

Linking community structure of small demersal fishes around Kodiak Island, Alaska, to environmental variables

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ABSTRACT: Juveniles and small adults of at least 75 species of demersal fishes were identified in trawl catches from the nearshore waters of Kodiak Island, Alaska, in August 1991 and 1992. We derived several indices to characterize community structure at each site, identified key environmental gradients along which community structure was organized, and identified those species whose abundances varied most strongly along these gradients. We related species richness, species diversity, and total catch per unit effort to environmental variables observed at each site. Species richness and diversity were highly variable among sites, but decreased significantly with salinity and were significantly higher on heterogeneous sediments. Standardized catch per unit effort for all species combined differed significantly among 5 geographic areas and was significantly higher on sediments with a high sand and/or mud content. Indices of species composition for each sampling site were obtained as the scores of ordination axes based on non-metric multidimensional scaling of Bray-Curtis dissimilarities between sites. The indices summarized different aspects of community composition and were associated with different species groups. The first and major index was primarily related to the depth-temperature gradient and contrasted a shallow, warm water species group with a deep, cold water group. Non-linear depth effects on most indices suggest relatively rapid changes in species composition in shallow water (0 to 50 m), and more gradual changes in the lower part of the depth range. While the depth-temperature gradient was the most important gradient along which species composition was structured, sediment composition and geographic area accounted for a significant proportion of the variance of each of the indices. While species composition changed most strongly along the depth-temperature gradient, species richness, diversity, and total abundance were not related to depth or temperature, suggesting that species composition changed independently of the overall abundance and of species richness and diversity.

KEY WORDS: Community structure · Demersal fish · Depth · Kodiak Island, Nearshore zone · Non-metric multidimensional scaling · Sediment composition

INTRODUCTION

The early juvenile stages of demersal fishes have rarely been studied in the Gulf of Alaska. Ichthyoplankton studies in the Kodiak Island region have provided information on the timing, distribution, and abundance of the eggs and larvae of many species on the continental shelf and inside bays (Dunn et al. 1981, Kendall et al. 1981, Kendall & Dunn 1984, Hermann et

al. 1996). The nearshore zone and bays around Kodiak are important nursery areas for larval and juvenile stages of numerous fish species (Harris & Hartt 1977, Blackburn 1979, Walters et al. 1985, Rogers et al. 1986).

While the nearshore area clearly plays an important role in the early life history of many commercial and non-commercial species, we know very little about the structure of these communities or of their distribution in relation to environmental variables in the North Pacific. Norcross et al. (1995, 1997) identified nursery area characteristics of the 4 most common flatfish species collected around Kodiak Island and found depth

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and sediment composition to be key variables in determining the distribution of juveniles of these species in the estuarine and nearshore zones.

In the deep ocean, many benthic communities are zoned with depth (Haedrich et al. 1980, Bianchi 1992a,b). The causes for the zonation are not clear but it has typically been related to differences in the physical environment, including temperature, sediment type, strength of currents, and topography (Day & Pearcy 1968, Rowe & Menzies 1969, Haedrich et al. 1975, Bianchi 1991, 1992a,b). Bianchi (1992a) examined the structure of the demersal community on the continental shelf and upper slope of Angola and found that groupings are primarily structured along the thermal, depth-dependent gradient and secondarily along gradients of bottom type and latitude. Depth is also the main gradient along which the fauna of the continental shelf and slope edge between the Gulf of Tehuantepec and the Gulf of Papagayo changes (Bianchi 1991), and similar results hold for the demersal assemblages of the continental shelf and upper slope off Congo and Gabon (Bianchi 1992b).

With the exception of coral reef studies (e.g. Alevizon et al. 1985, Sale et al. 1994), there have been few studies examining similar gradients in nearshore demersal fish communities. Blaber et al. (1994a) examined the community structure of demersal fishes in the Gulf of Carpentaria. They found that the distribution patterns of fishes are related to depth but not to other fac-

tors measured, including sediment type, salinity, temperature, and turbidity. Several studies have examined environmental variables that affect fish communities in shallow estuarine areas and found salinity and temperature to be the dominant factors influencing distribution (e.g. Thiel et al. 1995, Marshall & Elliott 1998).

The goal of this study is to characterize the community structure of small demersal fishes in a nearshore area of the Gulf of Alaska characterized by relatively deep bays in relation to environmental variables. Specific objectives are (1) to quantify different aspects of the community structure of small demersal fishes around Kodiak Island, (2) to examine relationships between indices of community structure and environmental variables at the sampled sites, and (3) to identify key environmental gradients along which the community is structured.

METHODS

Sample collection and processing. We quantitatively sampled 211 sites in the nearshore areas around Kodiak Island, Alaska, in August 1991 and August 1992. Trawling locations were often dictated by the availability of trawlable bottom. Sites were selected to encompass as many depths and sediment types as possible within the trawlable areas. In 1991, we sampled the east side of Kodiak Island between Chiniak Bay and Sitkinak Strait (Fig. 1). In 1992, sites in most bays on both the east and west side of the island were sampled. Collections were made from a 7.3 m skiff in Chiniak Bay and from a 24.7 m chartered trawling vessel in all other areas. Sites within a bay were typically between 3 and 15 km apart. Occasionally, several tows were made within a small area, but no replicate tows were taken at any one site.

At all except 19 sites, sediment was collected with a 0.06 m³ Ponar grab for analysis of grain size. A portable conductivity, temperature, and depth (CTD) probe (Seabird Seacat Profiler SB19) was deployed to within 1 to 5 m of the bottom to measure temperature and salinity at all except 8 sites. Bottom temperature and salinity were extracted from the CTD record for each site. Sediment size was determined using a simplified sieve/pipette procedure by which the weight percents of gravel, sand and mud were obtained (Folk 1980). Complete environmental data were available for a total of 187 sites.

Fishes were collected on rising tides during daylight hours using a modified 3.7 m plumb staff beam trawl with a double tickler chain, 7 mm stretch mesh and a codend liner of 4 mm bar mesh (Gunderson & Ellis 1986). The depth to warp ratio was approximately 1:8 for sites less than 10 m, 1:5 at 10 to 20 m sites, and 1:3

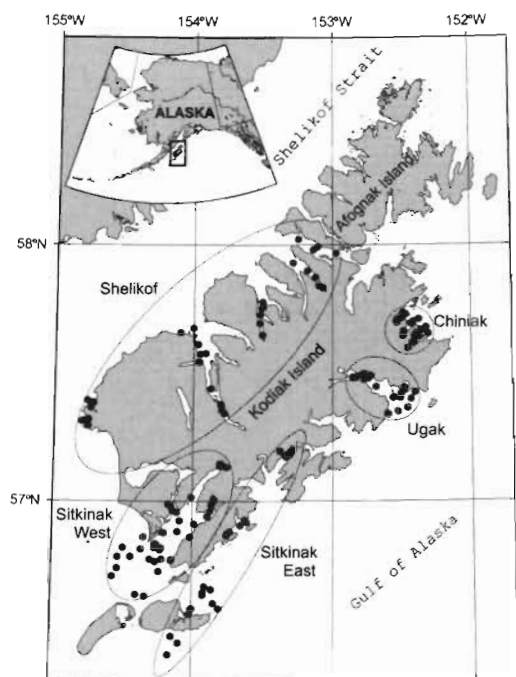


Fig. 1. Map of Kodiak Island, Alaska, showing (●) site locations and 5 geographical areas used in analysis

at deeper sites. Tows from both skiff and trawler were of 10 min duration at a towing speed of approximately 0.5 to 1 m s⁻¹.

