KELP BED VARIABILITY AND FISH POPULATION DYNAMICS IN KACHEMAK BAY, ALASKA

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IN KACHEMAK BAY, ALASKA

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ABSTRACT

Understanding interactions between kelp beds and fishes is essential because anthropogenic changes and natural variability in these beds (composition, density, and distribution) may affect available habitat for fishes. In Alaska, little is known about the annual and seasonal variability of macroalgal cover in kelp beds and corresponding changes in associated fish populations. This study investigated natural variability using monthly SCUBA surveys in Kachemak Bay, Alaska from May 2002 to September 2003. Ten shallow (approximately 7m water depth) nearshore kelp beds with varying degrees of macroalgal cover were surveyed visually for fishes and kelp, and measurements of environmental variables were collected. These kelp beds had a persistent, perennial-dominated understory with sporadic, sparse populations of annual canopy kelp. Understory and canopy kelps had affinities with greater bottom structure, and annual kelp density was greatest during periods with higher temperatures. Hexagrammids, especially kelp greenlings, existed year-round in the more structurally complex beds and were typically more abundant during periods with higher temperatures, and at sites with denser annual kelp populations. Most other fishes were transient and generally present only during summer months. Monthly changes in kelp and fish communities reflected a strong seasonal component.

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INTRODUCTION

The definition and identification of fish habitat is a challenging goal for marine scientists. The physical and financial obstacles to unbiased observation in the subtidal zone contribute to the dearth of understanding in much of the world's most productive habitats. However, given the widespread dependence of the world's human population on aquatic resources and various national and international mandates to protect the ecology of underwater environments, it is imperative that managers have the information necessary to ensure sustainability of coastal and oceanic habitats worldwide.

The multi-layered subtidal communities formed by marine macroalgae in the shallow, rocky nearshore zones of the world's cold water coastal zones are critical habitat for many fishes. These kelp forests are among the most productive aquatic biomes on earth and support numerous organisms, such as invertebrates, fishes, marine mammals, and other algal species (Steneck et al. 2002). Kelp forests are most common between 40-60° latitude in both of earth's hemispheres, though they exist in less dense stands supporting fewer fish and kelp species as far north as the Beaufort Sea in the Arctic (Dunton 1985). The range of kelp is limited by light in higher latitudes and by high temperatures and the associated low nutrient concentrations in low latitudes (Dayton 1985, Steneck et al. 2002). Almost all kelp species rely on stable substrate for holdfast attachment, and the persistence and stability of kelp beds are at least partly determined by suitable space and bottom type (Mann 1973, Estes et al. 1978, Dayton 1985). Depending on species and given appropriate substrate, kelp can form stands to approximately 25 meters water depth, with some perennial understory species dominating the deeper depths (Vadas 1968, Mann 1973, Estes and Duggins 1995). Canopy kelps can attain heights of up to 20 meters and may strongly influence the associated understory community structure due to shading and the dampening of currents and surge (Rosenthal and Lees 1976, Reed and Foster 1984, Levin 1993, Edwards 1998).

Kelp forest composition and density varies with latitude. In the eastern Pacific Ocean, the perennial kelp *Macrocystis pyrifera* dominates the canopy along the central

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Because this manuscript was prepared for submission to a journal, its figures and tables are located at the end of the text rather than embedded within it.

coast of California. This species forms dense stands that are generally stable, persistent habitats with little seasonal and annual variation (Dayton 1985, Steneck et al. 2002). Although characterized by sparse understory communities due to shading, the midwater structure afforded by this canopy kelp provides abundant cover for consistently dense and rich fish communities (e.g., Bodkin 1986, Dayton 1985). In contrast, kelp beds of the higher latitudes of the northeastern Pacific are characterized by annual canopy-forming kelps, *Alaria fistulosa* and *Nereocystis luetkeana,* resulting in wide seasonal and annual fluctuations in canopy cover (O'Clair and Lindstrom 2000). In addition, the physical structure afforded by these annual canopy kelps differs greatly from that of the perennial *Macrocystis* and as a result, the northern kelp beds are characterized by much less midwater structure. *Alaria fistulosa* forms a narrow, ribbon-like blade with a gas-filled, centralized midrib from seafloor to surface and *N. luetkeana* consists of a hollow, rope-like stipe extending from the seafloor to a floating, gas-filled pneumatocyst at the surface. *Alaria fistulosa* ranges from the Eastern Aleutians to south central Alaska, while *N. luetkeana* extends from south central Alaska to northern California (Dayton 1985, Steneck et al. 2002). Both these annual canopy kelps rarely grow in densities that shade the understory to exclusion of other kelps (Estes and Duggins 1995). Instead, these beds often contain dense understory kelp communities consisting of annual and perennial kelp species, which exist in widely varying densities in the seasonal or perennial absence of any canopy-forming kelp.

Although little is known about the overall and seasonal importance of kelp beds to fishes in Alaska, such importance has been well demonstrated elsewhere. Studies have documented increased species richness, diversity, and abundance of fishes characterize vegetated subtidal areas compared with similar areas without vegetation (Briggs and O'Connor 1971, Orth and Heck 1980, Sogard and Able 1991, Connolly 1994, Lazzari and Tupper 2002, Wyda et al. 2002). Fishes may inhabit kelp beds for a variety of reasons, based on life stage and type of cover. Some examples include the use of kelp beds by fishes for spawning and/or mating (Haegele et al. 1981, Hay 1985, Haegele and Schweigert 1985, Merrill 1989, Stekoll 1989), nurseries for new recruits (Ebeling and

Laur 1985, Carr 1989, Love et al. 1991, Levin 1994), feeding (North and Hubbs 1968, Quast 1971, Schmitt and Holbrook 1985, Hoeisaeter and Fossaa 1993), predator avoidance (Schmitt and Holbrook 1985, Carr 1992, Gotceitas et al. 1994, Sarno et al. 1994, Gotceitas et al. 1995), and as shelter from currents (Jackson and Winant 1983). While these studies are informative for basic ecological relationships, they may not be directly comparable to Alaska because of its more highly variable environmental conditions. Recent studies conducted in Prince William Sound (Dean et al. 2000), southeastern Alaska (Johnson et al. 2003), and near Kodiak Island (Hegwer 2003) suggest the kelp beds in Alaska's rocky nearshore zones are important to certain fishes (including rockfishes and greenlings) but utilized by fewer species overall than more southern kelp beds. Given the economic importance of both commercial and recreational fishing in Alaska, resource managers should have a better understanding of kelp bed habitats and the fish resources dependent on them. Specific information for Alaska is needed to provide a basis for the determination and protection of critical habitat areas.

Physical habitat structure is also important to fishes. Structural complexity of habitat provides shelter from predation (Hixon and Beets 1993) and water movement (Garcia-Charton and Perez-Ruzafa 1998), a place for feeding, reproduction, recruitment (Carr 1989, Sale 1991 and 1999, Levin 1993, Steele 1997, Aburto-Oropeza and Balart 2001) and post-recruitment (Jones 1991) events and can affect the behavior of individual fishes (Hixon and Beets 1993). The importance of physical structure, such as the measures of rugosity, verticality, and substrate size, has been documented for temperate and tropical reef fish assemblages (Bell and Galzin 1984, Callum and Ormond 1987, Garcia-Charton and Perez-Ruzafa 1998 and 2001, Aburto-Oropeza and Balart 2001). Although numerous studies in Alaska demonstrate the importance of substrate type to commercially-important bottom fishes such as Pacific halibut, little is known about any affinities of fishes to structure in the shallow, rocky nearshore coastal zones typical of much of the state.

Prior studies in Kachemak Bay were conducted primarily during summer months and described either fish or kelp communities, but do not address in detail the relationships and ecology. Inventories of kelp species (Rosenthal and Lees 1976) and documentation of kelp growth and species composition (Lees and Driskell 1981) have been conducted in Kachemak Bay. A recently initiated study (Schoch 2001) will monitor the long-term extent of beds containing *Nereocystis luetkeana* canopy kelp. However, little information is available for this region relating fishes to kelp, physical habitat, or other habitat variables. The bulk of the fish data collected in Kachemak Bay have been from deep water, targeting commercially important bottom fishes such as Pacific halibut *(Hippoglossus stenolepis)* or demersal fishes such as Pacific cod (*Gadus macrocephalus)* and walleye pollock (*Theragra chalcogramma)* (Bechtol 1997, Abookire et al. 2000). All prior work in Kachemak Bay involving fishes or kelp occurred primarily during summer (Rosenthal and Lees 1976, Rosenthal 1979, Lees et al. 1980, Lees and Driskell 1981, Abookire et al. 2000, Schoch 2001, Chenelot et al. 2001, Chenelot 2003). Little is known about seasonal variation of the algal community and any influence this may have on associated fish communities in Alaska. This study investigates seasonal variability in the rocky nearshore kelp beds and associated fish assemblages in a region typical to the south central region of Alaska and well known for its productive commercial and recreational fisheries.

