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SPATIAL AND TEMPORAL PATTERNS IN THE GULF OF ALASKA GROUNDFISH COMMUNITY IN RELATION TO THE ENVIRONMENT

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

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DOCTOR OF PHILOSOPHY

By

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Abstract

The GoA supports a rich demersal fish community dominated by gadids, pleuronectids, sablefish (*Anoplopoma fimbria*) and rockfishes (*Sebastes* spp.). This study describes the structure of the juvenile and adult groundfish communities of the Gulf of Alaska (GoA) in relation to their environment and along spatial and temporal gradients. Abundance data were obtained from trawl surveys of juvenile groundfishes in the nearshore areas of Kodiak Island (1991-1996), shrimp-trawl surveys in the same areas (1976-1995), and triennial bottom trawl surveys of adult groundfishes on the GoA shelf and upper slope (1984-1996). Species richness, species diversity, total abundance, and multivariate indices of species composition for each station sampled were statistically related to depth, temperature, salinity, sediment composition, geographic location, and time of sampling to identify spatial and temporal patterns in community structure. The observed patterns were then related to local and large-scale atmospheric and oceanographic trends. Both juvenile and adult groundfish communities were primarily structured along the depth gradient. The abundance of juvenile groundfishes decreased with depth from 0 to 100m, whereas the abundance of adults increased with depth to a peak at 150-200m. Species richness and diversity of the adult community had a significant peak at 200-300m. Spatial patterns suggested higher abundances, lower species richness and diversity, and a different species composition of demersal fishes in the western GoA compared to the eastern GoA. These large-scale spatial patterns appear to be related to differences in upwelling between the eastern and western GoA. A 40% increase in total groundfish biomass on the GoA shelf and upper slope was estimated between 1984 and 1996. Significant changes in species composition occurred in the nearshore areas of Kodiak Island in the early 1980s, from a community dominated by shrimp and small forage fishes to one dominated by large piscivorous gadids and flatfishes. The change in species composition in the nearshore community appeared to be linked to an increase in advection in the Alaska Current. Increased flow around the GoA may enhance the supply of

nutrients and plankton on the shelf and upper slope, resulting in an increase in overall productivity of the pelagic and demersal biota.

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Chapter 1: Introduction

Fisheries scientists and managers have an increasing interest in ecosystem approaches to research and management (Samson and Knopf 1996; Yaffee et al. 1996; Boreman et al. 1997; Langton and Haedrich 1997). Although considerations of the ecosystem consequences of fishing are not a new development (Rice 1999), policy makers have only recently begun to apply ecosystem principles to fishery conservation and management activities (Anonymous 1996). Although the objectives vary (Larkin 1996), ecosystem management is now a commonly stated goal of fisheries management throughout the world. The North Pacific Fisheries Management Council (NPFMC) is currently in the process of developing goals and policies to formally implement an ecosystem approach in the management of Bering Sea and Gulf of Alaska (GoA) groundfish fisheries (Witherell 1998). Ecosystem considerations that are already incorporated in North Pacific groundfish management include conservative harvest limits, spatial and temporal allocation of harvest, bycatch limits, and a limit on total harvest.

Sound ecosystem management must be based on multispecies relationships and overcome the current focus on individual species (Langton and Haedrich 1997; National Research Council 1999). Current fisheries management is dominated by single-species approaches and single-species models are the primary tools for stock assessment. Multispecies approaches to management have so far met with limited success in providing reliable estimates of stock abundance (Daan and Sissenwine 1991; Magnusson 1995). However, they have yielded valuable insights into the dynamics of multispecies assemblages (Daan and Sissenwine 1991). Fishing not only affects the target species, but also has significant effects on other components of the ecosystem. As the goals of fisheries management shift towards considering the ecosystem consequences of fishing, fishery scientists will have to look beyond the single-species level at multispecies assemblages and ecological communities.

In order to incorporate relationships among different species into research and management, multispecies approaches are clearly required. Existing multispecies approaches include multispecies virtual population analysis and other multispecies stock dynamics models (Hilborn and Walters 1992; Magnusson 1995), ecosystem models that include a limited number of species or species groups (Laevastu et al. 1982; Bryant et al. 1995), trophic mass-balance models (Christensen and Pauly 1996), and multivariate statistical techniques. Multivariate methods have been used in fisheries applications to examine the biogeography of fishes (Colvocoresses and Musick 1984; Gomes et al. 1992; Mahon et al. 1998), to relate community structure to oceanographic features (Morin et al. 1992; Pearcy et al. 1996), and to examine changes in species composition over time (Gabriel 1992; Saila 1993; Farina et al. 1997).

In the ecosystem context, one of the goals of studying multispecies relationships is to understand, and eventually to predict the effects of environmental variation and fishing on fish communities. Numerous studies have examined how individual species respond to environmental changes and fishing (Beamish and McFarlane 1989; Beamish 1995), but few studies to date have considered effects on whole fish communities (Gomes et al. 1995; Farina et al. 1997; Hansson 1998). The relative effects of fishing and environmental fluctuations on fish stocks are often difficult to separate (National Research Council 1999). For example, environmental conditions at least contributed to the major changes observed in Newfoundland groundfish stocks over the period from 1985 to 1991 (Hutchings and Myers 1994; Gomes et al. 1995), although these changes are generally attributed to overexploitation (Hutchings and Myers 1994).

To analyze multispecies assemblages and their response to environmental changes and fishing, estimates of the abundance or recruitment of multiple species are required. In the case of groundfish species, trawl surveys routinely gather information on the relative abundances of commercial and non-commercial species. Information from these surveys is often analyzed on a species-by-species basis only, thus ignoring much of the information inherent in multispecies surveys. A more 'holistic' approach is usually the domain of community ecology, a field that has spawned the development of numerous multivariate statistical techniques for the analysis of patterns in community composition over space and time (Gauch 1982; Jongman et al. 1995).