All fishes were identified in the field to the highest possible taxonomic separation or frozen and returned whole to the laboratory for identification. Fishes were counted and total length was measured to the nearest mm. Catches were standardized to CPUE as individuals 1000 m⁻². The towing distance was estimated based on GPS positions where available or on the average speed and tow duration. The area swept was computed from the estimated tow distance and effective width of the net (Gunderson & Ellis 1986).

Environmental variables. We analyzed catch composition in relation to depth, bottom temperature, bottom salinity, and percentages of gravel, sand, and mud in the sediment. We further investigated differences between 5 distinct geographical areas (Fig. 1). The areas were Chiniak (84 stations), Ugak Bay (21), Sitkinak East (26), Sitkinak West (44), and Shelikof (36). Areas Sitkinak East (SE) and Sitkinak West (SW) were separated in the analysis because they are physically separated by a relatively narrow and shallow sill in Sitkinak Strait and are subject to different oceanographic influences (Chilton 1997). All bays on the Shelikof Strait side were combined for analysis due to the relatively small number of samples within each bay. An electronic copy of the data including species abundances and environmental information is available from the authors upon request.

The environmental variables included 2 groups of highly correlated variables. Depth and temperature were highly correlated, thus their effects could not be separated reliably. Likewise, the percentages of gravel, sand, and mud in the sediment were naturally highly correlated. To reduce the number of variables and avoid problems with collinearity we extracted major principal components from each of these groups (Johnson & Wichern 1992).

Indices of community structure. We computed 4 descriptive measures of community structure for our analysis: (1) the number of species captured at each site, (2) species diversity, estimated by the complement of Simpson's index (Magurran 1988, Krebs 1989), (3) total CPUE of all species combined at each site, and (4) indices of species composition based on an ordination of pair-wise site dissimilarities.

In analyzing the number of species per site and species diversity, we assumed that each sample estimated the composition of the local community at the sampling site. Thus, indices were computed for each site and related to environmental variables associated with that site. The number of species per site is a measure of species richness for the habitat represented by the site. Because we expected the number of species, and pos-

sibly species diversity, to be related to the area sampled by the trawl, we included area swept as one explanatory variable when examining patterns in species richness and diversity. The complement of Simpson's D (1-D) is a measure of species diversity, which can be interpreted as the probability that 2 randomly chosen individuals belong to different species (Krebs 1989). Simpson's D is independent of any theory of the frequency distribution of species abundances, but tends to be positively correlated with sample size. We examined trends in diversity with sample size prior to analysis and found no significant relationship.

As another quantitative descriptor of the fish community we calculated total CPUE as an index of total fish abundance at each site. For statistical comparisons we used log-transformed CPUE since the raw CPUE values were approximately log-normally distributed.

Indices of species composition were obtained for each site from a site-by-species matrix of the standardized CPUE of all species by site. For each genus or family that contained specimens that were not identified to species, data were combined and analyzed as a group. Rare species were eliminated prior to further analysis as recommended by Saila et al. (1996). A genus or a species was included in the analysis if it occurred at more than 5% of the sites (>10 sites), yielding 35 taxa for consideration (Table 1).

Indices of species composition were related to environmental variables using indirect gradient analysis (Gauch 1982, Digby & Kempton 1987, Ter Braak 1995). Specifically, we used non-metric multidimensional

Table 1 Number of species collected in August 1991 and August 1992 around Kodiak Island, Alaska, by family. *: no fish were identified to the species level

Family	No. of species
Cottidae	23
Pleuronectidae	12
Agonidae	10
Stichaeidae	7
Gadidae	4
Hexagrammidae	4
Osmeridae	2
Bathymasteridae	2
Zoarcidae	2
Rajidae	1
Clupeidae	1
Cyclopteridae	1
Cryptacanthodidae	1
Pholidae	1
Zapruidae	1
Trichodontidae	1
Ammodytidae	1
Bothidae	1
Scorpaenidae	*
Liparidinae	*

scaling (NMDS), which has proven useful in analyzing marine community data (Field et al. 1982, Clarke 1993, Clarke & Ainsworth 1993). NMDS uses a measure of between-site dissimilarity and arranges all sites in a k -dimensional space such that the rank-order of the between-site dissimilarities corresponds as closely as possible to the rank-order of between-site distances.

Indices of species composition were constructed based on an approach described in Field et al. (1982) and extended by Mueter & Norcross (unpubl.):

(1) The matrix of CPUE data was transformed by taking the fourth root, thereby decreasing the influence of abundant species. The effect is similar to a log transformation but the fourth root transformation is preferred with the dissimilarity measure used in our analysis (Field et al. 1982).

(2) Dissimilarity in species composition between each pair of sites was computed from the transformed CPUE data using the Bray-Curtis measure of dissimilarity.

(3) The resulting matrix of Bray-Curtis site dissimilarities was used as input for NMDS. Goodness of fit was evaluated using the stress criterion as defined in Kruskal (1964). Kruskal's stress measures how closely the pair-wise distances in the final NMDS configuration approximate the true distances in the dissimilarity matrix. A stress of 0.1 or lower is considered a good fit (Kruskal 1964). We increased the number of axes until a stress of less than 0.1 was achieved in the final configuration. As the orientation of axes derived from NMDS is arbitrary, we rotated the solution such that the first axis corresponds to the axis of maximum variation.

(4) Finally, the scores along each of the rotated axes of the final configuration were used as indices of species composition. To interpret the indices in terms of species abundances we related the scores at each site to CPUEs of individual species using scatterplots and Spearman rank correlations. Different indices were strongly rank correlated with different groups of species and were interpreted as representing different, independent aspects of community composition. It is important to note that the correlation analysis was only used to identify those species that are most strongly associated with a particular index. Rank correlations between scores and species abundances cannot be tested for significance, as the abundances themselves are used to derive the scores.

Relating indices of community structure to environmental variables. We examined relationships between community structure and environmental variables using generalized additive models (GAM, Hastie & Tibshirani 1990). A GAM is a non-parametric regression that uses smooth functions of the predictor variables in place of linear functions and allows different

probability distributions for the data. We assumed that errors were normally distributed. The dependent variables (number of species, Simpson's index of species diversity, total CPUE, and indices of species composition) were modeled as the sum of non-parametric functions of the hypothesized independent variables. The non-parametric function we used was a smoothing spline with the equivalent of approximately 4 degrees of freedom. If no evidence of non-linearity was found, linear terms were substituted for smoothing splines. As a measure of goodness of fit and for comparing models the deviance criterion is used and plays the role of the residual sum of squares in linear regressions. As a measure of model fit we provide a pseudo coefficient of determination, the fraction of the total deviance explained by the model, as a surrogate for the familiar R^2 (Swartzman et al. 1992). The coefficient was computed as 1 minus the ratio of the deviance of the best fitting model to the deviance of the model that only uses the overall mean (the null model). All available variables were initially included as predictors. A step-wise procedure based on the Akaike information criterion (Hastie & Tibshirani 1990) was used to select a subset of significant variables and to choose whether a linear relationship between the dependent variable and any of the independent variables was adequate. Residuals from the final model for each dependent variable were examined for violations of normality and for outliers.

RESULTS

During the cruises in August 1991 and August 1992 we captured a total of 29749 bottom fishes belonging to 1 of 75 identified species from 20 families (Table 1). The most abundant species were rock sole *Pleuronectes bilineatus*, flathead sole *Hippoglossoides elassodon*, and Pacific cod *Gadus macrocephalus* with 9862 (33%), 2481 (8.3%), and 2073 (7.0%) specimens, respectively (Table 2). Rock sole were captured at more sites than any other species (159 of 211 sites, Table 2). Thus rock sole was the most ubiquitous as well as the most abundant species in the nearshore waters of Kodiak Island with densities in August as high as 650 ind. 1000 m⁻².