METHODS

The objectives of this study were to assess relationships of fish to habitat structure and kelp densities and of fish to seasonal variations in the kelp community. Relationships were determined among structural habitat descriptors (verticality, rugosity, and substrate size), canopy and understory kelp densities, and the presence of fishes. In other studies, densities of fishes were associated positively with complexity of substrate (e.g. Aburto-Oropeza and Balart 2001) and density or biomass of understory kelp (e.g. Bodkin 1986, Dean et al. 2000). This study sought to determine if similar trends exist for northern kelp beds, such as those found in Kachemak Bay. Seasonal variation in densities of understory and annual canopy kelps and fish presence was also examined. Because macroalgal communities in Alaska vary seasonally with the growth and senescence of annual kelps, changes in kelp densities and communities can be quantified and compared with associated fishes. More fishes were present in kelp beds during periods with greater densities of understory kelp in other locations in Alaska (Dean et al. 2000, Hegwer 2003).

Study location, sites, and habitat variables

Kachemak Bay was designated as the newest and largest National Estuarine Research Reserve in the United States in 1999. It is the southernmost inlet on the Kenai Peninsula, which forms the eastern shore of Cook Inlet in Alaska (Figure 1). This region has the world's second-largest tidal range, with fluctuations of up to ten meters. Kachemak Bay is approximately 60 kilometers wide at the mouth, tapering to a width of about three kilometers at the shallow estuarine head, and is about 50 kilometers long. Hydrologic inputs are highly variable and seasonal. The Fox River at the head of Kachemak Bay and several glaciers on the south shore provide freshwater input during summer. Much of the northern shore and head of Kachemak Bay is relatively shallow with muddy, silty substrate, while the southern shore is characterized by cobble and bedrock in the shallow nearshore subtidal zone due to differences in current flow (Driskell 1979). There are strong oceanic influences from the Gulf of Alaska at the mouth (Miller and Britch 1975).

Ten sites were chosen at approximately mid-bay along the south shore based on their structural habitat characteristics, presence of kelp communities, and accessibility (Figure 2). Large sandy areas and a distance of at least 200 meters separated all sites from each other. Sites were in approximately seven meters water depth. All ten sites contained understory kelp populations providing varying degrees of macroalgal cover, and five sites contained the canopy-forming kelp, *Nereocystis luetkeana.*

Structural habitat descriptors were measured once for each site. Verticality, a subjective measure ranging from one (for low structural relief) to five (high), was assigned to each site (Bodkin 1986). Rugosity and substrate size were measured once for each quadrat in each transect surveyed in each site during September 2003. Rugosity provides a measure of habitat complexity on a small spatial scale (Garcia-Charton and

Perez-Ruzafa 2001) and is defined as the ratio of the true distance contour along the bottom to a one-meter horizontal distance (Luckhurst and Luckhurst 1978, Leum and Choat 1980, Garcia-Charton and Perez-Ruzafa 1998). Rugosity was measured by using a one-meter-long PVC bar to which a series of five-millimeter chain links were attached at one end. The bar was held horizontally with the chain-attached end resting on the substrate, and the chain was then draped along the substrate beneath the bar. These chain links were counted and a rugosity measure calculated for each quadrat, averaged per transect. The dominant substrate size was estimated by measuring the diameter of the bottom type comprising greater than 50% of the quadrat (Garcia-Charton and Perez-Ruzafa 2001). When no substrate type dominated the area in a quadrat, the percentages and size estimates of each type were noted. These measurements were categorized as ranging from one (for sand/silt) to five (bedrock) and an average value was calculated for each site. Measurements of each of these structural habitat characteristics occurred in only one month, so temporal variability cannot be determined from these data. However, these structural characteristics were not expected or observed to vary greatly over time.

Study design

SCUBA surveys were conducted to quantify densities of kelp, the presence of associated fishes, and to compare them over time. A total of seventeen visual surveys were conducted monthly between May 2002 and September 2003. At each site, three 30m x 4m transects (120m^2 each) were surveyed monthly for both fishes and kelp cover. The starting point of each transect was selected haphazardly, beginning from the boat anchor dropped in the approximate center of the study area. Transect direction was taken from a random compass bearing that maintained the requisite habitat and depth contour. All transects were separated by a randomly selected distance of at least five meters. Surveys took place during daylight hours from a small Achilles inflatable boat or Boston Whaler. Three sites had strong tidal currents (Herring Islands, Jakolof Bay, and Outside Jakolof Bay), so these surveys coincided with high and low slack tides. The remaining seven sites were sampled at all tidal stages. During three sampling periods (July, October, and November 2002), only nine sites could be sampled due to turbidity and poor visibility (missing MacDonald Spit, Anisom Point, and MacDonald Spit, respectively). Water temperature was measured monthly at each site using wrist-mounted dive computers, and it is the only physical factor with a seasonal component analyzed in this study. Horizontal visibility was estimated at each site for each survey as the distance from which the anchor was visible. Visibility also varied among sampling periods, but was consistently at least a transect width (2m on each side) and not included in the analyses. Each survey had two parts: a kelp survey and a fish survey. These surveys were conducted concurrently along the same transects by separate divers.

For the kelp survey, ten 0.25m^2 quadrats were examined per 120m^2 transect. Quadrat placement was determined by random kick cycles along transects. All understory kelps in each quadrat were counted and identified to species. Because all understory kelp species were structurally similar (in size and overall shape), they were later grouped as "annual understory" or "perennial understory" based on the life history of each species for the statistical analyses. Analyses were conducted on the average understory kelp densities per transect (number of annual or perennial individuals per 120m^2). Because canopy individuals were encountered more rarely than those comprising the understory, all *Nereocystis luetkeana* individuals present within each 120m^2 transect were counted to better quantify their presence and contribution.

Fish surveys were conducted in two parts (Bodkin 1986). Such visual SCUBA surveys are widely accepted as the best means for non-destructive sampling of fishes (Bodkin 1986 and 1988, Levin 1991 and 1993, Carr 1994) and have been used in numerous studies in various coastal habitats in other parts of the world. When workers are well trained, observer bias is shown to be low (Davis and Anderson 1989, Thompson and Mapstone 1997). To further minimize observer bias, the same diver (J. Hamilton) conducted all fish surveys except April 2003. From the starting point, all fishes observed within the boundary of each 120m^2 transect and within one meter of the bottom were counted and identified to species whenever possible. The return swim was along the same transect and conducted in midwater, approximately three meters off the bottom. All fishes within visual range and more than one meter above the bottom were counted and identified to species. However, fishes were observed more than one meter above the substrate on only one occasion, so the midwater transect data were not included in any analyses. Because few fishes were observed, the three most abundant families (Hexagrammidae, Scorpaenidae, and Gadidae) were analyzed by family group. All other fishes were observed rarely and were lumped as "other fishes" for the analyses.

Analyses and statistics

Statistical analyses were comprised of linear models and multivariate approaches using STATISTICA v.6 (Statsoft, Tulsa, OK, USA). One-way analysis of variance was used for temporal variation of water temperature. Pair-wise correlation analysis (using Pearson's correlation coefficient, r) was performed between kelp groups (based on average canopy, annual understory, and perennial understory kelp densities [number per $120m^2$]) and physical habitat data (water temperature: °C per month; rugosity, verticality, substrate size: average values per $120m^2$). Results were considered significant at $\alpha < 0.05$. Using values per $120m^2$ transect enabled realistic comparison of the physical variables and the densities of the relatively sparse canopy and more abundant understory kelps. Due to missing understory kelp data in the first month of sampling, all data collected in May 2002 were omitted from the analyses involving kelp. Because of the low number of occurrences, fish counts were converted to presence/absence data and logistic regression was applied. Independent variables were the four log-transformed physical variables (temperature: $\log_{10}$ [value per month]; substrate size, rugosity, and verticality: $\log_{10}$ [average values per $120m^2$]) and the three log-transformed kelp groups (canopy and annual/perennial understory groups: $\log_{10}$ [number of kelps per $120m^2$]). Analyses were conducted separately for each major fish family (composing at least 20% of total abundance). Cluster analysis (Clifford and Stephenson 1975) and multidimensional scaling (MDS; Field et al. 1982) were used to examine site variability in the fish and kelp communities and how these relate to structural complexity. Averages of all data were calculated by site across months and years for the ordination analyses.

Densities (number per $120m^2$ transect) of fishes and kelps were considered by species and the physical variables used were substrate size, rugosity, and verticality (water temperature did not vary among sites within months so was not used in this analysis). The Bray and Curtis dissimilarity coefficient (Bray and Curtis 1957) was used and the Euclidean distance calculated for fish, kelp, and physical variables.

RESULTS

Structural site characteristics varied from complex (rocky outcrops, large boulders and bedrock) to homogeneous (low physical relief, small cobble and sand) (Table 1). Clustering techniques partitioned the ten sites into two general structural complexity groups based on dissimilarities among the three structural characteristics (Figure 3). Water temperature varied significantly among months ($F_{12,456} = 1983.2$, $p < 0.001$, Figure 4). Temperature ranged from 1.8°C in winter to 11.0°C in summer and was the only physical variable that did not vary among sites. Water temperatures also differed significantly between years ($F_{1,456} = 1028.6$, $p < 0.001$), and were higher in 2003.

