increasingly complex habitats can be beneficial to fish, however fish use of these complex habitats is poorly understood in northern latitudes, particularly for juvenile fish. The potential effects of macroalgal density and substrate complexity on nearshore fish communities were examined in Kachemak Bay, Alaska. Fish were collected from multiple sand, understory, and understory and canopy sites, along with substrate and algal complexity measurements. SMURF's, light traps, shrimp pots, and SCUBA visual surveys were all employed in these collections. Fish abundance and composition varied temporally across habitats. Adult fish communities were comparable among similar habitats, with younger fish assemblages being similar across macroalgal sites but distinctly separate from sandy sites. The dominant fish included gadids, pleuronectids, hexagrammids, and sebastids. Larger gadids were captured in all three habitats, while smaller individuals were primarily encountered in macroalgal habitats. Pleuronectids were only captured in sandy sites. Adult hexagrammids were captured in macroalgal habitats; however, juveniles were not encountered. Adult sebastids were only encountered in understory sites, while smaller sebastids were captured in all three habitats. All dominant fish families were significantly different in habitat use both temporally and ontogenetically, but these differences were family specific with different families utilizing different habitats. Community analysis showed that different habitat complexities supported distinctly different fish assemblages and that these assemblages were predictable based on substrate composition and the presence or absence of kelp. This study indicates that different groups of fish may have different habitat preferences in Alaska's nearshore waters requiring different management strategies.

## INTRODUCTION

Habitat structural complexity can determine fish abundance and diversity (Bell and Galzin 1984; Roberts and Ormond 1987; Jones 1988; Bell et al. 1991; Hixon and Beets 1993; Warfe and Barmuta 2004) with habitats containing highly complex structure typically supporting higher abundance and diversity. It has been noted that increasingly complex habitats influence predator prey interactions (Hixon and Menge 1991; Hixon and Beets 1993), reduce water flow (Jackson and Winant 1983; Garcia-Charton and Perez-Ruzafa 1998), and can serve as areas for feeding, reproduction, and recruitment (Carr 1989; Sale 1991; 1999; Levin 1993; Steele 1997; Aburto-Oropeza and Balart 2001); all of which can be beneficial to fish populations. Many studies, which have investigated the effects of habitat complexity on fish populations, come from tropical regions where coral is the primary component increasing complexity. In general, much less is known about the effects of increased complexity afforded by rocky kelp habitats on temperate fish populations.

Habitat structural complexity in the nearshore environment contains two components; substrate topography and macrophyte density. Substrate topography, as defined by topographical variation in the substrate, can be attributed to either variation in the seafloor itself (sand, bedrock, etc.) or debris on the seafloor (boulders, cobbles, etc.). Substrate topography can drive fish distribution and abundance in habitats such as rock and coral reefs (Jones 1988; Hixon and Menge 1991; Hixon and Beets 1993; Garcia-Charton and Perez-Ruzafa 1998). The main mechanism thought to be responsible for this is a reduction in predation due to the increased amount of refuge available to prey species (Hixon and Beets 1993; Almany 2004a; Caley and St. John 1996). Increases in available refuge due to enhanced substrate topography also has been shown to reduce competition for space (Hixon and Menge 1991; Almany 2004b) as well as adding to niche dimensionality (MacArthur and Levins 1967), both of which potentially increase fish abundance and distribution.

In many aquatic systems such as lakes, lowland rivers, estuaries, and nearshore marine habitats, structure can be provided by vascular plants and macroalgae (Heck and Crowder 1991). This added structure can enhance habitat complexity. Many studies have examined fish use of seagrass habitats and deemed them essential to fish (Ogden 1988; Baelde 1990; Heck et al. 2003; Irlandi and Crawford 1997; Gotceitas et al. 1997; Eggleston et al., 1998; Laurel et al. 2003). Likewise, kelp beds are important to fish communities for a variety of reasons, depending on

species, age, and type of macroalgal cover. Fish use kelp beds as spawning/mating grounds (Haegele et al. 1981; Hay 1985; Haegele and Schweigert 1985; Merrill 1989; Stekoll 1989), nursery grounds (Ebeling and Laur 1985; Carr 1989; Love et al. 1991; Levin 1994), feeding grounds (North and Hubbs 1968; Quast 1971; Hobson and Chess 1976; Schmitt and Holbrook 1985; Singer 1985; Høisaeter and Fossaa 1993), for predator avoidance (Schmitt and Holbrook 1985; Carr 1992; Gotceitas et al. 1993; Sarno et al. 1994; Gotceitas et al. 1995), and as shelter from currents (Jackson and Winant 1983).

Many fish habitat interaction studies primarily focus on adult fish, however, it has been suggested that settling larval fish select structurally complex habitats due to increased microhabitats (Almany 2004a). This could lead to a nonrandom distribution of juveniles and subsequently drive adult distribution (Almany 2004b). Post settlement juvenile predation can also be reduced in areas of increased structural complexity (Beukers and Jones 1997; Almany 2004a), ultimately impacting adult distribution. Kelp beds are particularly important for newly settled more vulnerable recruits and juveniles that use complex structure to avoid predators (Hartney 1996). Experimental evidence has shown that recruits and juveniles have a lower mortality rate in the presence of macroalgal cover (Savino and Stein 1989), and that predators, despite increased abundance of prey items, have a lower catch per unit effort in macroalgal stands (Anderson 1984). It also has been shown that juvenile fish shift from areas of low macrophyte density to areas of high macrophyte density in the presence of a predator (Holbrook and Schmitt 1988). Levin (1993) found that experimental removal of canopy kelp in the Gulf of Maine increased the overall cover of understory algal assemblages and resulted in a significant increase in temperate fish recruit density. Experimental kelp removals in California also have shown that adult mid-water species, such as rockfish, significantly decrease when canopy kelp is removed (Bodkin 1988). Thus, differences in inter-annual success of understory algae may affect survivorship of associated juvenile and hence adult fish.

Alaskan kelp beds are structurally very different than kelp beds elsewhere. In California, kelp beds are comprised primarily of perennial species, which results in kelp cover throughout the year. These perennial species include the giant kelp, *Macrocystis pyrifera* but also the large understory *Pterygophora californica* and *Eisenia arborea*, which stand erect above the substrate because of their woody stipes. The dominant canopy kelps in Alaska include the annual bull kelp, *Nereocystis luetkeana* and the annual ribbon kelp, *Alaria fistulosa*. Understory species,

including *Laminaria* spp., *Saccharina* spp., *Agarum clathratum*, *Costaria costata*, and *Cymathaere triplicate*, typically lie prostrate on the substrate because they are lacking a woody stipe. While *A. fistulosa* is the primary canopy-forming kelp in the Aleutians, *N. luetkeana* dominates most of Southcentral Alaska. The result of Alaska being dominated by annual canopy kelp is that there is little to no mid-water structure to act as fish refuge in winter months. *Macrocystis pyrifera* has blades along the stipe that provide structure through the water column while *N. luetkeana*, which is only present during summer months, has a stipe through the mid-water and blades only at the surface. However some mid-water structure is provided by juvenile *N. luetkeana* individuals as they grow toward the surface. The differences in physical structure provided and seasonal variability between Alaskan kelp beds and lower latitudinal regions may have different affects on the fish communities in these structurally distinct habitats.