Environmental variables

The depth of our sampling sites ranged from 1 to 167 m with relatively few sites below 120 m. Temperatures ranged from 4.0 to 11.9°C and its distribution was slightly skewed towards warmer temperatures. As in most nearshore areas there was a strong correlation

between depth and temperature ($r = 0.72$, Fig. 2). Because of the strong correlation, we were unable to separate temperature and depth effects. Therefore we used the first principal component from a principal component analysis of depth and temperature in place of the original variables. The new depth-temperature (DT) variable explained 86% of the variation in depth and temperature and had correlations of -0.92 and 0.92 with depth and temperature respectively. DT was positive at warm, shallow sites and negative at deep, cold sites.

Salinities at most sites ranged from 29.9 to 32.7 psu, with a few unusually high (>33 psu) and 2 unusually low values (27.1 and 24.0 psu). The percentage of gravel in the sediment ranged from 0 to 100% and had

a bimodal distribution. Ninety-eight sites did not contain any gravel and over 75% of the sites had less than 5% gravel. There were relatively few sites with intermediate percentages but a number of sites sampled contained 90 to 100% gravel in sediment samples. The distribution of sand was skewed towards higher percentages because of the large number of trawls on sandy sediment. Mud content in sediment samples ranged from 0 to 99%, with a relatively uniform distribution over the entire sampled range. A few sites contained some cobble in the sediment. Video observations and torn nets confirmed the presence of occasional large boulders on sandy or gravelly sediment.

Gravel, sand, and mud content of the sediment were naturally highly correlated and their first 2 principal

Table 2. List of groundfish species and taxa collected in August 1991 and August 1992 around Kodiak Island, Alaska. Sites: number of sites at which each group was captured, No.: total number of specimens caught, and Rank: Rank order of numerical abundance (No.). Groups shown are those used for analysis

Family	Scientific name	Common name	Sites	No.	Rank
Gadidae	<i>Gadus macrocephalus</i>	Pacific cod	106	2073	3
	<i>Theragra chalcogramma</i>	Walleye pollock	81	786	11
Hexagrammidae	<i>Hexagrammos</i> spp.	Greenlings	61	367	14
	<i>Ophiodon elongatus</i>	Lingcod	29	111	23
Cottidae	<i>Dasycottus setiger</i>	Spinyhead sculpin	21	118	22
	<i>Gymnocanthus</i> spp.	<i>Gymnocanthus</i> spp.	72	385	13
	<i>Hemilepidotus</i> spp.	Irish lords	49	173	18
	<i>Icelinus borealis</i>	Northern sculpin	59	940	9
	<i>Myoxocephalus</i> spp.	<i>Myoxocephalus</i> spp.	82	1346	6
	<i>Radulinus asprellus</i>	Slim sculpin	17	76	28
	<i>Triglops</i> spp.	<i>Triglops</i> spp.	28	154	19
	<i>Enophrys</i> spp.	<i>Enophrys</i> spp.	12	30	33
	<i>Psychrolutes sigalutes</i>	Soft sculpin	33	318	16
	<i>Podothecus acipenserinus</i>	Sturgeon poacher	97	847	10
Agonidae	<i>Pallasina barbata</i>	Tube-nose poacher	48	127	21
	<i>Aspidophoroides bartoni</i>	Aleutian alligatorfish	15	31	32
	<i>Bathyagonus</i> spp.	<i>Bathyagonus</i> spp.	59	449	12
	<i>Anoplagonus inermis</i>	Smooth alligatorfish	14	62	29
Liparidinae	<i>Liparis</i> spp.	Snailfishes	79	229	17
Bathymasteridae	<i>Bathymaster</i> spp.	<i>Bathymaster</i> spp.	24	96	26
	<i>Ronquilus jordani</i>	Northern ronquil	28	108	24
Zoarcidae	<i>Lycodes</i> spp.	<i>Lycodes</i> spp.	27	1152	7
Stichaeidae	<i>Lumpenus</i> spp.	<i>Lumpenus</i> spp.	134	1980	4
Pholidae	<i>Pholis</i> spp.	<i>Pholis</i> spp.	21	78	27
Pleuronectidae	<i>Atherestes stomias</i>	Arrowtooth flounder	50	340	15
	<i>Hippoglossoides elassodon</i>	Flathead sole	92	2481	2
	<i>Pleuronectes isolepis</i>	Butter sole	37	143	20
	<i>Pleuronectes bilineata</i>	Rock sole	159	9862	1
	<i>Pleuronectes asper</i>	Yellowfin sole	97	1890	5
	<i>Microstomus pacificus</i>	Dover sole	13	25	34
	<i>Pleuronectes vetulus</i>	English sole	19	42	30
	<i>Platichthys stellatus</i>	Starry flounder	11	34	31
	<i>Pleuronectes quadrituberculatus</i>	Alaska plaice	18	104	25
	<i>Psettichthys melanostictus</i>	Sand sole	12	24	35
	<i>Hippoglossus stenolepis</i>	Pacific halibut	92	1053	8
Other species				1715	
Total				29749	

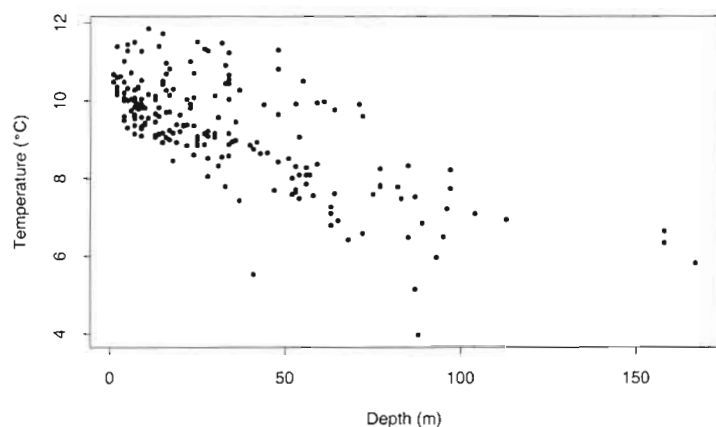


Fig. 2. Scatterplot of temperature versus depth for all sites sampled in August 1991 and August 1992

components explained nearly all (>99%) of the variation in sediment composition. The first component (S1) contrasted sand with gravel and mud. It had high positive values for sediments with a large non-sand component, intermediate values for mixed sediments, and high negative values for sediments that contained pri-

marily sand. The second component (S2) contrasted gravel with mud and was high for sediments rich in gravel and low (negative) for sediments with a high mud content.

The final set of explanatory variables used in modeling indices of community structure consisted of 1 DT variable, salinity, 2 sediment variables (S1 and S2), and geographic area. Each regression that included 1 or both of the sediment variables was also compared to a regression that included a categorical sediment variable with 6 levels in place of the continuous sediment variables. The 6 levels were pure gravel (G), sand (S), or mud (M) if the sediment contained at least 95% of 1 of these sediment types and mixed gravel, mixed sand, or mixed mud if the sediment contained less than 95% of any 1 sediment type.

Relating indices of community structure to environmental variables

Regression results from the best fitting additive models for each dependent variable are presented as smoothed trends depicting the standardized effect of each covariate on the dependent variable (Figs. 3 to 10). To allow comparisons of the relative effects of different covariates, all y-axes within each figure are drawn to the same scale. Species richness (number of species) in our samples ranged from 1 to 19 species with a mean of 9.7 species (standard deviation = 3.9 species) per sample. It was significantly and non-linearly related to area swept, the sediment variable S2, salinity, and geographic area (Fig. 3, pseudo $R^2 = 0.35$). As expected, the number of species increased with the area sampled, but leveled off at 600 to 700 m^2 . Ignoring the effects of other covariates, the number of species averaged 7.7 if the area swept was under 500 m^2 , 9.8 if the area swept was between 500 and 1000 m^2 and 9.9 for larger areas.

