Abstract—We analyzed data from National Marine Fisheries Service bottom trawl surveys carried out triennially from 1984 to 1996 in the Gulf of Alaska (GOA). The continental shelf and upper slope (0–500 m) of the GOA support a rich demersal fish fauna dominated by arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and Pacific Ocean perch (*Sebastes alutus*). Average catch per unit of effort (CPUE) of all ground-fish species combined increased with depth and had a significant peak near the shelf break at 150–200 m. Species richness and diversity had significant peaks at 200–300 m. The western GOA was characterized by higher CPUEs and lower species richness and diversity than the eastern GOA. Highest CPUEs were observed in Shelikof Strait, along the shelf break and upper slope south of Kodiak Island, and on the banks and in the gullies northeast of Kodiak Island. Significant differences in total CPUE among surveys suggest a 40% increase in total groundfish biomass between 1984 and 1996. A multivariate analysis of the CPUE of 72 groundfish taxa revealed strong gradients in species composition with depth and from east to west, and a weak but significant trend in species composition over time. The trend over time was associated with increases in the frequency of occurrence and CPUE of at least eight taxa, including skates (Rajidae), capelin (*Mallotus villosus*), three flatfish species, and Pacific Ocean perch, and decreases in frequency of occurrence and CPUE of several sculpin (*Myoxocephalus* spp.) species. Results are discussed in terms of spatial and temporal patterns in productivity and in the context of their ecological and management implications.

Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska

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The continental shelf and upper slope of the Gulf of Alaska (GOA, Fig. 1) support a diverse community of demersal fishes. This community includes many commercial species that support rich bottom trawl and longline fisheries with landings averaging approximately 250,000 metric tons per year over the past two decades (NPFMC[1]). The commercially most important species during the past decade have been walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), other flatfish species (Pleuronectidae), rockfish (*Sebastes* spp.), and sablefish (*Anoplopoma fimbria*). Arrowtooth flounder (*Atheresthes stomias*), although currently the dominant demersal species by biomass, is a minor component of total landings.

Triennial bottom trawl surveys have been carried out since 1984 to assess the abundance and distribution of the main commercial species in the GOA (Martin, 1997). The surveys also provide data on noncommercial fish species and other associated benthic megafauna. At least 140 species of fishes belonging to 33 families were collected during the 1996 GOA bottom trawl survey (Martin, 1997). Rockfish (Scorpaenidae) were the best represented family with 25 species, followed by sculpins (Cottidae, 24 species) and flatfishes (Pleuronectidae, 16 species). Data from similar bottom trawl surveys have been used to investigate the ecology and zoogeography of fish assemblages in many parts of the world, including the North Pacific (Gabriel

and Tyler, 1980; Rogers and Pikitch, 1992; Jay, 1996). However, to our knowledge there have been no studies in which demersal fish assemblages from the GOA shelf and slope were examined.

To understand, and eventually to predict, the effects of environmental variations on fish stocks, scientists and managers increasingly advocate ecosystem approaches to research and management (Yaffee et al., 1996; Langton and Haedrich, 1997). Ecosystem management must be based on multispecies relationships and overcome the current focus on individual species (Langton and Haedrich, 1997). An important prerequisite for successful multispecies approaches is an understanding of the species structure of fish communities in space and time.

The purpose of this paper is to identify spatial and temporal patterns in the composition of the demersal fish community from the GOA. Specific objectives are 1) to identify the main environmental and spatial gradients along which the groundfish community is structured, and 2) to identify long-term changes in the composition of the groundfish community.

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[1] NPFMC (North Pacific Fisheries Management Council). 1997. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fisheries Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501.
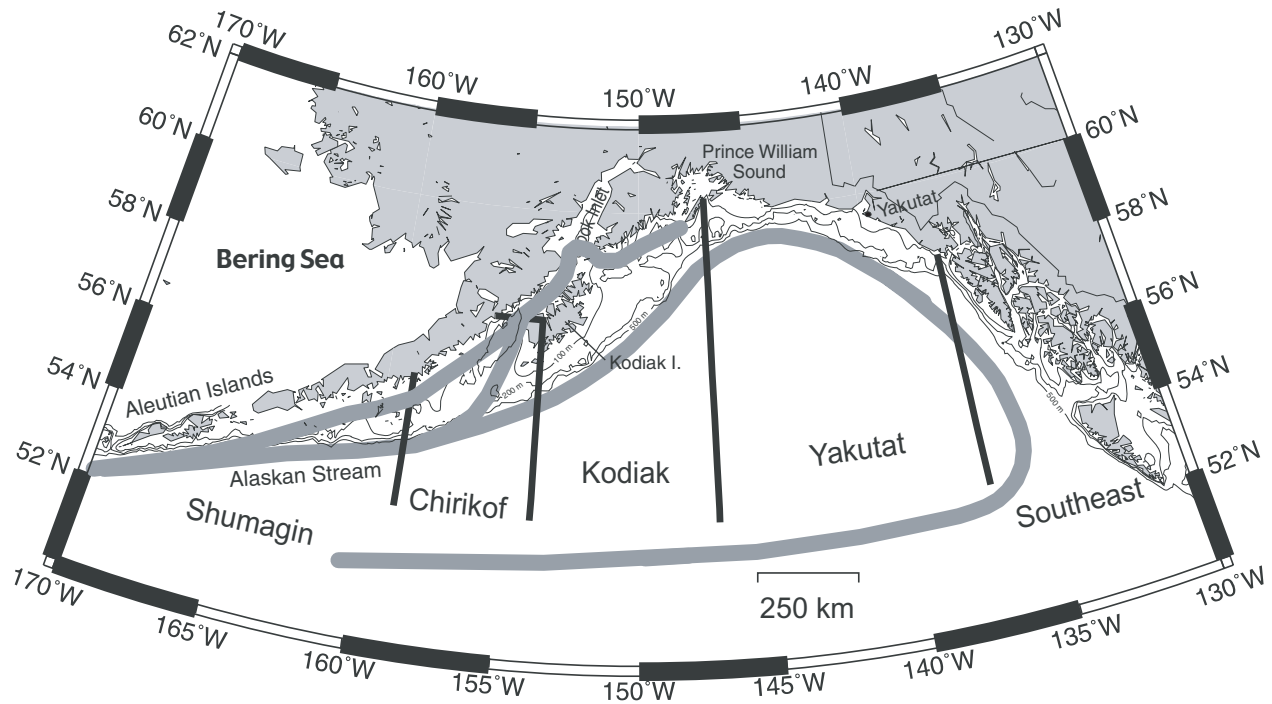
Figure 1

Bathymetric and geographic features of the Gulf of Alaska between 130°W and 170°W. The black vertical lines separate the five areas used in the survey design and analysis. Thin lines indicate 100 m, 200 m, and 500-m isobaths. The large shaded lines summarize major circulation patterns.

Materials and methods

Study area

Our study area included the continental shelf and the upper continental slope along the perimeter of the GOA to a depth of 500 m (Fig. 1). The total study area is approximately 300,000 km², extending over a distance of 2600 km from Southeast Alaska to the western Aleutian Islands.

Data sources

All fisheries data for this study were obtained from the Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service (NMFS) in Seattle, WA. Personnel from AFSC have executed bottom trawl surveys of groundfish stocks in the GOA on a triennial basis since 1984 (Table 1). All surveys were conducted during the summer with chartered fishing vessels and were based on a stratified random sampling design. The GOA was divided into five areas, three in the western GOA (Shumagin, Chirikof, Kodiak) and two in the eastern GOA (Yakutat, Southeast, see Fig. 1) and four depth strata (0–100 m, 100–200 m, 200–300 m, 300–500 m). Depth strata within each area were further subdivided into 2–5 strata based on the type of geographical area (e.g. banks, gullies, shelf, and slope), resulting in a total of 49 strata. Some modifications were made to the stratification scheme after 1987. Our analysis was based on current stratum boundaries. Details of the

sampling design, data collection, and sample processing are described in Brown (1986), Martin and Clausen (1995), Stark and Clausen (1995), and Martin (1997). In our analysis we excluded data from the 0–100 m stratum in the southeast area because it is mostly untrawlable and was not sampled during three out of five surveys; thus we used a total of 48 strata in the analysis. We further excluded all hauls that were classified as unsatisfactory in the database.

Several types of fishing gear were used in the bottom trawl surveys between 1984 and 1996. A poly-Nor'eastern high opening bottom trawl equipped with rubber bobbin roller gear has become the standard gear for GOA bottom trawl surveys (Munro and Hoff, 1995) and was used for at least part of the survey in all years (Table 1). In addition, an older Nor'eastern trawl (gear type 160) was used during parts of the 1984 and 1990 survey and two different Japanese trawls (Table 1) were used during the 1984 and 1987 joint Japanese-American surveys. Fishing effort for each gear type was spread out over most of the sampling region within each year and one gear type (gear type 172) was used during all surveys, allowing us to estimate gear differences.

Data analysis

Our analysis was based on standardized catch per unit of effort of 72 fish taxa collected in the bottom trawl surveys. Catches were standardized to weight per unit area (kg/km²), where the area swept by the trawl was estimated

Table 1

Number of quantitative hauls used in analysis by gear type, start and ending dates of survey, minimum, maximum, and average depth of hauls, and number of haul locations for which bottom temperature was obtained. Note changes in gear from 1984 to 1990, which were associated with a decrease in the average tow duration. Gear types: 160 = Nor'eastern trawl; 172 = poly-Nor'eastern high opening bottom trawl; 710 = Japanese poly trawl; 717 = Japanese poly trawl with roller gear.

	1984	1987	1990	1993	1996
Total number of hauls	867	758	705	774	807
Gear type: no. of hauls	(160: 430)	(172: 380)	(160: 166)	(all: 172)	(all: 172)
	(172: 133)	(717: 378)	(172: 539)		
	(710: 304)				
Starting date	Jun 3	May 22	Jun 4	Jun 6	May 22
Ending date	Oct 2	Sep 10	Sep 9	Sep 7	Jul 30
Average depth (m)	167	150	167	156	157
Maximum depth (m)	499	499	494	488	479
Minimum depth (m)	16	20	20	22	20
Temp. measurements	563	298	285	726	716

from the measured distance trawled and estimates or measurements of the width of the net opening. Taxa to include in the analysis were selected according to the following criteria: 1) all species consistently identified to species level and occurring at least at 1% of the stations, 2) taxa that were not consistently identified to species level were combined by genus or, if necessary, by family, 3) if, after grouping taxa, a species, genus, or family was present at less than 1% of the stations within each year, it was not included in the analysis.

As an initial estimate of abundance trends, we computed gulf-wide averages of CPUE for each species by year. CPUEs from the Japanese trawls used in 1984 and 1987 were adjusted to the US standard trawl gear by using fishing power coefficients provided in Tables 28 and 31 in Munro and Hoff (1995). Following standard NMFS methods (Martin, 1997), we averaged estimated CPUEs by stratum, weighted the averages by stratum area, and combined them to obtain area-wide averages.

From a haul-by-taxon matrix of CPUE data, we computed univariate and multivariate indices to examine spatial and temporal patterns in community structure. For each haul we computed species richness (number of species), species diversity (Shannon-Wiener index), and total CPUE of all groundfish taxa combined as univariate measures of community structure. We considered three indices of species diversity (Shannon-Wiener, Simpson's D, Fisher's α) and chose the Shannon-Wiener index because it showed little dependence on sample size in simulations, was approximately normally distributed (which facilitates statistical comparisons), and is widely used in the ecological literature. In addition, we computed multivariate indices of species composition based on Bray-Curtis dissimilarities of root-root transformed CPUEs and nonmetric multidimensional scaling (NMDS) as described in Mueter and Norcross (1999). Indices of species composition were computed separately for each year and were related to

explanatory variables to describe the major gradients in species composition by year. To examine trends in species composition over time, catches were averaged by stratum instead of using individual hauls, reducing the 3911 hauls to 240 within-year strata (5 years × 48 strata). An NMDS ordination of the stratum-by-species matrix was then used to test specifically for significant trends in species composition over time. We computed the linear combination of ordination axes that maximized the correlation with year and tested whether the correlation was significantly higher than would be expected by chance by using randomization tests. This linear combination was used as an index representing changes in species composition over time (time index). Species that were most strongly associated with the time index were identified based on scatterplots and Spearman rank correlations between the index and individual species abundances, and changes in these species were examined in more detail.