Multivariate analyses of trawl survey data have been used to examine the composition of demersal fish assemblages in many parts of the world, including the North Pacific (Gabriel and Tyler 1980; Rogers and Pikitch 1992; Jay 1996). To date, there have not been similar studies examining demersal fish assemblages on the GoA shelf and slope. Understanding patterns in the structure of groundfish communities and understanding the effects of environmental changes and fishing on species composition are important prerequisites for successful multispecies management. To improve our understanding of these relationships, this study examines spatial and temporal patterns in the structure of the GoA groundfish communities.

The main goals of the study are to describe the community structure of juvenile and adult groundfishes in relation to their environment and to identify long-term changes in relative species composition. In Chapter 2, I provide a brief description of the study area including the major geomorphologic and hydrographic features, a brief history of the groundfish fishery, and a summary of our current understanding of large-scale environmental variability in the Northeast Pacific and its impacts on the oceans and their biota. Chapter 3 gives an overview of the methods I used to analyze compositional data from multispecies surveys. I examined community structure separately for three components of the groundfish community. Juvenile and small adult demersal fishes in nearshore areas of Kodiak Island were examined to characterize community structure in relation to depth, temperature, and sediment composition based on collections done in 1991 and 1992 (Chapter 4). Long-term changes in the species composition of the groundfish community around Kodiak Island between 1976 and 1995 were examined in seven nearshore areas (Chapter 5). Spatial and temporal patterns in the composition of the adult demersal fish community on the GoA shelf and upper slope (0-500 m) were examined between 1984 and 1996, based on triennial resource assessment surveys (Chapter 6). Chapter 7 examines some possible causes for the observed patterns in the groundfish community. Patterns in community structure are compared between the juvenile and adult groundfish community in Chapter 8. Chapter 9 concludes with a brief summary of the major findings and discusses some implications for management.

Chapter 2: The Gulf of Alaska

Geology

The Gulf of Alaska (GoA) is bounded by mountains that were primarily formed by the collision of the Pacific and North American lithospheric plates. Strong seismic activity and extremely steep topography characterizes this boundary region. The coastal mountain range, with elevations in excess of 4000 m, is separated by the continental shelf from abyssal depths in excess of 3000 m in the eastern GoA and 5000 m in the Aleutian Trench. The continental shelf, shaped by the forces of plate tectonics, ice and ocean currents, ranges from 5 to 200 km in width (Royer 1998) and is characterized by an extremely irregular topography. Islands, banks, ridges, and numerous troughs or gullies cutting across the shelf (Fig. 2.1) were carved by glaciers, which extended to the shelf break during the Pleistocene period (Hampton et al. 1986). Today the remaining glacial fields, some of the largest in the world, are an important source of fine-grained sediments and freshwater.

The major input of sediment occurs in the northeastern GoA (Alsek River, Copper River, Bering Glacier, and Malaspina Glacier, Fig. 2.1) and at the head of Cook Inlet. Sediments are transported to the west with the prevailing currents and are deposited on the shelf along the coast. Because of the large supply of fine glacial sediments, the troughs and banks between Cross Sound and the Kenai Peninsula are characterized by gray and clayey mud and by the absence of coarse material (Hampton et al. 1986). Sediments in Cook Inlet are much sandier due to strong tidal currents. Finer sediments are transported out of Cook Inlet and are deposited in Shelikof Strait as fine sand, silt, and clay.

The shelf around Kodiak and west of Kodiak Island to Unimak Pass receive little modern sediment. Relict glacial debris is prevalent, with coarse-grained deposits (pebbly, gravelly sand) on the banks and finer sediment in the gullies. Coarse sediment on the banks includes shell fragments and volcanic material from nearby islands. Volcanic ash is also common in the silt