Species richness was lowest at the extremes of sediment variable S2, corresponding to sediments with high percentages of either mud or gravel (Fig. 3). This pattern became more obvious when the categorical sediment variable was substituted for S2 in the regression (Fig. 4). Species richness was significantly lower on pure sediments, particularly on mud and gravel, compared to mixed sediments. Without taking the effects of other covariates into account, the number of species on pure gravel, sand, and mud averaged 7.1, 9.7, and 6.0, species, respectively, while it averaged 10.3, 10.3, and 10.4 on mixed gravel, mixed sand, and mixed mud, respectively.

Species richness decreased significantly along the salinity gradient for salinities over approximately

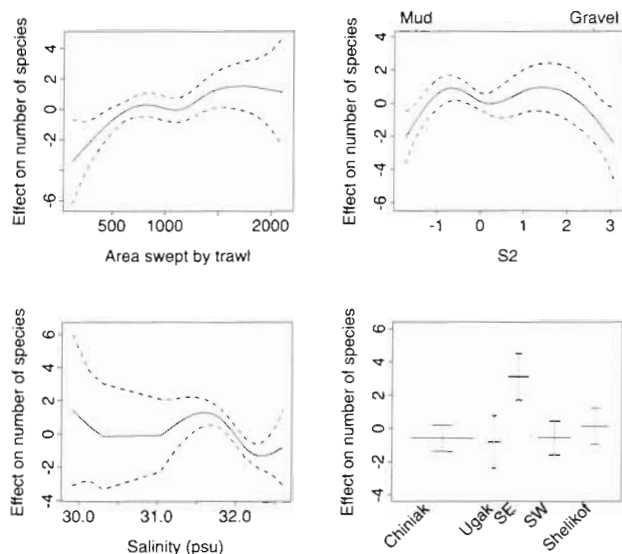


Fig. 3. Estimated relationship between number of species and significant explanatory variables. Tickmarks along x-axis indicate values of observations. Dashed lines indicate approximate 95% confidence limits of the regression lines. Horizontal lines in lower right plot indicate mean response with 95% pointwise confidence intervals. The width of the bars is proportional to the number of observations in each area. Fitted lines in each panel are adjusted for the effects of all other variables. Standardized effects in each plot (y-axes) are on the same scale for comparison. Effects are standardized because the estimated number of species at a given value of a variable is dependent upon the levels of all other variables. S2 = second component, SE = Sitkinak East, SW = Sitkinak West

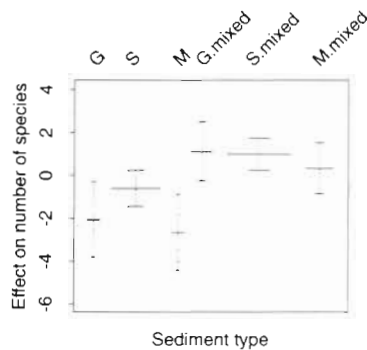


Fig. 4. Estimated effect of sediment type on the number of species, after accounting for effects of area swept and differences among geographic areas with 95% pointwise confidence intervals. G = gravel, S = sand, M = mud

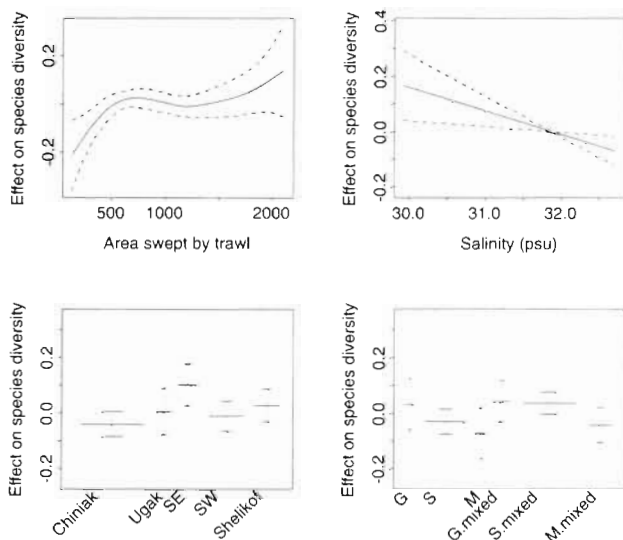


Fig. 5. Estimated relationship between species diversity and significant explanatory variables. For explanation of plots, see Fig. 3. G = gravel, S = sand, M = mud

31.7 psu. No clear effect of salinity on the number of species was apparent at salinities below 31.7 psu, due to wide confidence intervals resulting from the small number of samples (Fig. 3). Species richness was significantly higher in area SE compared to all other areas. The number of species averaged 12.6 in SE, while the mean in the other areas ranged from 8.9 to 10.3.

Species diversity as measured by the complement of Simpson's index was highly variable, but was significantly related to area swept, salinity, geographic area, and sediment type (Fig. 5). Only a very small portion (pseudo $R^2 = 0.17$) of the variability in species diversity was accounted for by the model. In parallel with species richness, diversity increased with area swept, leveling off at approximately 600 m². Diversity de-

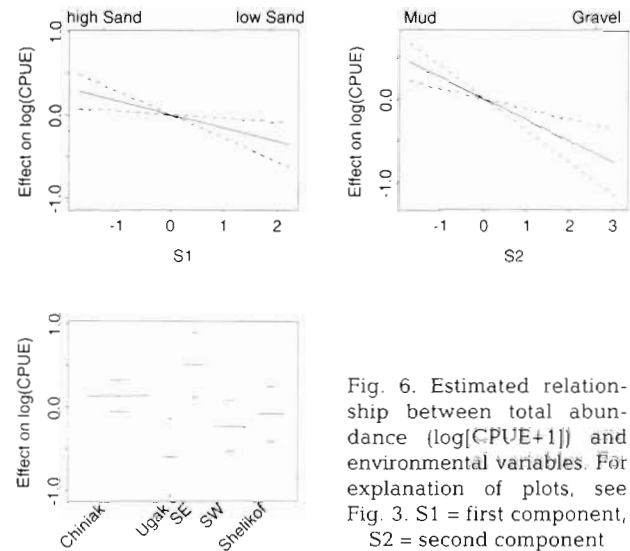


Fig. 6. Estimated relationship between total abundance ($\log[CPUE+1]$) and environmental variables. For explanation of plots, see Fig. 3. S1 = first component, S2 = second component

creased linearly with salinity over the range of salinities sampled. Like species richness, diversity was highest in area SE. Species diversity tended to be significantly lower on pure sand, pure mud, and mixed mud sediments (Fig. 5); however, the effect was less pronounced than for species richness. Trends in diversity closely followed those in species richness, with the possible exception of a relatively high diversity on pure gravel, in spite of a low number of species.

Total abundance, as measured by $\log(CPUE+1)$, decreased significantly along the sediment gradients S1 and S2 and differed significantly among the 5 geographical areas (Fig. 6); however, only a very small proportion (pseudo $R^2 = 0.18$) of the overall variability was explained by these trends

CPUE tended to be lower on sediment with a high non-sand component (large S1) and a high gravel content (large S2). A comparison of CPUE among the 6 sediment types confirmed that, on average, the lowest abundances were obtained on gravel, and the highest values were observed on sand, mixed mud, and mixed sand sediments (Table 3). Among the 5 areas, highest abundances were observed in areas SE and Chiniak Bay (Fig. 6).