Depth, geographic location, bottom temperature (measured by sensors attached to the gear), Julian day, year, gear type, and area swept were included in the analysis as explanatory variables. Geographic location was represented in the analysis either as a categorical variable by using the five statistical areas depicted in Figure 1 or by using alongshore distances (AD). Alongshore distance was computed by projecting each station onto a line that approximately followed the shelf break and measuring the distance along this line from its origin in the southeast part of the study area (km 0) to the westernmost point (km 2600). Temperature was not measured for all hauls (Table 1); thus all regressions were done both with and without temperature included. Gear type was included in all models to account for potential differences among gear types. Area swept was only included for examining trends in species richness and diversity because the number of species per haul was expected to increase with the area sampled. All other indices were based on standardized CPUEs.

Generalized additive models (GAM, Hastie and Tibshirani, 1990) and linear models were used to relate univariate and multivariate indices, individual species CPUEs, and presence-absence data to the independent variables. Additive models were used to allow for nonlinear relationships between the dependent and independent variables. A GAM is a nonparametric regression that uses smooth functions of the independent variables in place of linear functions and allows different probability distributions for the data. We initially assumed that species richness followed a Poisson distribution (counts), that the Shannon-Wiener index, log-transformed CPUEs, and all indices of species composition followed a normal distribution, and that presence-absence data followed a binomial distribution. The dependent variables were then modeled as the sum of nonparametric functions (smoothing splines) of the hypothesized independent variables. If no evidence of nonlinearity was found, linear terms were substituted for the smoothing splines. Residuals from each regression model were examined for violations of the underlying assumptions (error distribution and homogeneity of variance) and for outliers. Specifically, we examined residuals graphically by means of histograms, quantile-quantile plots, and plots of residuals against time and against other covariates. We further conducted formal tests of goodness-of-fit of the residuals against the assumed error distributions after each model fit. Model fits were generally deemed adequate, unless noted otherwise in the results.

To identify and evaluate the significance of relationships between species composition and explanatory variables we first chose the most appropriate regression model, then quantified the contribution of each explanatory variable to the model fit. A stepwise procedure based on the Akaike information criterion (Hastie and Tibshirani, 1990) was used to select a subset of significant variables. As a measure of model fit we computed a pseudo-coefficient of determination (pseudo-r^2), or the fraction of the total deviance explained by the model, as a surrogate for the familiar r^2 (Swartzman et al., 1992). The importance of individual variables in the model fits was evaluated similarly by using a pseudo-coefficient of partial determination based on reduced models that exclude the variable of interest (= 1 – deviance of best model/deviance of reduced model).

Trends in the abundance of those species that were strongly associated with the time index were examined in greater detail by haul. For this analysis we treated zero and nonzero catches separately to test for 1) changes in the catch rate of a species over time based on positive catches only (CPUE-where-present) and 2) changes in the frequency of occurrence of a species over time (by estimating the probability of a nonzero haul). To test for changes in the CPUE-where-present of these species, we used an analysis of covariance model of the following form:

$$\log(CPUE\text{-}where\text{-}present) = area + depth\ stratum +$$
$$gear + (area \times depth\ stratum) + \beta \times year.$$

Errors were assumed to be normally distributed, thus CPUE-where-present was assumed to follow a lognormal distribution. A separate linear time trend was estimated and evaluated for significance within each depth stratum in each area (β parameters). The interaction term (*area × depth stratum*) was omitted if it was not significant at the 5% level. Strata within the same statistical area and depth stratum were pooled, unless fitting separate regression lines to each of the 48 strata improved the overall fit significantly. If the slope of the regression did not differ among areas or depth strata at the 5% level, data were further pooled across areas or depth strata (or both) to obtain the most parsimonious model.

The probability of nonzero hauls was estimated similarly using a logistic regression model (McCullagh and Nelder, 1989):

$$\log\left(\frac{\Pr(CPUE > 0)}{1 - \Pr(CPUE > 0)}\right) = area + depth\ stratum +$$
$$gear + (area \times depth\ stratum) + \beta \times year,$$

where the number of positive catches (CPUE>0) was assumed to follow a binomial distribution. The most parsimonious models for each species were used to test the null hypothesis that there was no significant (linear) trend in the catch rate (CPUE-where-present) or frequency of occurrence (Pr{CPUE>0}) over time. The null hypothesis was rejected if the slope β was significantly different from zero at the 5% level.

Results

Arrowtooth flounder had the highest average CPUE (kg/km²) and the highest frequency of occurrence during all surveys (Table 2). Walleye pollock was second in most years, followed by Pacific cod and Pacific halibut. However, in 1996, the estimated CPUE of Pacific Ocean perch exceeded that of pollock, cod, and halibut. Sablefish, five other flatfish species, two *Sebastes* species, and Atka mackerel (*Pleurogrammus monopterygius*) were other important species by CPUE (> 200 kg/km², Table 2). The most abundant species, including gadids and most of the flatfishes, were generally also the most widespread species in the survey (>50% frequency of occurrence). In spite of relatively high CPUEs, rockfishes, Atka mackerel, and yellowfin sole (*Limanda aspera*) had low frequencies of occurrence (4–40%), indicating high local abundances and a more restricted spatial distribution.

Independent variables used in the analysis of species richness, diversity, CPUE, and species composition were moderately correlated (Table 3). The largest correlations were between area swept and year (–0.452), due to a reduction in haul duration after 1987, between depth and temperature (–0.407), and between Julian day and alongshore distance (–0.383). Depth and bottom temperature on the shelf and slope are invariably confounded and their effects may generally be difficult to separate. The confounding between Julian day and AD was extreme in some years (e.g. r=–0.79 in 1993) because sampling vessels traveled from west to east during most surveys. However

Table 2

All groundfish taxa included in analysis and their estimated average CPUE (kg/km²) by year and for all years combined. CPUEs were computed for each haul, averaged by stratum, weighted by stratum area, and combined to obtain area-wide averages. FO denotes overall frequency of occurrence for all years combined in percent.

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
Atheresthes stomias [1]	arrowtooth flounder	3790	3339	6499	5298	5574	4900	91
Theragra chalcogramma [1]	walleye pollock	2431	3139	2873	2586	2320	2670	74
Gadus macrocephalus [1]	Pacific cod	1876	1516	1424	1397	1821	1607	73
Hippoglossus stenolepis [1]	Pacific halibut	1415	1410	1118	2007	1936	1577	77
Sebastes alutus [1]	Pacific Ocean perch	753	823	535	1649	2629	1278	40
Anoplopoma fimbria [1]	sablefish	753	1379	731	844	492	840	52
Hippoglossoides elassodon [1]	flathead sole	912	783	828	643	689	771	57
Lepidopsetta spp. [1]	rock sole	515	668	531	590	695	600	44
Sebastes polyspinis [1]	northern rockfish	135	475	365	356	337	334	20
Pleurogrammus monopterygius	Atka mackerel	153	98	101	73	1179	321	5
Glyptocephalus zachirus [1]	rex sole	187	269	335	297	245	266	67
Microstomus pacificus [1]	Dover sole	164	263	329	291	266	263	55
Limanda aspera [1]	yellowfin sole	313	192	196	277	162	228	7
Sebastes ciliatus [1]	dusky rockfish	87	505	91	194	255	227	20
Sebastes aleutianus [1]	rougheye rockfish	153	227	165	212	156	183	34
Rajidae unident.	skate (unidentified)	139	129	164	205	274	182	33
Clupea pallasi	Pacific herring	186	511	60	53	3	163	8
Sebastes zacentrus	sharpchin rockfish	23	274	131	81	220	146	10
Albatrossia pectoralis	giant grenadier	115	96	81	155	175	124	3
Sebastolobus alascanus	shortspine thornyhead	126	127	68	114	177	122	24
Sebastes variegatus	harlequin rockfish	9	247	60	32	68	83	11
Thaleichthys pacificus	eulachon	24	56	95	119	110	81	32
Isopsetta isolepis [1]	butter sole	80	71	59	102	71	77	7
Platichthys stellatus [1]	starry flounder	50	63	35	137	93	76	5
Sebastes borealis	shortraker rockfish	59	137	43	69	69	75	8
Sebastes proriger	redstripe rockfish	18	90	92	101	51	71	4
Squalus acanthias	spiny dogfish	34	34	65	114	96	69	16
Hemilepidotus jordani	yellow Irish lord	49	46	40	40	61	47	27
Sebastes brevispinis	silvergray rockfish	16	18	48	65	82	46	7
Ophiodon elongatus	lingcod	15	32	35	53	80	43	10
Hemitripterus bolini	bigmouth sculpin	54	35	29	19	14	30	18
Lamna ditropis	salmon shark	27	43	42	26	11	30	1
Myoxocephalus spp.	sculpin (unidentified)	37	23	18	22	30	26	9
Parophrys vetulus [1]	English sole	11	28	26	28	15	22	7
Somniosus pacificus	Pacific sleeper shark	1	1	6	29	72	22	1
Zaprora silenus	prowfish	13	24	15	28	23	21	11
Pleuronectes quadrituberculatus [1]	Alaska plaice	7	16	20	9	17	14	4
Microgadus proximus	Pacific tomcod	5.03	34.67	6.32	9.01	5.78	12.16	2
Sebastes babcocki	redbanded rockfish	4.88	6.21	11.20	12.53	15.54	10.07	11
Hydrolagus colliei	spotted ratfish	13.06	8.16	6.32	7.08	12.65	9.45	6
Hexagrammos decagrammus	kelp greenling	3.89	8.17	13.87	8.21	6.69	8.16	8
Sebastes reedi	yellowmouth rockfish	1.69	0.89	6.39	12.14	3.15	4.85	1
Sebastes ruberrimus	yelloweye rockfish	2.10	10.17	3.29	3.88	3.70	4.63	3
Sebastes helvomaculatus	rosethorn rockfish	1.99	5.12	2.50	2.54	7.71	3.97	4
Sebastes melanops	black rockfish	1.14	3.75	4.65	0.86	7.89	3.66	1
Bathymaster signatus	searcher	2.08	2.05	5.39	3.04	4.38	3.39	15
Trichodon trichodon	Pacific sandfish	7.56	3.71	2.45	1.76	0.52	3.20	3
Malacocottus spp.	sculpin (unidentified)	4.33	2.97	2.40	3.55	1.63	2.97	14
Cryptacanthodes giganteus	giant wrymouth	0.76	3.26	3.98	1.17	2.77	2.39	1
Lycodes palearis	wattled eelpout	0.86	1.75	3.10	3.16	2.30	2.23	11

Table 2 (continued)