This study examined the differential effects of substrate complexity and macroalgal density on the abundance and distribution of the juvenile and adult nearshore fish community in Kachemak Bay, Alaska. Specifically, multiple gear types were used in habitats of varying structural complexity to address three questions (1) does habitat complexity affect the abundance of total juvenile and adult fish, (2) does habitat complexity have differential affects on the distribution and abundance of juvenile and adult fish of different families, and (3) does habitat complexity drive the juvenile and adult fish community in a given habitat type. It was predicted that (a) increasingly complex habitats would have higher abundances of both juvenile and adult fish, (b) habitat complexity would have differential affects depending on family of fish, and (c) the fish community would vary independently of habitat complexity and not be predictable based on habitat type.

## MATERIALS AND METHODS

This study was conducted from June 2005 to September 2006 in Kachemak Bay, Alaska (Fig. 1). Kachemak Bay is located on the southern tip of the Kenai Peninsula (59°33'25"N 151°35'50"W) and drains into the Gulf of Alaska by way of Cook Inlet. Kachemak Bay is comprised of both marine and estuarine environments. The head of the bay is highly estuarine, fed by seven glaciers and the Fox River. The mouth of the bay is strongly influenced by both deepwater and surface currents from the Gulf of Alaska.

Nine sites were selected along the southern shore of the bay based on water depth and substrate and macroalgal complexity (Fig. 1). Three replicate sites had highly complex substrates in addition to understory and canopy kelp species (canopy sites), three replicate sites had highly complex substrates amid understory kelp species (understory sites), and three replicate sites were sandy with low substrate complexity and no macroalgae (sand sites) (Fig. 1). All sites were approximately the same size (2827 m<sup>2</sup>) and depth (11 m), and were separated by at least 1 km.

## HABITAT

Macroalgal density was surveyed monthly throughout the study, whereas substrate measurements were only conducted twice as they were not expected to change. At each site, three 30 x 2 m (60 m<sup>2</sup>) transects were examined via SCUBA to quantify seasonal variation in the kelp community. The dominant understory kelp in this region includes *Laminaria* spp., *Saccharina* spp., *Agarum clathratum*, *Costaria costata*, and *Cymathaere triplicate* (Chenelot 2003; Hegwer 2003; Hamilton 2004). Six randomly placed 0.25 m<sup>2</sup> quadrats were examined per 60 m<sup>2</sup> transect. All understory juvenile (< 20 cm) and adult (>20 cm) kelps in each quadrat were counted and identified to species. Structurally, understory kelps are very similar with comparable sizes and blade widths, thus they were grouped into two functional understory kelp groups for analysis, juvenile and adult. The only canopy forming species encountered was *Nereocystis luetkeana*, which, in this region is more sparsely distributed compared to understory species. All kelp individuals contributing to the canopy (> 2 m above the substrate) within each 60 m<sup>2</sup> transect were counted and termed adults. *Nereocystis luetkeana* individuals that were less than 2 m above the substrate and encountered in the 0.25 m<sup>2</sup> quadrats were counted and termed juveniles.

Rugosity and dominant substrate size were measured in May 2005 and September 2006 along nine 30 m transects at each site via SCUBA. Rugosity is a measure of substrate topography and is a ratio of the topographical distance compared to a straight line distance. Rugosity was measured using a 1 m polyvinyl chloride (PVC) bar with a length of small mesh (5 mm diameter) chain attached to one end. At six random points along each 30 m transect, the PVC bar was laid perpendicular to the transect, the chain was then placed in the same direction but allowed to drape and follow the substrate topography. At the end of the PVC bar, the chain was marked and then straightened and measured to provide the rugosity ratio. Dominant substrate

size was measured by selecting six random points along each 30 m transect and measuring substrate diameter directly beneath that point.

## FISH COLLECTIONS

Juvenile and adult fish were collected or observed using a variety of methods during neap tidal cycles from June 2005 to September 2006. Standard Monitoring Units for the Recruitment of Fish (SMURFs) (Steele et al. 2002; Findlay and Allen 2002; Ammann 2004) and light traps (Anderson et al. 2002) were used to catch smaller (< 10 cm) fish and shrimp pots and diver visual surveys (Bodkin 1986, Hegwer 2003; Hamilton 2004) were used to capture larger fish (> 10 cm). SMURF's and light traps were fished in mid-water depths and shrimp pots, diver visual surveys, and SMURF's surveyed the benthos. SMURF's were deployed in both mid-water and benthic regions.

SMURFs were adopted from (Ammann 2004) and comprised of 1 x 0.35 m diameter cylinders of fine plastic mesh (2.5 cm), which contained a folded section of larger mesh plastic (5 x 7.5 cm). Three SMURFs were deployed per site every month: two in the benthic region (1 m off the substrate) and one in the mid-water (6 m off the substrate). SMURFs were deployed via SCUBA onto moorings and soaked for 48 hours as increased intervals have shown a decrease in recruitment (Ammann 2004). SMURFs were retrieved via SCUBA by enclosing them in a diver propelled collapsing type hoop net or BINCKE net to prevent fish escape. The net frame measured 1 x 1 m, was constructed of PVC and was strung with 4.76 mm Ace square mesh netting to form a 1.5 m deep cod end (adopted from Anderson and Carr 1998). BINCKE net and SMURF were then brought aboard and rinsed vigorously with seawater into a 100 l tote and sieved through a 1 cm sieve.

Three light traps were deployed in the mid-water (6 m off the substrate) per site every month and were adopted from Anderson (2002) and Calvert (2005). Light traps were deployed and retrieved 48 hours later via mooring lines. Light traps were constructed of a 19 l translucent water container with four funnels facing inward, a PVC pipe with a 330  $\mu$ m mesh bottom, and two waterproof battery powered Light Emitting Diode (LED) dive flashlights (PrincetonTec. Attitude<sup>®</sup>) illuminating the trap. As the trap is retrieved the contents drain through the 330  $\mu$ m sieve, which is then unscrewed and rinsed.

Two shrimp pots baited with herring were randomly deployed at least 5 m apart per site every month. Shrimp pots were collapsible, constructed of an 86 cm rectangular metal frame covered with 1.25 cm nylon netting and had two 10 cm entrances. Traps were deployed and retrieved via mooring lines from a boat in which fish were brought onboard, processed, and then released.

SCUBA visual surveys were conducted along three 30 x 2 m (60 m<sup>2</sup>) swath transects per site every month during daylight hours. Mooring lines at the center of each site marked the point from which a random distance between 4 and 8 m designated the point at which each transect would begin. This was in an effort to minimize over-sampling of the mooring region. Visual surveys consisted of two search patterns; the first as the diver swam out the transect in search of more mobile species within 2 m of the substrate and those scared off easily, the second as the diver swam back the transect conducting a more detailed search of the substrate and macroalgae to identify more cryptic species.

