

Abstract—Understanding the interactions between kelp beds and nearshore fish is essential because anthropogenic changes and natural variability in these beds may affect available habitat for fishes. In this study fish communities were investigated in south-central Alaska kelp beds characterized by a range of substrate complexity and varying densities of both perennial understory kelps and annual canopy kelps. Many of the observed fish species, as well as understory and canopy kelps, were positively associated with structurally complex substratum. Targeted canopy and understory kelp beds supported seasonal populations of adult and juvenile Pacific cod (*Gadus macrocephalus*), rockfishes (*Sebastes* spp.), and year-round populations of greenlings (*Hexagrammos* spp.). Monthly changes in kelp and fish communities reflected seasonal changes; the densities of some species were greatest during periods with higher temperatures. This work illustrates the importance of structurally complex kelp beds with persistent understory kelp populations as important fish habitat for several commercially and recreationally important fishes.

Implications of substrate complexity and kelp variability for south-central Alaskan nearshore fish communities

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Marine macroalgal communities in the shallow, rocky, nearshore zones are among the most productive aquatic biomes on earth and provide important habitat for invertebrates, fishes, and marine mammals (Steneck et al., 2002). Although the importance of kelp bed variability (including kelp density, distribution, and species composition) to fishes has been demonstrated in Alaskan waters (Dean et al., 2000; Hegwer, 2003; Hamilton, 2004; Calvert, 2005), the role of seasonality in these habitats is poorly understood, particularly in regions with seasonal extremes, such as the subarctic (but see Calvert, 2005). Furthermore, although the persistence and stability of kelp beds are at least partly determined by suitable space and substratum type (Dayton, 1985), the importance of overall habitat complexity (i.e., kelp cover and substrate topography) to kelp-associated fish species has not been investigated in Alaska.

Previous studies in Alaskan kelp beds have shown positive correlations between the presence of fishes and the density (or biomass) of understory algae (Dean et al., 2000; Hegwer, 2003; Hamilton, 2004). Researchers elsewhere have also agreed with these findings (Dayton, 1985) but have demonstrated relationships between fish density or biomass and the relative abundance of the canopy kelp *Macrocystis pyrifera* (Bodkin,

1986; Carr, 1994). *Macrocystis* forms dense stands that are generally stable and provide persistent habitat; beds composed of this perennial species exhibit relatively little seasonal and annual variation in structure (Dayton, 1985; Steneck et al., 2002). In contrast, northern Pacific canopy kelps are annuals (*Alaria fistulosa* and *Nereocystis luetkeana* [hereafter *Nereocystis*]) that afford much less midwater structure. As a result, vertical relief in northern Pacific kelp beds is often seasonally restricted to, and is more consistently provided by, physical structure of the seafloor and the perennial understory kelp species. The importance of physical structure (described by the measures of rugosity, substrate size, and verticality) to temperate and tropical reef fish assemblages has been documented (Aburto-Oropeza and Balart, 2001; Garcia-Charton and Perez-Ruzafa, 2001), but little is known about the importance of the physical structure of kelp and substrate to fishes in the northern Pacific rocky nearshore zones.

The objectives of this study were to assess relationships of fish to habitat structure and to seasonal variability in kelp communities. We determined the relationship of fishes to habitat structure (classified according to rugosity, size of substrate, and verticality) and kelp densities. Because north Pacific macroalgal communities vary

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seasonally with the growth and senescence of annual kelps, changes in the kelp communities were correlated with associated fish abundances.

Materials and methods

Study sites

This study was conducted in Kachemak Bay, the southernmost inlet on the western shore of the Kenai Peninsula, in south-central Alaska. Ten sites were chosen based on their structural characteristics and the presence of kelp communities (Fig. 1). All sites contained understory kelp, providing varying degrees of macroalgal cover, and five sites contained the canopy-forming kelp *Nereocystis*. A distance of at least 200 m (predominantly sandy bottom) separated all sites from each other. Sites were situated at a water depth of approximately 7 m.