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
Eopsetta jordani	petrale sole	0.97	0.83	0.61	2.77	3.68	1.77	2
Mallotus villosus	capelin	1.47	0.17	0.51	0.42	4.98	1.51	7
Lycodes brevipes	shortfin eelpout	0.13	0.84	0.79	2.41	2.17	1.27	8
Dasycottus setiger	spinyhead sculpin	1.33	0.49	0.89	1.88	0.83	1.08	11
Aptocyclus ventricosus	smooth lumpsucker	0.74	1.29	1.77	0.37	0.56	0.95	2
Podothecus acipenserinus	sturgeon poacher	0.19	0.42	1.23	2.34	0.33	0.90	5
Sebastes elongatus	greenstriped rockfish	0.05	0.22	0.59	0.91	1.20	0.59	1
Sebastes wilsoni	pygmy rockfish	0.00	1.38	0.30	0.01	0.96	0.53	1
Myctophidae	lanternfish (unidentified)	0.19	0.19	0.11	1.52	0.53	0.51	4
Triglops spp.	sculpin (unidentified)	0.37	0.32	0.68	0.40	0.61	0.48	6
Stichaeidae	prickleback (unidentified)	0.58	0.05	0.51	0.70	0.41	0.45	4
Sebastes crameri	darkblotched rockfish	0.02	0.13	0.59	0.99	0.41	0.43	1
Hexagrammos stelleri	whitespotted greenling	0.17	0.56	0.64	0.33	0.27	0.39	1
Lyopsetta exilis	slender sole	0.10	0.07	0.29	0.77	0.59	0.37	5
Cyclopteridae (Liparidinae)	snailfish	0.30	0.23	0.30	0.28	0.04	0.23	3
Hemilepidotus hemilepidotus	red Irish lord	0.07	0.29	0.05	0.32	0.10	0.16	1
Cottidae	sculpin (unidentified)	0.25	0.00	0.28	0.08	0.01	0.12	1
Gymnocanthus spp.	sculpin (unidentified)	0.16	0.03	0.00	0.06	0.06	0.06	1
Eumicrotremus orbis	Pacific spiny lumpsucker	0.02	0.08	0.03	0.07	0.04	0.05	2
Lycodes diapterus	black eelpout	0.08	0.05	0.00	0.01	0.02	0.03	2
Sarritor frenatus	sawback poacher	0.03	0.03	0.01	0.04	0.04	0.03	2
Bathyagonus nigripinnis	blackfin poacher	0.02	0.01	0.01	0.01	0.00	0.01	1
Total		14,786	17,286	17,436	18,400	20,662	17,714	

[1] Catches for 1984 and 1987 were adjusted by using fishing power coefficients in Tables 28 and 31 in Munro and Hoff (1995). Other flatfishes were adjusted by using rock sole coefficients.

Table 3
Pairwise Pearson's correlation coefficients among independent variables used in the statistical analysis.

	Depth	Alongshore distance	Gear temperature	Julian day	Year
Alongshore distance	−0.326*				
Gear temperature	−0.407*	−0.203*			
Julian day	0.129*	−.383*	0.330*		
Year	−0.026	−0.035	−0.266*	−0.306*	
Area swept	0.012	0.184*	0.019	0.145*	−0.452*

* Highly significant (P=0.01)

the direction of sampling was reversed in some years, providing some contrast.

Species richness, as measured by the number of species per haul, was initially modeled as a Poisson variable (counts). However, an analysis of the distribution of the observed numbers and of residuals from the fitted models suggested that it could more appropriately be modeled as a normally distributed variable (see below). We fitted models assuming either a Poisson or a normal distribution and found that the estimated patterns were virtually identical and in both cases the same model was selected as

best model. Only results based on the normal distribution are presented. Species richness was highly variable and the best model explained a small portion of the overall variability (Pseudo-r^2=0.25). The average number of species increased with area swept (Fig. 2), which may be expected if species area relationships established for terrestrial ecosystems also hold in the marine environment. The number of species tended to peak at intermediate depths (200–300 m) and was highest in the eastern GOA (Table 4), decreasing steadily west of Prince William Sound (km 1100, approximately 147°W). Species richness appeared
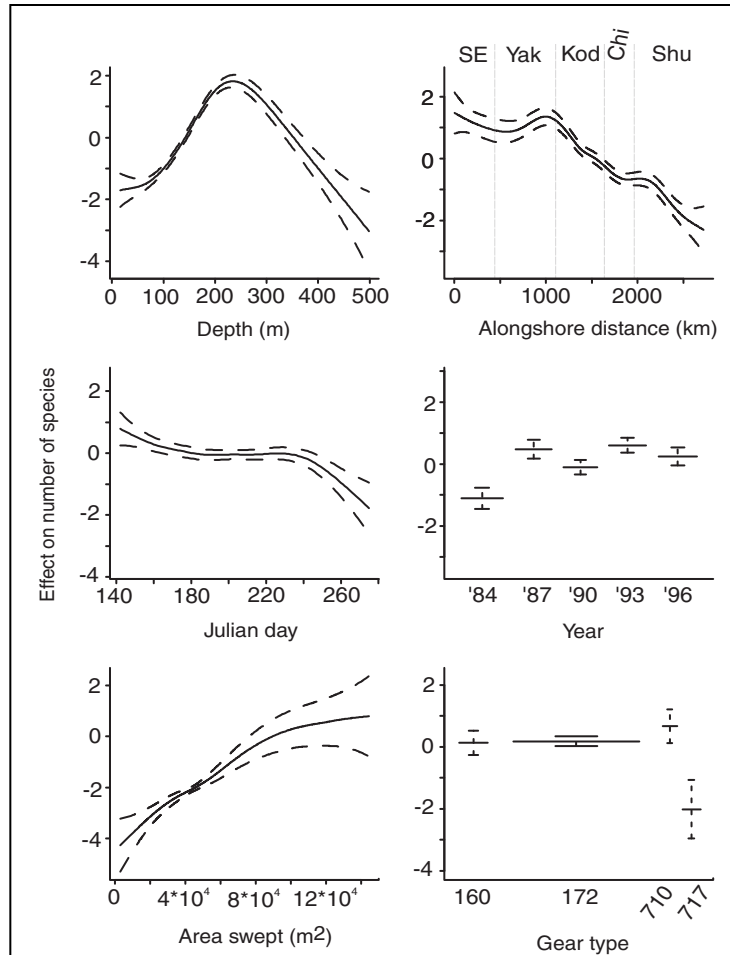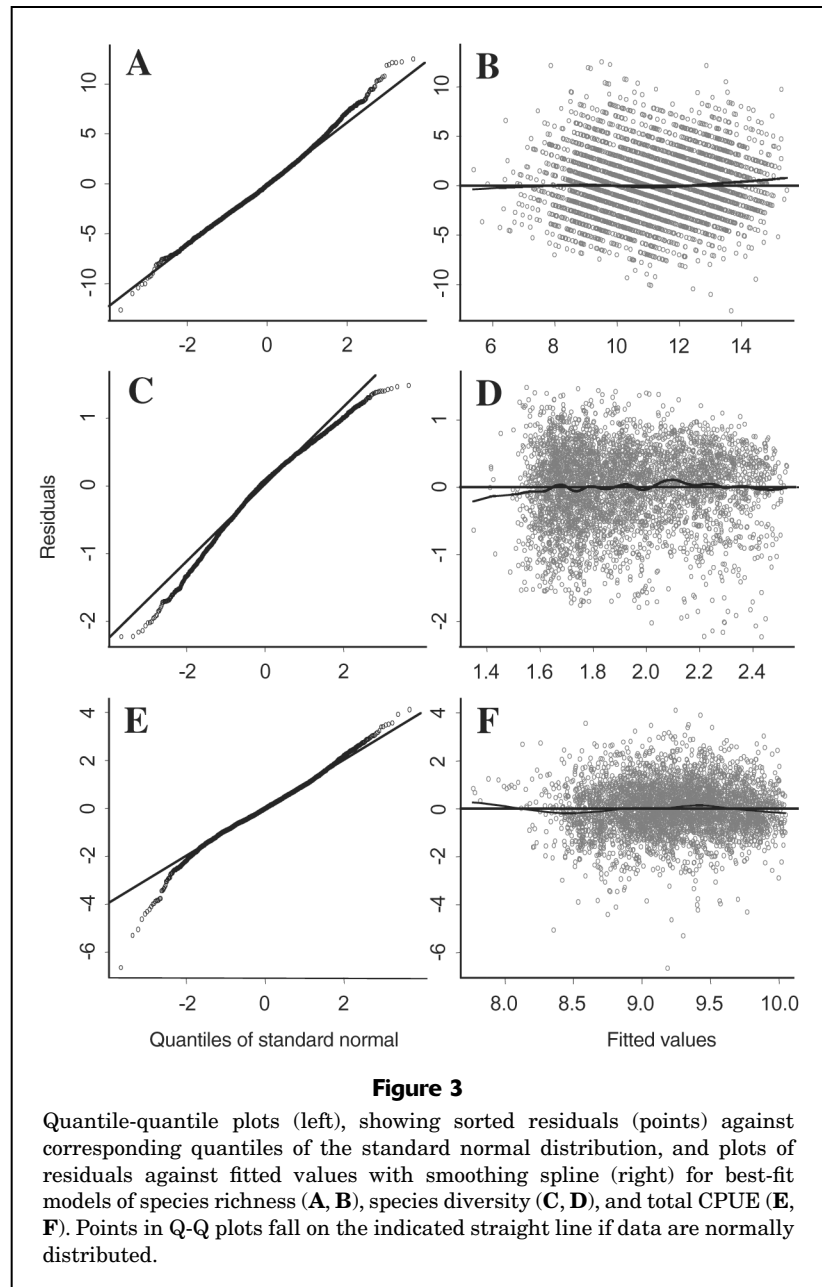
Figure 2

Estimated trends in number of species per haul by depth, alongshore distance, Julian day, year, area swept, and gear type. Alongshore distance was measured along the 200-m depth contour from east to west. Major geographic regions from east to west are Southeast (SE), Yakutat (Yak), Kodiak (Kod), Chirikof (Chi), and Shumagin (Shu). Dashed lines indicate approximate 95% confidence limits of the regression lines. Horizontal lines in lower right plots indicate mean response with 95% pointwise confidence intervals. Width of bars is proportional to number of observations. Fitted lines in each panel are adjusted for the effects of all other variables. Standardized effects in each plot (y-axes, no units) are on the same scale for comparison. Effects are standardized because the estimated CPUE at a given value of a variable is dependent upon the levels of all other variables.

to decrease during the last month of the survey season and showed some variation across years (Fig. 2). There was no consistent trend in species richness with temperature (not shown). One of the Japanese trawls (gear type 717, Fig. 2) tended to have a much smaller number of species per haul on average, suggesting a low catchability for at least some species. Residuals from the best model were close to normally distributed (Fig. 3, A and B) and showed no apparent trends with any of the covariates or over time.

Only a very small portion of the variability in species diversity (Shannon-Wiener index) was accounted for by the best regression (Pseudo-r^2=0.17). Depth had the strongest effect on species diversity with highest diversities observed at intermediate depths (Fig. 4). Diversity generally increased with the number of species, which showed a very similar trend with depth (Fig. 2). Diversity was higher in the eastern Gulf and decreased west of Prince William Sound (Figs. 4 and 5). It showed little variation over time, both within the survey period and across years. However,

Figure 3

Quantile-quantile plots (left), showing sorted residuals (points) against corresponding quantiles of the standard normal distribution, and plots of residuals against fitted values with smoothing spline (right) for best-fit models of species richness (**A**, **B**), species diversity (**C**, **D**), and total CPUE (**E**, **F**). Points in Q-Q plots fall on the indicated straight line if data are normally distributed.

Table 4

Average number of groundfish species caught per haul by depth stratum and geographic area, not adjusted for effects of other variables.