All fish captured or observed were identified to the lowest taxonomic level (Mecklenburg et al. 2002; Eschmeyer et al. 1983; Kessler 1985; Goodson 1988; Kramer and O'Connell 1995; Matarese et al. 1989; O'Clair and O'Clair 1998) however, analysis was performed at the family level. Captured fish were measured to the nearest cm whereas fish observed in diver surveys were estimated in 5 cm size classes. As it is impossible to verify sexual maturity and therefore life stage in fish that are not captured, analysis was performed on two size classes of fish; smaller fish (< 10 cm) and larger fish (> 10 cm).

## STATISTICAL ANALYSES

Linear and multivariate techniques were used to examine environmental habitat variables and fish abundance data with STATISTICA v.6 (Statsoft, Tulsa, OK, USA) and PRIMER v.6 (PRIMER-E, Plymouth, UK). Cluster analysis (Clifford and Stephenson 1975) and multidimensional scaling (MDS; Field et al. 1982) were used to examine variability among sites based on environmental habitat data. Data were log (x + 1) transformed, ranked, and then resemblance was calculated based on Euclidean distances. One-way analysis of variance (ANOVA) was used to test for spatial variation in temperature, salinity, and dissolved oxygen among sites. Results were considered significant at  $\alpha < 0.05$ . Repeated measures ANOVA was used to test for significance in spatial and temporal variation in kelp density and fish abundance

across habitat types. Cluster analysis and MDS were used to examine variation in the fish community across habitat types based on average densities of fish per site in each of the dominant families (comprising at least 3% of total abundance). Data were  $\log(x + 1)$  transformed and the Bray Curtis dissimilarity coefficient (Bray and Curtis 1957) was calculated.

## RESULTS

### HABITAT

Habitat structural complexity ranged from low (sandy areas with no kelp) to highly complex (understory and canopy kelp regions with large boulders) and varied temporally with kelp densities. Cluster analysis grouped the nine sites into three distinct groups based on the similarity of six habitat variables (juvenile understory density, adult understory density, juvenile canopy density, adult canopy density, rugosity, and dominant substrate size) (Fig. 2). The six kelp sites grouped separately from the sand sites indicating differences in substrate complexity and kelp density (Fig. 2). The three canopy sites grouped separately from the understory sites indicating differences in the kelp community (the presence of *Nereocystis luetkeana*) (Fig. 2).

Both substrate complexity measurements were significantly different based on habitat type (Table 1). Post-hoc analysis of rugosity revealed that sandy sites were driving this difference with kelp sites not being significantly different (Tukey's HSD,  $p = 0.198$ ). Understory sites did however have slightly higher mean values ( $1.35 \pm 0.017$  s.e.) than canopy sites ( $1.31 \pm 0.017$  s.e.). Post-hoc examination of dominant substrate size also showed that the sandy sites, having much less complex substrates, were driving this result with kelp sites not being significantly different (Tukey's HSD,  $p > 0.202$ ). Canopy sites did have slightly higher mean substrate size ( $20.52 \text{ cm} \pm 0.51$  s.e.) than understory sites ( $19.23 \text{ cm} \pm 0.56$  s.e.).

Kelp communities showed spatial and strong seasonal variation. Understory kelp density was significant over time and by habitat (Table 1), which was expected. Post-hoc analysis revealed significant differences in understory density among the three habitats (Tukey's HSD,  $p < 0.0001$ ). Sand sites had the lowest mean understory kelp density ( $0.08 / 0.25 \text{ m}^2 \pm 0.02$  s.e.) followed by the understory sites ( $3.04 / 0.25 \text{ m}^2 \pm 0.02$  s.e.), and canopy sites ( $4.40 / 0.25 \text{ m}^2 \pm 0.15$  s.e.). Canopy kelp density was also significant over time and by habitat (Table 1). Canopy sites contained significantly more *Nereocystis luetkeana* ( $\bar{x} = 5.20 / 60 \text{ m} \pm 0.77$  s.e., Tukey's

HSD,  $p < 0.0001$ ) than understory sites ( $\bar{x} = 0.10 / 60 \text{ m}^2 \pm 0.05 \text{ s.e.}$ ) and *N. luetkeana* was not encountered at sand sites.

## FISH

A total of 2732 fish from fifteen families and twenty four species were either captured or observed (Table 2). Of these, four families dominated in total abundance contributing at least 10% of the total catch: Gadidae 29.1%, Pleuronectidae 18.9%, Hexagrammidae 16.9%, and Sebastidae 16.2%. These four families cumulatively contributed 81.1% to the total catch.

Repeated measures ANOVA of total fish abundance showed significant variation over time, by depth, family, and habitat, but was not significant when comparing total abundance of smaller versus larger fish (Table 3). Total fish abundance was highly seasonal (Figs. 3 and 4), which is attributed to increased abundances in summer and decreases in winter. Total fish abundance varied significantly over depth with higher abundances in the benthos (CPUE =  $0.137 \pm 0.009 \text{ s.e.}$ ) compared to mid-water (CPUE =  $0.036 \pm 0.013 \text{ s.e.}$ ). Post-hoc analysis revealed similar abundances of smaller fish in both the mid-water and benthos (Tukey's HSD,  $p > 0.17$ ), thus the variation in adult fish distribution is driving the significant differences in total fish abundance by depth. Since no large fish were encountered in the mid-water and smaller fish showed no significant variation by depth, these samples were pooled thus removing depth as a covariate. Significant differences were identified in total fish abundance when examining different families of fish (Tables 2 and 3). Overall habitat use was significantly different with highest total fish abundances in understory kelp sites (CPUE =  $0.110 \pm 0.015 \text{ s.e.}$ ) followed by sand sites (CPUE =  $0.083 \pm 0.012 \text{ s.e.}$ ), and lastly canopy kelp sites (CPUE =  $0.066 \pm 0.012 \text{ s.e.}$ ). Ontogenetically, fish abundances were not significantly different but smaller fish were slightly more abundant (CPUE =  $0.095 \pm 0.011 \text{ s.e.}$ ) than larger fish (CPUE =  $0.077 \pm 0.011 \text{ s.e.}$ ). However, the interaction between habitat and life stage was significant (Table 3), with post-hoc analysis revealing smaller fish being more abundant in sand habitats ( $0.14 \pm 0.02 \text{ s.e.}$  vs., large fish  $0.05 \pm 0.01 \text{ s.e.}$  Tukey's HSD,  $p < 0.013$ ) driven by small pleuronectids (Fig 3), and larger fish being more abundant in understory habitats ( $0.19 \pm 0.02 \text{ s.e.}$  vs. small fish  $0.09 \pm 0.02 \text{ s.e.}$ , Tukey's HSD,  $p < 0.004$ ), driven by large sebastids (Fig. 4).

The four dominant families (Gadidae, Pleuronectidae, Hexagrammidae, and Sebastidae) were significantly different in temporal distribution, average abundance of small versus large

fish, and spatial distribution across habitat (Table 4). However these four fish families utilized each habitat differently, both ontogenetically and temporally, depending on the family of fish. This instigated the need for individual analysis.