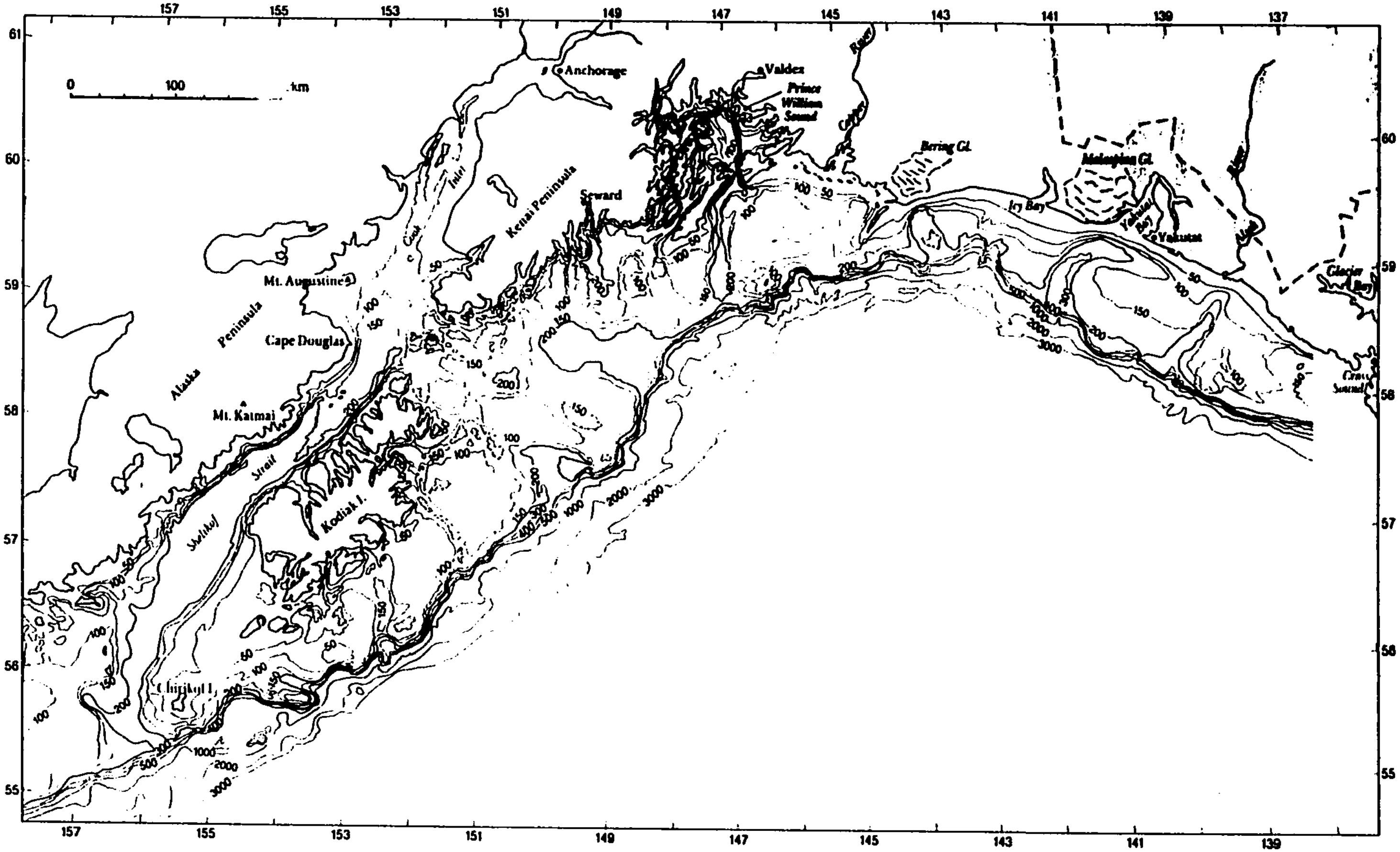

Figure 2.1: Bathymetric and geographic features of the central part of the study area.

fraction. Near the shelf edge, intermittent concentrations of calcareous foraminifera are found (Hampton et al. 1986).

The eastern GoA, from Cross Sound to Vancouver Island, is characterized by a narrow shelf with coarse, clastic sediments. Volcanic sediments are not present and fine sediments are rare, except for mud in deep narrow channels between islands (Hampton et al. 1986).

Hydrography

The cyclonic subarctic gyre of the Northeast Pacific dominates water circulation in the GoA. The southern limb of the gyre is the North Pacific Current flowing east between about 30 and 45°N. When the North Pacific Current reaches the west coast of North America it bifurcates into a southward flowing branch, the California Current, and a northern branch, the Alaska Current (Reed and Schumacher 1986). The Alaska Current follows the coast of British Columbia and Southeast Alaska, then turns westward along the continental slope off the coast of Alaska. It continues as the Alaskan Stream along the south side of the Alaska Peninsula and the Aleutian Arc with speeds ranging from 30 to 100 cm s^{-1}. A variable portion of the Alaskan Stream turns south near the tip of the Alaska Peninsula and recirculates as part of the subarctic current (the northern part of the North Pacific Current) to form the Alaskan Gyre (Reed and Schumacher 1986).

The primary driving forces for the circulation in the GoA are winds and freshwater input from adjacent landmasses. Winds over the GoA are strongly related to the strength and position of the Aleutian Low, a low-pressure area resulting from the passage of storms along the Aleutian storm track (Wilson and Overland 1986). The center of the Aleutian Low is typically over the eastern Bering Sea in the summer, over the GoA in early winter, and over the western Aleutians throughout the winter months. These patterns reflect strong seasonality in storm intensity and frequency, which in turn causes strong seasonality in coastal forcing. During the winter intense alongshore winds cause downwelling and increased water transport around the Alaskan Gyre. In the summer the Eastern Pacific High Pressure system expands into the GoA and the associated weak and variable winds cause a relaxation in downwelling, and possibly slight divergences and upwelling along the coast, particularly in the western GoA.

Climatic variability in the Northeast Pacific and its impact on the marine environment of the Gulf of Alaska

Variability in the Northeast Pacific climate occurs at interannual, interdecadal, and longer time scales (Ware 1995) with major impacts on regional marine fish stocks (Beamish 1995; Francis et al. 1998). Much of the atmospheric variability is associated with the strength and position of the Aleutian Low Pressure System in winter (Ware 1995). Variability in the Aleutian Low is related to El Nino-Southern Oscillation (ENSO) events in the tropics (Mysak 1986; Trenberth and Hurrell 1994) and to large scale atmospheric patterns in the Northern Hemisphere. These patterns have been described by a variety of indices such as the North Pacific Index (NPI, Trenberth and Hurrell 1994), Aleutian Low Pressure Index (ALPI, Beamish and Bouillon 1993), Northeast Pacific Pressure index (NEPPI, Emery and Hamilton 1985), Bi-decadal oscillation (BDO, Ware 1995), and most recently, the Pacific Decadal Oscillation (PDO, Mantua et al. 1997). In contrast to the tropics, which are dominated by short-frequency variations, the decadal time scale is more important in the northern North Pacific, which may be a result of positive feedback mechanisms between the atmosphere and ocean (Trenberth and Hurrell 1994).

Changes in atmospheric circulation patterns on the decadal scale and their impacts on upper ocean conditions have received much attention in recent years. Atmospheric variability is associated with variations in sea surface temperatures (Trenberth and Hurrell 1995) and affects thermal conditions to at least 250 m depth both in the central GoA (Hanava 1995) and on the shelf (Royer 1989). Sea surface temperature records from the eastern subarctic North Pacific indicate the existence of alternating warm and cool eras with an average period of roughly 17 years (Hollowed and Wooster 1992; Wooster and Hollowed 1995). During cool eras the Aleutian Low is weak and located further west than usual. Northerly winds inhibit northward flow along the Alaskan coast, flow in the Alaskan Gyre is weak, flow in the California Current is strong and upwelling there is enhanced (Hollowed and Wooster 1992). During periods of a strong Aleutian Low located over the eastern GoA, surface flow in the Alaska Current is intensified (Ingraham et al. 1998), resulting in periods of strong circulation in the GoA and diminished flow in the California Current (Hollowed and Wooster 1992). Southerly winds on the eastern limb of the Aleutian Low inhibit upwelling and advect warm and moist air into the eastern North Pacific, while offshore northerly winds on the west side of the low cool the central North Pacific.