Depth stratum (m)	No. of species/haul (SE)	Area	No. of species /haul (SE)
0–100	9.5 (0.12)	Shumagin	9.7 (0.11)
100–200	11.5 (0.08)	Chirikof	10.5 (0.12)
200–300	13.2 (0.13)	Kodiak	11.6 (0.11)
300–500	10.9 (0.15)	Yakutat	12.5 (0.14)
		Southeast	12.8 (0.20)

Figure 4

Trends in species diversity (Shannon-Wiener index) by depth, alongshore distance, Julian day, and year (area swept and gear type were not significant). For details see Figure 2.
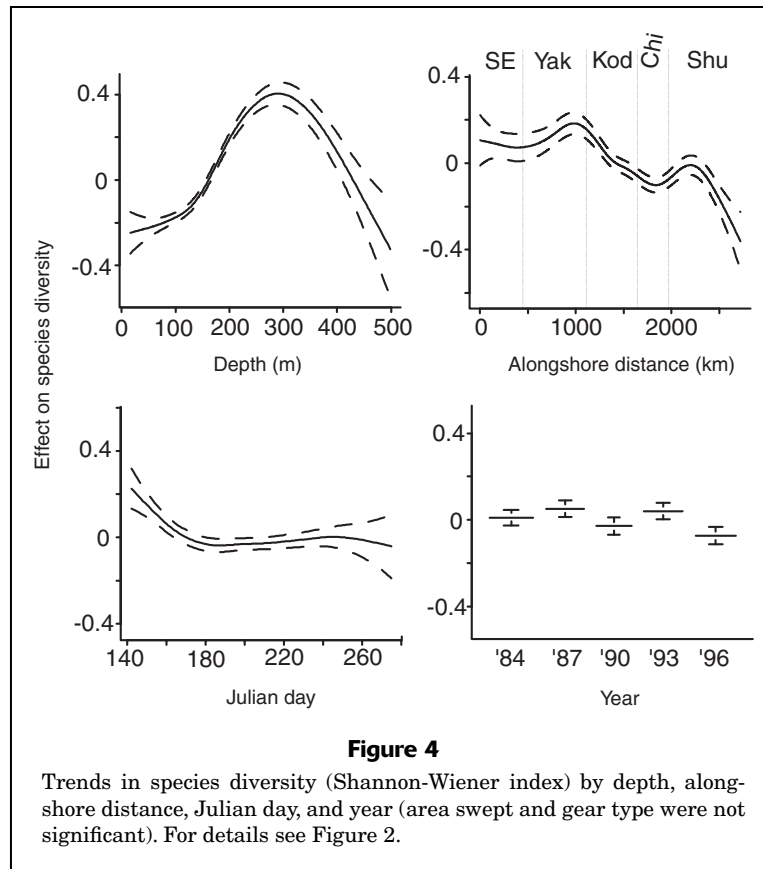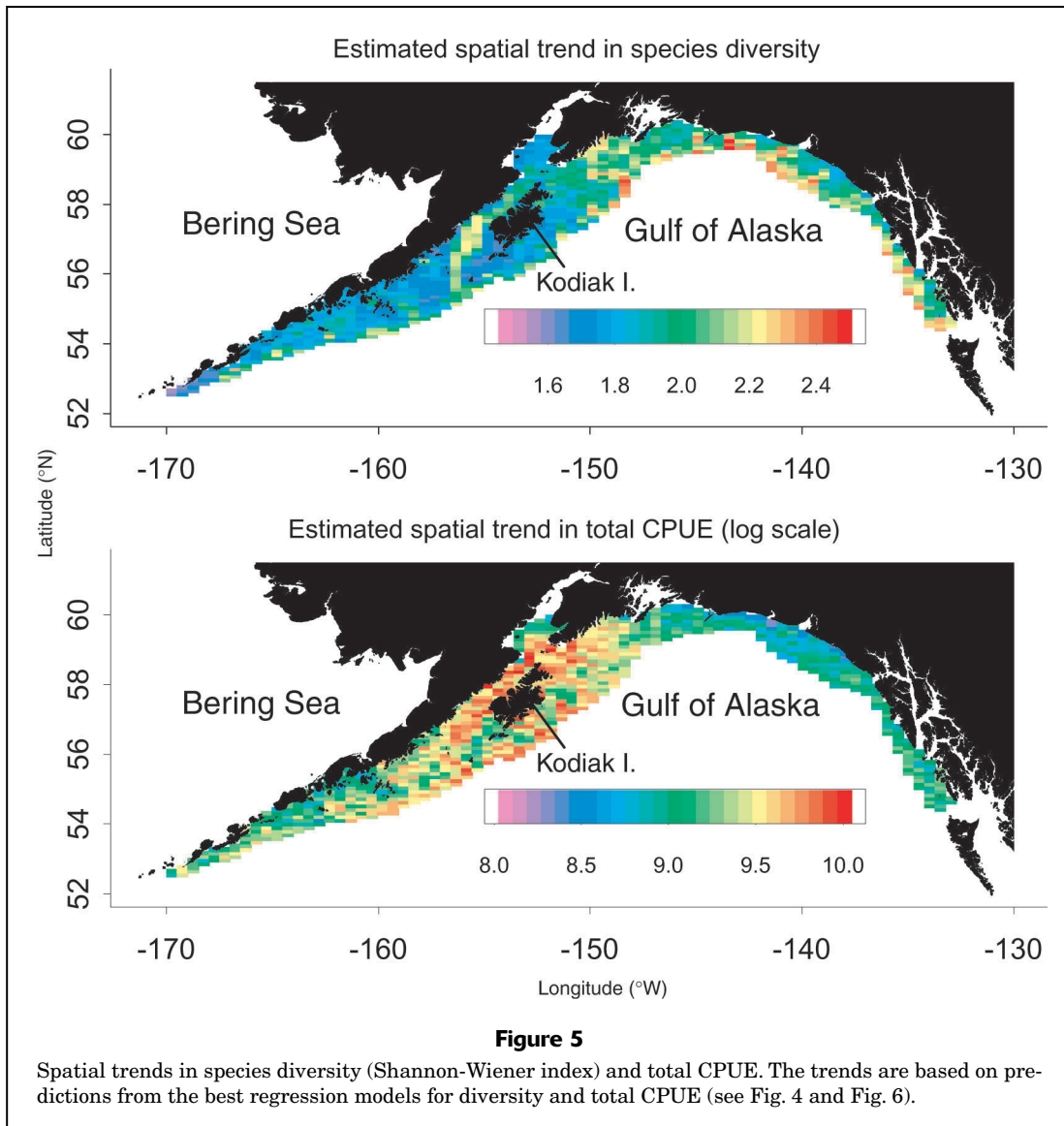
95% confidence intervals suggest a significant drop in species diversity between 1993 and 1996. Area swept and temperature did not enter the best model, suggesting they had no strong effect on species diversity. Diagnostic plots indicated approximate normality and no apparent trends in the residuals (Fig. 3, C and D).

Total biomass (CPUE) showed strong trends with depth and alongshore distance (Fig. 6) but had high variability around these trends (Pseudo-r^2=0.14). Average CPUE increased sharply with depth to about 150 m—a trend that reflected, on average, approximately a doubling of CPUE between the shallowest sampling stations and stations at 150–200 m depth. A similarly strong gradient exists in the alongshore direction between Yakutat (km 700) and the Kodiak Island area (km 1500), where total CPUE has a pronounced maximum. Estimates of the spatial trend suggested that highest CPUEs are found around Kodiak Island, particularly in Shelikof Strait, along the shelf break and upper slope, and on the banks and in the gullies northeast of Kodiak Island (Fig. 5). Total CPUE appeared to decrease significantly after approximately Julian day 240 (Aug. 28); however, Julian day was confounded with alongshore distance (r =–0.38, Table 3) and the effect could in part be due to lower abundance in the eastern GOA, which was often sampled later than other areas. Gear effects were significant and indicated a lower catch rate for one of the Japanese trawls (gear 717, Fig. 6). The estimated time trend (Fig. 6) indicated a significant increase

in total CPUE between 1984 and 1996 (P<0.001), based on a chi-square test of the difference in residual deviances (Hastie and Tibshirani, 1990). We estimated that the combined CPUE of all groundfish species included in the analysis increased from a gulf-wide average of 14,786 kg/km^2 in 1984 to 20,600 kg/km^2 in 1996 (Table 2), representing an increase of 40%. No significant effect of temperature on total CPUE was found. Diagnostic plots indicated approximate normality and no apparent trends in the residuals (Fig. 3, E and F).

The biomass of 72 groundfish species in 240 stratum/year combinations could effectively be summarized by an NMDS ordination in three dimensions (stress=0.085). Our findings suggested that the main gradients along which species composition varied were depth and alongshore distance, whereas temperature and temporal gradients (within and between years) had relatively minor effects on these indices of species composition. The first two dimensions (axes 1 and 2) of the ordination accounted for 67% and 19% of the overall variation respectively. An ordination plot of the first two axes indicated that the sample strata were most clearly separated along the depth gradient (Fig. 7). The alongshore gradient was roughly perpendicular to the depth gradient and clearly distinguished areas Southeast from the other areas (Fig. 7). Yakutat strata occupy an intermediate position between the Southeast strata and strata in other areas. Kodiak, Chiniak, and Shumagin were similar in species composition, as sug-

Figure 5

Spatial trends in species diversity (Shannon-Wiener index) and total CPUE. The trends are based on predictions from the best regression models for diversity and total CPUE (see Fig. 4 and Fig. 6).

gested by a substantial overlap in the location of strata in the ordination diagram. A three-way analysis of variance for each of the three axes by depth stratum, area, and year indicated highly significant differences for all three axes between depth strata and geographic areas, but weak and nonsignificant differences among years (Table 5), suggesting a relatively stable species composition from 1984 to 1996. Residuals from the ANOVA for axis 1 and 3 were approximately normally distributed and showed no apparent violations of the ANOVA assumptions. Residuals for axis 2 had a very long-tailed distribution, but an analysis of variance based on ranks yielded very similar results; therefore the conclusions appear to be robust.

Ordinations of individual hauls within each year confirmed that depth and alongshore distance explained much of the variation in species composition within years. The species composition in each year was effectively sum-

marized by ordinations in five dimensions with Kruskal's stress values that were very close to 0.1 in all years (axes 1–5 in Table 6). The first axis of all five ordinations accounted for 42–47% of the variation in species composition. This axis, as well as most of the other axes, was most strongly related to the depth gradient in all years (Table 6). Alongshore distance appeared to explain a relatively small proportion of the variance in species composition. However the pseudo-coefficients of partial determination for alongshore distance typically increased substantially if Julian day was excluded from the model because of high correlations between Julian day and alongshore distances. Regressions of the axes on depth and alongshore distance alone resulted in pseudo-r^2 values that were very close to those from models that included Julian day. Furthermore, residuals from these models were not significantly related to Julian day for any year ($P>0.5$) based on linear regres-

Figure 6

Trends in total CPUE by depth, alongshore distance, Julian day, year, and gear type. For details see Figure 2

Figure 7

Plots of the first two axes from an NMDS (multidimensional scaling) ordination of 48 strata sampled during each of fivfe years. Distances between two points (strata) in the ordination diagram approximately reflect their dissimilarity in terms of species composition. Symbols indicate depth strata (**A**) and geographic area (**B**).

sions). These findings suggest that species composition within the summer remains relatively stable over the 14–16 week survey period.

To examine effects of temperature on species composition we used only those hauls from the 1993 and 1996 data for which temperature measurements were available (n=726 and n=716 respectively, Table 1). Results for other years are not reported because of the relatively small number of temperature measurements. The available temperature data for earlier years were often localized in certain strata, whereas large areas had few if any measurements. The lack of contrast did not allow definite conclusions with regards to the temperature effect. For 1993 and 1996, we repeated the GAM analysis for the five axes of species composition with temperature included. Temperature effects were apparently large. However, wide confidence intervals and inconsistent patterns between years suggest that the apparent effects were at least in

part due to confounding of temperature with alongshore distance and depth. Therefore we first adjusted for the effects of depth and alongshore distance using the regression models summarized in Table 6. Temperature explained a small but significant portion of the remaining residual variation in three of the ordination axes in both 1993 and 1996 (Pseudo-r^2 values <0.1).