Kelp communities were variable in species composition and density (Table 2). Five of ten sites (Anisom Point, Herring Islands, Hesketh Island, MacDonald Spit, and Outside Jakolof Bay) contained the canopy kelp *Nereocystis luetkeana* in 2002, whereas only two sites (Herring Islands and MacDonald Spit) had this species in 2003. Canopy individuals persisted throughout the winter at one site (Herring Islands). The most canopy individuals were observed in late October 2002, and canopy kelp existed in very low densities (fewer than five per $120m^2$ transect at the five sites originally containing canopy) November through April with no canopy individuals seen on any transects in May 2003 (Figure 5). Canopy kelp had significant, positive relationships with temperature, substrate size, and verticality (Table 3). Understory kelp communities were variable but denser than the canopy. Understory kelps were present every month (Figure 6) with perennial kelp composing the majority of total relative abundance in all months except late October 2002. Perennial understory kelps were found on all transects in all sites with an overall equal contribution from perennial *Laminaria* spp. and *Agarum* *clathratum* (Table 2). The annual understory kelp *Laminaria saccharina* composed at least 75% of the annual kelp relative abundance in any month, and *Costaria costata* contributed at most 2%. As a group, annual understory kelps were significantly and positively correlated with temperature, while the perennial group was not (Table 3). Significant, positive correlations existed for both annual and perennial understory groups with all three structural variables measured (verticality, rugosity, and substrate size; Table 3).

The presence of some fishes was associated with season, year, physical habitat characteristics, and kelp. Four hundred twenty-two fishes from eight families and fifteen species were sighted on 34% of total transects surveyed (Table 4). Three families (Hexagrammidae [greenlings], Scorpaenidae [rockfishes], and Gadidae [codfishes]) each composed at least 20% of the total abundance and together accounted for more than 80% of all fishes sighted. Infrequently sighted fishes included those in the families Pholidae (gunnels, 6% of sightings), Cottidae (sculpins, 3%), Pleuronectidae (flatfishes, 2%), and others (including ronquils, searchers, and unidentified fishes, 5%). Grouped together, these rare fishes composed 17% of total sightings. Pooled across all species and sites, logistic regression indicated that the presence of total fishes differed significantly among months and between years (Table 5) with more fishes sighted in 2003 (Table 6). Fishes were present in all months, and the most sightings occurred in August 2003 (fishes observed on 97% of transects) and the fewest in March 2003 (23%). There were significant, positive associations of fish presence (all fish species pooled across months, years, and sites) with temperature and substrate size, as well as with the densities of both canopy and annual understory kelp (Table 5). Greenlings (primarily the kelp greenling, *Hexagrammos decagrammus*) accounted for the majority of sightings (35% of total abundance) and their presence did not differ significantly among months (Table 5). The presence of greenlings was significantly associated with rugosity (a negative association), temperature, substrate, and annual understory kelp density (positive for these three). Sightings of schooling species such as rockfishes (*Sebastes* spp., primarily the black rockfish, *S. melanops*) and Pacific cod (*Gadus macrocephalus*) occurred infrequently though these groups accounted for the greatest numbers of fishes seen on any one transect (Figure 7). As a result, densities of rockfishes and codfishes exhibited the greatest variability in sightings per month in the fish groups (Table 4), primarily during the second summer (Table 6, Figure 7). There was no significant difference in presence of rockfishes among months, but there were significant temporal differences in presence of codfishes (Table 5). Considering the major families observed in this study, only the presence of rockfishes showed significant annual variability (Table 5) with more in 2003 (Table 6). The presence of rockfishes and codfishes was significantly and positively associated with temperature only (Table 5). The presence of all other fishes did not relate significantly to temperature, any structural variables, or any kelp groups. Although these results consider only sightings of adult fishes, large schools (thousands of individuals) of juvenile codfishes (predominately *G. macrocephalus*) were observed at all sites during August and September 2002. The juvenile codfish schools observed in summer 2003 were much smaller (at most, tens of individuals). These sightings were not included in any analyses in this study due to difficulties in their accurate quantification.

Comparison of cluster dendrograms and MDS plots showed similar patterns of spatial variation among the fish and kelp groups. With all biological data averaged across months and years, five sites exhibiting greatest structural complexity grouped together with higher counts of fishes and kelp (Figures 8 and 9, respectively). Similarly, the three structurally homogenous sites grouped consistently with lower values for both fishes and kelp. Two sites (Little Jakolof Bay and Outside Jakolof Bay) showed inconsistencies in these groupings. Little Jakolof Bay (with a lower complexity designation) grouped in the lower fish abundance group but the higher macroalgal count group. Outside Jakolof Bay (higher complexity designation) grouped in the lower density groups for both kelp and fishes.

DISCUSSION

Fish diversity and overall abundance in kelp bed habitats of the highly productive Gulf of Alaska appear low compared to similar, more temperate coastal habitats. Visual

SCUBA surveys conducted in Alaska kelp beds have resulted in low overall fish counts (Dean et al. 2000, Hegwer 2003, Calvert unpublished data, this study) whereas studies incorporating similar methods in California kelp beds documented higher fish diversity and abundance (Ebeling et al. 1985, Bodkin 1986 and 1988, Carr 1989, Levin 1993).

Previous studies in Alaska kelp beds have shown positive correlations between presence of fishes and understory algal density or biomass (Dean et al. 2000, Hegwer 2003). Some investigations in California agreed with these findings (DeMartini and Roberts 1990, Levin 1993), although most California studies discussed relationships between fish density or biomass and the relative abundance of vertical structure afforded by the perennial canopy kelp, *Macrocystis pyrifera* (i.e., Carr 1989 and 1994, Bodkin 1986 and 1988, Dayton et al. 1998). Alaska's kelp beds differ from those in California because the more northern canopy kelps are annuals. In Kachemak Bay, the significant, positive association of total fishes with the density of the annual canopy kelp, *Nereocystis luetkeana,* suggests that areas characterized by better *N. luetkeana* growth have greater fish densities. In one northern California study, four times more kelp greenling were found in *N. luetkeana* beds than were seen in the present study (Bodkin 1986). *Nereocystis luetkeana* beds in California were similarly important to rockfishes (Bodkin 1986, Love et al. 1991, Danner et al 1994).

The existence of high understory kelp densities in canopy-containing sites may be of greater importance to fishes than the canopy itself in Kachemak Bay. Both the greenling group and general fishes were positively associated with annual understory kelp density. In addition, fishes in the present study were nearly always observed in close association with the understory. This agrees with Dean et al. (2000) and Rosenthal (1979) who showed that understory kelp is important habitat to greenlings in south central Alaska, particularly since the majority of sightings in the present study were in this group. Perhaps the perennial-dominated understory of northern kelp beds provides a small degree of habitat stability for some fishes at least part of the year.

The variability in Kachemak Bay fish and kelp populations may be partially attributable to the extremely seasonal nature of the northern environment compared to southern locations. A significant, positive association between fish presence (fishes in general and the major families observed in the present study) and temperature indicates seasonal variability in the fish communities associated with kelp communities in Kachemak Bay. Fish communities inhabiting seasonally and annually variable kelp beds in the north must endure a wider variety of environmental variables over the course of a season, year, or lifetime than those occupying the stable, perennial canopy-dominated kelp beds of more temperate zones. The importance and magnitude of seasonal cues varies among kelp and fish species throughout their ranges, but include temperature, photoperiod, turbidity, increased frequency of storms and surge in winter, and the availability of prey and nutrients. However, the thresholds of many of these environmental factors are to some extent temperature-dependent (Dayton 1985), providing an easily quantified surrogate variable for seasonality in the present study. Kelp beds (and associated fishes) at the northern edge of their range are subject to wide fluctuations in all of these factors, as well as wide inter-annual variation in intensity and duration of seasonal factors. It is these extremes that make studying these habitats difficult or impossible during all but summer, thus the paucity of consistent seasonal data in the north.

Increased storm frequency affects shallow subtidal habitats by increasing mechanical damage to kelp (Dayton 1985, Mann 1973) and foraging difficulty for fishes (Ebeling et al. 1980). Surge tends to influence movement of fishes to deeper water during the winter months. Rockfishes in Puget Sound moved to shallower water in summer and deeper water in winter (Moulton and Miller 1987), possibly avoiding increased surge during winter months. While greenlings were observed in the shallow, rocky nearshore sites every month in the present study, rockfishes and codfishes were observed rarely during all but summer. Healthy understory populations have been observed in this area on rocky substrate at depths of up to 16m (J. Hamilton, pers. obs.) and Kachemak Bay fish populations may shift seasonally to similar habitats in adjacent, deeper water (Rosenthal 1979).