Study design

At each site, transects ($n=3$) were surveyed monthly to quantify kelp densities and fish presence between May 2002 and September 2003. A haphazard starting point was selected for each transect from which a random direction was taken. Although visibility varied among sampling periods, transects were surveyed when visibility was at least a transect width (2 m on each side) or more and therefore such visibility was not included in the analyses. Because of turbidity and poor visibility at this site, MacDonald Spit was not sampled in July and November 2002 and Anisom Point was not sampled in October 2002. Each survey had two components (a kelp and a fish survey), which were conducted concurrently by two separate divers.

Physical habitat variables

Physical habitat variables (rugosity, substrate size, and verticality) were measured once for each site in September 2003. Rugosity and substrate size were measured for every quadrat at all sites during September 2003. Rugosity provides a measure of habitat complexity on a small spatial scale and is defined as the ratio of the true distance contour along the bottom to a one-meter horizontal distance (Leum and Choat, 1980). Rugosity was measured by using a 1-m bar with a series of 5-mm links attached at one end. The bar was held horizontally with the link end resting on the substrate. The links were then draped along the substrate beneath the bar. These links were counted

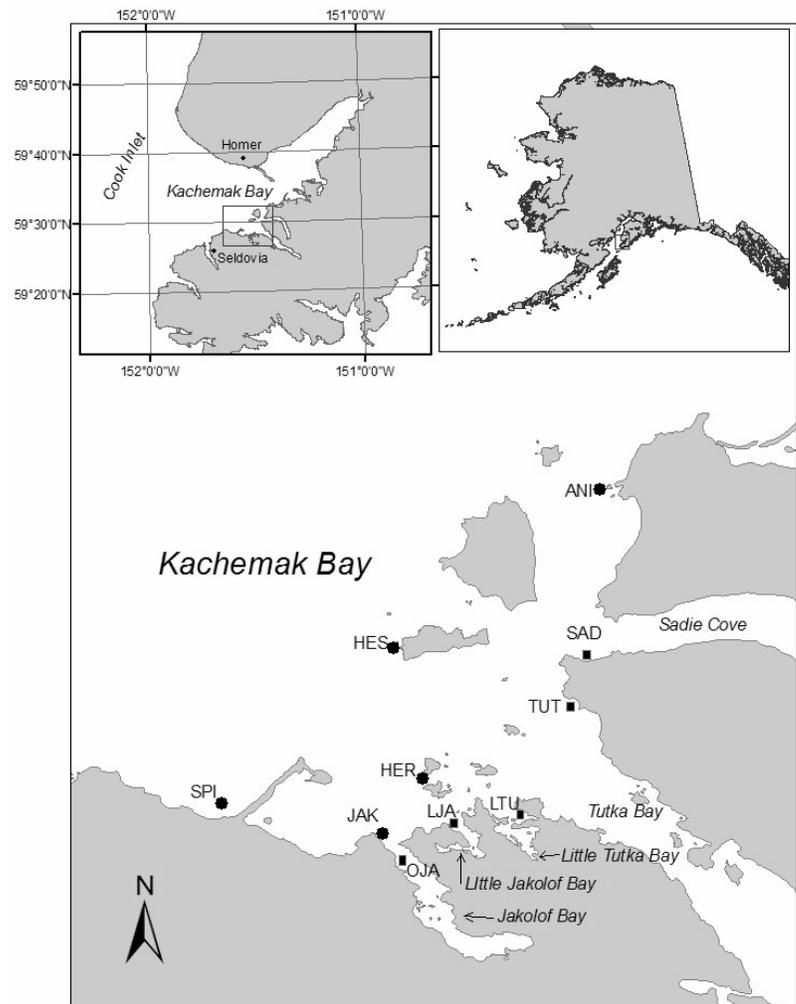


Figure 1

Location of Kachemak Bay and study sites. Sites characterized by high structural complexity of the substratum are denoted with a circle and low structural complexity sites are denoted with a square. Study sites are abbreviated as follows: ANI=Anisom Point; HER=Herring Islands; HES=Hesketh Island; JAK=Jakolof Bay; LJA=Little Jakolof Bay; LTU=Little Tutka Bay; OJA=Outside Jakolof Bay; SAD=Sadie Cove; SPI=MacDonald Spit; and TUT=Tutka Bay.

and a rugosity measure was calculated for each quadrat and averaged per transect. Substrate size was determined by measuring the diameter of samples of the bottom relief (e.g., sand, cobble, bedrock) that composed greater than 50% of the quadrat (Garcia-Charton and Perez-Ruzafa, 2001). When no substrate type dominated, the percentages and sizes of each substrate type were noted. These measurements were categorized from one (sand or silt) to five (bedrock) and an average value was calculated for each site. Verticality, a subjective measure ranging from one (for low structural relief) to five (high), was assigned to each site (Bodkin, 1986). Monthly water temperature was also measured at each site.