Gadids, mainly Pacific cod (*Gadus macrocephalus*), were significantly different in seasonal distribution, mean abundance of small versus large fish, and average abundance across habitat type (Table 4). Smaller gadids were highly seasonal with highest abundances in summer and no fish in winter, whereas larger gadid abundances remained temporally consistent (Figs. 3a and 4a). These smaller fish, although highly seasonal, were significantly more abundant than larger fish (Table 2, Figs. 3a and 4a). Post-hoc analysis of habitat use revealed small fish utilizing kelp sites significantly more than sandy sites (Tukey's HSD,  $p < 0.02$ ), with slightly higher averages in canopy than understory sites (CPUE =  $0.511 \pm 0.129$  s.e. and  $0.687 \pm 0.164$  s.e.). Larger gadids were more cosmopolitan in their distribution (Fig. 4a).

The main pleuronectid encountered was the Rock sole (*Lepidopsetta bilineata*). This group showed significant differences in seasonal distribution, mean abundances of small versus large fish, and average abundance across habitat type (Table 4). Both small and large fish were highly seasonal, showing similar trends with increased abundances in summer decreasing to zero during winter (Figs. 3b and 4b). Small pleuronectids had significantly greater abundances than large fish (Table 2, Figs. 3b and 4b). Post-hoc examination of habitat use revealed small fish utilized sandy habitats exclusively (Tukey's HSD,  $p < 0.001$ , Fig. 3b) and large fish, although only found in sandy habitats (Fig. 4b), did not show significant differences among habitat types due to a large variance.

There were four dominant hexagrammids, Kelp greenling (*Hexagrammos decagrammus*), Whitespotted greenling (*Hexagrammos stelleri*), Rock greenling (*Hexagrammos lagocephalus*), and Masked greenling (*Hexagrammos octogrammus*). Hexagrammids were significantly different in temporal distribution, average abundance of small versus large fish, and average spatial distribution across habitats (Table 4). Larger fish showed a strong seasonal trend with highest abundances in summer and decreasing in winter (Fig. 4c). Smaller fish were almost absent from the study, with few individuals encountered only in summer (Fig. 3c). Since small fish were infrequently encountered and large fish were encountered often, a significant difference in small versus large fish abundance was evident (Table 2, Figs. 3c and 4c). Post-hoc analysis of large hexagrammid habitat use revealed a strong preference toward kelp habitats

(Tukey's HSD,  $p < 0.001$ ), with slightly higher averages in understory sites than canopy sites (CPUE =  $0.456 \pm 0.045$  s.e. and CPUE =  $0.355 \pm 0.035$  s.e., respectively).

Sebastids consisted of mainly Black rockfish (*Sebastes melanops*) and Dusky rockfish (*Sebastes ciliatus*). This group was significantly different in temporal distribution, average abundance of small vs. large fish, and average spatial distribution across habitat (Table 4). Both small and large fish were highly seasonal showing increased abundances in summer and decreasing to zero in winter (Figs. 3d and 4d). Large fish had significantly higher abundances than small fish (Figs. 3d and 4d). Post-hoc examination revealed that smaller fish were ubiquitous across habitat types (Fig. 3d), however larger fish utilized understory habitats almost exclusively (Tukey's HSD,  $p < 0.001$ , Fig. 4d).

Fish community cluster dendrograms for total abundance, smaller, and larger fish revealed distinct relationships between fish community and habitat type (Fig. 5). For total fish abundance, three distinct groups were evident (Fig. 5a). The first and most similar were the understory kelp sites, with the fish community being at least 83% similar within these sites. The second most similar were the canopy kelp sites, which were at least 81% similar. The least similar were the sand sites, being at least 68% similar. Overall, the kelp sites were more similar to one another than to the sandy sites, being 73% similar. The entire fish community across all sites and habitats was 47% similar (Fig. 5a). A cluster dendrogram for the smaller fish community revealed two distinct groups (Fig. 5b). The more similar of these two groups contained all of the kelp sites, grouping together with at least 76% similarity. The remaining sand sites grouped out with at least 67% similarity. The smaller fish community across all sites and habitats was 53.41% similar. Three distinct groups were evident for the larger fish community (Fig. 5c). The first and most similar of these were the canopy sites with the larger fish community being at least 85% similar. The second most similar group contained the understory kelp sites and were at least 84% similar. The least similar of the three groups were the sand sites being only 65% similar. Overall, the kelp sites were more similar to one another than to the sandy sites, being 65% similar. The entire larger fish community across all sites and habitats was 47% similar (Fig. 5c).

## DISCUSSION

Although habitat complexity can be a determinate of fish abundance and diversity in many cases (Bell and Galzin 1984; Roberts and Ormond 1987; Jones 1988; Bell et al. 1991; Hixon and Beets 1993; Almany 2004a; Warfe and Barmuta 2004, and others), examinations of how the added complexity afforded by macroalgal density effects fish populations have been sparse (Carr 1994; Willis and Anderson 2003; Hamilton 2004), especially in higher latitudes. Most studies on the effects of habitat complexity on fish distribution come from tropical regions and involve coral reefs. Furthermore, many studies fail to examine the different effects habitat complexity has on different fish families (Hixon and Beets 1993; Almany 2004a), neglecting the fact that fish utilize habitats differently depending on fish family and/or species.

From this study it does not appear that habitat structural complexity is a determinate of total fish abundance in these macroalgal environments. Canopy sites were the only to contain canopy kelp, providing structure in the mid-water, and also had the highest understory kelp density, therefore this habitat was the most highly complex. It was expected that fish abundances would be largest in this habitat, however total fish abundance was greatest in the understory kelp habitat. Similar trends were found when examining ontogenetic differences in habitat use, with highest small fish abundance at the sand sites and greatest large fish abundance at the understory sites. These data do not support the first hypothesis that increasingly complex habitats would have higher abundances of both juvenile and adult fish. Others have documented similar trends with total fish abundance in kelp environments not being driven by kelp density (Angel and Ojeda 2001; Willis and Anderson 2003). This is likely a result of different fish families or species utilizing habitats differently, making broad characterizations about total fish abundance difficult and demonstrating the need for a species specific approach.

Differential effects of habitat complexity were exhibited by the four dominant fish families (Gadidae, Pleuronectidae, Hexagrammidae, and Sebastidae). All families had different habitat preferences among the three varying levels of habitat complexity examined in this study. Smaller gadid fish were most frequently captured in macroalgal habitats while larger fish were cosmopolitan in their distribution. Based on length data, smaller (< 10 cm) gadids (primarily Pacific cod *Gadus macrocephalus*) were likely young of the year and larger fish (between 10 and 40 cm) were likely still juveniles of ages 1, 2, or 3 (Abookire et al. 2001). Pacific cod are schooling fish typically associated with demersal habitats and were usually sighted within 2 m of

the substrate. However, these fish were rarely sighted within the understory kelp and would swim in schools slightly above the kelp. As a diver approached, fish would typically move closer to the kelp and then utilize the kelp for cover (Markis personal observation). The highly significant association between smaller young of the year gadid abundance and macroalgal presence suggests the potential for these areas to be used as a nursery, feeding ground, and refuge. Larger Pacific cod were rarely sighted during diver surveys but pot data suggest uniform distribution across habitats. Overall, these data suggest that Pacific cod are increasing their use of different habitats as they become larger, potentially no longer needing the kelp refuge. These results contradict those of Abookire et al. (2006) who found no association between Pacific cod distribution and macroalgal or eelgrass distribution. However, that study did find Pacific cod distribution to be positively correlated with sea cucumber mounds and salinity around Kodiak Island (< 200 km from Kachemak Bay). Other studies have found positive correlations between Pacific cod and macrophyte distribution. As example, both Laur and Haldorson (1996) and Dean et al. (2000) found Pacific cod to be associated with eelgrass in Prince William Sound, Alaska. The temporal distribution of Pacific cod in this study followed that of Matarese et al. (2003) with individuals being captured from April to August and not during winter months. It is likely that in winter, they are moving offshore into the deeper waters of the shelf break region (Connors et al. 2006).