In the kelp community, recent aerial surveys during two consecutive summers showed variability in size, location, and presence of *Nereocystis luetkeana* canopies in Kachemak Bay (Schoch 2001), illustrating great inter-annual variability that may be apparent in short temporal scales. Such variability was also observed in the present study, in that three of five sites originally containing canopy kelp did not recruit canopy individuals the second summer. Although this canopy species is considered an annual, Chenelot et al. (2001) found *N. luetkeana* individuals that persisted to reproduce into a second summer, as also observed in one site in the present study. A previous study of seasonality in northern understory kelp communities (Mann 1973) found the greatest growth rates for annual understory kelps in summer, but growth rates for perennial kelps were greatest in late winter and early spring (also Rosenthal and Lees 1976, Lees and Driskell 1981). These findings may explain the lack of a relationship between perennial understory kelp density and temperature in the present study. In addition, they support the positive relationships found between temperature and annual kelp in both the canopy and the understory in this study, illustrating seasonal variation of the kelp communities in Kachemak Bay.

As demonstrated elsewhere, some habitat characteristics may influence fish community structure in this region. In California kelp beds, Bodkin (1986) found a significant correlation between densities of fishes and bottom relief. The significant, positive association in the present study of total fishes with substrate size suggests a similar trend for Kachemak Bay. In particular, greenlings in the present study associated most consistently with kelp beds that had a predominately rocky (i.e., large cobble/bedrock) and structurally complex bottom habitat. During summer, rockfishes in Puget Sound inhabited low-relief rocky kelp beds (Matthews 1990) and in Prince William Sound they were positively associated with slope (Dean et al. 2000). In the present study, however, rockfishes and codfishes were not associated with any bottom structure at any time of year, perhaps due to the sporadic sightings of these species. The lack of association of rockfishes and codfishes with any structural habitat variables or kelp may reflect the transient nature and seasonal association of these fishes with kelp at the depth sampled. Again, however, the rarity of fishes observed higher than one meter above the substrate in the present study indicates that bottom structure may be important to the observed fishes, if perhaps indirectly by also being appropriate substrate for kelp habitat. Structural complexity, as defined in the present study, was important to both fishes and kelps in that greater physical complexity was associated with greater overall densities in these communities, and vice versa. These findings may enable managers to identify potentially important nearshore fish habitat based on easily quantified structural habitat variables alone. However, due to the design of the present study and the others cited here, the separate effects of physical structure and structure provided by kelp cannot be distinguished. Additional research focusing on the separation of kelp and structural habitat characteristics through manipulative experimentation is required for such understanding.

It is difficult to account for all meaningful factors influencing a natural system, particularly without knowing the recent history of the community (Dayton et al. 1998). Because little is known about interactions between kelp and fish communities and their natural variability in south central Alaska, investigation of the more obvious, small-scale processes over an entire year is necessary. As this study was observational, inferences based upon it cannot be attributed unequivocally to cause and effect relationships. Instead, factors outside the scope of this study may be of equal or greater influence on the patterns observed. Physical factors such as size of the kelp beds and related edge effects, salinity fluctuations and freshwater runoff, degree and direction of exposure to light and tidal currents, and the frequency of storm events almost certainly play a significant role in the structuring of these communities. In addition, biological factors that may influence algal community structure include inter- and intra-species competition (Estes et al. 1978, Duggins 1980) and herbivory (Ebeling et al. 1985, Tegner et al. 1995). A growing body of evidence points to the importance of temporal and spatial scales in the study of ecological processes (i.e., Dayton and Tegner 1984, Wiens et al. 1986, Dethier and Duggins 1988, Powell 1989, Foster 1990). At the depth surveyed in the present study, structurally complex Kachemak Bay kelp beds appear to provide critical habitat throughout the year for greenling species only. However, this habitat is also used seasonally by rockfishes and (adult and juvenile) codfishes and importance for these groups is implied as well. This work provides a description and baseline of shallow nearshore kelp beds and associated fish communities in Kachemak Bay, Alaska on a spatial scale of tens of kilometers over seventeen consecutive months. These findings are suitable for comparison with relationships found within kelp bed habitats at similar scales in other areas.

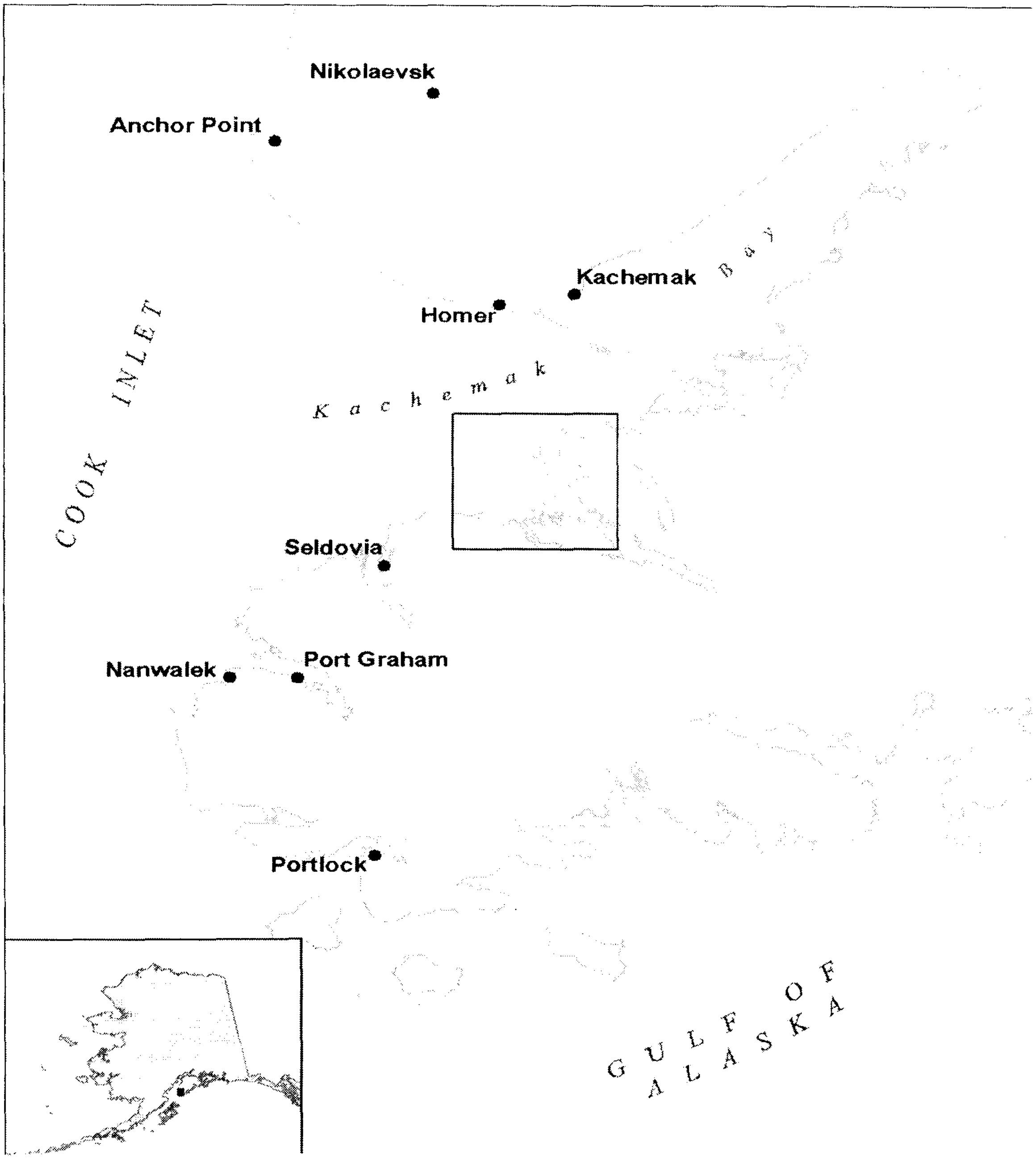

Figure 1. Location of study area (central box) detailed in Figure 2.