Surveys of kelp and fish

For surveys of kelp, randomly placed 0.25-m² quadrats ($n=10$) were examined per 120-m² transect. 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 grouped as “annual” (*Costaria costata*, *Cymathere triplicata*, and *Laminaria saccharina*,) or “perennial” (*Agarum clathratum*, *L. bongardiana*, and *L. yezoensis*) understory for statistical analyses. All data collected in May 2002 were omitted from the analyses involving kelp because understory data for that month were incomplete. Analyses were conducted on the average understory kelp densities per transect to enable comparison with the relatively sparse densities of the canopy kelp and fish communities. Because *Nereocystis* was relatively rare, all individuals were counted within each 120-m² band transect.

For fish surveys, all fishes observed within each transect and within one meter of the bottom (30 m × 4 m × 1 m = 120 m³) were enumerated and identified to species whenever possible. Because few fishes were observed, the three most abundant families (Hexagrammidae, Scorpaenidae, and Gadidae) were analyzed by family group. All other fishes were rarely observed and were grouped as “other fishes” for the analyses.

Statistical analyses

Statistical analyses were performed by using multivariate approaches and linear models with STATISTICA vers. 6 (Statsoft, Tulsa, OK). Cluster analyses were used to examine site variability in the kelp and fish communities and how this variability relates to structural complexity. Averages of all data were calculated by site across month and year for the ordination analyses. Kelp and fish densities were considered by species with the physical variables of rugosity, substrate size, and verticality. The Bray and Curtis dissimilarity coefficient (Bray and Curtis, 1957) was used and the Euclidean distance was calculated for physical variables, kelp, and fish. Water temperature did not vary among sites within months and was not used in our analysis. A one-way ANOVA was used for temporal variation of water temperature. Partial correlation analysis (with Pearson's correlation coefficient, r) was performed between kelp groups (based on average annual understory, perennial understory, and canopy kelp densities [no./120 m²]) and physical habitat data (rugosity, substrate size, and verticality; average values per 120 m²; water temperature: °C per month) while controlling for potentially intercorrelating variables. These results were considered significant at $\alpha < 0.05$. Because of the low number of fish observed, fish counts were converted to presence or absence data and logistic regression was applied. Independent variables were the four log-transformed physical variables (rugosity, substrate size, and verticality: \log_{10} [average values per 120 m²]; temperature: \log_{10} [value per month],) and the three log-transformed kelp groups (annual under-

story kelp, perennial understory kelp, and canopy kelp: \log_{10} [number of kelps per 120 m²]). Analyses were conducted separately for each fish family that composed at least 20% of total abundance (Hexagrammidae, Scorpaenidae, and Gadidae).

Results

Physical habitat variables

Substrate in the study sites varied from complex (rocky outcrops, large boulders, and bedrock) to homogeneous (small cobble and sand). The ten sites were partitioned by clustering techniques into two general structural complexity groups based on dissimilarities among the three measured structural characteristics (rugosity, substrate size, and verticality; Fig. 2A). Water temperature varied significantly among months ($F_{12,456}=1983.2$, $P < 0.001$). 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 than 2002.

Surveys of kelp and fish

A comparison of cluster dendrograms revealed patterns of spatial variation among the kelp and fish groups that mirrored the substrate trends. When all biological data (understory and canopy kelp densities and fish presence) were averaged across months and years, five sites grouped with higher counts of kelp and fish exhibited the greatest structural complexity (Fig. 2, B [kelp] and C [fish]). Similarly, three of the structurally homogenous sites were grouped consistently with lower values for both kelp and fish. Two sites (LJA and OJA) showed inconsistencies in these groupings. Little Jakolof Bay (with a lower complexity designation) was in the higher macroalgal count group but in the lower fish abundance group. Outside Jakolof Bay (with a higher complexity designation) was in the lower density groups for both kelp and fish.