Pleuronectids were captured almost exclusively in sandy habitats. Pleuronectid (primarily Rock sole *Lepidopsetta bilineata*) spatial distribution followed that reported by Abookire et al. (2001), with individuals inhabiting sandy shallow habitats. Temporal distribution followed those reported by Matarese et al. (2003), with individuals encountered from April to November and absent in winter. The data presented here confirm habitat associations reported by Abookire et al. (2001) and Matarese et al. (2003) and specifically excludes pleuronectid association with rocky macroalgal habitats through close examination over an entire annual cycle.

Larger hexagrammid distribution was highly significant in macroalgal habitat types but with smaller fish being absent. Many studies have documented adult hexagrammid associations with kelp (Eschmeyer et al. 1983; Dean et al. 2000; Hamilton 2004); however juvenile distribution is not well understood. Gomelyuk and Leunov (1999) describe juvenile masked greenling (*Hexagrammos octogrammus*) inhabiting the rocky littoral zone and being territorial in the Sea of Japan. Since this study focused on subtidal marine habitats, fish inhabiting the rocky

littoral regions may have been missed, which could explain their absence. Hexagrammid larvae are planktonic, residing in the neuston until development is complete through the extended juvenile transformation stage (Matarese et al. 1989). This likely keeps larval and early juvenile fish offshore on the Gulf Shelf edge, however juveniles should be recruiting into the nearshore. The reason for the absence of juvenile hexagrammids in this study is unknown.

Unexpectedly, smaller sebastids were encountered in all habitats. If these smaller fish were influenced by the added complexity provided by both substrate and macroalgae, increased abundances would be expected in the more complex kelp habitats. With over half of the smaller sebastids coming from SMURF captures, it is important to understand how SMURF's function. SMURF's provide artificial structure to which fish are attracted. Fish must choose the artificial habitat over a biogenic habitat when SMURF's are deployed in areas with moderate to high habitat complexity. Fish are probably less likely to inhabit artificial SMURF's in areas with ample natural biogenic refuge. In sandy areas with no refuge, fish are more likely to inhabit the artificial traps, accounting for higher than would be expected CPUE rates in sandy sites. Similar behavior was observed by Nanami and Nishihira (2003) when transplanting coral into a sandy environment. With the likelihood that SMURF's may have higher CPUE values in areas lacking natural biogenic refuge, it is believed that the cosmopolitan distribution of smaller sebastid fishes is a result of this gear bias and that natural distribution would more closely follow that of larger fish. Larger sebastids were almost exclusively captured in understory habitats. Either the added complexity provided by the canopy kelp *Nereocystis luetkeana* is having a negative affect on sebastids or there is some other parameter that was not detected through the substrate measurements conducted. Although this study did measure rugosity and dominant substrate size to describe substrate characteristics that could be driving differences in fish distribution, Friedlander and Parish (1998) and Almany (2004a) describe substrate crevice characteristic (such as size, depth, diameter, and number of holes) as being factors that contribute to fish abundance. It is possible that understory and canopy sites had differing crevice characteristics and that this is responsible for the differences in larger sebastid abundances.

The results of this study also support the second hypothesis that habitat complexity would have differential affects depending on fish family. This is similar to Willis and Anderson (2003) and Almany (2004a), who also found varying affects of habitat complexity on fish assemblages both by species and ontogeny, mainly driven by predation. Although this study did not examine

predation, it is likely one of the main forces driving the differences seen in these complex habitats with prey availability, competition, and juvenile recruitment also likely candidates. The differential effects of fish abundance and diversity presented here point out the need for examining fish habitat on a more detailed level such as family or even species, in order to tease apart complicated interactions between marine fish and habitat.

Habitat complexity had a deterministic affect on the overall fish assemblage. The three different habitats all had distinct fish communities. These results fail to support the third hypothesis that the fish community would vary independently of habitat complexity. The smaller fish community was similar across all macroalgal habitats indicating that the added canopy structure was not critical to smaller fish. These smaller fish may be utilizing the understory kelp much like many juvenile fish utilize seagrass habitats in other regions (Ogden 1988; Baelde 1990; Laurel et al. 2003). The larger fish community, being separated into three groups based on habitat complexity, was affected either positively or negatively by the added canopy kelp complexity. Although many studies document fish associations with canopy forming kelp (Carr 1994; Dean et al. 2000; Hamilton 2004; and others), none of the dominant fish families had increased abundances in canopy sites. This suggests there are negative effects of canopy kelp on certain fish families. These results demonstrate the importance of habitat complexity and its potential to drive fish populations.

In conclusion this was a broad look at habitat use for multiple life stages of fish across different nearshore habitats. Several conclusions from this study may be applicable to other regions, or work done in the future. First, different families of fish are utilizing habitats in different ways spatially, temporally, and ontogenetically and that broad conclusions about fish abundance in any particular time, habitat, or life stage are tenuous at best. This study points out that overall fish abundance was significantly different in habitats of varying structural complexity, but closer examination showed that different fish families respond in varying ways to added habitat complexity. Second, no single standardized method can be used for sampling fish in complex nearshore environments. This is especially true for the early life history stages. This study used multiple gear types with varying degrees of effectiveness in an effort to try and characterize the fish community as accurately as possible. Last, these different habitats are driving different fish communities depending on the presence of understory and/or canopy kelp. Future studies and/or management actions should take into consideration the differential effects

of varying levels of habitat complexity as they may be driving the fish community within any given habitat.

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Table 1. One-way and repeated measure ANOVA for habitat complexity measurements.

<b>Rugosity</b>	SS	df	MS	F	P
Habitat	11.25	2	5.62	129.040	<b>&lt;0.00001</b>
Error	19.83	455	0.04		
<b>Dom. Sub. Size</b>					
Habitat	51088.79	2	25544.39	496.315	<b>&lt;0.00001</b>
Error	28822.13	560	51.47		
<b>Understory</b>					
Time	1593.07	15	106.20	11.968	<b>&lt;0.00001</b>
Error	7365.27	830	8.87		
HABITAT	8266.49	2	4133.25	398.151	<b>&lt;0.00001</b>
HABITAT*Time	1499.22	30	49.97	4.814	<b>&lt;0.00001</b>
Error	17232.65	1660	10.38		
<b>Canopy</b>					
Time	1224.31	15	81.62	3.705	<b>0.00002</b>
Error	2820.00	128	22.03		
HABITAT	2542.72	2	1271.36	55.914	<b>&lt;0.00001</b>
HABITAT*Time	2392.39	30	79.75	3.507	<b>&lt;0.00001</b>
Error	5820.89	256	22.74		

Table 2. Total number of small and large fish captured by gear type in benthic and mid-water samples. Families comprising less than 3% of the total catch were grouped into Other (- indicates no fish).