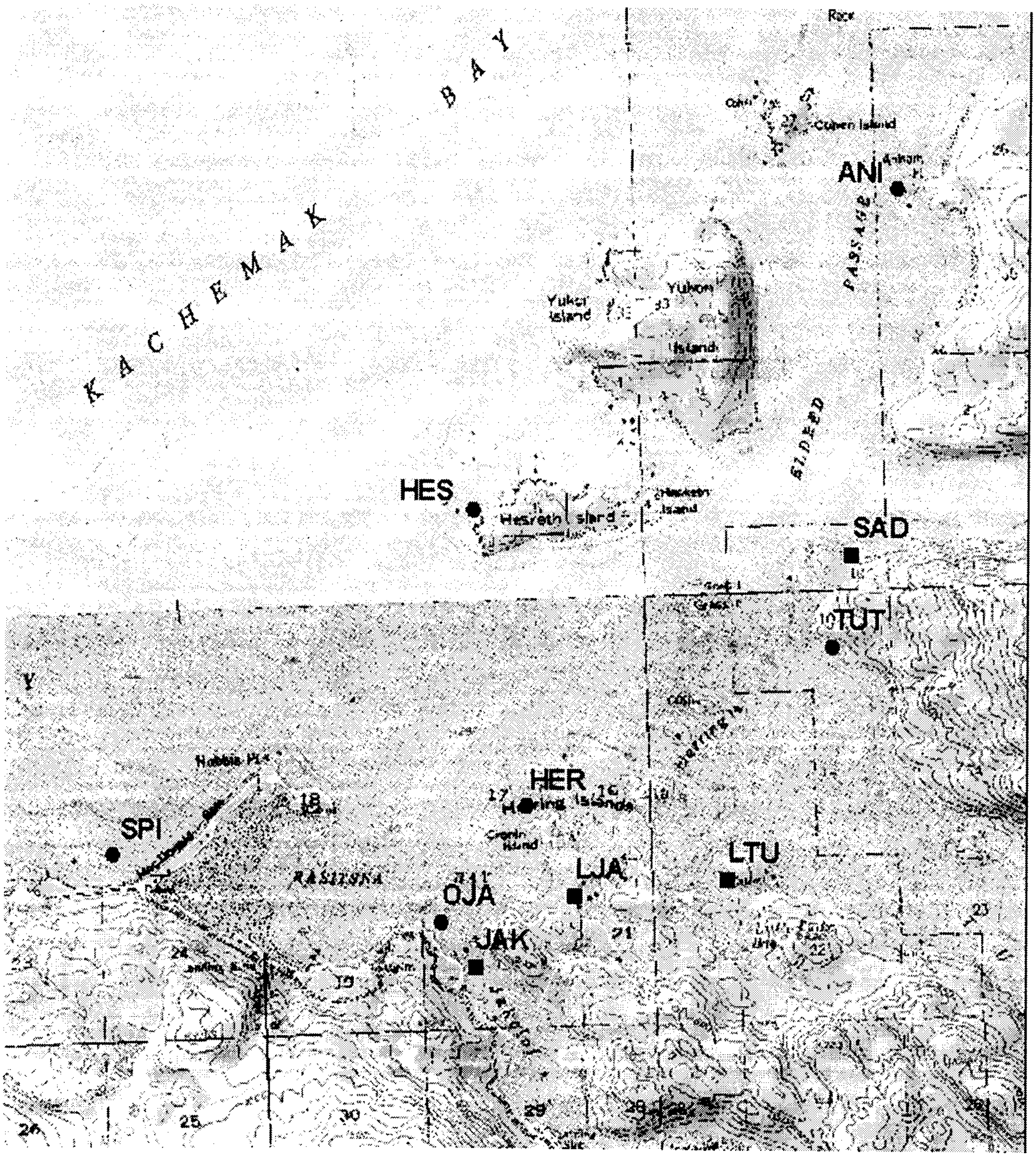

Figure 2. Location of study sites. Sites characterized by high structural complexity are denoted with a circle and low structural complexity sites are designated by a square (Figure 3). See Table 1 for definition of abbreviations.

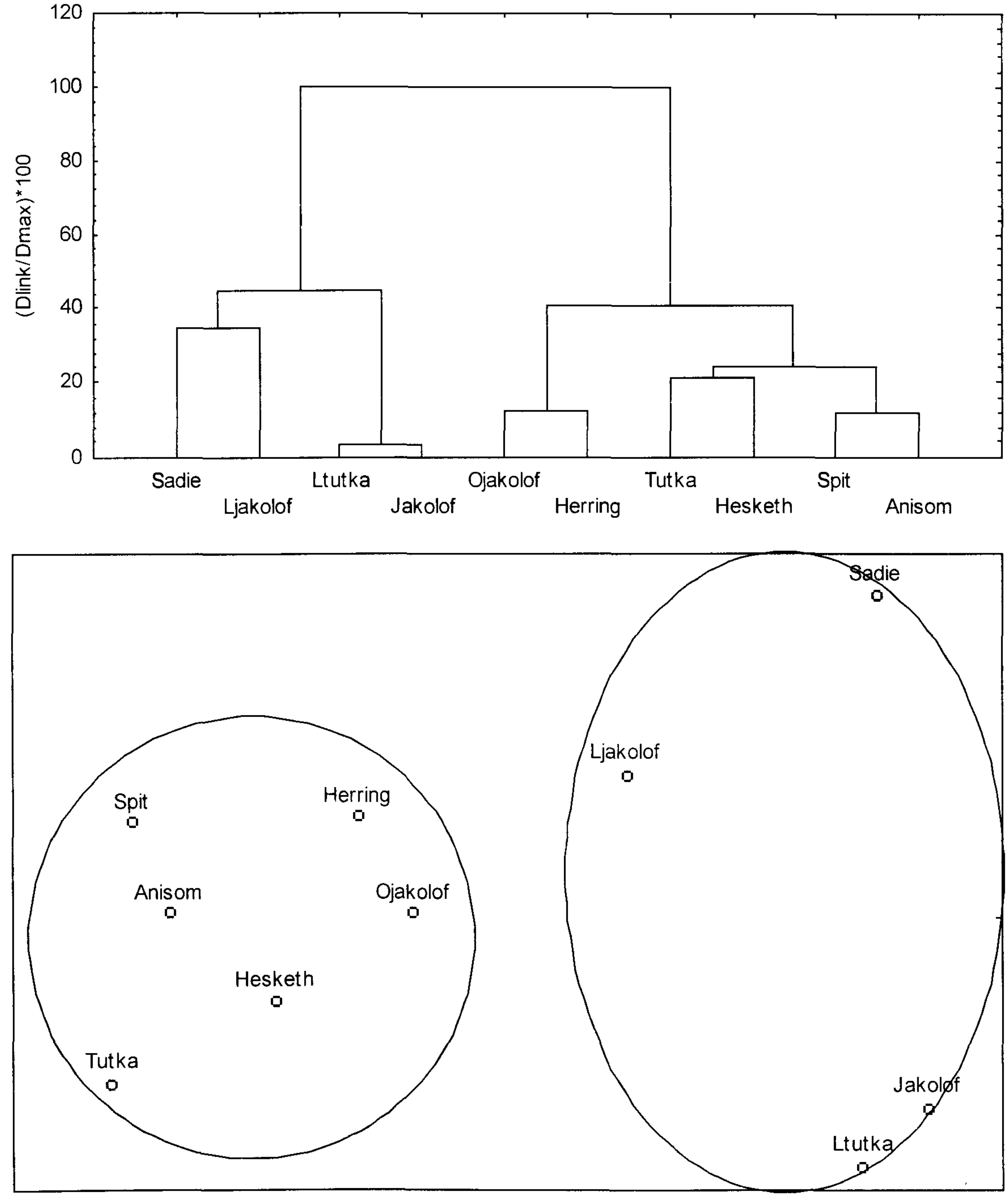

Figure 3. Cluster dendrogram (top) and multidimensional scaling ordination (MDS, complete linkage: bottom) for structural habitat variables (substrate size, rugosity, and verticality) at each site. Circled groups indicate sites with less than 50% dissimilarity between structural variables.

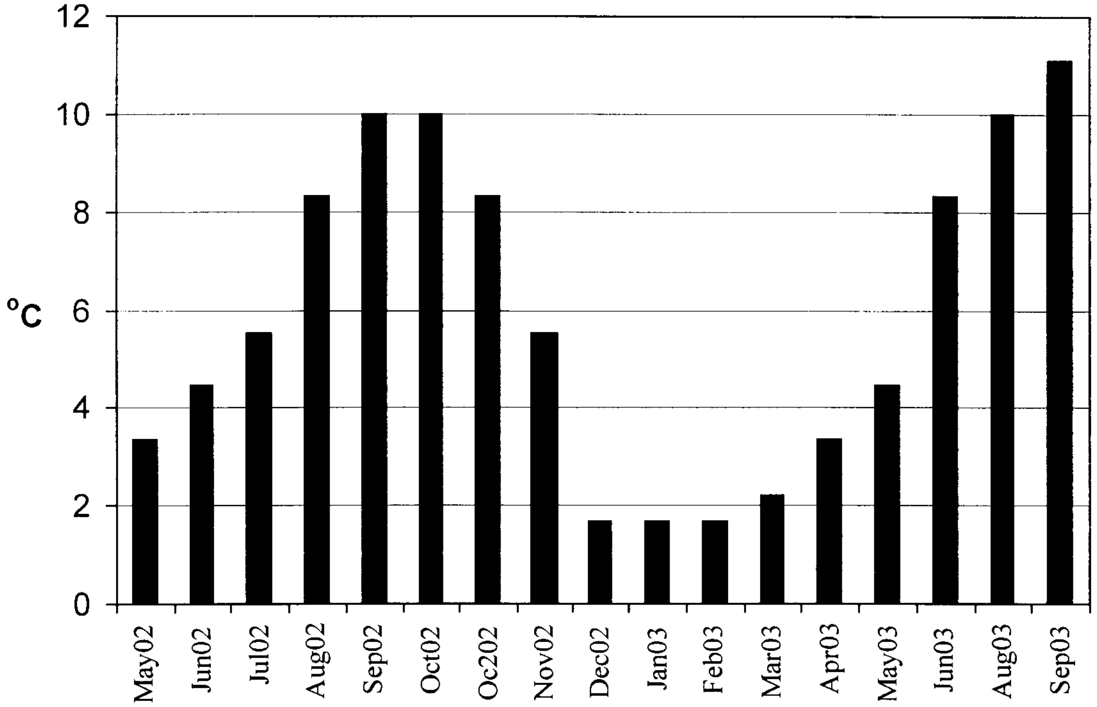

Figure 4. Monthly variation of water temperature. Temperatures were consistent among sites within months. N = 167 total observations.