Six indices of species composition were obtained for each site by an NMDS ordination based on site dissimilarities. Six dimensions were required to reduce the stress of the final NMDS configuration to 0.092, below our target value of 0.1. Each of the 6 indices was modeled separately as a function of the explanatory variables. The indices will be referred to as Axis 1 through Axis 6. The 6 dimensions accounted for 33, 17, 14, 13, 12, and 10% of the overall variation, respectively. Thus the first 2 axes accounted for approximately half the variation in the NMDS ordination.

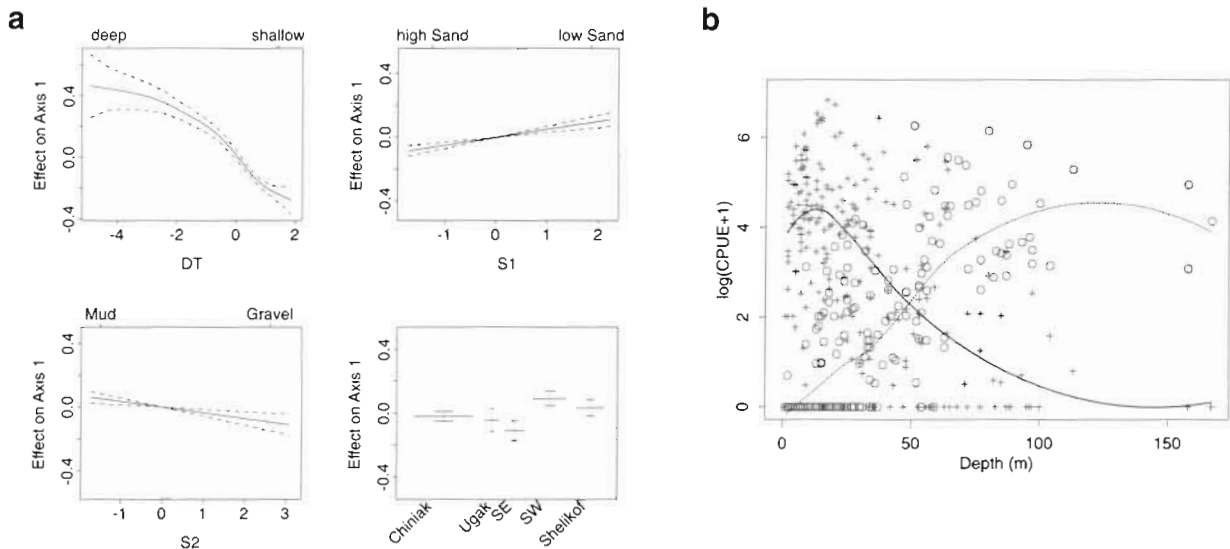


Fig. 7. (a) Estimated relationship between Axis 1 and environmental variables (for explanation of plots, see Fig. 3, DT = depth-temperature, S1 = first component, S2 = second component) and (b) scatterplot of the total abundances of the 2 species groups defined by Axis 1 against depth. Combined abundance of shallow water group (*G. macrocephalus*, *Hexagrammos* spp., *O. elongatus*, *Myoxocephalus* spp., *P. acipenserinus*, *P. barbata*, *P. bilineata*, and *H. stenolepis*) indicated by crosses and solid line. Combined abundance of deep water group (*D. setiger*, *Psychrolutes* spp., *Bathyagonus* spp., *Lycodes* spp., *A. stomias*, and *H. elassodon*) indicated by circles and dotted line. Smoothed abundance trends were estimated using a robust, locally weighted smoother. See Table 2 for full genus names

To aid interpretation of the indices we first related each of the 6 indices to the CPUEs of all species. Scatterplots of individual species CPUEs against Axes 1 to 6 indicated that relationships were generally monotone. Therefore, we used simple Spearman rank correlations to summarize relationships between the indices of species composition and the CPUE of individual species (Table 4). A species was considered to be associated with an index if it had a rank correlation with the index of 0.3 or higher. This value was chosen after examining the scatterplots, which showed clearly obvious relationships between a species and an index for all correlations larger than 0.3. For example, the first index (Axis 1) had strong positive rank correlations with the CPUE of *Dasycottus setiger*, *Bathyagonus* spp., *Lycodes* spp., *Atherestes stomias*, and *Hippoglossoides elassodon*.

and strong negative rank correlations with the CPUE of a group of 9 other species (Table 4), thus contrasting these 2 groups of species.

All variables except salinity explained a significant proportion of the variance of 1 or more of the indices. The first 4 indices of species composition were significantly related to the DT variable and to both sediment variables. Axes 5 and 6 had very low pseudo coefficients of determination even for the best fits (pseudo $R^2 = 0.19$ and 0.22 , respectively) and were difficult to interpret in terms of species composition. They were therefore not considered further for this study.

The first index was primarily related to the DT gradient (Fig. 7a). The variable DT had by far the largest coefficient of partial determination for Axis 1 (Table 5). Thus, species that were positively correlated with Axis 1 were more abundant at the deeper, colder sites, while those that are negatively correlated with Axis 1 tended to be shallow water or warm water species (Table 4, Fig. 7b). Axis 1 was also weakly associated with area, indicating that the deep water group was more abundant in areas SE and Shelikof on the west side of Kodiak island, while the shallow water group was more abundant in areas Chiniak, Ugak, and SE on the east side of the island. Linear relationships between Axis 1 and the sediment variables indicated a preference of the shallow water group for sediments with a relatively high sand content (S1 small) and more gravel than mud (S2 large), compared to the deep water group (Fig. 7a).

Table 3. Mean CPUE \pm 1 standard deviation (SD) by sediment type for 208 samples with known sediment type collected in 1991 and 1992

Sediment type	Mean CPUE (No. 1000 m ⁻²)	SD
Gravel	47	34
Sand	156	146
Mud	93	90
Mixed gravel	133	206
Mixed sand	202	195
Mixed mud	156	112

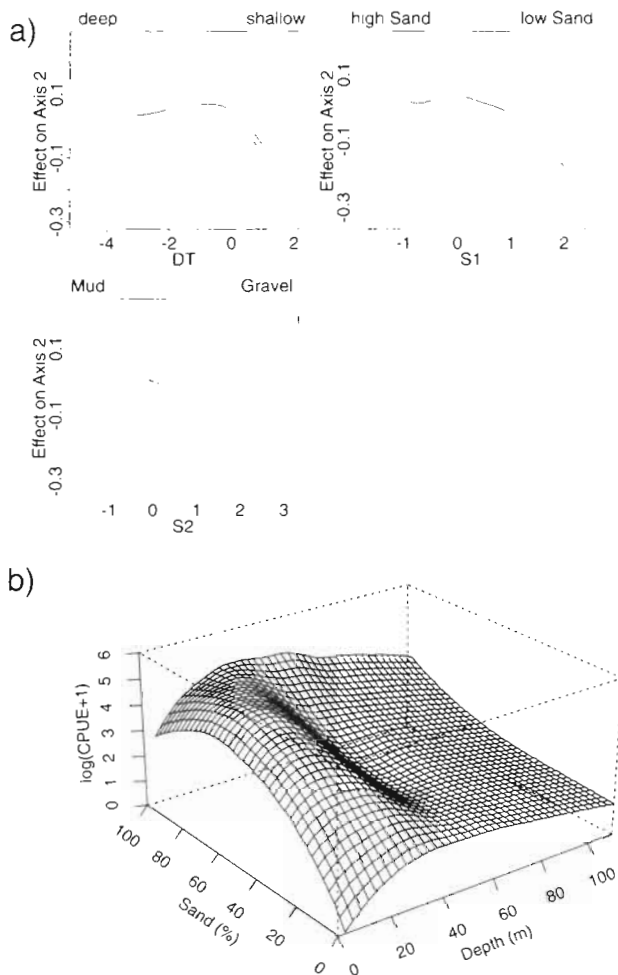
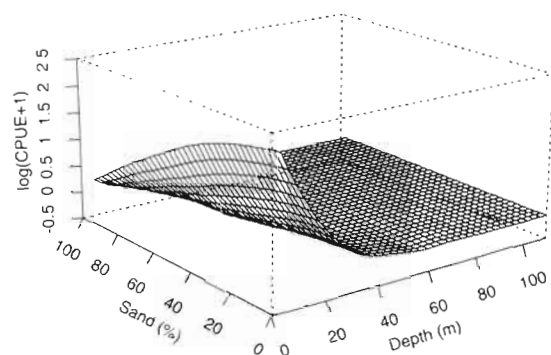