Many studies have shown that dramatic changes in both the physical and biological environment occurred in the Northeast Pacific in the late 1970s. This regime shift was associated with the intensification and an eastward shift in the average position of the Aleutian Low, an increase in coastal air temperatures, increases in coastal SST, intensification of the circulation in the GoA, and decreased flow in the California Current. The shift in average conditions may have been particularly intense because warming phases of the decadal scale variation and low frequency variations coincided in the late 1970s (Ware 1995).

Effects of the observed changes in the atmosphere and ocean on biological communities have been documented, although data on phytoplankton, zooplankton, and higher trophic level species are much less extensive than data on physical variability. Modeling results suggest that the changes in the physical environment between the 1970s and 1980s imply an increase in primary and secondary production in the Gulf of Alaska due to a shoaling of the mixed layer (Polovina et al. 1995). There is some evidence that primary productivity in the GoA increased after the regime shift, although decreases in Chl *a* after 1975 were observed in much of the subarctic Pacific (Sugimoto and Tadokoro 1997) and Chl *a* concentrations at Ocean Station P (50°N, 145°W) have remained stable over a 27 year period (Wong et al. 1995). In situ ^{14}C primary production at Ocean Station P between 1984 and 1990 was much higher than in the 1950s and 1960s, but this may largely be due to improvements in sampling techniques (Wong et al. 1995). In contrast, Venrick (1995) documented a doubling of Chl *a* concentrations in the deep layer of the central North Pacific, presumably due to an increase in winter storm activity.

However, the observed doubling does not imply a corresponding increase in productivity but may indicate a shift in species composition resulting from low light conditions that favor phytoplankton species with a higher Chl *a* content. Lack of a positive correlation between wind intensity during winter and Chl *a* concentrations during the following summer in the subarctic Pacific (Sugimoto and Tadokoro 1997) does not support the hypothesis that an intense Aleutian Low leads to enhanced primary production in the GoA. Thus evidence for increases in primary production or phytoplankton biomass in the GoA following the regime shift in the late 1970s is weak.

In contrast, the evidence is strong that variations in the abundance of zooplankton stocks are associated with variations in the Aleutian Low and associated changes in ocean conditions. Brodeur and Ware (1992) show a large increase in zooplankton biomass in the central Gulf of Alaska between the 1950s/60s and the 1980s, while at the same time there was a corresponding decrease in zooplankton biomass in the California Current region (Roemmich and McGowan 1995; Brodeur et al. 1996). Thus secondary production does not vary uniformly throughout the Northeast Pacific but appears to be out of phase in the two production regimes. Recently, a similar out-of phase pattern has been documented for the abundance of salmon in the two regions (Hare et al. 1999).

Interpretation of patterns in the abundance of phytoplankton, zooplankton, and higher trophic level species is complicated by the effects of both bottom-up and top-down forcing. Chl *a* and zooplankton biomass are negatively correlated at the interannual scale (Sugimoto and Tadokoro 1997), suggesting top-down controls on phytoplankton abundance. When averaged over the decadal time scales, there is a positive correlation between Chl *a* and zooplankton biomass (Sugimoto and Tadokoro 1997), suggesting that an increase in phytoplankton productivity will lead to increases in the average levels of both Chl *a* and zooplankton over time. A negative correlation between pink salmon catches and zooplankton abundance in the central North Pacific may indicate top-down effects of pink salmon on zooplankton abundances.

The observed increase in productivity in the Northeast Pacific has had major impacts on upper trophic levels in the region. The biomass of all species of salmon, particularly sockeye, chum, and pink salmon, increased greatly in the late 1970s (Beamish and Bouillon 1993; Hare and Francis 1995). Brodeur and Ware (1995) also documented large shifts in abundance of non-salmonid large nekton in the Northeast Pacific including salmon shark, Pacific pomfret, jack mackerel, albacore, and three squid species. Except for jack mackerel all species had much higher catch rates for surveys done in the late 80's compared to surveys in the late 1950's.

Although the evidence is less conclusive, large-scale changes in the Northeast Pacific not only affected pelagic species but also had effects on demersal fish populations. Increased zooplankton production has been related to strong year-classes in sablefish (McFarlane and Beamish 1992) and may influence other groundfish populations through increases in larval survival or adult growth rates. Sixteen groundfish stocks in the Bering Sea, Aleutian Islands, GoA, off the west coast of Canada, and off the west coast of the United States had seven years of synchronous strong recruitment between the late 1950s and late 1980s (Hollowed and Wooster 1995). For a number of these stocks the probability of strong year-classes was different between cold and warm eras, corresponding to periods of a weak and strong Aleutian Low, respectively. Even more species showed a difference in average production between the different temperature eras (Hollowed and Wooster 1995).

Many hypotheses have been advanced to explain observed relationships between environmental variation and recruitment or abundance of fishes. They generally relate to starvation, transport, or predation of larval and early juvenile stages, although these effects cannot always be separated. Wooster and Bailey (1989) reviewed hypotheses relating to variability in recruitment and concluded that there is no simple, unified hypothesis to explain recruitment. Instead of focusing on the recruitment dynamics of individual fish stocks, they suggest examining large-scale changes in environmental conditions that may allow us to predict major shifts in fish communities. Hypotheses that have been advanced to explain the observed relationships between large-scale environmental conditions and marine production in the

Northeast Pacific focus on decadal-scale variability in atmospheric circulation and its impacts on circulation in the Alaskan Gyre (Brodeur et al. 1996), on mixed layer depth (Polovina et al. 1995), and on water column stabilization (Gargett 1997). A review of these and other hypotheses can be found in Francis et al. (1998) and McGowan et al. (1998).