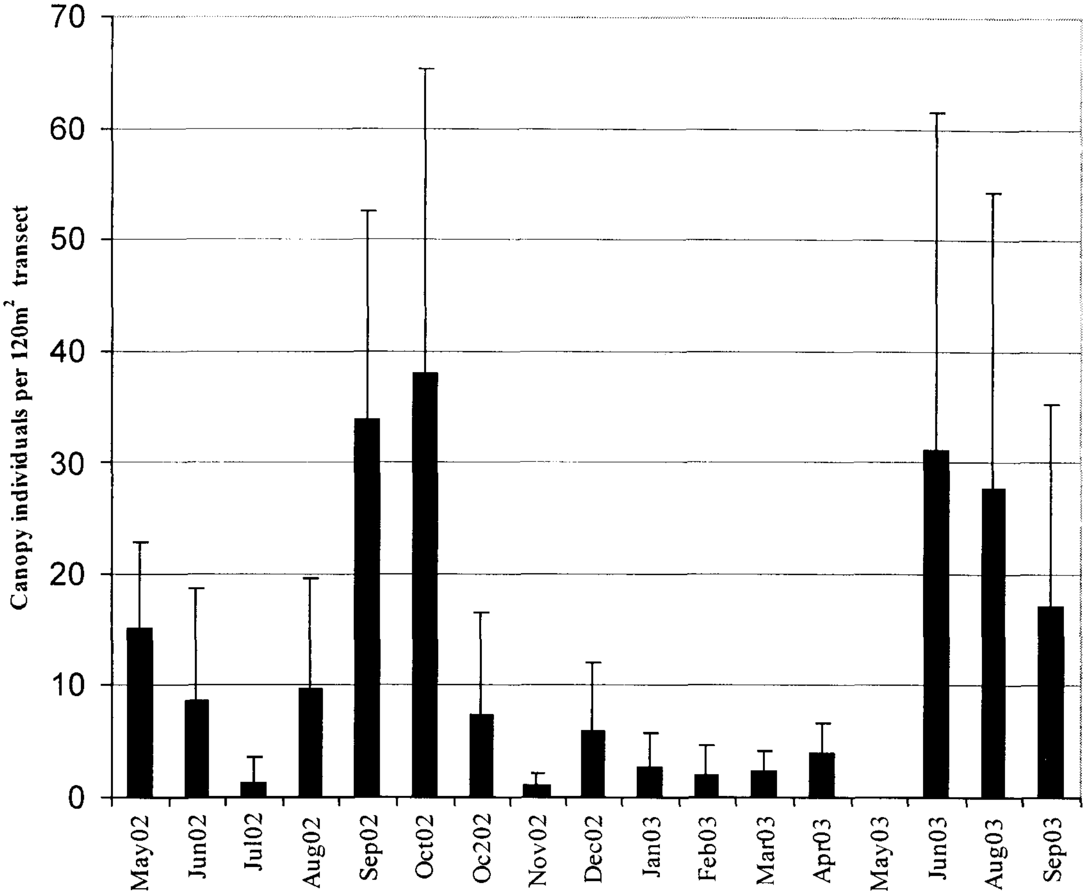

Figure 5. Monthly variation of *Nereocystis luetkeana* density. Values are the average number of canopy individuals per transect, averaged across the five sites initially containing canopy. Error bars represent standard error (N = 248 transects).

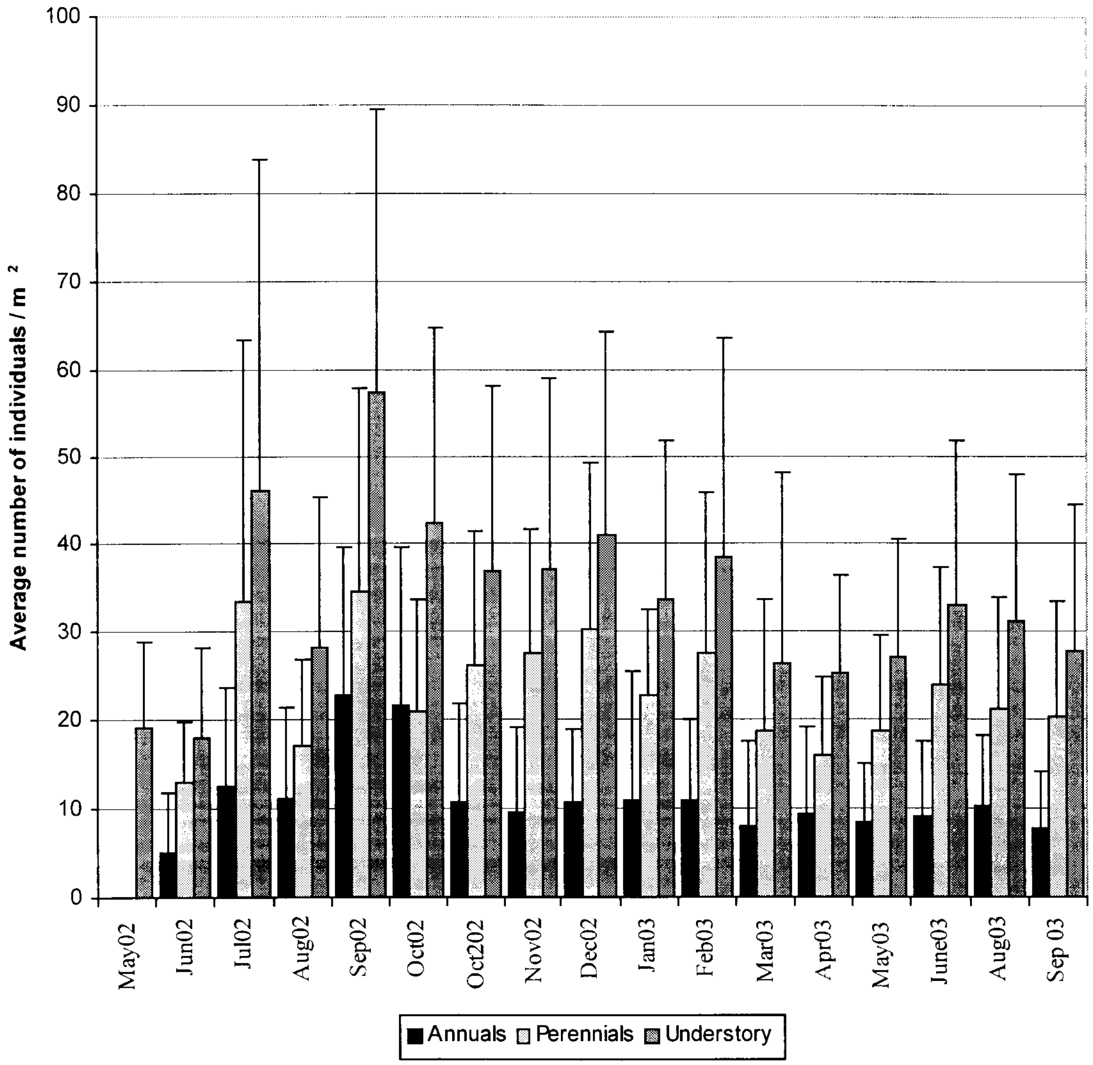

Figure 6. Monthly variation of the density of understory kelp groups. Understory is comprised of pooled "annuals" and "perennials." In May 2002, the understory is the only reported value since there was no differentiation between annual and perennial *Laminaria* spp. Error bars represent standard error (N = 503 transects).