	Benthic Samples						Midwater Samples				Total Small	Total Large	Total
	Diver Visual		Shrimp Pot		SMURF		SMURF		Light Trap				
	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large			
Gadidae	497	10	7	67	-	-	-	-	215	-	719	77	796
Pleuronectidae	351	34	-	29	-	-	-	-	103	-	454	63	517
Hexagrammidae	6	257	1	192	-	-	-	-	3	-	12	449	461
Sebastidae	32	368	-	-	27	-	15	-	1	-	75	368	443
Cottidae	47	40	-	86	55	-	16	-	5	-	123	126	249
Bathymasteridae	-	83	-	13	-	-	-	-	-	-	0	96	96
Clupeidae	-	54	-	-	-	-	-	-	7	-	7	54	61
Unidentified	11	16	-	-	-	-	1	-	-	-	12	16	28
Stichaeidae	1	10	-	1	1	-	2	-	10	-	14	11	25
Other	2	9	-	-	1	-	2	-	9	-	14	9	23
Ammodytidae	-	11	-	-	-	-	-	-	7	-	7	11	18
Liparidae	-	-	-	-	5	-	6	-	4	-	15	0	15
<b>Total</b>	<b>947</b>	<b>892</b>	<b>8</b>	<b>388</b>	<b>89</b>	<b>-</b>	<b>44</b>	<b>-</b>	<b>364</b>	<b>-</b>	<b>1452</b>	<b>1280</b>	<b>2732</b>

Table 3. Repeated measures ANOVA of total fish abundance. Life stage represents differences in small vs. large fish. Depth refers to differences in mid-water versus benthic samples.

	SS	df	MS	F	P
Life Stage	1.61	1	1.6149	1.2502	0.26354
Family	68.11	7	9.7298	7.5326	<b>&lt;0.00001</b>
Depth	53.33	1	53.3290	41.2861	<b>&lt;0.00001</b>
Time	89.47	15	5.9647	4.6178	<b>&lt;0.00001</b>
Error	10106.21	7824	1.2917		
Habitat	6.78	2	3.3882	3.1365	<b>0.04346</b>
Habitat x Life Stage	38.53	2	19.2670	16.2464	<b>&lt;0.00001</b>
Error	16903.43	15648	1.0802		

Table 4. Repeated measures ANOVA of the four dominant families of fish (comprising at least 10% of the total abundance) Gadidae, Pleuronectidae, Hexagrammidae, and Sebastidae. Life stage represents differences in small vs. large fish.

<b>Gadidae</b>	SS	df	MS	F	P
Life Stage	77.387	1	77.387	14.904	<b>0.00012</b>
Time	249.013	15	16.601	3.197	<b>0.00004</b>
Error	5244.189	1010	5.192		
Habitat	33.34	2	16.670	4.659	<b>0.00958</b>
Error	7227.644	2020	3.578		
<b>Pleuronectidae</b>					
Life Stage	39.591	1	39.591	19.473	<b>0.00001</b>
Time	51.296	15	3.420	1.682	<b>0.04888</b>
Error	2053.446	1010	2.033		
Habitat	135.832	2	67.916	33.491	<b>&lt;0.00001</b>
Error	4096.285	2020	2.028		
<b>Hexagrammidae</b>					
Life Stage	52.5008	1	52.501	136.542	<b>&lt;0.00001</b>
Time	13.9768	15	0.932	2.423	<b>0.00180</b>
Error	388.3494	1010	0.385		
Habitat	24.1487	2	12.074	47.117	<b>&lt;0.00001</b>
Error	517.6509	2020	0.256		
<b>Sebastidae</b>					
Life Stage	25.062	1	25.062	11.044	<b>0.00092</b>
Time	106.387	15	7.092	3.126	<b>0.00005</b>
Error	2291.895	1010	2.269		
Habitat	82.005	2	41.002	18.262	<b>&lt;0.00001</b>
Error	4535.394	2020	2.245		