Any links between increased primary production in the central subarctic Pacific and production of the coastal groundfish community are highly speculative since the dominant GoA groundfish species are primarily distributed within the Coastal Downwelling Domain (Ware and McFarlane 1989), away from the center of the gyre. No data are available to examine changes in primary or secondary production over the GoA shelf. However, it has been suggested that species on the shelf and inshore areas rely on production from outside their distributional range. A large proportion of zooplankton prey on the continental shelf surrounding the GoA may be supplied through onshore advection (Cooney 1984), which is prevalent throughout most of the year. Another possible source of zooplankton prey is the advection of zooplankton rich water via the Subarctic Current after its bifurcation into the Alaska Current and California Current. Variable flow in the Alaska Coastal Current may thus affect groundfish populations through changes in transport rates that lead to variations in the supply of nutrients and plankton, as well as variations in temperature and other water mass characteristics.

Temperature, transport, and food supply are among the factors that determine vital processes of fishes (growth, reproduction, etc) and ultimately determine recruitment and biomass levels. Recruitment patterns in many fish stocks are characterized by periods of above-average recruitment followed by periods of below-average recruitment. For example, the walleye pollock (*Theragra chalcogramma*) population in the GoA produced a number of strong year-classes in the late 1970's, and has had below average recruitment since then (NPFMC 1997). The cumulative effects of a period of above average recruitment usually result in increased abundance of a species and vice versa. Synchronous changes in a number of stocks over several years, as postulated by Hollowed and Wooster (1992), will result in marked shifts in relative species abundance. Thus large-scale environmental variability in the GoA is likely to contribute to variability in species composition of the groundfish community, independent of the impacts of fishing.

Groundfish fisheries in the Gulf of Alaska

The GoA supports a highly productive groundfish fishery with annual landings that averaged 257,000 mt in the period from 1981 to 1992 (Low 1993). The most important commercial species were walleye pollock, Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), other flatfish species, Pacific Ocean perch (*Sebastes alutus*), other rockfish species, and sablefish (*Anoplopoma fimbria*). Estimates of total abundance show that over the last decade the GoA has been dominated by pollock, arrowtooth flounder (*Atheresthes stomias*), and Pacific cod (NPFMC 1997). Historically, there was an apparent succession of three dominant species from Pacific Ocean perch in the 1960s to walleye pollock in the late 1970s/early 1980s to arrowtooth flounder in the 1990s.

Although total commercial catch has remained relatively stable, the catch and abundance of individual species have fluctuated widely. The ratio of highest to lowest catches between 1981 and 1992 ranged from 3-fold for Pacific halibut to over 30-fold for thornyhead rockfish (*Sebastolobus alascanus*). The abundance of most species varies on an interannual as well as on an interdecadal time scale. Large fluctuations in stock size are apparent in biomass estimates and large interannual variations in recruitment have been documented for many species (NPFMC 1997). The available recruitment data suggest that some populations (e.g. walleye pollock and Pacific Ocean perch) are dominated by few strong year-classes or short series of strong year-classes, whereas recruitment in other species (e.g. Pacific halibut, arrowtooth flounder, sablefish) displays less extreme fluctuations and is characterized by longer term trends (NPFMC 1997).

Recruitment of large, slow-growing flatfish species shows strong autocorrelation and appears to be related to decadal-scale forcing (Hollowed et al. 1998), whereas gadids in the GoA appear to respond to higher-frequency forcing related to local conditions (Megrey et al. 1995), or to ENSO events (Hollowed and Wooster 1995; Hollowed et al. 1998). For both flatfishes and gadids, changes in the GoA following the regime shift of the late 1970s appeared to favor recruitment success, resulting in increases in the average level of recruitment and biomass (Hollowed et al. 1998).

Groundfishes in the GoA are harvested mainly by trawlers, hook and line longliners and pot fishermen. The North Pacific Fishery Management Council (NPFMC), one of eight regional councils established by the Magnuson-Stevens Fishery Conservation and Management Act in 1976 to oversee management of the nation's fisheries, has primary responsibility for groundfish management in the GoA. The NPFMC has jurisdiction over the Exclusive Economic Zone (EEZ) off Alaska and manages groundfishes in the GoA as well as the Bering Sea and Aleutian Islands. Species managed by the NPFMC include cod, pollock, flatfish, mackerel, sablefish, and rockfish species. The Council also makes allocative and limited entry decisions for halibut, although the U.S. - Canada International Pacific Halibut Commission (IPHC) is responsible for conservation of halibut. Other large Alaska fisheries such as salmon, crab and herring are managed primarily by the State of Alaska.

Whereas trends in stock biomass and recruitment of the major commercial species have been examined previously, very little is known about trends in most of the non-commercial species. Therefore this study examines patterns and trends in the abundance of both commercial and non-commercial species.

Chapter 3: Methods

To meet the goals of the study I analyzed trawl survey data from three data sources. The first is a survey of juvenile groundfishes conducted in a number of nearshore areas around Kodiak Island in 1991 and 1992 (juvenile survey, Chapter 4). The second is a shrimp trawl survey conducted in nearshore areas around Kodiak Island between 1976 and 1995 by the Alaska Department of Fish and Game personnel (shrimp survey, Chapter 5). This survey targeted primarily shrimp but incidentally caught large juvenile and adult groundfishes. The third and most extensive data set was based on resource assessment surveys conducted on the entire Gulf of Alaska shelf and upper slope by National Marine Fisheries Service (NMFS) personnel (adult survey, Chapter 6) between 1984 and 1996. Spatial and temporal trends in the shrimp survey and the adult survey were used in Chapter 7 and were related to environmental trends. The juvenile survey was extended to include samples obtained from 1993 to 1996 in the central GoA for a comparison of patterns in the juvenile and adult surveys (Chapter 8).

Each of the trawl surveys collected information on the abundance of a large number of species at a large number of sites. Abundances were estimated as the combined weight of all individuals of a species collected in a given haul. No weight data was available for the juvenile survey, thus abundances were estimated as the number of individuals per haul. All surveys included estimates of the width of the net opening and the length of each tow, thus the area swept by the trawl could be estimated and catches at each site were standardized to catch-per-unit-effort (CPUE) in units of numbers or weight per unit area. CPUEs were not comparable among surveys as the surveys used very different gear types. In addition to CPUE data, environmental variables and information on the location and time of sampling were available for each site.