Fig. 8. (a) Estimated relationship between Axis 2 and environmental variables (for explanation of plots, see Fig. 3, DT = depth-temperature, S1 = first component, S2 = second component) and (b) smoothed trend surfaces of abundance for the 2 species groups defined by Axis 2 as a function of depth and sand. A group that is more abundant at intermediate to deep sites on sediments rich in sand (combined abundance of *P. acipenserinus*, *Lumpenus* spp., *A. stomias*, *P. isolepis*, *P. bilineata*, and *P. asper* shown on left) is contrasted with a group that tends to be more abundant on coarser sediments with a high gravel content and in very shallow water (combined abundance of *Hexagrammos* spp., *Hemilepidotus* spp., and *Pholis* spp. as shown on right). Smoothed trend surfaces were estimated using a robust, locally weighted smoother. See Table 2 for full genus names



Axis 2 was primarily related to the first sediment variable (Table 5, Fig. 8a). Species positively correlated with the index (Table 4) tended to be more abundant on sandy and muddy sediments compared to species negatively correlated with the index, which were more commonly found on coarse sediments with a low sand and high gravel content. The value of Axis 2 also dropped sharply at high values of the DT variable (shallow, warm sites), indicating that the group of positively correlated species tended to have low abundances at shallow or warm sites, whereas species that were negatively correlated with the index tended to be more abundant in intermediate to deep or cold water. These general trends are obvious in the smoothed trends of the abundances of the 2 groups plotted by depth and percent sand (Fig. 8b).

Species that were positively correlated with Axis 3 (Table 4) comprise a species group that was more abundant on fine muddy sediments (S2 small) with a low sand content and in very shallow, warm water (S1 large, Table 5, Fig. 9a). These species are contrasted with a group on sediments high in sand and gravel,

which had a deeper distribution. The trends in abundance were more obvious for the latter group (Fig. 9b).

Axis 4 was primarily related to area and depth (Table 5). Species that were negatively correlated with the index (Table 4) comprise another shallow water group. Unlike the shallow group defined by Axis 1, this group tended to be more abundant on muddy sediments (S2 small) with a relatively low sand content (Fig. 10a). Species that were positively correlated with the index were more abundant in Chiniak Bay, at greater depths and on sediments with a high percentage of gravel (Fig. 10a). Smoothed abundance trends by depth and S2 (Fig. 10b) indicate the presence of interactions between these variables, as the trend in abundance along S2 appeared to depend on depth.

DISCUSSION

Our study suggests that the small demersal fish community in shallow nearshore areas around Kodiak

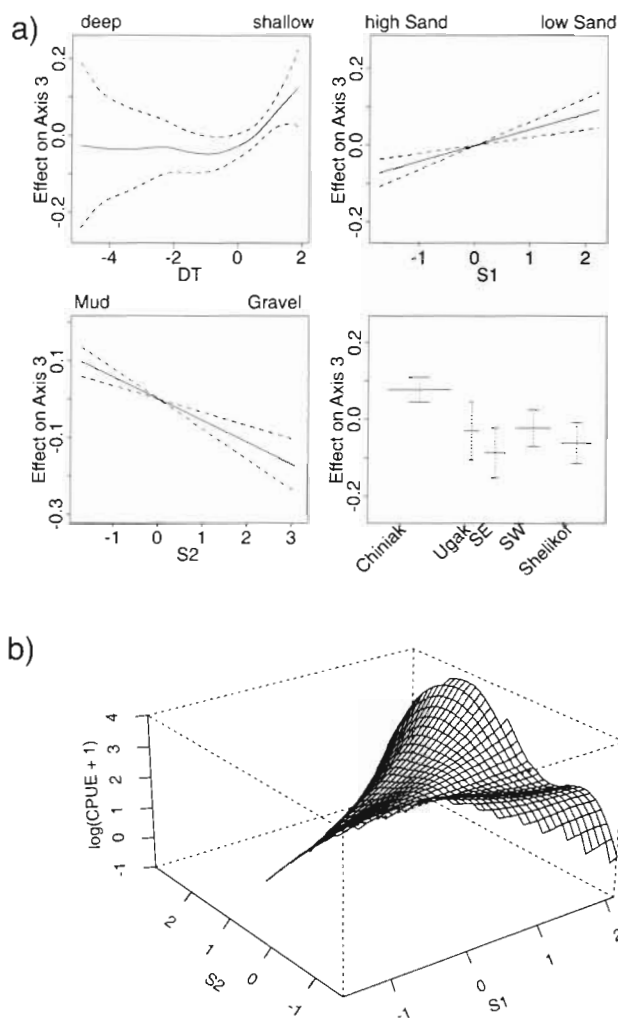


Fig. 9. (a) Estimated relationship between Axis 2 and environmental variables (for explanation of plots, see Fig. 3, DT = depth-temperature, S1 = first component, S2 = second component) and (b) smoothed trend surfaces of abundance ($\log(\text{CPUE} + 1)$) for the 2 species groups defined by Axis 3 as a function of sediment variables. Combined abundance of species positively correlated with Axis 3 (*Hexagrammos* spp., *Myoxocephalus* spp., and *P. asper*) plotted on left, combined abundance of species negatively correlated with Axis 3 (*G. macrocephalus*, *T. chalcogramma*, *I. borealis*, *R. asprellus*, *Triglops* spp., and *Psychrolutes* spp.) on right. Smoothed trend surfaces were estimated using a robust, locally weighted smoother. See Table 2 for full genus names

Island was primarily structured along gradients of DT and sediment composition. Our analysis encompassed communities from a wide range of habitats including shallow nearshore areas at the heads of long fjords, areas within deep muddy portions of several bays, as well as the Sitkinak Strait area which is subject to very strong tidal currents. It is remarkable that across all these habitats there existed a consistent, strong gradient in species composition along the DT gradient (Figs. 7 to 10).

Strong depth-dependent gradients are also found in the demersal fish communities inhabiting continental slope regions of the North Atlantic and Mediterranean Sea (Bianchi 1991, 1992a, Moranta et al. 1998), the continental shelf off Oregon (Day & Percy 1968), the abyssal North Atlantic (Haedrich & Krefft 1978, Merrett 1992), and the continental shelf off Sendai Bay, Japan (Fujita et al. 1995). In contrast to these studies we sampled a much narrower depth range and our sites were primarily located inshore.