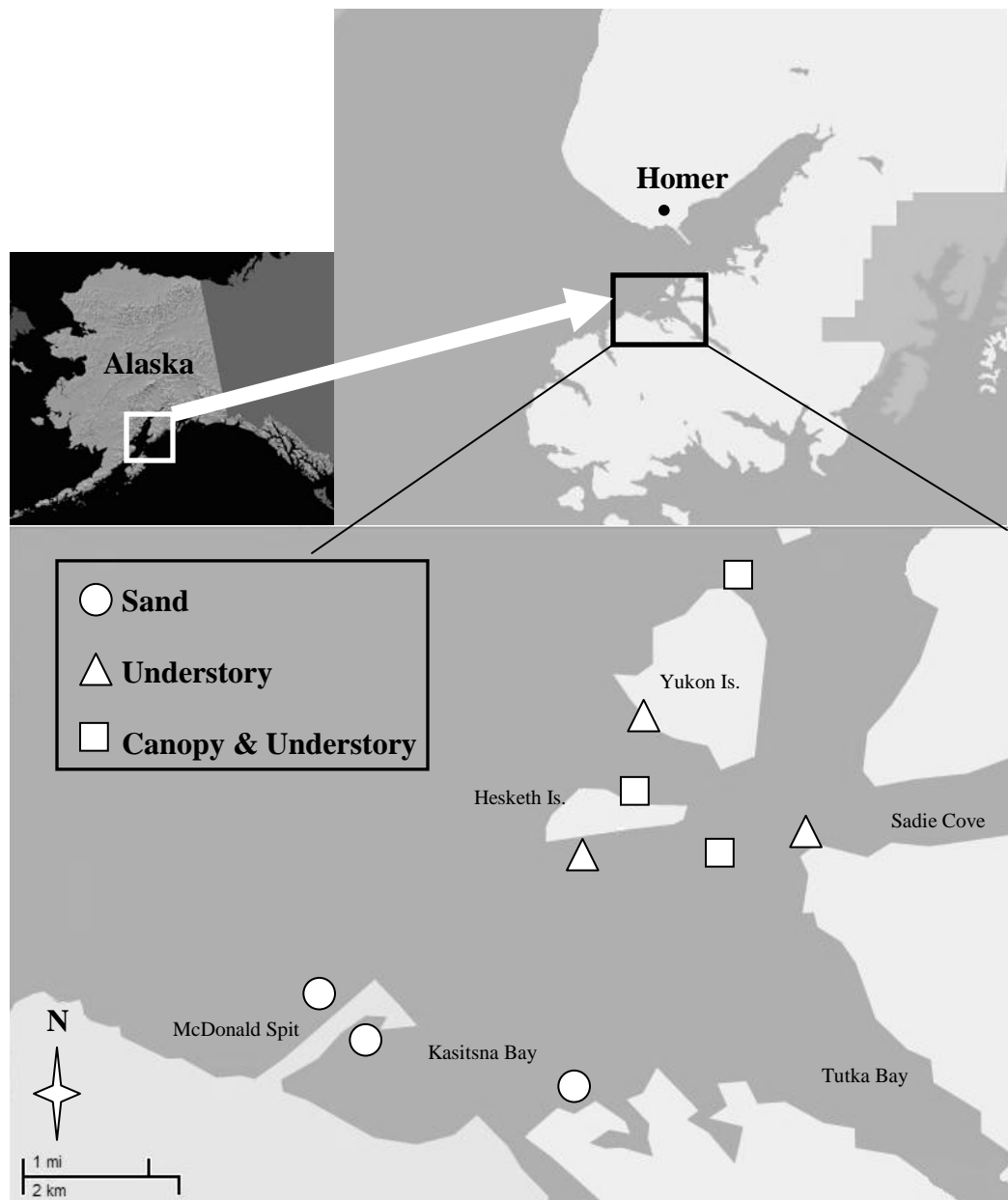


Figure 1. Location of study sites within Kachemak Bay, Alaska. Sand, understory kelp, and understory and canopy kelp sites represented by circles, triangles, and squares, respectively.

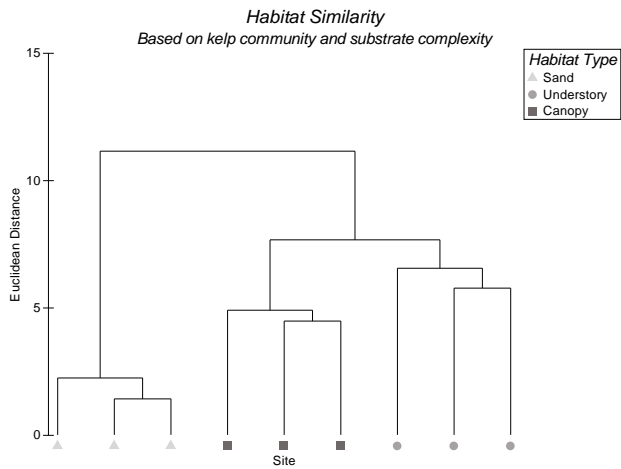


Figure 2. Cluster analysis depicting similarity among sites based on environmental habitat data. Average kelp density was calculated for each site for juvenile and adult understory and juvenile and adult canopy kelp. Data were  $\log(x + 1)$  transformed, ranked, and then resemblance was calculated based on Euclidean distances. Sand, understory, and canopy sites depicted by light, medium and dark grey respectively.

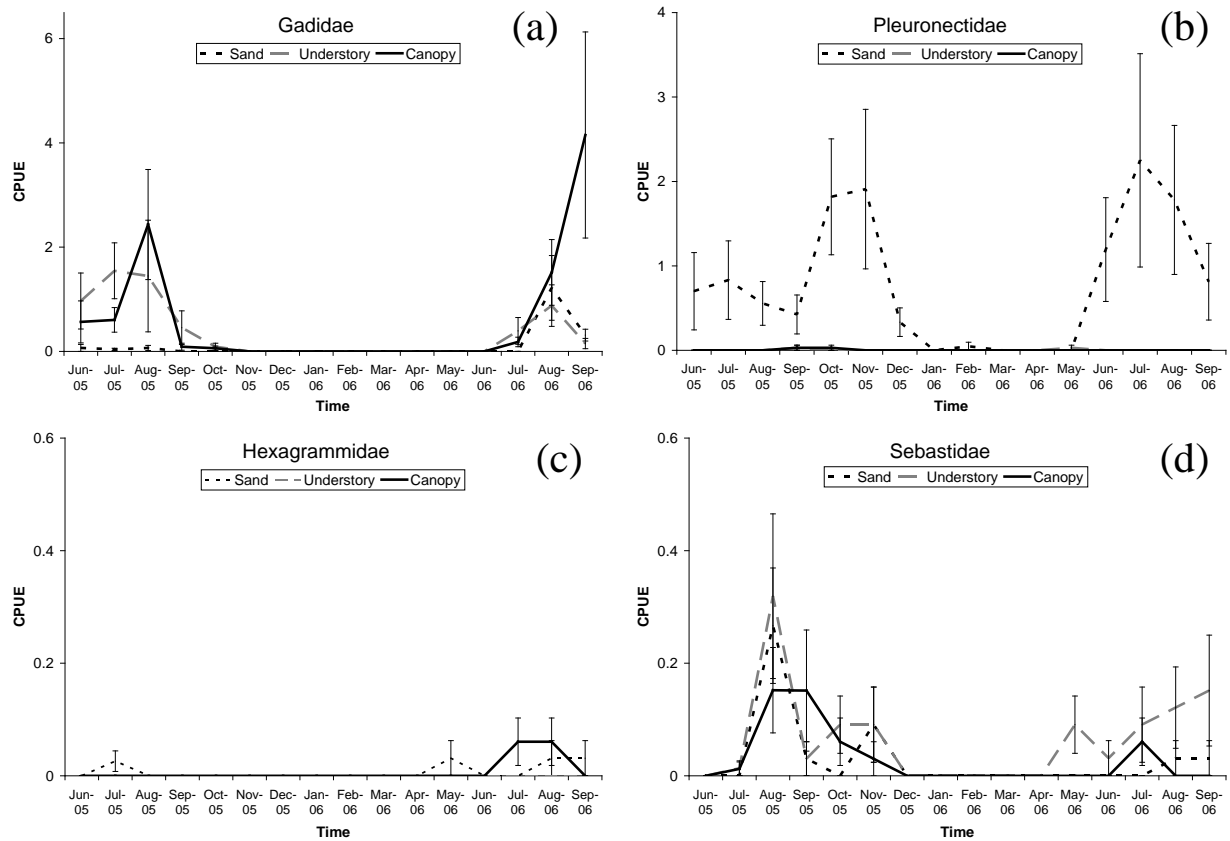


Figure 3. Mean CPUE ( $\pm 1$  SE) of (a) Gadidae, (b) Pleuronectidae, (c) Hexagrammidae, and (d) Sebastidae fishes (< 10 cm) captured or encountered in either sand, understory, or canopy habitats over time. Only families comprising more than 10% of total catch are depicted.