Kelp communities were variable in species composition and density over space and time and understory kelp communities were considerably denser than the canopy kelp. Understory kelps were present every month and perennial kelp dominated in all months except late October 2002 (Fig. 3). The annual understory kelp *C. costata* contributed at most 2% to the annual kelp relative abundance in any month, whereas *L. saccharina* composed at least 75%. Annual understory kelps were found in greatest densities during periods with warmer water temperatures; perennial kelps, however, were not significantly correlated with temperature (Table 1). Perennial understory kelps were found on all transects; an overall equal contribution was made by *A. clathratum* and the perennial *Laminaria* species (*L. bongardiana* and *L. yezoensis*, densities lumped together). Both annual and perennial understory kelps were found in

greatest densities in sites with higher values for rugosity and verticality, although, curiously, not for substrate size (Table 1). Five sites (ANI, HER, HES, OJA, and SPI) contained *Nereocystis* in 2002, compared to two

sites (HER and SPI) in 2003. Canopy kelp persisted throughout the winter at one site (HER). The greatest number of canopy kelp individuals was observed in October 2002, the lowest densities (fewer than 5 *Nereocystis*/120 m² transect) were observed from November through April, and no canopy kelp was observed in May 2003 (Fig. 4). Canopy kelp was more abundant during months with higher water temperatures and in sites with larger substrate and greater vertical relief, but, unlike the understory kelp, was negatively correlated with rugosity (Table 1).

The presence of some fishes was associated with season, year, physical habitat characteristics, and kelp. Four hundred twenty-two fishes representing 15 species from eight families were sighted on 34% ($n=171$) of transects surveyed. 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%), Cottidae (sculpins, 3%), Pleuronectidae (flatfishes, 2%), and others (including ronquils, searchers, and unidentified fishes, 5%). Fish presence varied over time (Table 2); more fishes were sighted in 2003 (2.59 ± 6.92 fish/transect) than in 2002 (0.63 ± 0.96 fish/transect). More fish (considering all fish species pooled across months, years, and sites) were seen during periods with higher temperatures and in sites characterized by larger substrate and greater densities of annual understory and canopy kelp (Table 2). Greenlings (primarily kelp greenling [*Hexagrammos decagrammus*]) accounted for the majority of sightings (35% of total abundance) and their presence did not differ among months (Table 2). Greenlings were most commonly seen in sites with low rugosity values and larger substrate (i.e., boulder to bedrock), and during periods with warmer water temperatures and higher densities of annual understory kelps.

Schooling species, such as rockfishes (primarily the black rockfish [*S. melanops*]) and adult Pacific cod (*Gadus macrocephalus*), were observed infrequently. However, these groups accounted for the greatest number of fish seen on any one transect and exhibited the greatest variability in sightings per month in the fish groups, primarily during summer 2003 (Fig. 5). There was no difference in the presence of rockfishes among months, but there were significant temporal differences for codfishes (Table 2). Considering the major families observed in this study, only the presence of rockfishes showed significant annual variability (Table 2)—more in 2003 (1.23 ± 5.83 fish/transect) than in 2002 (0.08 ± 0.42 fish/transect). Both rockfishes and codfishes were most commonly seen during periods with higher water temperatures (Table 2). Although these results are based only on 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