Blaber et al. (1994a) examined the community structure of demersal fishes in the Gulf of Carpentaria over a depth range similar to the one in our study. They found that the distribution patterns of fishes are related to depth but not to other factors measured, including sediment type. Similarly, there is no correlation between adult fish assemblages and sediment type off the north-eastern United States (Colvocoresses & Musick 1984). Unlike Blaber et al. (1994a) and Colvocoresses & Musick (1984), we found a strong relationship between indices of species composition and sediment variables (Table 5). This discrepancy may be due to differences in the responses of juvenile or small fishes and large adults to sediment composition. While both Blaber et al. (1994a) and Colvocoresses & Musick (1984) sampled primarily large adult fishes, our study sampled juveniles and small adults only. Furthermore, the beam trawl used in our study sampled fishes on a much smaller spatial scale. Auster et al. (1991) investigated the small-scale distribution of fish and shellfish species on the outer continen-

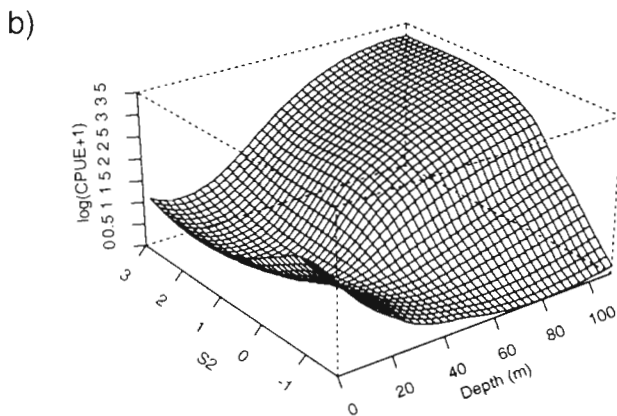
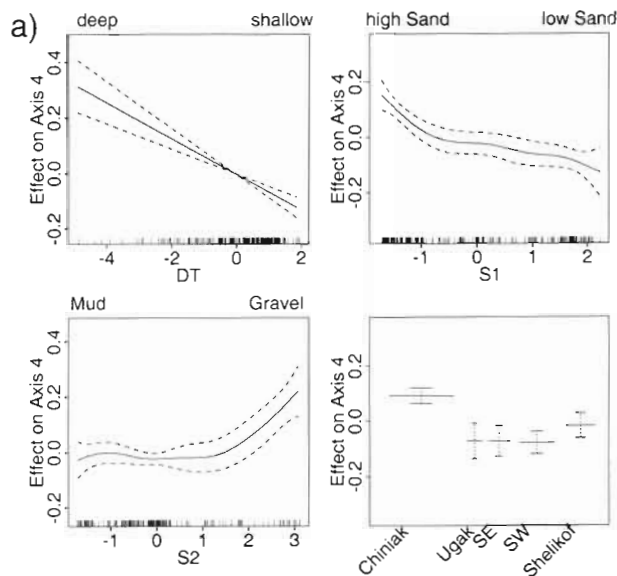
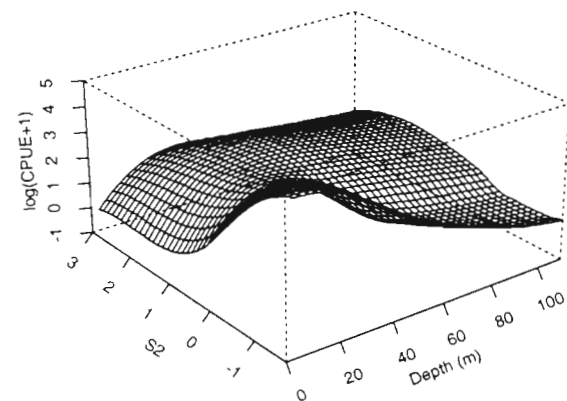


Fig. 10. (a) Estimated relationship between Axis 4 and environmental variables (for explanation of plots, see Fig. 3, DT = depth-temperature, S1 = first component, S2 = second component) and (b) smoothed trend surfaces of abundance ($\log(\text{CPUE}+1)$) for the 2 species groups defined by Axis 4 as a function of depth and S2. Combined abundance of species positively correlated with Axis 4 (*I. borealis*, *P. barbata*, Liparidinae, and *P. quadrituberculatus*) on left, combined abundance of species negatively correlated with Axis 4 (*T. chalcogramma*, *Gymnocanthus* spp., *Lumpenus* spp., and *P. asper*) on right. See Table 2 for full genus names



tal shelf of the Middle Atlantic Bight using a remotely operated vehicle equipped with a video camera. They found strong species-specific relationships between the small-scale distribution of several species and micro-habitat features including sediment type. Auster et al. (1991) suggest that it is topographic structures associated with certain sediments that are important, rather than sediment composition itself. These structures may serve as shelters or as functional aids to foraging.

While the effects of depth and temperature are often examined separately (Colvocoresses & Musick 1984, Blaber et al. 1994a, Norcross et al. 1997), we made no attempt to do so in this study because these parameters are invariably confounded. By only including a single DT factor that captured most of the variations in depth and temperature we avoided problems with collinearity that can significantly weaken statistical conclusions. To separate the effects of depth and temperature, seasonal observations or larger contrasts in temperature at depth are required.

Sediment composition at our sampling sites did not reflect the full range of bottom types available around Kodiak Island. Sampling was limited to trawlable bottom types and we could not include any hard-bottom surfaces. Observations from a remotely operated vehicle during the 1992 cruise indicated much lower abundances of small fishes on hard bottom, but the results have not been quantified. Laboratory studies of juvenile flatfishes indicate a clear preference of several flatfish species for fine-grained sediment (Moles & Norcross 1995) and it is unlikely that juveniles of these species would be found in untrawlable areas. Little is known about the bottom type preferences of other species included in our study.

Bottom salinity in the study area was not related to any of our indices, suggesting that salinity over the observed range was not an important determinant of the distribution of fishes and that species composition may be insensitive to the observed variations in bottom salinity. This is consistent with earlier findings that

Table 4. Spearman correlations between 6 indices of species composition (Axes 1 to 6) and CPUE of individual species. Only correlations exceeding 0.3 are shown. For common names of species see Table 2

Species	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
<i>Gadus macrocephalus</i>	-0.496		-0.412		0.322	
<i>Theragra chalcogramma</i>			-0.583	-0.423		
<i>Hexagrammos</i> spp.	-0.468	-0.461	0.348			
<i>Ophiodon elongatus</i>	-0.388				0.338	
<i>Dascyllus setiger</i>	0.466					
<i>Gymnocanthus</i> spp.				-0.413	-0.448	
<i>Hemilepidotus</i> spp.		-0.300				-0.325
<i>Icelinus borealis</i>			-0.466	0.302		-0.391
<i>Myoxocephalus</i> spp.	-0.464		0.307			-0.511
<i>Radulinus asprellus</i>			-0.376			
<i>Triglops</i> spp.			-0.422			
<i>Psychrolutes sigalutes</i>			-0.474			
<i>Podothecus acipenserinus</i>	-0.333	0.628				
<i>Pallasina barbata</i>	-0.362			0.325		
<i>Bathygonus</i> spp.	0.662					
<i>Anoplagonus inermis</i>			-0.317			
<i>Liparidinae</i>				0.456		-0.500
<i>Bathymaster</i> spp.						-0.338
<i>Lycodes</i> spp.	0.511					
<i>Lumpenus</i> spp.		0.304		-0.351	0.469	-0.371
<i>Pholis</i> spp.	-0.295	-0.302				
<i>Atheresthes stomias</i>	0.328	0.438	-0.334			
<i>Hippoglossoides elassodon</i>	0.773					
<i>Pleuronectes isolepis</i>		0.432				
<i>Pleuronectes bilineata</i>	-0.674	0.495				
<i>Pleuronectes asper</i>		0.400	0.354	-0.313		
<i>Pleuronectes quadrituberculatus</i>				0.388		
<i>Hippoglossus stenolepis</i>	-0.682					

presence/absence patterns and abundances of 4 flatfish species around Kodiak Island are not related to salinity (Norcross et al. 1995, 1997). The observed salinities suggest that freshwater influence at our sampling sites was minimal and did not affect community structure. This is in sharp contrast to shallow estuarine areas, where salinity can be a dominant factor determining the distribution of species (Marshall & Elliott 1998). Unlike indices of species composition, both species richness and diversity of the juvenile groundfish community in our study appeared to decrease along the salinity gradient, a trend that we cannot currently explain. Given the narrow range of salinities observed, we were surprised to find a significant trend along the short salinity gradient. The result is opposite to trends observed in some shallow estuaries where species richness has been observed to increase along the salinity gradient (Thorman 1986, Marshall & Elliott 1998). It is possible that this is a spurious result because salinities at a station will vary over the tidal cycle and our sampling design did not control for tidal stage.