To identify which species were most strongly related to the major gradients we computed rank correlations between each species and the three axes of species composition based on the NMDS ordination of strata averages. We considered all species that had a positive or negative rank correlation of at least 0.4 with one of the axes for further examination, based on a visual inspection of scatterplots. Species associated with the first two axes were clearly separated along gradients of depth and alongshore distance (Figs. 8 and 9). The first axis was positively correlated with a number of deep-water species that were

Table 5
Analysis of variance of three axes of species composition by statistical area, depth stratum, and year.

Effect	df	Sum of squares	Mean squares	F-value	P-value
Axis 1					
Depth stratum	3	129.793	43.264	613.856	0.000
Area	4	10.350	2.588	36.713	0.000
Year	4	0.665	0.166	2.358	0.056
Depth stratum:area	11	1.756	0.160	2.265	0.014
Depth stratum:year	12	0.412	0.034	0.487	0.920
Area:year	16	0.291	0.018	0.258	0.998
Depth stratum:area:year	44	0.839	0.019	0.271	1.000
Residuals	145	10.220	0.070		
Axis 2					
Depth stratum	3	6.601	2.200	37.581	0.000
Area	4	27.771	6.943	118.587	0.000
Year	4	0.346	0.087	1.478	0.212
Depth stratum:area	11	1.091	0.099	1.694	0.080
Depth stratum:year	12	0.366	0.030	0.521	0.899
Area:year	16	1.017	0.064	1.086	0.374
Depth stratum:area:year	44	0.815	0.019	0.317	1.000
Residuals	145	8.489	0.059		
Axis 3					
Depth stratum	3	0.478	0.159	1.231	0.301
Area	4	9.541	2.385	18.423	0.000
Year	4	0.615	0.154	1.188	0.318
Depth stratum:area	11	3.080	0.280	2.163	0.019
Depth stratum:year	12	0.212	0.018	0.137	1.000
Area:year	16	0.698	0.044	0.337	0.992
Depth stratum:area:year	44	1.365	0.031	0.240	1.000
Residuals	145	18.773	0.129		

more abundant in the eastern GOA, but generally had a broad geographic distribution. The deep-water species included several rockfish species, rex sole (*Glyptocephalus zachirus*), Dover sole (*Microstomus pacificus*), sablefish, and myctophids. The alongshore distribution of CPUE suggests that many species displayed local maxima in biomass on the scale of 100–200 km (Fig. 8). The first axis was negatively correlated with a group of shallow-water species that were typically more abundant in the western GOA. The shallow-water group included a number of flatfish species, gadids, and sculpins. Many of the shallow water species had pronounced peaks in biomass at the longitude of Kodiak Island (km 1400–1700) and between the Shumagin Islands and Sanak Island (km 2000–2200).

The second axis was positively correlated with a "shelf break" group. Most of the species in this group had a pronounced peak in biomass near 200 m and were found primarily in the eastern GOA (Fig. 9). The group included a number of rockfish species, as well as lingcod (*Ophiodon elongatus*), petrale sole (*Eopsetta jordani*), and slender sole (*Lyopsetta exilis*). Species that were negatively or positively associated with the third axis (not shown) were not differentiated along gradients of depth and alongshore

distance, suggesting that the third axis, which accounted for 14% of the overall variation, was related to other, unidentified gradients.

Finally, we examined trends in species composition over the 12-year period from the first survey in 1984 to the most recent survey in 1996 in more detail based on the NMDS ordination of species CPUEs averaged by stratum (Fig. 7). Although the individual indices of species composition were not significantly different among years (Table 5), a canonical correlation between the ordination axes and time (survey years) indicated a highly significant trend ($P<0.001$) in species composition. The linear combination of ordination axes that maximized the correlation with survey year was used as an index for the trend in species composition ("time index"). The index increased in most areas and depth strata between 1984 and 1996. Eight species that were positively correlated with the time index showed significant and increasing trends in either CPUE-where-present or frequency of occurrence for at least two area-depth stratum combinations (Fig. 10). Skates were most strongly associated with the index and showed a widespread increase in CPUE-where-present and frequency of occurrence, particularly in the Chirikof,

Table 6

Results from NMDS (multidimensional scaling) ordinations of species CPUEs in five dimensions (axes 1–5) by year, and GAM (generalized additive models) results for regressions of axis scores on depth, alongshore distance, and Julian day. Variance indicates proportion of overall variation accounted for by each axis. Stress indicates Kruskal's stress values for each ordination. Numbers for the full model indicate pseudo-r^2 values for the best model fit (1 – deviance of the best fitting model/deviance of the null model). Numbers following individual variables indicate pseudo-coefficient of partial determination, computed from a reduced model that excluded the variable (= 1 – deviance of best model / deviance of reduced model). Only coefficients of determination exceeding 0.1 are shown. Coefficient of determination for Julian day did not exceed 0.1 in any year or for any axis. AD = alongshore distances.

Year		Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Stress
1984	Variance	44%	19%	14%	12%	11%	0.102
	Full model	0.84	0.28	0.26	0.58	0.13	
	Depth	0.74		0.19	0.42		
	AD	0.12	0.13		0.12		
1987	Variance	42%	22%	14%	12%	10%	0.100
	Full model	0.77	0.22	0.32	0.36	0.21	
	Depth	0.67	0.11	0.28	0.19	0.17	
	AD	0.15			0.24		
1990	Variance	42%	21%	15%	12%	10%	0.096
	Full model	0.83	0.37	0.29	0.34	0.16	
	Depth	0.69	0.23	0.17	0.27	0.10	
	AD	0.11	0.12	0.17			
1993	Variance	47%	18%	13%	11%	11%	0.098
	Full model	0.81	0.24	0.37	0.49	0.31	
	Depth	0.71		0.26	0.42	0.27	
	AD				0.21		
1996	Variance	44%	20%	14%	12%	10%	0.099
	Full model	0.78	0.22	0.31	0.55	0.34	
	Depth	0.71	0.11	0.18	0.40	0.17	

Kodiak, and Yakutat areas (Figs. 10 and 11). Another elasmobranch (Pacific sleeper shark, *Somniosus pacificus*), two osmerids (capelin, *Mallotus villosus*, and eulachon, *Thaleichthys pacificus*), three flatfish species (Dover sole, rex sole, and arrowtooth flounder), and one rockfish species (Pacific Ocean perch, *Sebastes alutus*) increased significantly in one or more areas and depth strata (Fig. 10). The frequency of occurrence of capelin in the trawl survey increased significantly, whereas CPUE-where-present did not change or, in some cases, decreased significantly. Closer examination revealed that the increase in frequency of occurrence occurred primarily between 1993 and 1996 (Fig. 12). Capelin were caught in 14% of all hauls in 1996, compared to only 7% in 1993. Changes in the CPUE-where-present of three flatfish species differed among species. Although Dover sole increased primarily in the eastern GOA (Yakutat and Southeast), rex sole increased most strongly in the Chirikof area (Fig. 10). In contrast, arrowtooth flounder increased in all areas, but only in the 0–100 m depth stratum. Although all three flatfish species increased significantly over time, estimates of their gulf-wide average CPUEs were highest in 1990 and declined from 1990 to 1996 (Table 2). Both the frequency of occurrence and CPUE-where-present of Pacific Ocean perch increased strongly in the Chirikof area, and frequency of occurrence decreased in the Yakutat area.

CPUE-where-present of the four species that were negatively correlated with the time index did not decrease significantly, and, in the case of rock sole (*Lepidopsetta* spp.), even increased in some areas (Fig. 13). However, frequency of occurrence decreased significantly for three of the species, particularly for bigmouth sculpin (*Hemitripterus bolini*, Fig. 13).

Discussion

Research survey data provide standardized indices of relative abundance that often track abundance trends more accurately than methods that use commercial catch data (Pennington and Stromme, 1998). However, results need to be interpreted with caution because the catchability of species may change over time owing to changes in survey gear, vessel type, spatial distribution, or the length composition of a population. In our study we were particularly concerned that differences in gear type (Table 1) might bias our results. We opted to include gear type directly into the analysis as a "nuisance" variable, instead
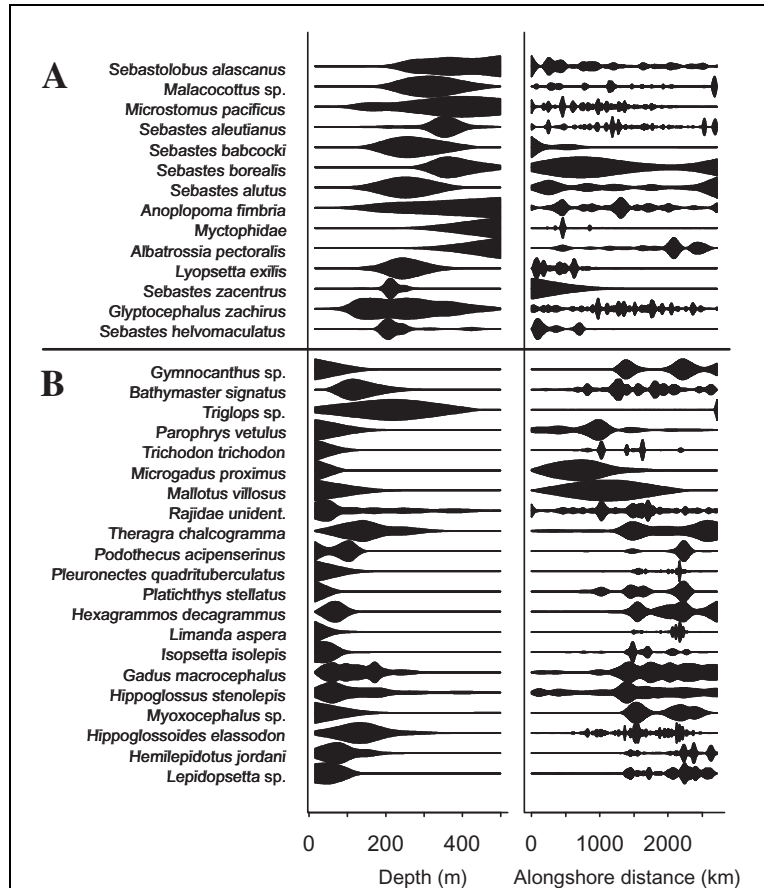
Figure 8

Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (**A**) or negative (**B**) association with the first index of species composition derived from an NMDS ordination of abundances averaged by strata. Widths of dark bands are proportional to average CPUE of a given species. Average CPUE as a function of depth and alongshore distance was estimated by using a scatterplot smoother (cubic smoothing spline). Degree of smoothing was determined by cross-validation for each species separately.

of standardizing the CPUE of each species to a common gear standard prior to analysis because of large uncertainties in the estimation of fishing power coefficients (Munro and Hoff, 1995). The estimated differences among gear types agreed qualitatively with results in Munro and Hoff (1995) for those species for which these authors estimated fishing power. Nevertheless, differences among gear types may have biased some of our results. In spite of these problems, the survey data used in our study provided the best available indicator of relative changes in species composition and distribution for many species of ecological or commercial interest.

The observed trends in species richness, diversity, and biomass, as well as in the CPUE of individual species, showed that depth is an important gradient structuring the groundfish community in the GOA, and that the shelf break and upper slope (at 150–300 m) is a particularly important depth range. Strong depth-dependent gradients are found in many other demersal fish communities inhabiting shelf and upper slope regions (Colvocoresses and Musick, 1984; Gomes et al., 1992; Blaber et al., 1994; Fujita et al., 1995; Jay, 1996; Farina et al., 1997; Mahon et al., 1998). Distinct depth preferences of many individual species (Fig. 8) result in a turnover of species along the depth gradient and lead to the observed patterns in richness, diversity, and biomass. Similar to the altitude gradient in terrestrial environments (Brown and Lomolino, 1998), depth appears to be the major ecological gradient structuring benthic communities in the ocean from shallow, nearshore areas (Mueter and Norcross, 1999) to the abyssal plain (Merrett, 1992).