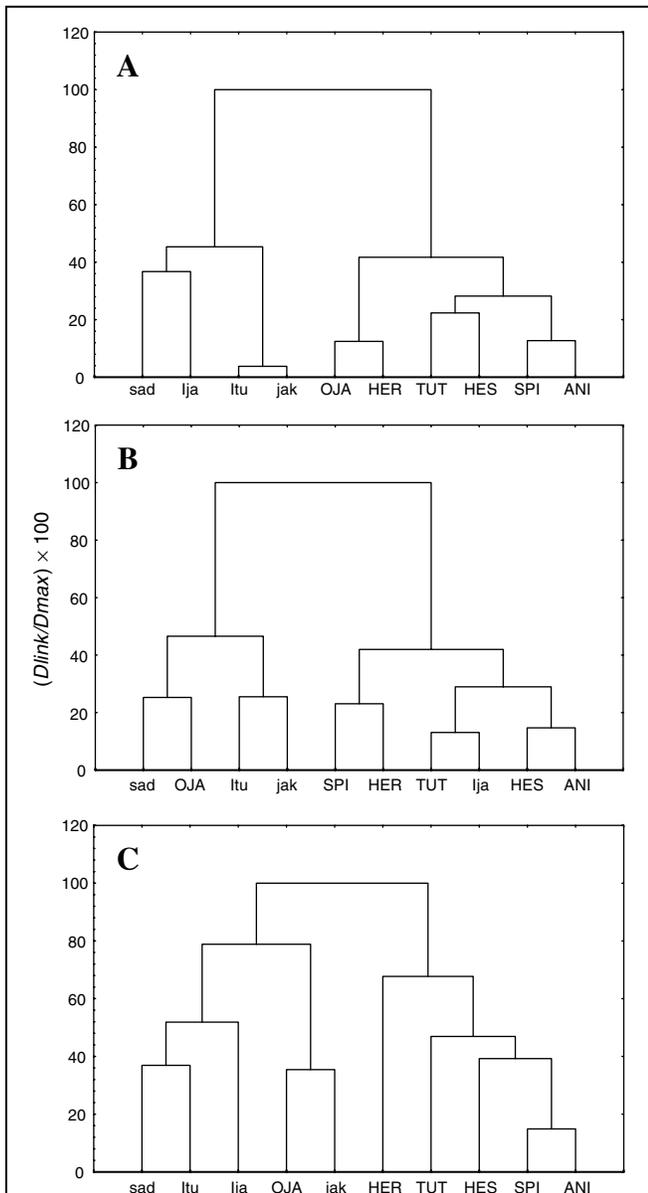


Figure 2

Cluster dendrograms based on percent dissimilarities of variables among sites. (A) Structural habitat descriptors (rugosity, substrate size, and verticality); (B) Kelp communities; and (C) Fish communities. Site abbreviations indicate relative structural complexity (lower case=low complexity; upper case=high complexity). Study sites are abbreviated as follows: ANI=Anisom Point; HER=Herring Islands; HES=Hesketh Island; JAK=Jakolof Bay; LJA=Little Jakolof Bay; LTU=Little Tutka Bay; OJA=Outside Jakolof Bay; SAD=Sadie Cove; SPI=MacDonald Spit; and TUT=Tutka Bay.

Table 1

Partial correlation analysis (Pearson's correlation coefficient, r) between physical variables and kelp groups ($n=473$ transects). Values are considered significant at $P < 0.05$. Rugosity provides a small-scale measure of habitat complexity and is the ratio of the true distance contour along the bottom to a one-meter horizontal distance. Substrate size is based on the average diameter of the substrate comprising the majority of a 0.25-m² quadrat. Verticality was assigned to each site on the basis of overall vertical relief.