Based on site-by-species matrices of CPUE, I computed various indices of community structure including measures of species richness, species diversity, catch-per-unit-effort (CPUE) and multivariate indices of species composition. Each of the indices describes a different aspect of community structure. As a measure of species richness I used the number of species per haul.

In community ecology, species richness is often estimated as the expected number of species in a sample with a fixed number of individuals (Krebs 1989). I chose to use the simpler measure of 'number of species per haul' for two reasons. First, the expected number of species as estimated, for example, by the rarefaction method (Krebs 1989) makes restrictive assumptions about the distribution of individuals in space that are rarely met. In practice, the distribution of most species tends to be clumped (Krebs 1989) as is the case for juvenile flatfishes around Kodiak Island (Norcross and Mueter 1999). Second, I was primarily interested in how many species an area of a given size supports and how this may vary among different sites. Because the size of the area sampled by the trawl differed among sites I expected the number of species identified at a site to increase with the area swept. Therefore area swept was taken into account when comparing species richness among sites by including it as a covariate in all statistical analyses. For statistical comparisons of species richness I assumed that species counts followed a Poisson distribution. Empirical distributions of the number of species per tow suggested that the Poisson assumption was justified for the adult survey, whereas the number of species per tow in the juvenile survey had a bimodal distribution and was over-dispersed relative to the Poisson distribution (Fig. 3.1). However, a Chi-square test rejected the Poisson fit for both the juvenile ($\chi^2 = 99.3$, $p < 0.001$) and adult surveys ($\chi^2 = 280$, $p < 0.001$).

In addition to species richness, itself often considered a measure of diversity, I computed other measures of diversity that take into account the number of species as well as the evenness of relative species abundances. A wide variety of diversity measures have been suggested in the literature (Pielou 1975; Washington 1984; Magurran 1988), but no consensus has been achieved on which index to use. I chose to use Simpson's index of diversity for the juvenile data set because it is based on the number of individuals in the sample and has some theoretical justification, without making restrictive assumptions about the frequency distribution of the number of individuals per species (Krebs 1989). For the adult survey, I used the Shannon-Wiener index because Simpson's index cannot be applied to weight data. The Shannon-Wiener index had the advantage that it appeared to be relatively independent of sample size in simulations (Mueter,

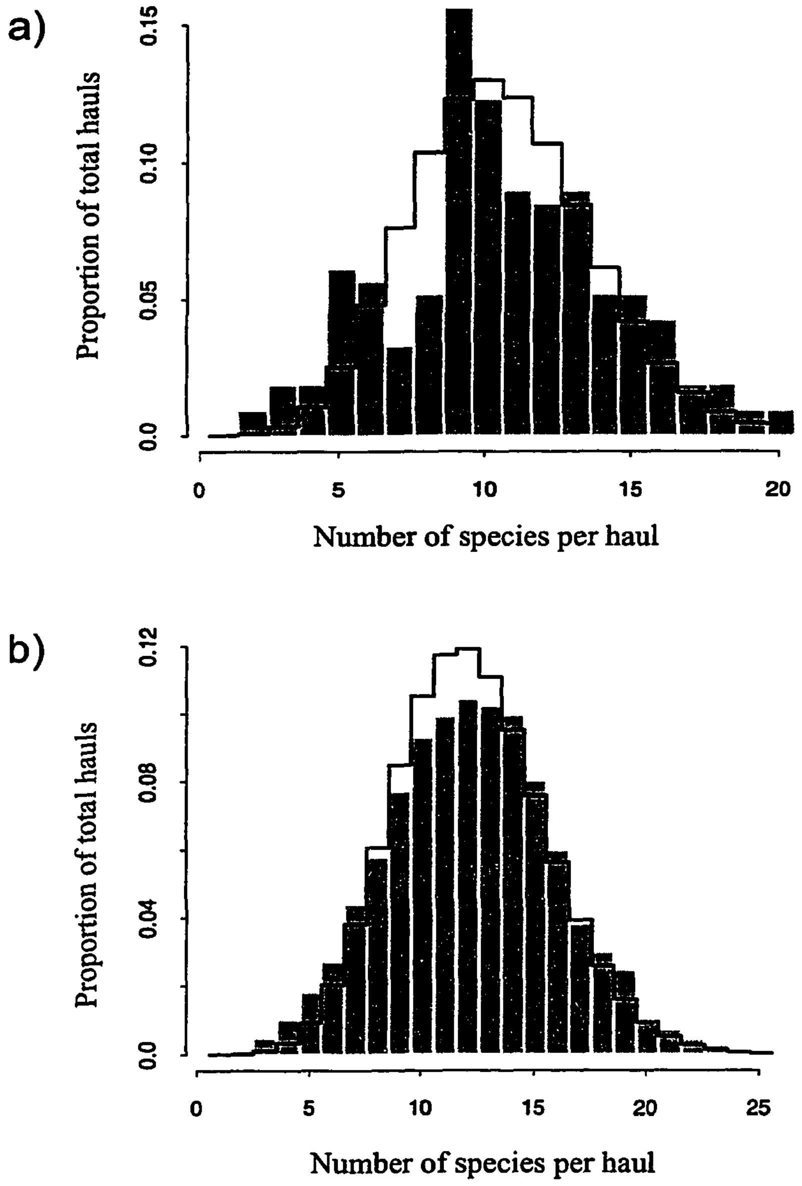

Figure 3.1: Distribution of the number of species per haul in (a) 211 hauls sampled during juvenile survey and (b) 3911 hauls sampled during adult survey (NMFS triennial bottom trawl survey). Dark line represents best Poisson fit with estimated Poisson means of $\lambda = 9.5$ (a) and $\lambda = 11.2$ (b).

unpublished data), and typically had a distribution that was close to normal. Magurran (1988) claims that repeated measures of diversity are usually normally distributed, implying that statistical tests based on the normal distribution can be used for the comparison of diversity among sites. In this study, the Shannon-Wiener index computed for each haul of the adult survey approximately followed a normal distribution, whereas Simpson's index of diversity, which is constrained to be between 0 and 1, had a skewed distribution with a short right tail for data from the juvenile survey (Fig. 3.2).