Our results suggest a pronounced peak in species richness, diversity, and total biomass at intermediate depths. Species richness as well as biomass of demersal fish com-
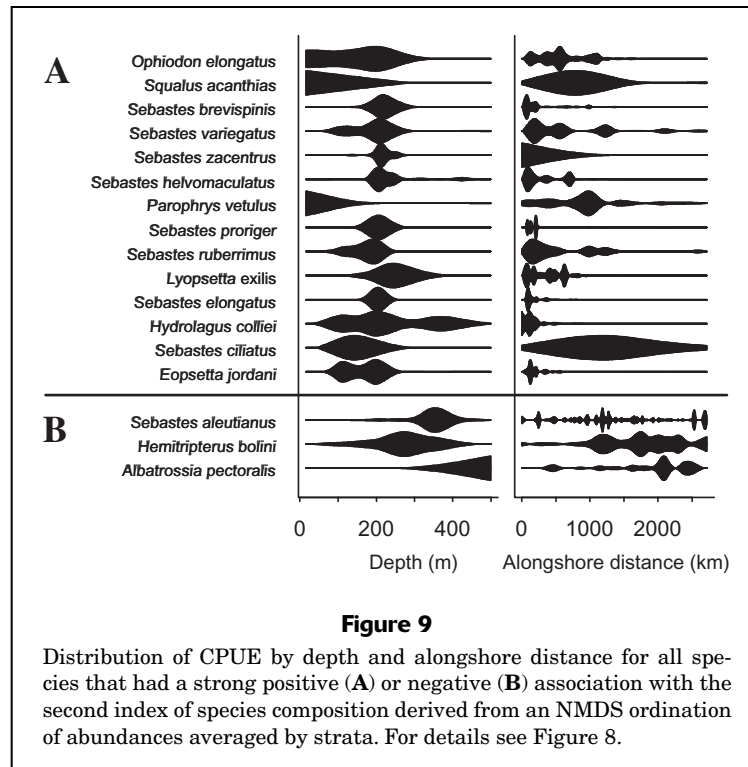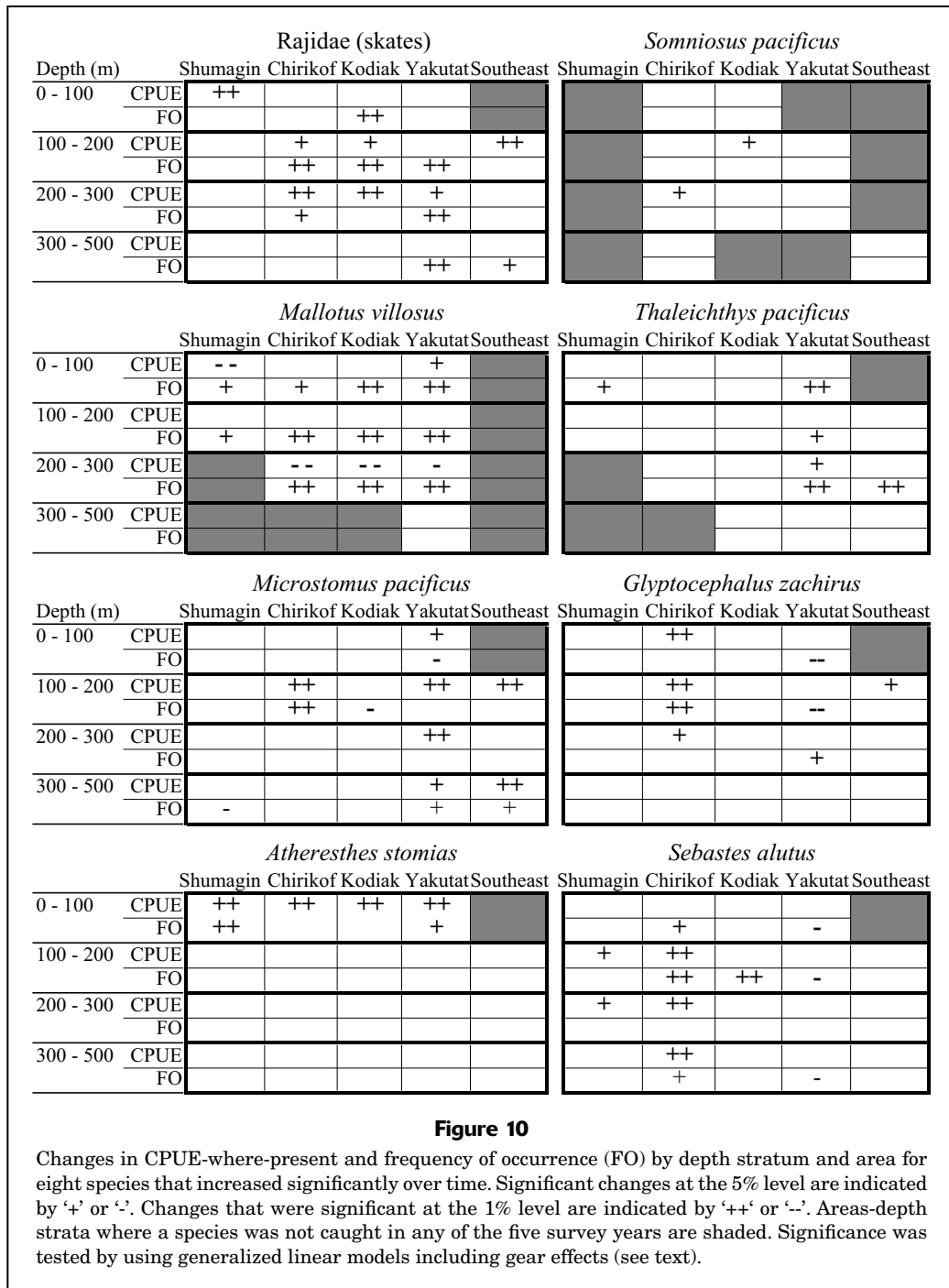
Figure 9

Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (**A**) or negative (**B**) association with the second index of species composition derived from an NMDS ordination of abundances averaged by strata. For details see Figure 8.

munities are generally higher on the continental shelf than on adjacent slope regions, reflecting a strong gradient with depth (Day and Pearcy, 1968; Colvocoresses and Musick, 1984; Farina et al., 1997). In contrast to our results for the GOA, these studies did not find peaks in richness or biomass at intermediate depths. This may have been partly the result of aggregating data into relatively large depth ranges in those studies (and the associated loss in resolution), whereas our study examined patterns in richness and biomass along a continuous depth gradient.

We suggest that the high biomass of demersal fishes near the shelf break (in particular the biomass of flatfishes, rockfishes, and gadids) reflects favorable feeding conditions at this depth range. Favorable feeding conditions may result from enhanced benthic productivity or availability of suitable prey at this depth. The region along the shelf break and over the upper slope has high primary productivity that may be driven by shelf-break fronts, seasonal upwelling, strong alongshore currents, and tidal mixing (Parsons, 1986). Shelf-break fronts have frequently been observed in the GOA (Weingartner[2]) and can enhance phytoplankton and zooplankton biomass, particularly when coupled with upwelling (Mann and Lazier, 1991), which is common during the summer in the western GOA (Reed and Schumacher, 1986). We speculate that increased production in the water column becomes available to the benthos when sinking particles are consumed by larger

organisms such as shrimp or euphausiids, which are often concentrated near the shelf break and are consumed by demersal fish (Mackas et al., 1997; Robinson and Gomez-Gutierrez, 1998). The most abundant demersal fishes in the GOA, arrowtooth flounder and walleye pollock, as well as several rockfish species, have been shown to feed near or off the bottom on euphausiids, mysids, copepods, shrimps, and other fishes (Yang, 1993). Thus, a region of enhanced benthic productivity near the shelf break is consistent with the total biomass of groundfish being highest just inshore of the shelf break between 150 and 200 m (Fig. 6).

In addition to depth (or elevation), latitude is a major ecological gradient in both marine and terrestrial environments. Demersal fishes on the continental shelf off both the east coast of North America (Mahon et al., 1998) and the U.S. west coast (Jay, 1996) form loose assemblages that are clearly separated by latitude. Although the latitudinal extent of our study region is relatively small, we found strong alongshore (roughly corresponding to longitudinal) differences in community structure from the eastern GOA to the Aleutian Islands, with the steepest gradient between the Yakutat and Kodiak areas. This gradient was apparent in species richness and diversity (Figs. 2 and 4), total CPUE (Fig. 6), and indices of species composition (Fig. 7). The alongshore gradient is perpendicular to the depth gradient, with depth generally increasing in the offshore direction. However, these two variables were moderately correlated (–0.32, ranging from –0.20 to –0.44 in individual years), primarily due to the larger number of shallow stations in the western part of the study area and a relative lack of shallow stations in Southeast Alaska.
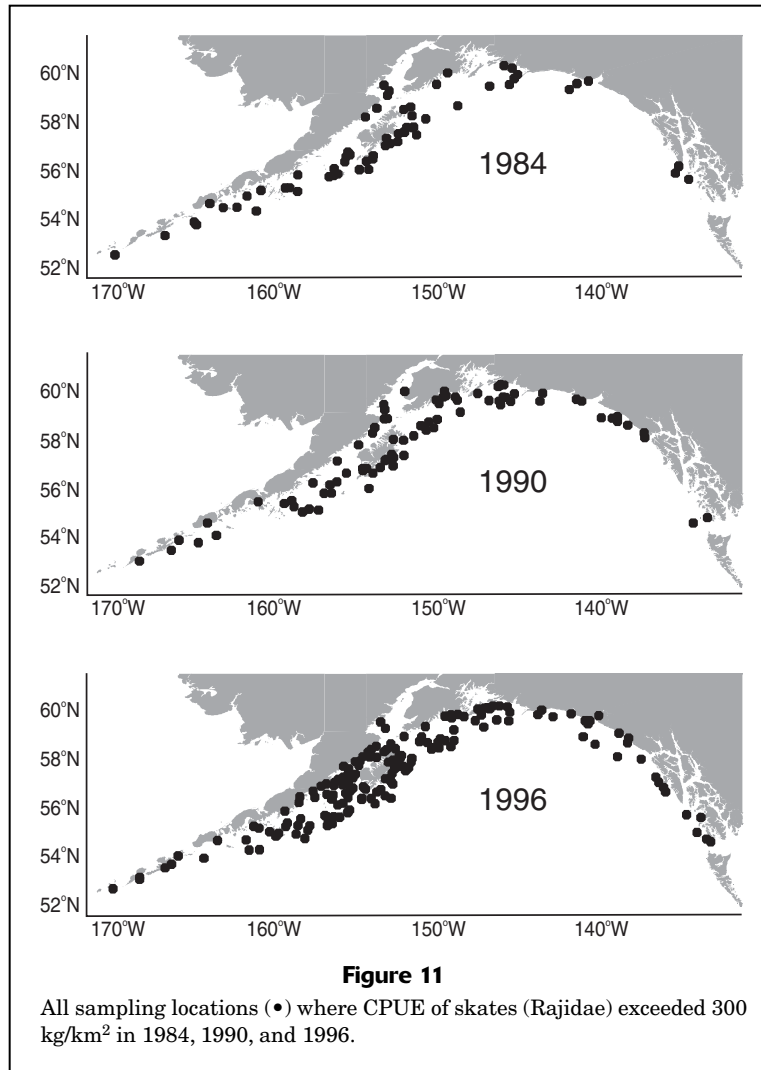
Figure 10

Rajidae (skates)

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE	++				▓
	FO			++		▓
100 - 200	CPUE		+	+		++
	FO		++	++	++	
200 - 300	CPUE		++	++	+	
	FO		+		++	
300 - 500	CPUE					
	FO				++	+

Somniosus pacificus

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE	▓			▓	▓
	FO	▓			▓	▓
100 - 200	CPUE	▓		+		▓
	FO	▓				▓
200 - 300	CPUE	▓	+			▓
	FO	▓				▓
300 - 500	CPUE	▓		▓	▓	
	FO	▓		▓	▓	