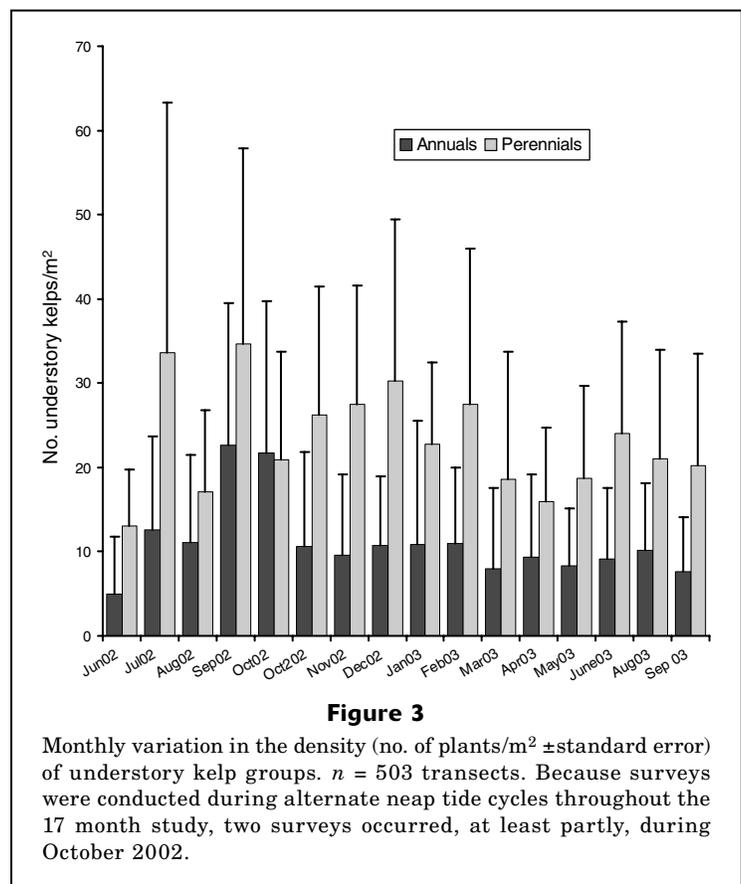
Kelp group	Temperature	Rugosity of substrate	Substrate size	Verticality of substrate
Canopy	0.18 $P < 0.001$	-0.32 $P < 0.001$	0.29 $P < 0.001$	0.09 $P < 0.001$
Annual understory kelp	0.17 $P = 0.001$	0.16 $P < 0.001$	0.01 $P = 0.790$	0.16 $P < 0.001$
Perennial understory kelp	0.02 $P = 0.685$	0.27 $P < 0.001$	-0.05 $P = 0.325$	0.26 $P < 0.001$

were composed of much fewer individuals (at most, tens of individuals/school). These juvenile codfishes were not included in any analyses in our study because of difficulties in accurately quantifying them.