Variations in DT and sediment composition explained much of the difference in species composition across a wide range of habitats. A large part of the variability remained unexplained (Table 5), even after

accounting for effects of the observed variables. The remaining variability may be due to random variations resulting from the relatively small sample sizes or may be attributable to other, unobserved variables. Other factors that may be of importance are the small-scale topography of the area (Auster et al. 1991), current speed and turbidity (e.g. Blaber et al. 1994b), and biological interactions including both food and predators.

Unlike species composition, neither species richness nor diversity of our samples appeared to be related to the DT gradient over the observed range. Day & Pearcy (1968) showed that the species richness of benthic marine fishes varies along the depth gradient and the highest number of species was observed in shallow water (<200 m). The entire depth range sampled in our study fell within the smallest depth stratum examined by Day & Pearcy (1968) and no trend in species richness or diversity within this limited depth range was apparent.

Species richness and diversity, though highly variable, significantly increased with the area sampled (Figs. 3 & 5). The observed relationship is similar in shape to the power model that is frequently used to describe the species-area relationship, although both the number of species as well as the size of the areas

considered were much smaller in our study. On average, species richness was significantly lower on 'pure' sediments, particularly on mud and gravel (Fig. 4). Species diversity showed a similar pattern, but tended to be higher on gravel than on sand and mud, and lower on mixed mud compared to other mixed sediments. Mixed mud sediments typically consisted of relatively homogenous areas with sediments ranging from fine sand to mud. Mixed sand, mixed gravel, and gravel typically contained large amounts of shell hash in various sizes and appeared to be the most heterogeneous and structurally complex bottom types in the area, based on video observations (Norcross unpubl. obs.). Spatial heterogeneity is typically associated with a higher diversity of animal species (Begon et al. 1990) and may explain the observed patterns.

Table 5. Contribution of each variable to the 'best-fit' models for Axes 1 to 4. The deviance for each of the variables refers to the deviance of a reduced model in which that variable is excluded from the model. Smooth non-linear functions of a variable were used if approximate *F*-tests and scatterplots indicated the presence of non-linear relationships. These variables are indicated by *f*(). Pseudo R^2 : pseudo coefficient of determination for the best model ($= 1 - \text{deviance of best model} / \text{deviance of null model}$) and to the pseudo coefficient of partial determination for reduced models ($= 1 - \text{deviance of best model} / \text{deviance of reduced model}$). Variables are listed in the order of their contribution to the fit. For further details see 'Methods'

Axis	Model df	Deviance	Pseudo R^2
1			
Null model	1	16.332	
Best model	11	4.156	0.75
<i>f</i> (DT)	7	9.127	0.55
Area	7	4.771	0.13
S1	10	4.751	0.13
S2	10	4.420	0.06
2			
Null model	1	8.124	
Best model	10	5.369	0.34
<i>f</i> (S1)	6	6.772	0.21
<i>f</i> (DT)	6	6.158	0.13
S2	9	5.881	0.09
3			
Null model	1	7.029	
Best model	11	4.559	0.35
S2	10	5.217	0.13
Area	7	5.154	0.12
S1	10	4.966	0.08
<i>f</i> (DT)	7	4.868	0.06
4			
Null model	1	5.265	
Best model	14	3.215	0.39
Area	10	3.976	0.19
DT	13	3.972	0.19
<i>f</i> (S2)	10	3.633	0.12
<i>f</i> (S1)	10	3.502	0.08

Total numerical abundance (CPUE) of small fishes provides a rough indicator of the capacity of a given area, but because it aggregates a variety of species and sizes it is at best a crude measure. Total CPUE tended to decrease as the gravel content in the sediment increased (Fig. 6), possibly indicating decreased abundances of small demersal fishes on coarse bottom. The presence of coarse sediment in this area is indicative of high current velocities due to strong tidal currents or of strong wind mixing in shallow areas. Tidal currents and strong mixing may represent sources of environmental stress that limit the abundance of small groundfishes. This trend could possibly be due to sampling difficulties resulting from strong currents, which may decrease the effectiveness of the beam trawl. However, video observations seem to confirm that abundances of juvenile fishes are lower on coarse sediments (Norcross & Mueter 1999).

The 4 indices of species composition examined in our analysis describe different, independent aspects of community composition. Each index can be interpreted as representing 2 groups of species that were highly correlated (positively or negatively) with the index (Table 4), and each index in turn was related to different aspects of the environment (Table 5). Thus, species associated with each index appeared to respond to different environmental gradients or in different ways to the same gradients. Each index contrasted groups that respond in opposite ways to these gradients.

Relating indices to environmental variables allowed us to draw general conclusions regarding the response of an assemblage of fishes to environmental gradients, but the actual response of individual species may sometimes vary from that predicted. The more highly correlated the CPUE of an individual species is with one of the indices, the more likely it will follow the same trends as that in relation to environmental variables.

A potential drawback of using such indices of species composition is that species are not assigned to unique groups, as for example in cluster analysis. Several species in our analysis were strongly associated with 2 or more indices (Table 4). The principal advantage of using indices is the fact that they are statistically well behaved, unlike the CPUEs of individual species, which do not lend themselves to a straightforward statistical analysis. Our main goal was to search for generalizations and detect major patterns in species composition. The use of a reduced number of indices allowed us to detect general patterns in the relationship between species composition and environmental variables and to assess their statistical significance.

All 4 indices that we examined were significantly related to the DT variable and to both sediment variables, suggesting that small groundfishes partition the available habitat to a considerable degree based on these variables. A strong depth or DT gradient in bottom fishes and other benthic organisms has been observed in many studies and has even been compared to the elevation gradient in the terrestrial environment (Brown & Lomolino 1998). However, it is not clear whether depth, temperature, or other confounding parameters are responsible for establishing and maintaining the gradient. Similarly, the association of species and species groups with sediment composition may indicate a true preference for a specific sediment type, or may be related to other parameters like the availability of food or shelter. At least some benthic fishes display clear sediment preferences, regardless of the availability of food or other parameters (Moles & Norcross 1995).

The simplest explanation for the observed patterns is that the juveniles of each species display distinct depth preferences, similar to adult groundfishes (Day & Percy 1968), and select their preferred sediment type within the occupied depth range. The causes of depth zonation are poorly understood but may be related to oceanographic conditions, the history of larval settlement in the area, physical factors like temperature, light, and pressure, and biotic interactions (Moyle & Cech 1988). Our analysis suggests strong non-linear effects of depth/temperature on all indices of species composition (Figs. 7 to 10). The patterns of change along the DT variable suggest that species composition changes rapidly in relatively shallow, warm water and more gradually in deeper, colder water. In contrast, effects of the sediment variables were typically linear or close to linear.

In summary, the species composition of the small demersal fish community around Kodiak Island changed primarily along gradients of DT and secondarily along gradients of sediment type as well as among geographic areas. While the DT variable was the most important variable along which species composition changed, the same variable was not significantly related to species richness, species diversity, or total CPUE. Therefore, species composition appeared to change independently of the overall abundance and of species richness and diversity.

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