Mallotus villosus

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE	- -			+	▓
	FO	+	+	++	++	▓
100 - 200	CPUE					▓
	FO	+	++	++	++	▓
200 - 300	CPUE	▓	- -	- -	-	▓
	FO		++	++	++	▓
300 - 500	CPUE	▓	▓	▓		▓
	FO	▓	▓	▓		▓

Thaleichthys pacificus

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE					▓
	FO	+			++	▓
100 - 200	CPUE					
	FO				+	
200 - 300	CPUE	▓			+	
	FO	▓			++	++
300 - 500	CPUE	▓	▓			
	FO	▓	▓			

Microstomus pacificus

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE				+	▓
	FO				-	▓
100 - 200	CPUE		++		++	++
	FO		++	-		
200 - 300	CPUE				++	
	FO					
300 - 500	CPUE				+	++
	FO	-			+	+

Glyptocephalus zachirus

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE		++			▓
	FO				--	▓
100 - 200	CPUE		++			+
	FO		++		--	
200 - 300	CPUE		+			
	FO				+	
300 - 500	CPUE					
	FO					

Atheresthes stomias

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE	++	++	++	++	▓
	FO	++			+	▓
100 - 200	CPUE					
	FO					
200 - 300	CPUE					
	FO					
300 - 500	CPUE					
	FO					

Sebastes alutus

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0 - 100	CPUE		+			▓
	FO		+		-	▓
100 - 200	CPUE	+	++			
	FO		++	++	-	
200 - 300	CPUE	+	++			
	FO					
300 - 500	CPUE		++			
	FO		+		-	

Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for eight species that increased significantly over time. Significant changes at the 5% level are indicated by '+' or '-'. Changes that were significant at the 1% level are indicated by '++' or '--'. Areas-depth strata where a species was not caught in any of the five survey years are shaded. Significance was tested by using generalized linear models including gear effects (see text).

Therefore, the alongshore trends may be partly due to differences in the distribution of sampling depth between the eastern and western GOA resulting from differences in topography. Nevertheless, we do not believe that the magnitude of correlations (Table 3) presents a serious problem for the general patterns that were observed for CPUE, diversity, and species composition.

Alongshore patterns in CPUE (Figs. 5 and 6) indicate a higher biomass of demersal fishes in the western GOA, particularly in 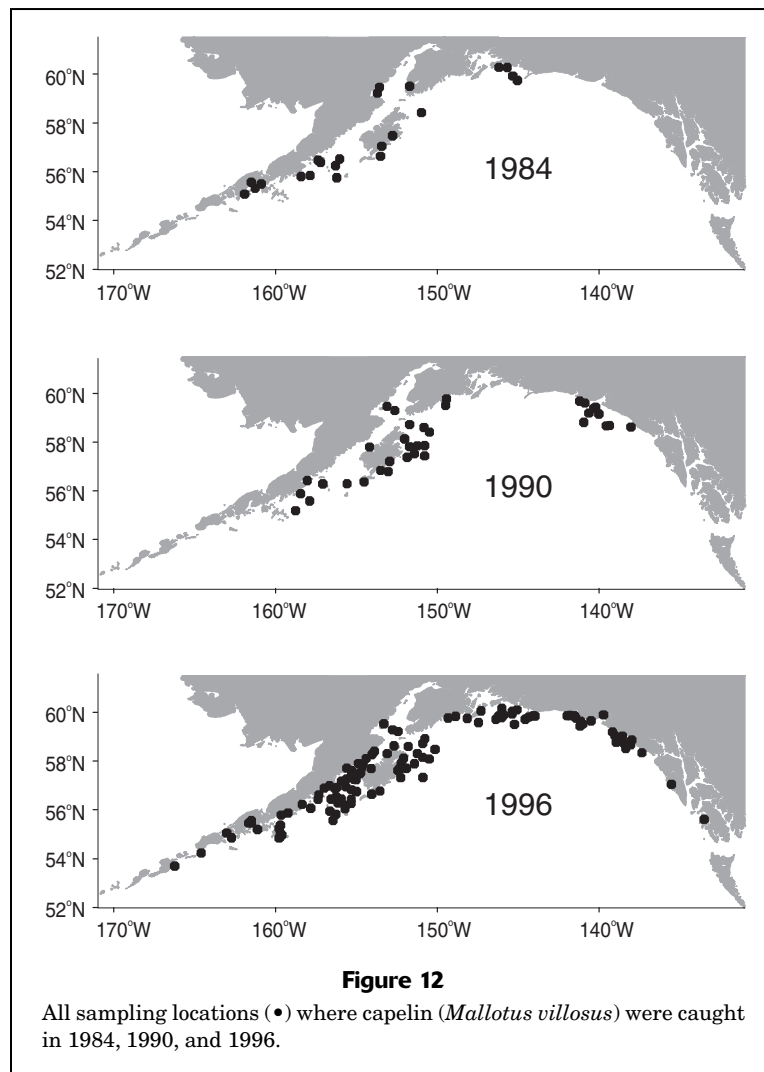the Kodiak Island area. If the higher bio-mass is related to the availability of food, this pattern may reflect higher benthic productivity in the Kodiak Island region. There are several pieces of evidence that suggest a higher productivity in this region. First, there is a higher benthic biomass and productivity of infaunal organisms on the Chirikof and Kodiak shelf, compared with the Yakutat and Southeast areas (Semenov, 1965, as cited in Feder and Jewett, 1986). Second, enhanced primary productivity in the western GOA is evident in estimates from coastsl zone color scanner (CZCS) data and from more

Figure 11

All sampling locations (•) where CPUE of skates (Rajidae) exceeded 300 kg/km^2 in 1984, 1990, and 1996.

recent SeaWifs data (Falkowski et al., 1998, see web site: http://seawifs.gsfc.nasa.gov/SEAWIFS.html). Third, the east–west gradient in productivity and biomass is consistent with differences in upwelling, which is generally more pronounced and more frequent in the western GOA (Reed and Schumacher, 1986). Fourth, the presence of strong tidal currents in the vicinity of Kodiak Island (Kowalik[3]) (see also Isaji and Spaulding, 1987) may further enhance demersal productivity (Mann and Lazier, 1991). Fifth, strong alongshore currents, advection, and nutrient input from major rivers may contribute to a higher productivity in the western GOA and around Kodiak Island. Finally, lower productivity in the eastern GOA may be related to the limited shelf area in this part of the Gulf. Broader shelf areas such as that in the central Gulf of Alaska around Kodiak Island are generally believed to be more productive because of increased nutrient enrichment.

There is evidence from many areas around the world that high productivity is associated with a high biomass of demersal fishes and vice versa. For example, Farina et al. (1997) showed that on the continental shelf and upper slope in the Mediterranean Sea upwelling areas with high primary productivity correlate with a high biomass in the upper trophic levels, including demersal species, and with low species diversity. In contrast, low productivity areas have the greatest species richness and a smaller biomass of demersal fish. Our study suggests that the same general patterns observed by Farina et al. (1997) may hold for the continental shelf and upper slope of the GOA. The productive western GOA is characterized by a high demersal biomass and relatively low species diversity, which is attributable to the presence of a few highly abundant species of flatfish and gadids (including arrowtooth flounder, Pacific cod, walleye pollock). In contrast, the eastern GOA appears to be less productive and is characterized by a low biomass of demersal fishes and high species diversity, due to the presence of a large number of rockfish species with relatively low abundances.

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[3] Kowalik, Z. 2000. Personal commun. Institute of Marine Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775.

Figure 12

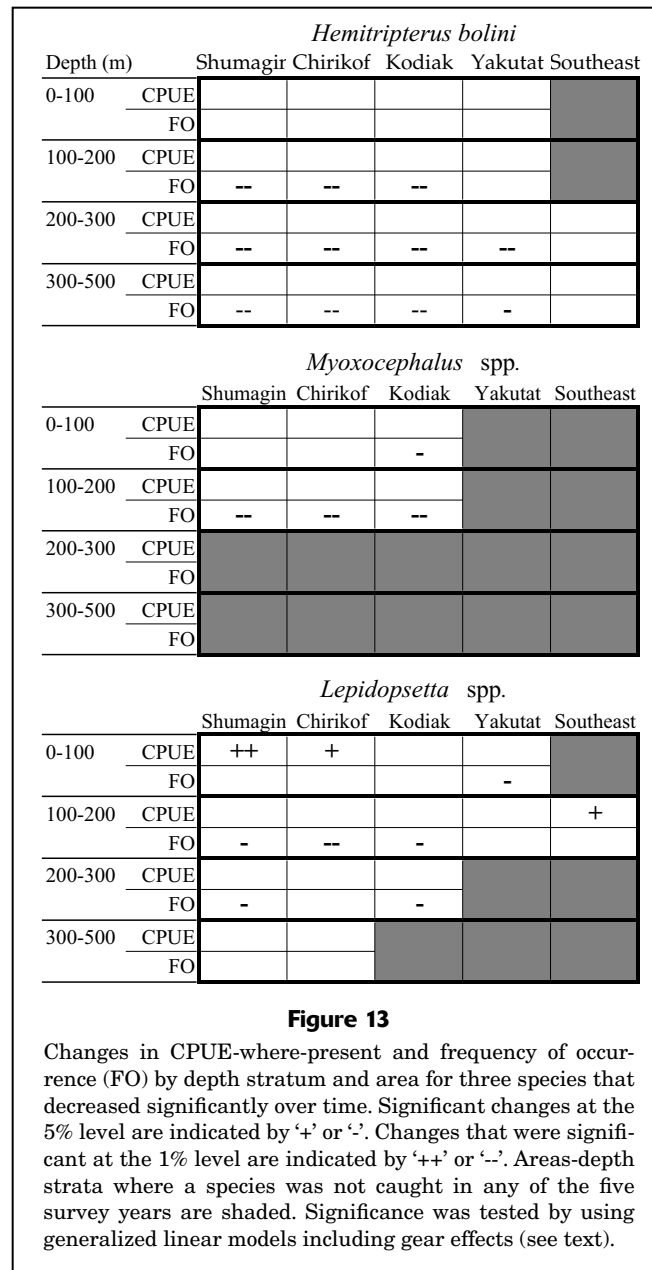All sampling locations (•) where capelin (*Mallotus villosus*) were caught in 1984, 1990, and 1996.

In contrast to strong spatial and depth gradients, there was little evidence for strong temporal gradients in the GOA groundfish community between 1984 and 1996, except for the pronounced increase in total CPUE and a potential decrease in species diversity after 1993. The species composition of the groundfish community in the GOA, as reflected in our indices, has remained relatively stable from 1984 through 1996. Furthermore, a visual comparison of the indices mapped by year (not shown) suggests that relative species composition is characterized by spatial patterns that were stable from 1984 to 1996. Similarly, no apparent shifts in individual species distributions were found. The apparent stability of spatial patterns in the GOA may simply reflect stability in species composition over the time period of the study, as well as a period of relatively moderate variations in the physical environment. It also suggests that recent levels of fishing may not have had a strong impact on the relative species composition, or possibly had a stabilizing effect. The observed composition of the groundfish community, which is

currently dominated by relatively long-lived species, may also contribute to its own stability.

Some of the most pronounced changes over time occurred in noncommercial species such as skates and capelin (Fig. 10). Whether these changes are directly or indirectly linked to fishing or are the result of environmental changes is currently unknown. Interestingly, capelin decreased in abundance in some areas and depth ranges but have been caught at an increasing proportion of the sampling stations in more recent surveys. These changes appear to reflect a "spreading out" of the population at relatively fixed numbers, possibly in response to the increasing abundance of large predatory fishes.