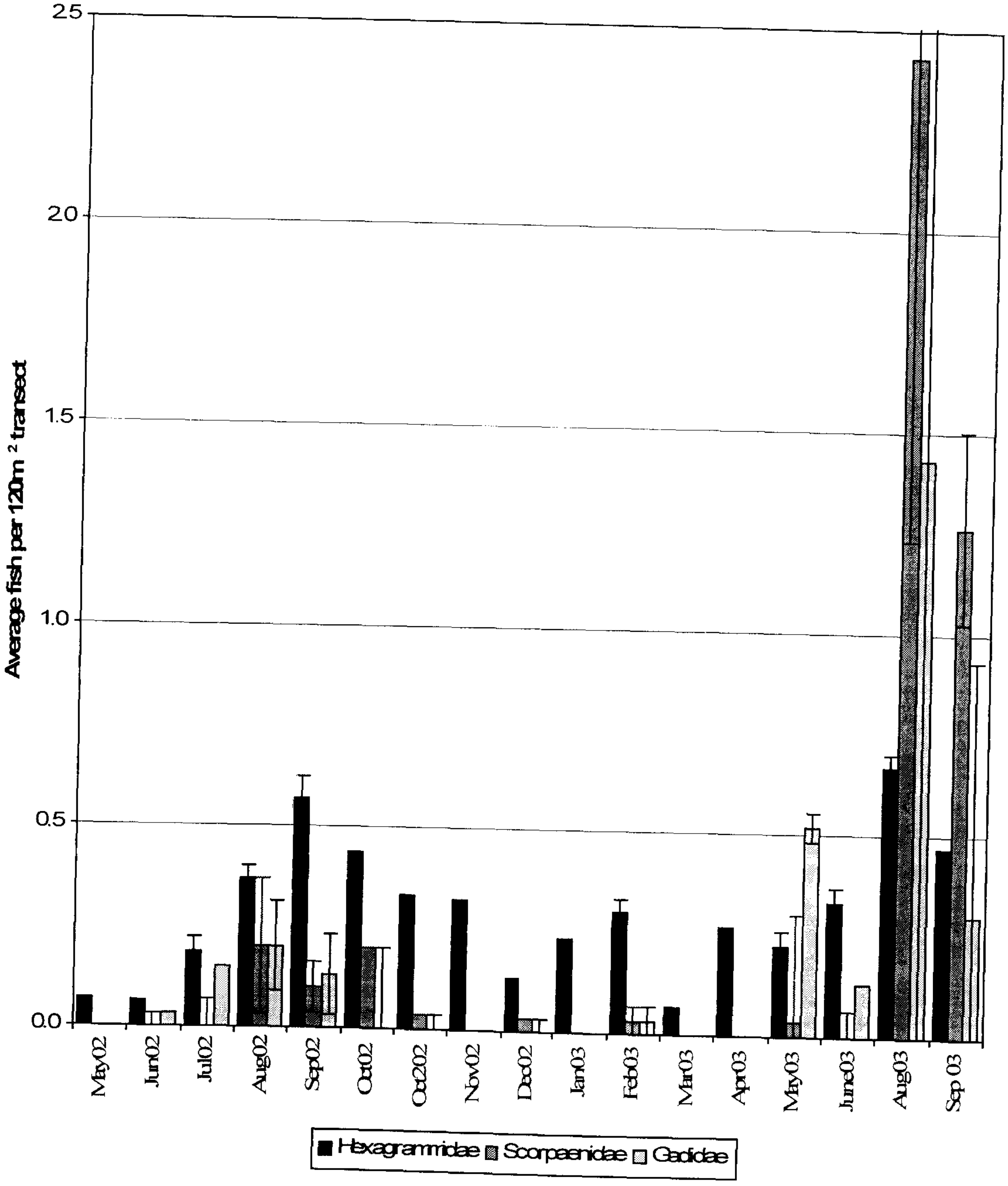

Figure 7. Monthly variation of major fish families averaged across sites. Only families comprising greater than 20% of total density were included. Standard error bars are shown (N = 503 transects).

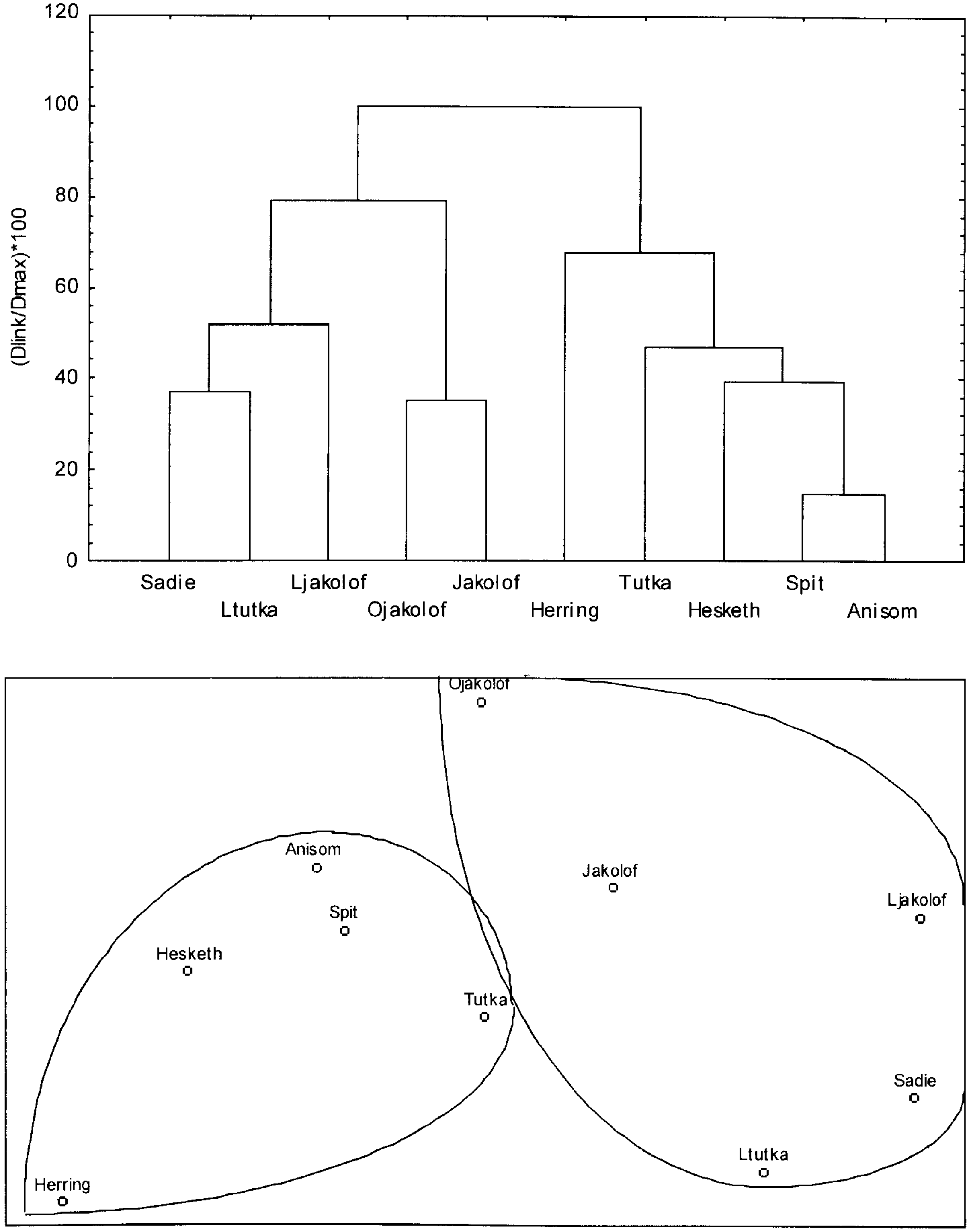

Figure 8. Cluster dendrogram and MDS ordination (complete linkage) for fish communities at each site. Circled groups indicate sites with less than 80% dissimilarity among fish communities.