In analyzing species richness and diversity, I assumed that each sample estimated the composition of the local community at the sampling site. Thus indices were computed for each site, rather than for data aggregated over large areas and/or time periods as recommended by many authors (Krebs 1989). This resulted in estimates that were extremely variable due to high sampling variability but allowed me to estimate trends in richness and diversity along continuous environmental gradients.

Total CPUE of all species combined was computed for each site as a measure of overall numerical abundance (juvenile survey) or fish biomass (shrimp survey, adult survey). CPUE estimates for individual species typically contain many zero values and are highly skewed. Total CPUE estimates from the surveys analyzed here followed a distribution that was approximately lognormal (Fig. 3.3). Therefore total CPUE was log-transformed prior to statistical analysis.

Species richness, diversity, and total CPUE provide simple univariate descriptors of different aspects of community structure that are indifferent to the actual species composition. Very different communities that have few or no species in common can have the same richness, diversity, or CPUE. To compare species composition we require indices that are not indifferent to the actual species that make up a community, i.e., measures that take into account the difference in abundance of a given species between two sites. Such measures are commonly referred to as similarity (or dissimilarity) measures (Washington 1984) and can be used as the basis for some multivariate ordination techniques. A brief review of ordination techniques commonly used in community ecology is included in Chapter 5.

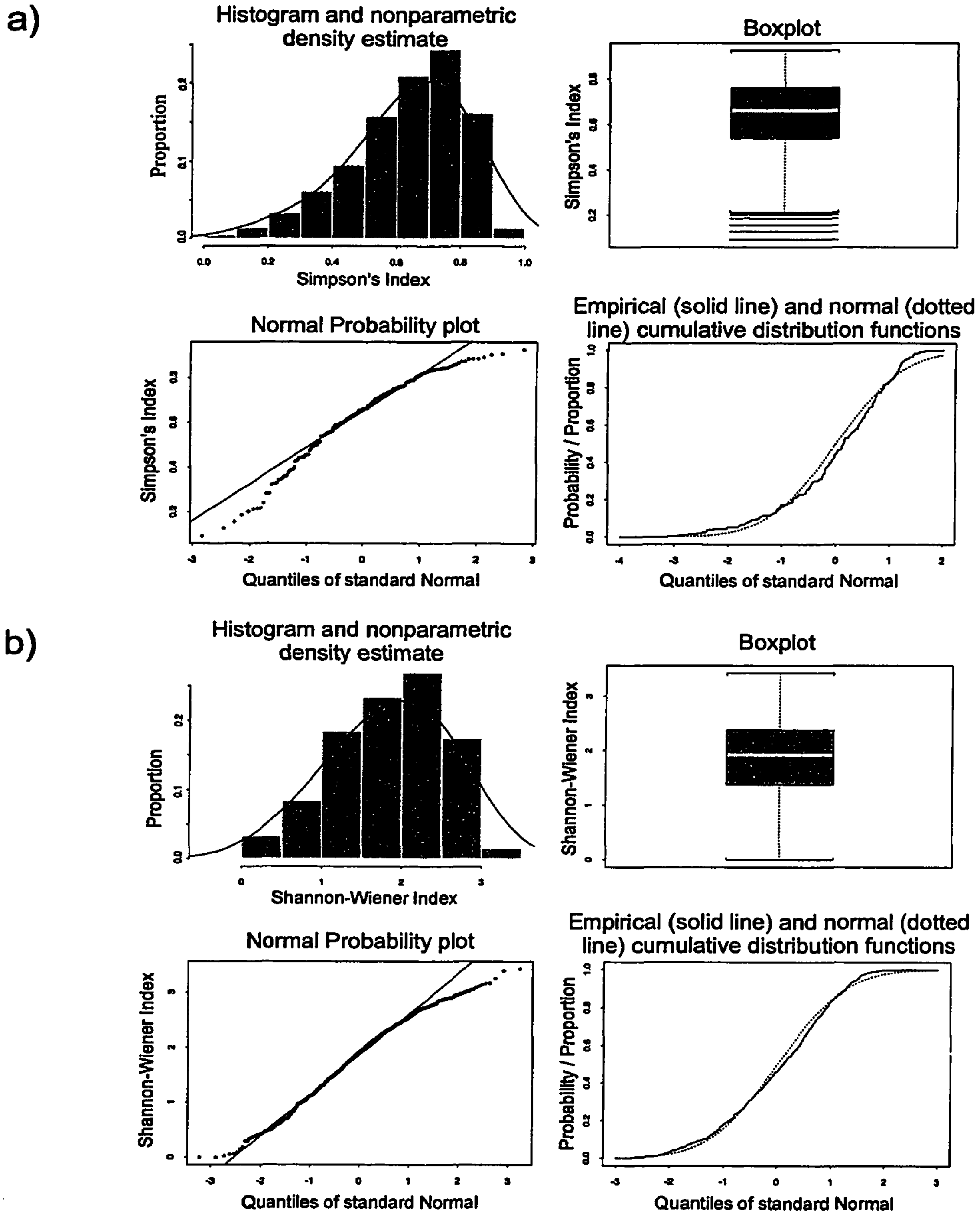

Figure 3.2: Distribution of (a) Simpson's index for 211 hauls from juvenile survey and (b) distribution of Shannon-Wiener index for 3911 hauls from adult survey.