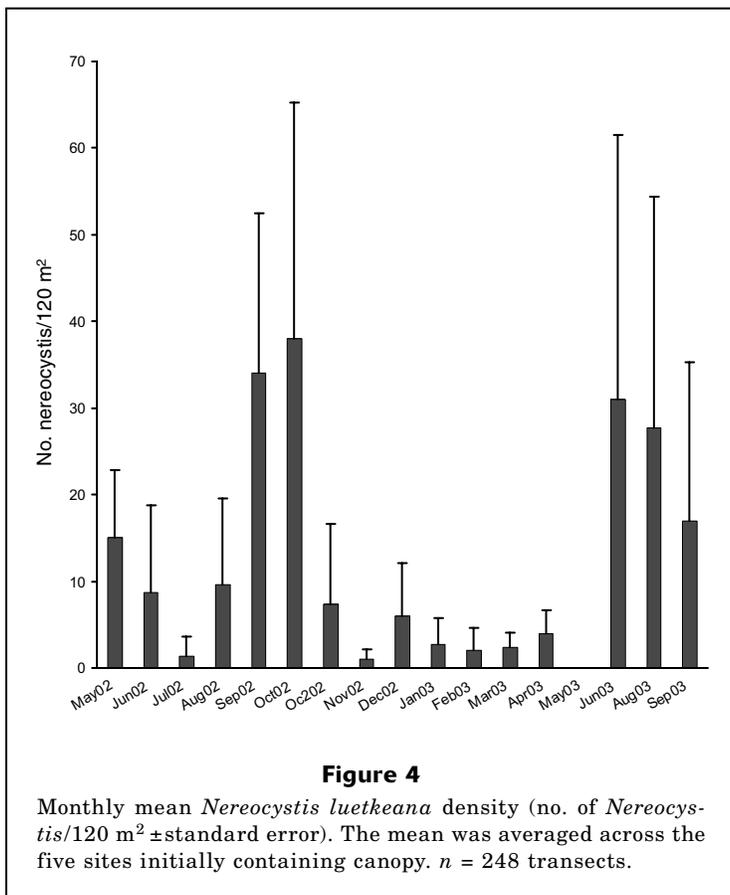
Discussion

Structural habitat complexity is important to both fish and kelps in that greater physical habitat complexity is associated with greater overall densities of fish in these communities. In particular, greenlings associated most consistently with kelp beds that had a predominately rocky (i.e., large cobble/bedrock) and structurally complex bottom habitat. The association of the dominant fish species in our study with relatively larger substrate and higher rock relief may indicate that south-central Alaska kelp-bed fishes follow the same trend (of a strong association of fish with kelp and rocky substrate relief) documented elsewhere. For example, in California kelp beds, significant correlations exist between fish density and bottom relief (Ebeling et al., 1980; Bodkin, 1986). However, rockfishes in Puget Sound inhabited low-relief rocky kelp beds during summer (Matthews, 1990) and in Prince William Sound were positively associated with relief (Dean et al., 2000). Rockfishes and codfishes in the present study were never associated with any bottom structure, perhaps because of the sporadic sightings of these species. The lack of association of rockfishes and codfishes with any physical habitat variables or kelp may reflect the transient nature and seasonal association of these fishes with kelp. However, the rarity of any fishes observed higher than one meter above the substratum in the present study indicates that bottom structure may be important to the fishes observed in our study, if perhaps indirectly, by also being appropriate substratum for kelp habitat.

The variability of Alaska kelp communities and associated fish populations may be partially attributable



to the extreme seasonal nature of the northern environment. Increased sightings of fish during periods characterized by warmer water indicate seasonal variability in fish communities associated with kelp communities. For example, although greenlings were observed in the shallow, rocky nearshore sites during every month in the present study, rockfishes and codfishes were rarely observed except in summer. Healthy understory kelp populations exist in this area on rocky substratum at depths of up to 16 m (first author, personal observ.) and fish populations may shift seasonally to similar



habitats in adjacent, deeper water. Puget Sound rockfishes tend to move to shallower water in summer and deeper water in winter (Moulton and Miller¹), possibly avoiding increased storm surge during winter months. Fish communities inhabiting seasonally and annually variable kelp beds in the north Pacific must be capable of enduring a wider variety of environmental variables over the course of a season, year, or lifetime than those occupying the relatively stable, perennial canopy-dominated kelp beds of more temperate zones. The importance and magnitude of seasonal cues vary among kelp and fish species throughout their ranges and the cues include temperature, photoperiod, turbidity, increased frequency of storms and surge in winter, and prey and nutrient availability (Ebeling et al., 1980, Dayton, 1985). However, the thresholds of many 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

¹ Miller, B. S., and L. L. Moulton. 1988. Characterization of Puget Sound fishes for the EPA Bay Program, p. 77–84. In Proceedings, First Annual Meeting on Puget Sound Research, vol. 1, Seattle, WA, March 18–19, 1988. Puget Sound Action Team, Office of the Governor, P.O. Box 40900, Olympia WA 98504-0900.

Table 2

Logistic regression results 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 kelp and annual and perennial understory kelp groups; n=473 transects), and physical habitat variables (water temperature, rugosity, substrate size, and verticality). Only significant values (P<0.05) are reported.

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

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 months and result in the paucity of consistent seasonal data in northern Pacific systems.

Aerial surveys of kelp beds in Kachemak Bay during three consecutive summers (2000–2002) showed significant differences in size, location, and presence of *Nereocystis* canopy (Schoch and Chenelot, 2004), illustrating great interannual variability that may be apparent on relatively 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 *Nereocystis* juveniles the second summer. Although this canopy kelp species is considered an annual, we observed *Nereocystis* individuals reproducing into a second summer.

Our findings of relatively more fishes inhabiting *Nereocystis* beds than understory-only kelp beds indicates that areas characterized by enhanced *Nereocystis* growth may have greater fish densities. In one northern California study, densities of kelp greenling in *Nereocystis* beds were four times greater than in the present study (Bodkin, 1986). *Nereocystis* beds in California were similarly more important to rockfishes (Bodkin, 1986; Love et al., 1991) than understory kelp alone. However, the existence of high understory kelp densities in the canopy-containing sites may be of greater importance to fishes than the canopy itself. In our study sites, both the greenlings and grouped fishes were positively associated with densities of annual understory. In addition, fishes in the present study were usually observed in close association with the understory and substratum as has been typical in other south-central Alaska studies (Rosenthal², Dean et al., 2000). The perennial-dominated understory of south-central Alaska kelp beds may provide a degree of habitat stability for some fishes for at least part of the year.