Other studies of groundfish communities have documented relatively stable spatial patterns in species composition over time periods of 10–20 years (Colvocoresses and Musick, 1984; Gabriel, 1992; Gomes et al., 1992; Jay, 1996). In contrast, Gomes et al. (1995) observed a sharp decline in the biomass and abundance of a number of commercial groundfish species on the Newfoundland-Labra-

Hemitripterus bolini

Depth (m)		Shumagir	Chirikof	Kodiak	Yakutat	Southeast
0-100	CPUE					(shaded)
	FO					(shaded)
100-200	CPUE					(shaded)
	FO	--	--	--		(shaded)
200-300	CPUE					
	FO	--	--	--	--	
300-500	CPUE					
	FO	--	--	--	-	

Myoxocephalus spp.

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0-100	CPUE				(shaded)	(shaded)
	FO			-	(shaded)	(shaded)
100-200	CPUE				(shaded)	(shaded)
	FO	--	--	--	(shaded)	(shaded)
200-300	CPUE	(shaded)	(shaded)	(shaded)	(shaded)	(shaded)
	FO	(shaded)	(shaded)	(shaded)	(shaded)	(shaded)
300-500	CPUE	(shaded)	(shaded)	(shaded)	(shaded)	(shaded)
	FO	(shaded)	(shaded)	(shaded)	(shaded)	(shaded)

Lepidopsetta spp.

Depth (m)		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0-100	CPUE	++	+			(shaded)
	FO				-	(shaded)
100-200	CPUE					+
	FO	-	--	-		
200-300	CPUE				(shaded)	(shaded)
	FO	-		-	(shaded)	(shaded)
300-500	CPUE			(shaded)	(shaded)	(shaded)
	FO			(shaded)	(shaded)	(shaded)

Figure 13

Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for three species that decreased significantly over time. Significant changes at the 5% level are indicated by '+' or '-'. Changes that were significant at the 1% level are indicated by '++' or '--'. Areas-depth strata where a species was not caught in any of the five survey years are shaded. Significance was tested by using generalized linear models including gear effects (see text).
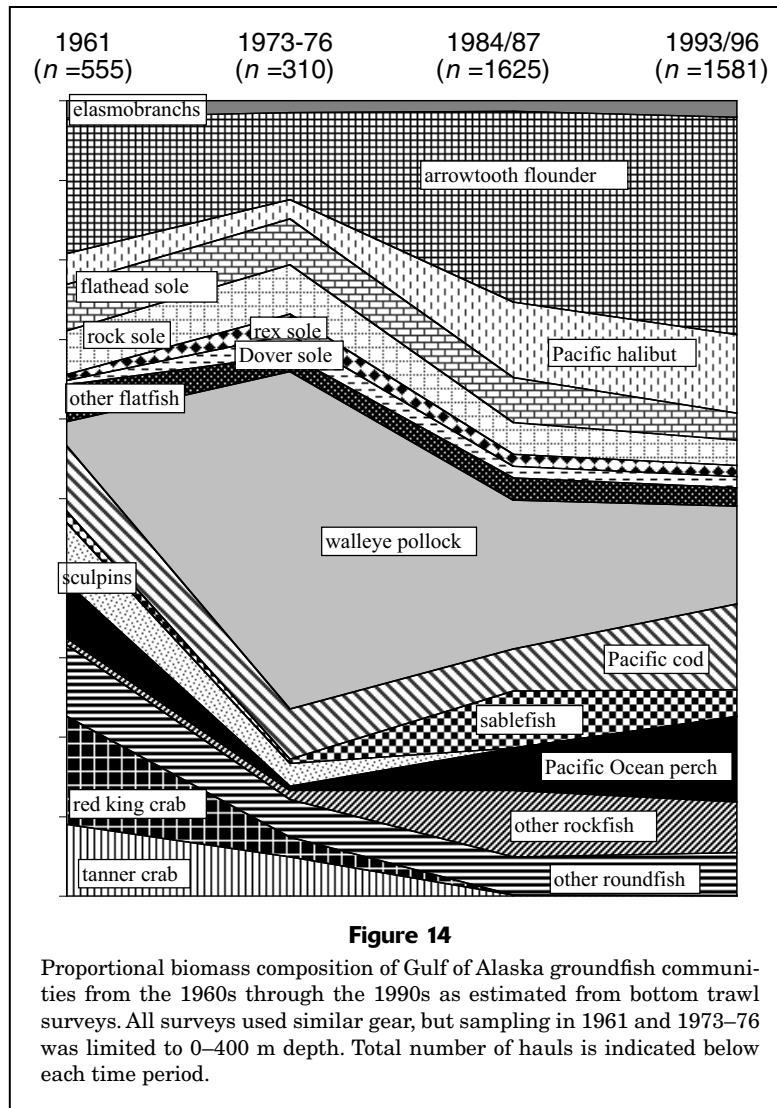
dor shelf from 1978 to 1991 and dramatic changes in the spatial distribution of groundfish assemblages after 1987. They attributed the changes primarily to intense exploitation, although environmental effects were likely at work as well. Similarly, on the continental shelf off Northwest Spain, significant decreases in commercial groundfish species, and a concurrent increase of several noncommercial species, can be attributed to a combination of fishing and environmental changes (Farina et al., 1997).

The recent period of stability in the GOA can be contrasted with a period of dramatic changes in the late 1970s and early 1980s that affected many parts of the North Pacific ecosystem including groundfish communities (e.g. Beamish, 1995). There is strong evidence of a shift in species composition of at least the nearshore demersal communities during this time period (Piatt and Anderson, 1996; Anderson and Piatt, 1999; Mueter and Norcross, 2000). Whether similarly dramatic changes occurred in offshore demersal communities is not known due to the lack of long time series for most species.

Estimated biomass trends for important commercial species based on recent stock assessment data (NPFMC[1]) and historical surveys (Ronholt et al.[4]) suggest that the

[4] Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948–1976: a historical review. Proc. rep., vols. 1–3, 872 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA.

Figure 14

Proportional biomass composition of Gulf of Alaska groundfish communities from the 1960s through the 1990s as estimated from bottom trawl surveys. All surveys used similar gear, but sampling in 1961 and 1973–76 was limited to 0–400 m depth. Total number of hauls is indicated below each time period.

composition of the groundfish community on the shelf and upper slope has changed substantially since the early 1960s. Resource assessment surveys were conducted in 1961 and 1973–76 with similar gear and covering much of the same area that was sampled during the later surveys. Survey data from the 1960s and 1970s have to be interpreted carefully because the sampling design, gear, and the spatial coverage of these surveys differ from the surveys done in the 1980s and 1990s.[4] In particular, no stations below 400 m or east of 136°W were sampled in the early surveys. In spite of these caveats, changes in species composition among surveys are likely to reflect actual changes, at least for taxa that occur primarily above 400 m and west of 136°W. The data suggest a dramatic decrease in the relative abundance of red king crab (*Paralithodes camtschaticus*) and Tanner crab (*Chionoecetes* spp.), which together accounted for 22% of total CPUE in 1961, and for less than 1% after the 1970s (Fig. 14). The data indicated that walleye pollock became the dominant species in the mid-1970s, peaked in the early 1980s, and

has declined in relative abundance since then. Arrowtooth flounder replaced walleye pollock as the dominant groundfish species in the 1980s and 1990s. Pacific Ocean perch and other rockfishes have increased substantially in biomass since the 1970s. Sablefish and Pacific halibut, two of the commercially most valuable species, made up a substantially larger proportion of the total CPUE in the 1980s and 90s compared to earlier decades (Fig. 14). The relative abundance of sculpins declined from about 8% in the early 1960s to less than 0.1% in the 1980s and 1990s. The observed difference is likely to reflect a real decline in sculpin abundance of several orders of magnitude between the 1960s and 1980s. The decline appears to continue into the 1990s, as suggested by a decrease in the frequency of occurrence and biomass of two of the most abundant sculpin taxa (bigmouth sculpin and *Myoxocephalus* spp., see Fig. 13, Table 2).

The observed increase in overall groundfish biomass in the GOA from the 1980s to the 1990s (Fig. 6) is consistent with increases in the productivity of the northeast Pacific

Ocean between the period of the 1960s and 70s and the 1980s and 90s. Polovina et al. (1995) suggested that the increase in primary and secondary productivity in the NE Pacific Ocean resulted from a shoaling of the mixed layer in the GOA by 20–30% associated with variations in the strength and position of the Aleutian low pressure system from the late 1970s to the late 1980s. Over the same time period large increases occurred in chlorophyll a levels (Venrick, 1995), zooplankton stocks (Brodeur and Pearcy, 1992; Brodeur et al., 1996), and upper trophic level species (Brodeur and Ware, 1995; Francis et al., 1998). Our study suggests that there has been a parallel increase in the biomass of demersal fish communities on the GOA shelf and upper slope since 1984, in response to the overall increase in productivity in the NE Pacific Ocean.

Given the increasing emphasis on ecosystem-based management, managers will have to rely on a variety of indicators in addition to traditional single-species biomass estimates to assess the status and health of an ecosystem (Yaffee et al., 1996). Indices of species composition like those used in this study, as well as survey-based assessments of noncommercial species, provide indicators that can help researchers in assessing changes in the community and can help managers in responding to such changes in a timely fashion.

Species richness and diversity are particularly simple, yet potentially very useful indices. The concept of marine biodiversity has received considerable attention in recent years (NRC, 1995) and should be included in planning and policy-making (Bengtsson et al., 1997). There is some evidence that bottom fishing can reduce the diversity of benthic communities (Collie et al., 1997) and, in turn, that changes in diversity can impact ecosystem function and productivity (Naeem et al., 1994). There was some indication in our study that the number of species and the diversity of the groundfish community in the GOA as measured by the Shannon-Wiener index decreased between 1993 and 1996 (Fig. 4). Although gear effects may have confounded differences among earlier surveys, the same gear and identical survey designs were used in both 1993 and 1996; thus the differences in species richness and diversity cannot be attributed to sampling effects and merit further study. The simple diversity indices used in our study were primarily chosen for practical considerations. Other indices, e.g. indices of beta-diversity, may be more appropriate for describing diversity of marine ecosystems and should be explored.

Multivariate techniques that summarize the major variation in species composition with a small number of indices (dimensions) provide another useful tool for monitoring changes in groundfish communities. Such indices provide sensitive indicators of change in community structure and can identify general trends that may not be apparent when using univariate measures (Austen and Warwick, 1989). The indices reduce the noise from random fluctuations of many individual stocks and the resulting "signal" may be used to test statistically for differences in species composition among areas or time periods, as well as helping to identify those species that show significant trends.

Another important part of an ecosystem approach to management is the monitoring of the abundance of non-commercial species, in addition to commercial species. Changes in the abundance of skates, sculpins, and other noncommercial species are examples of potentially important trends that may go undetected if management agencies focus on the assessment of commercial species only. Although these species comprise a small proportion of total biomass, such trends may be an early indication of changes in the groundfish community due to changes in the environment or fishing. Such monitoring, along with the monitoring of environmental variables, will further help to understand how and why groundfish communities change in response to environmental variation.

Current fisheries management often fails to account for the ecological complexities inherent in fish communities (Roberts, 1997). This is hardly surprising because of the focus of most stock assessment on individual stocks and on stock-recruitment relationships. Prediction becomes increasingly difficult as other species and environmental relationships are added to models. Nevertheless, the complexities should not discourage researchers from trying to understand species relationships and the response of species and communities to environmental variation and harvesting.

Knowledge of such relationships can improve management in several ways. First, it can help to explain why stocks are fluctuating in particular ways and help managers devise management strategies that take into account such fluctuations. Second, it can improve our understanding of multispecies or community-level relationships and can lead to better assessment methods that take such relationships into account. Third, it can lead to predictive hypotheses that can be explored and tested through rigorous research programs and adaptive management procedures. Ultimately, improved understanding of ecosystem processes will improve fisheries management only if it can reduce uncertainties in prediction. Thus the challenge remains to develop improved models that account for species relationships and environmental influences.

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