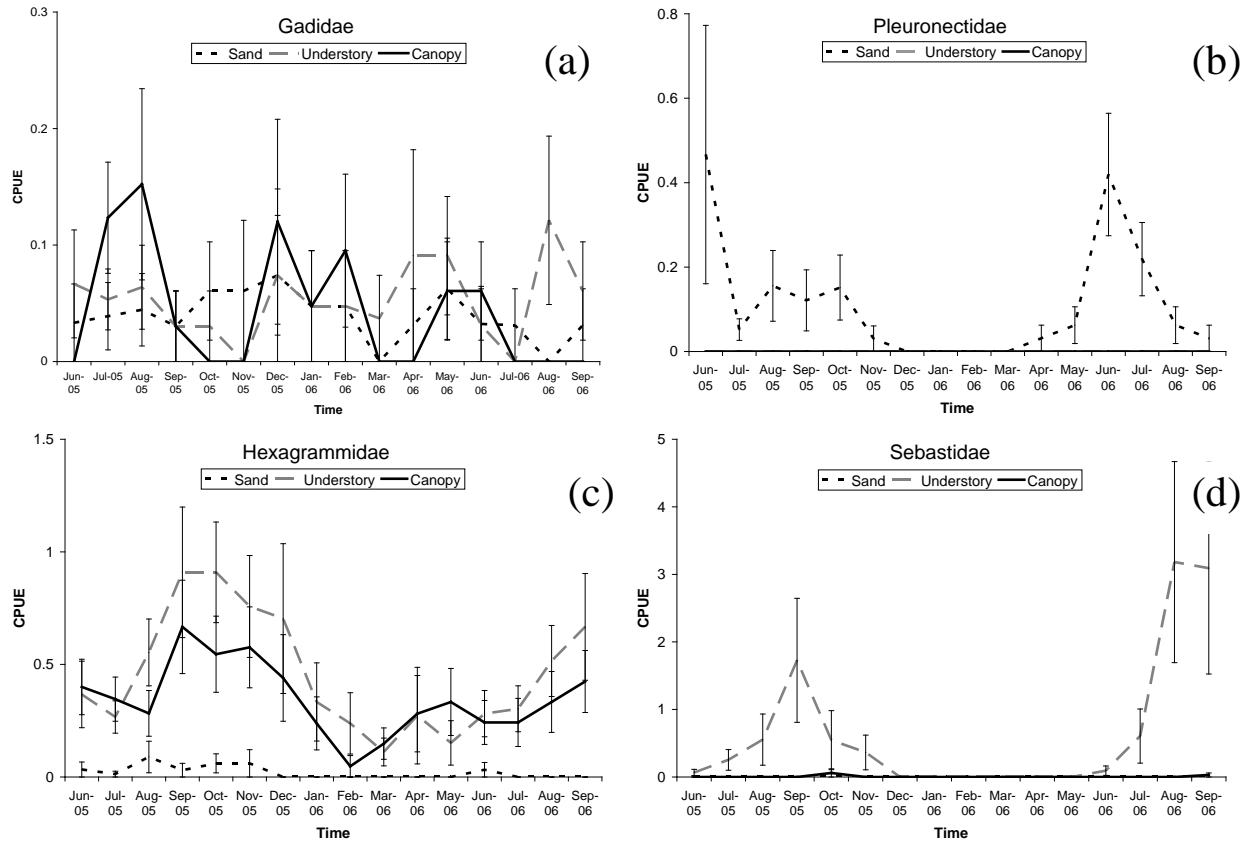


Figure 4. Mean CPUE ( $\pm 1$  SE) of (a) Gadidae, (b) Pleuronectidae, (c) Hexagrammidae, and (d) Sebastidae fishes (> 10 cm) captured or encountered in either sand, understory, or canopy habitats over time. Only families comprising more than 10% of total catch are depicted.

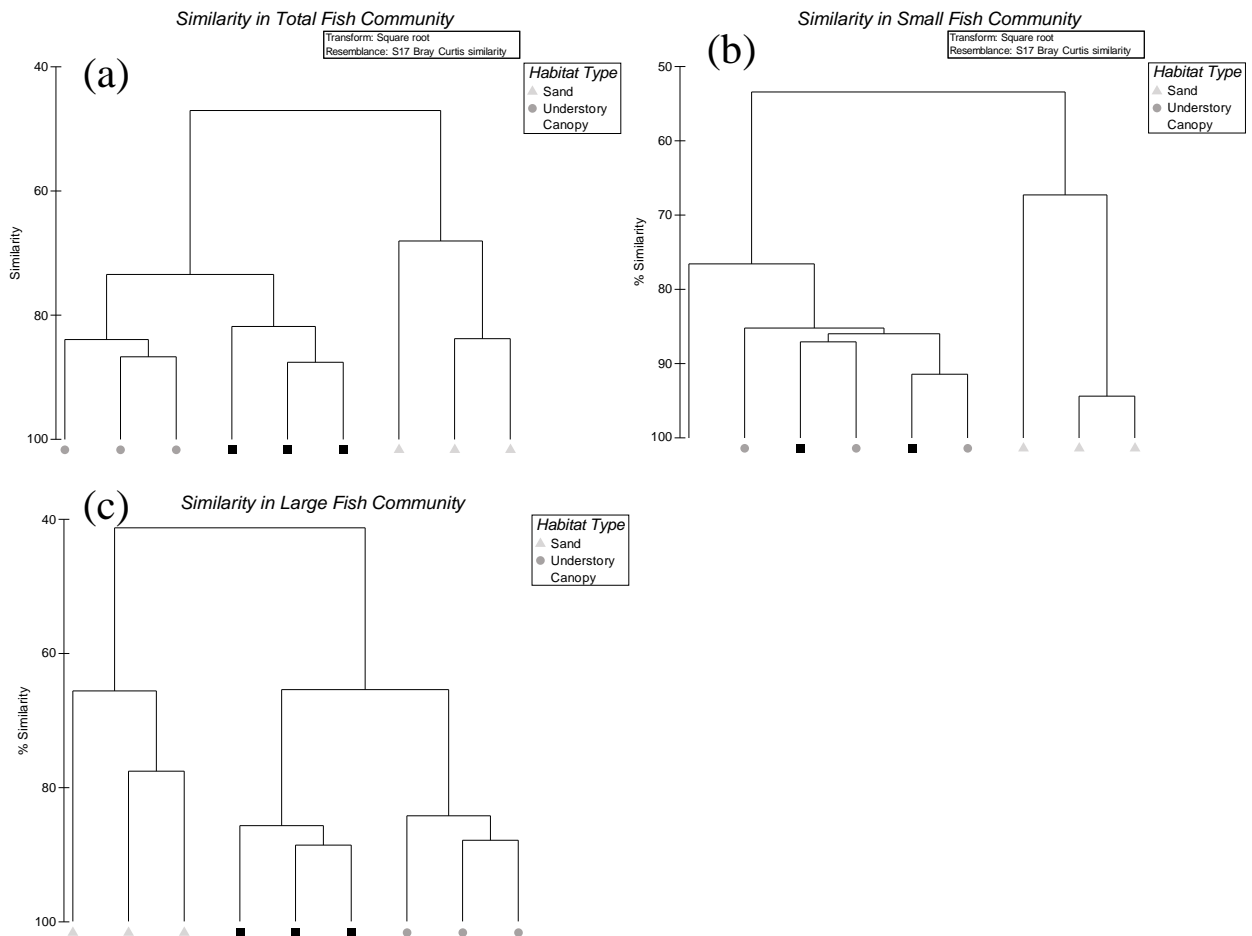


Figure 5. Cluster analysis depicting the similarity in the fish community among sites for (a) total, (b) smaller, and (c) larger fish abundance based on average densities of fish per site in each of the dominant families (comprising at least 3% of total abundance). Data were  $\log(x + 1)$  transformed and the Bray Curtis similarity coefficient was calculated. Sand, understory, and canopy sites depicted by light, medium and dark grey, respectively.

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