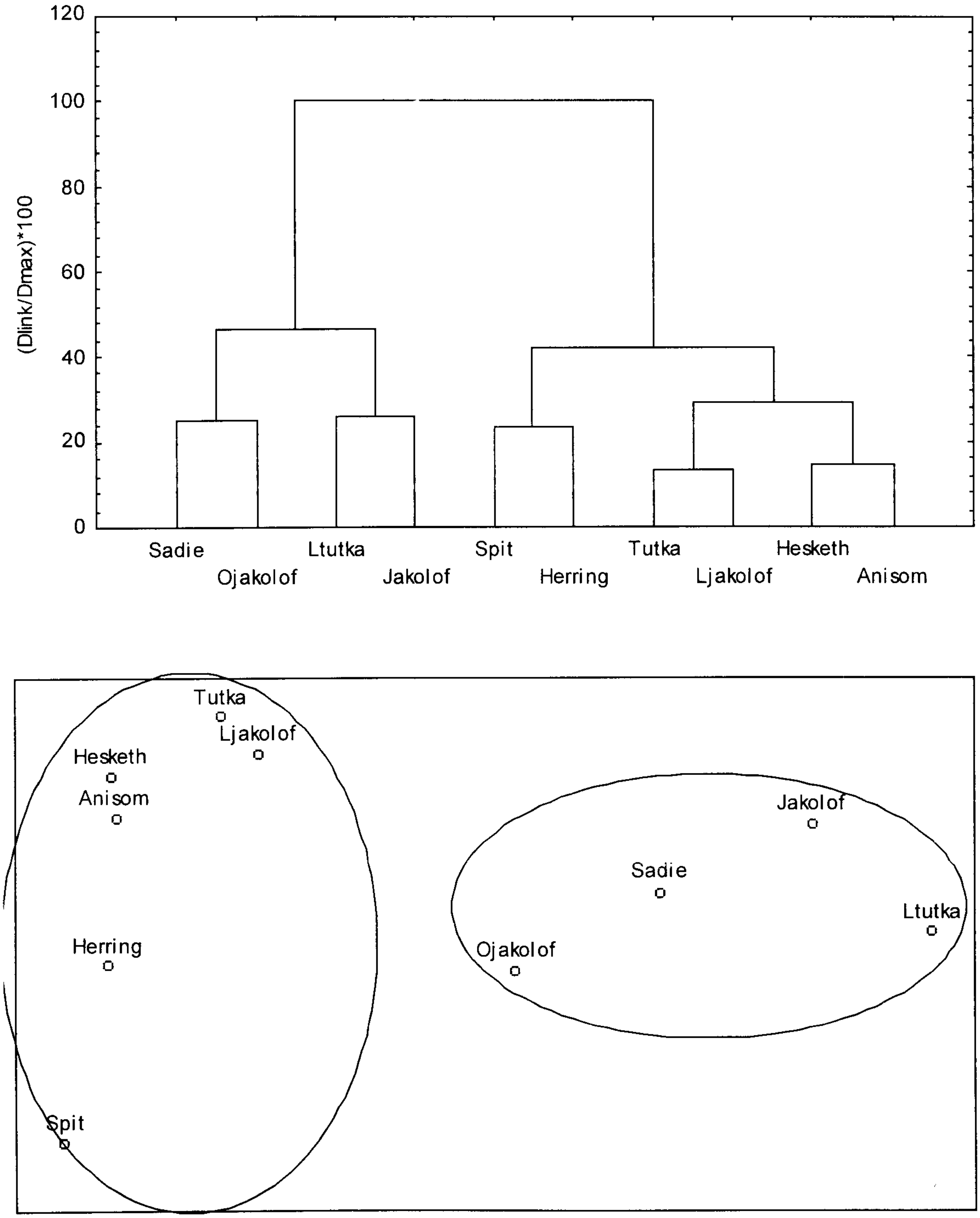

Figure 9. Cluster dendrogram and MDS plot (complete linkage) for kelp communities at each site. Circled groups indicate sites with less than 50% dissimilarity between kelp communities.

Table 1. Site variation of structural characteristics. Complexity designation is based on cluster analysis and multidimensional scaling plots (Figure 2), and represent groupings of sites with less than 50% dissimilarity. Site variation of rugosity and substrate measurements is based on quadrat averages while verticality measure is by site (see methods for details).

Site (abbreviation)	**Complexity designation**	**Rugosity (std. dev.)**	**Substrate (std. dev.)**	**Verticality**
Anisom Point (ANI)	High	1.38 (0.25)	3.8 (1.6)	5
Herring Islands (HER)	High	1.30 (0.29)	2.0 (2.0)	5
Hesketh Island (HES)	High	1.27 (0.20)	3.1 (1.9)	4
Outside Jakolof Bay (OJA)	High	1.18 (0.07)	1.9 (0.5)	4
MacDonald Spit (SPI)	High	1.20 (0.12)	4.6 (1.0)	5
Jakolof Bay (JAK)	Low	1.07 (0.06)	1.2 (0.5)	1
Little Jakolof Bay (LJA)	Low	1.21 (0.16)	1.0 (1.8)	3
Little Tutka Bay (LTU)	Low	1.10 (0.08)	1.3 (0.8)	1
Sadie Cove (SAD)	Low	1.11 (0.14)	0.5 (1.3)	2
Tutka Bay (TUT)	High	1.72 (0.39)	4.1 (0.2)	4

Table 2. Average number of kelp individuals / m^2 across all months and sites (N = 473 transects and May 2002 omitted due to missing data). "Maximum" indicates the greatest density of kelp individuals (number / m^2) observed for the respective groups and species. The headings "% transects" and "% sites" indicate frequency of kelp presence on transects and in sites, respectively.

Kelp group, *species name*	**Mean**	**St. Dev.**	**Maximum**	**% transects**	**% sites**
Canopy (*Nereocystis luetkeana)*	0.01	0.05	0.48	21%	50%
Understory (all species)	34.32	23.07	158.40	100%	100%
Perennials	21.77	16.85	113.20	100%	100%
Agarum clathratum	12.18	10.31	65.60	92%	100%
Laminaria spp.	10.98	13.79	76.80	85%	100%
Annuals	11.16	11.61	59.60	87%	100%
Laminaria saccharina	9.92	10.88	58.00	81%	100%
Cymathere triplicata	0.50	1.69	14.40	18%	60%
Alaria marginata	0.65	4.18	46.00	7%	50%
Costaria costata	0.04	0.22	3.20	5%	50%

Table 3. Pair-wise correlation analysis (Pearson's correlation coefficient, r) between physical variables and kelp groups (N = 473 transects). May 2002 was omitted due to missing data. Bolded values indicate significance at $p < 0.05$.

Kelp group	Temperature	Rugosity	Substrate	Verticality
Canopy	**0.19** **$p < 0.001$**	-0.04 $p = 0.435$	**0.27** **$p < 0.001$**	**0.22** **$p < 0.001$**
Understory (all species)	**0.09** **$p = 0.042$**	**0.51** **$p < 0.001$**	**0.45** **$p < 0.001$**	**0.51** **$p < 0.001$**
Perennial species	0.02 $p = 0.685$	**0.48** **$p < 0.001$**	**0.41** **$p < 0.001$**	**0.48** **$p < 0.001$**
Annual species	**0.16** **$p = 0.001$**	**0.34** **$p < 0.001$**	**0.32** **$p < 0.001$**	**0.35** **$p < 0.001$**

Table 4. Average number of fish sighted per 120 m^2 transect across all months and sites. N = 503 transects. The "total" column indicates total number of fishes sighted by family and/or by species in the study. Bolded entries indicate fishes designated by families or groups.

Family or group name, common name (*species name*)	**Total**	**Mean**	**Std.Dev**
Hexagrammidae	**148**	0.296	0.646
Kelp greenling, pooled (*Hexagrammos decagrammus*)	69	0.145	0.410
Kelp greenling, male	23	0.044	0.206
Kelp greenling, female	46	0.093	0.317
White-spotted greenling (*Hexagrammos stelleri*)	39	0.078	0.284
Rock greenling (*Hexagrammos lagocephalus*)	20	0.040	0.216
Masked greenling (*Hexagrammos octogrammus*)	15	0.030	0.213
Scorpaenidae	**130**	0.260	2.534
Black rockfish (*Sebastes melanops*)	114	0.228	2.518
Dusky rockfish (*Sebastes ciliatus*)	10	0.020	0.189
Gadidae	**86**	0.172	1.705
Pacific cod (*Gadus macrocephalus*)	83	0.166	1.704
Walleye pollock (*Theragra chalcogramma*)	3	0.006	0.077
Cottidae	**12**	0.024	0.153
Red Irish lord (*Hemilepidotus hemilepidotus*)	6	0.012	0.109
Yellow Irish lord (*Hemilepidotus jordani*)	3	0.006	0.077
Pleuronectidae (unspeciated)	**9**	0.018	0.133
Crescent gunnel (*Pholis laeta*)	25	0.050	0.289
Alaskan ronquil (*Bathymaster caeruleofasciatus*)	4	0.008	0.089
Sturgeon poacher (*Podothecus acipenserinus*)	2	0.004	0.063
Other (unidentified)	**20**	0.040	0.288
Total fish (all species)	**422**	0.844	3.142

Table 5. Summary of logistic regression on the presence of fishes by families and by total abundance. Only families composing greater than 20% of the total fish abundance are included. Independent variables are time (N = 503 transects for tests of "month" or N = 208 transects for test of "year," the comparison of June to September of years 2002 and 2003), kelp densities (canopy and perennial/annual understory groups; N = 473 transects), and physical variables (water temperature, rugosity, verticality, and substrate size). n = total transects with fishes present. Only significant values are reported, $p < 0.05$.

Analysis group	**Independent variable**	**n**	**Parameter estimate**	**Standard error**	**Wald's X^2**	**p-value**
Hexagrammidae	Annual understory	105	0.62	0.17	12.65	< 0.001
	Temperature	107	4.26	0.91	22.15	< 0.001
	Rugosity	107	-2.48	1.15	4.66	0.031
	Substrate size	107	1.90	0.47	16.11	< 0.001
Scorpaenidae	Year	16	0.64	0.29	4.67	0.031
	Temperature	21	9.00	3.00	13.00	< 0.001
Gadidae	Month	27	0.27	0.08	12.19	0.001
	Temperature	27	4.28	1.62	6.96	0.008
Total fish	Month	168	0.08	0.03	10.19	0.001
	Year	95	0.28	0.13	4.61	0.032
	Annual understory	164	0.21	0.10	3.99	0.046
	Canopy	164	0.66	0.32	4.37	0.037
	Temperature	164	5.12	0.78	43.13	<0.001
	Substrate size	164	0.80	0.38	4.49	0.034

Table 6. Annual variability in kelp and fish populations. Averages are for kelp groups and fish families during summer months (June to September in the years 2002 and 2003). All values are the average number of individuals per $120m^2$ transect. Only fish families comprising greater than 20% of total abundance are shown. N = 208 transects.

Family or group name	**2002 Average (std.dev)**	**2003 Average (std.dev)**
Canopy kelp	1.49 (4.10)	2.52 (9.29)
Perennial understory kelp	2911.32 (2570.67)	2611.73 (1572.87)
Annual understory kelp	1534.37 (1601.50)	1078.93 (918.30)
Hexagrammidae	0.30 (0.60)	0.49 (0.85)
Scorpaenidae	0.08 (0.42)	1.23 (5.83)
Gadidae	0.13 (0.53)	0.62 (3.88)
Total fish (all species)	0.63 (0.96)	2.59 (6.92)

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