It is difficult to account for all factors influencing a natural system, particularly without knowing the recent history of the community. Because little is known

² Rosenthal, R. J. 1979. A preliminary assessment of composition and food webs for demersal fish assemblages in several shallow subtidal habitats in lower Cook Inlet, Alaska, 58 p. In Final report by Dames and Moore, Inc., 800 Cordova Street, Suite 101, Anchorage, AK 99501, for Alaska Department of Fish and Game. Commercial Fisheries Division, 211 Mission Rd., Kodiak, Alaska 99615.

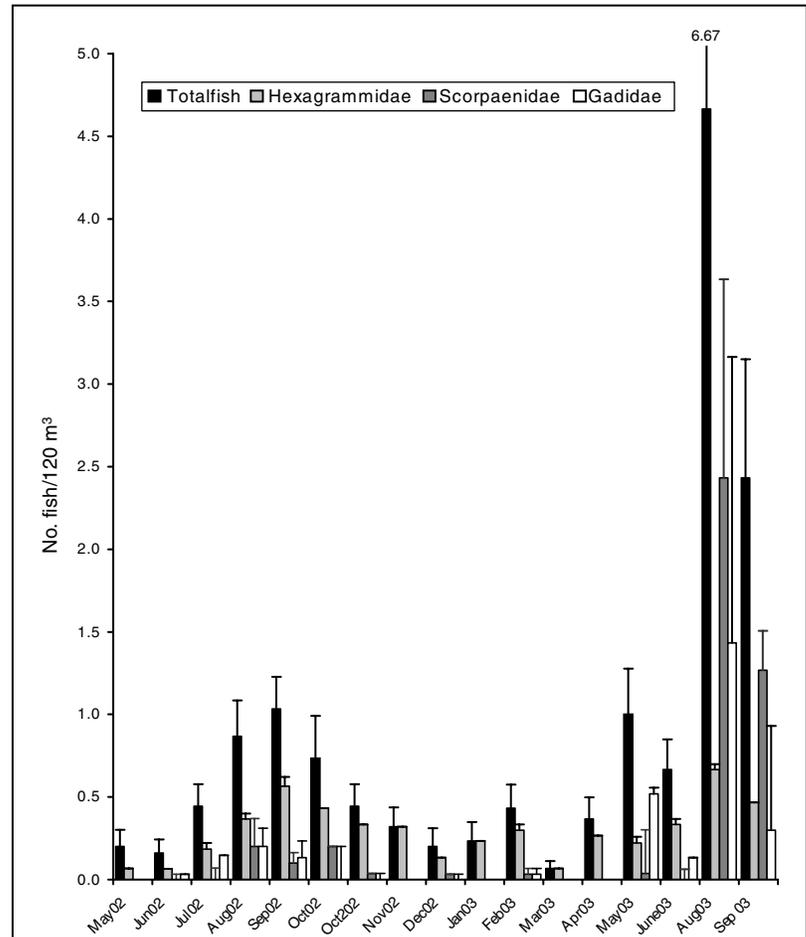


Figure 5

Monthly variation of major fish families (no. of fish/120 m³ ± standard error) averaged across sites. Only families comprising greater than 20% of total density were included. $n = 503$ transects.

about interactions between kelp and fish communities and their natural variability in south-central Alaska, investigation of more obvious, small-scale processes over an entire year is necessary. Physical factors, such as size of the kelp beds and related edge effects of the habitat, salinity fluctuations and freshwater runoff, degree and direction of exposure to light and tidal currents, and the frequency of storm events may play a significant role in structuring these dynamic communities. In addition, biological factors that may influence algal community structure include inter- and intra-species competition and herbivory. A growing body of evidence points to the importance of temporal and spatial scales in ecological processes (i.e., Dayton and Tegner, 1984; Wiens and Addicott, 1986; Foster, 1990). The structurally complex kelp beds surveyed in the present study appear to provide critical habitat throughout the year for greenling species. However, this habitat is also seasonally important to rockfishes and codfishes (both adult and juvenile).

This work provides a description and baseline information on the structural characteristics of south-central Alaska's nearshore kelp beds and associated fish communities, and provides insight on the importance of seasonality. These findings may enable managers to identify potentially important nearshore fish habitat from relatively easily quantified structural habitat variables. The identification of critical habitat areas for juvenile and adult fishes is essential for sustainable management, and the importance of habitat structure in and influence of seasonality on these habitats has been further illuminated by this work.

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