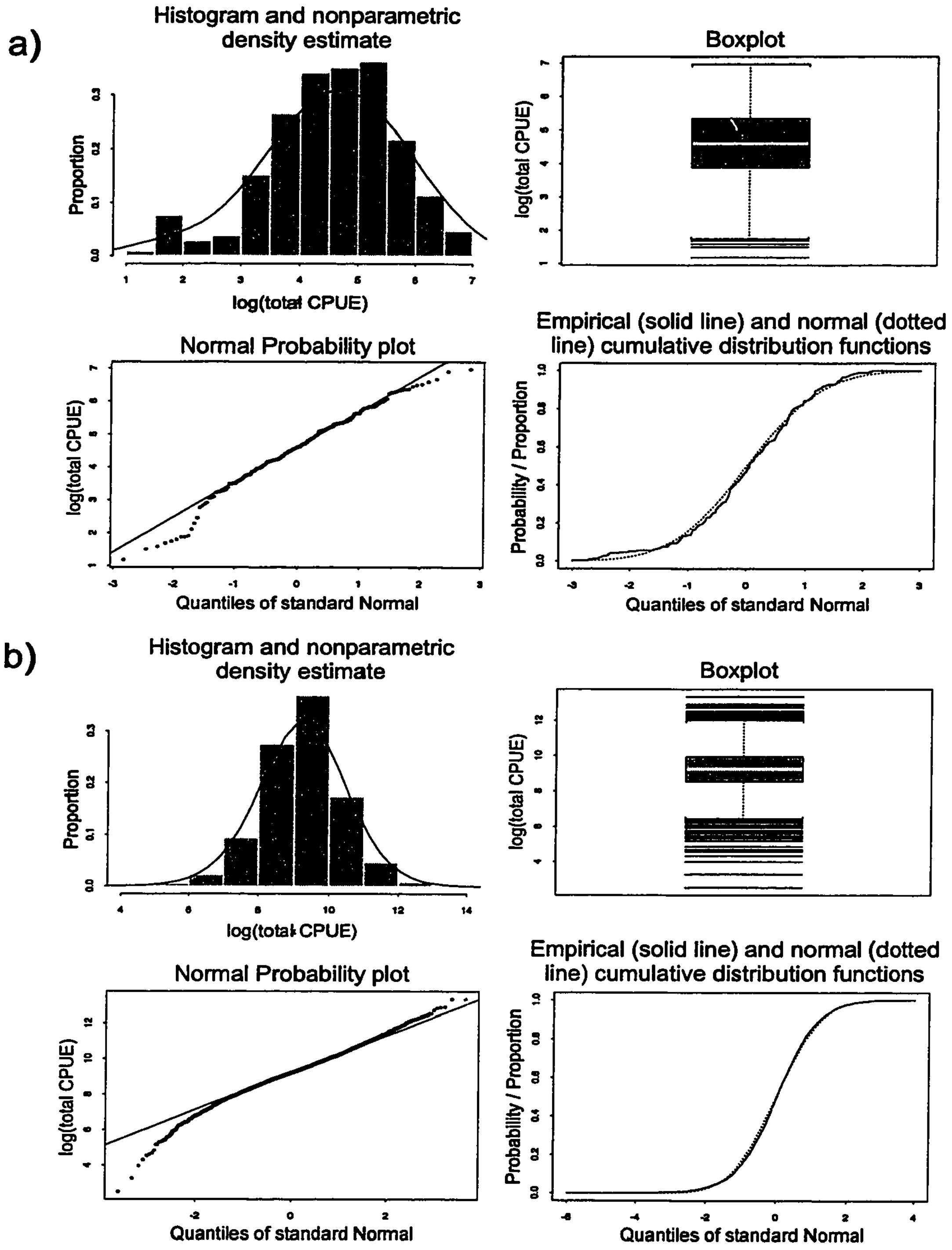

Figure 3.3: Distribution of (a) log-transformed total CPUE for 211 hauls from juvenile survey and (b) log-transformed total CPUE for 3911 hauls from adult survey.

For the analyses in Chapters 4-6 I used the Bray-Curtis dissimilarity measure, followed by a nonmetric multi-dimensional scaling (NMDS) ordination (Kruskal 1964), to summarize patterns in species composition. A justification for the use of the Bray-Curtis measure in conjunction with NMDS ordination is given in Chapter 5. To obtain multivariate indices of species composition and to relate variation in species composition to environmental variables I used the following sequence of steps:

1. Sampling sites were selected from a clearly defined area and time frame in accordance with the goals of the study. The choice of sites to include in the analysis depended on the underlying sampling design and the availability of relevant environmental data. For example, a number of sites sampled during the juvenile survey were excluded from analysis because one or more important environmental variables were not measured.
2. Species to be included in the analysis were selected and combined into species groups at an appropriate level of aggregation. Several authors suggest eliminating rare species as they can distort inferred patterns in species composition (Koch 1987; Saila et al. 1996). Alternatively, rare species can be aggregated at higher taxonomic levels. There is little guidance on how to aggregate species, particularly if not enough is known about the biology of these species to combine functionally similar guilds (e.g. Green et al. 1987). In my experience taxonomically related species generally show similar responses to ecological gradients and can typically be combined without distorting ordination patterns. Grouping species at higher taxonomic levels may be unavoidable if specimens were not consistently identified to the species level. The aggregation of species into groups often requires a series of subjective judgements. It is important to decide on a level of aggregation before the analysis is carried out, rather than searching for a level of aggregation that yields 'desired' results.
3. A site-by-species matrix of abundances was constructed and data were transformed in order to reduce the influence of a few stations and species with very high abundances. I followed a recommendation by Field et al. (1982) to use the fourth-root transformation, which in its

effect is similar to a log-transformation, but has the advantage that it is invariant to scale changes when used with the Bray-Curtis index of dissimilarity.

4. Many authors recommend a data standardization prior to the ordination. I generally used unstandardized data but repeated the analysis on standardized data for comparison. Data may be standardized in one of several ways: (a) Standardization of sites (rows) by dividing abundances in each row by the row total. In the resulting site-by-species matrix, abundances at each site sum to one, (b) standardization of species (columns) to equal maximum abundance by dividing each column by the maximum abundance in the column, such that the maximum value in each column is one, (c) standardization by site total, followed by a standardization to equal species maxima (double standardization), (d) standardization of species by removing the mean and dividing by the standard deviation. This is not appropriate for species abundance data with a large number of zeros.

Standardization can have important effects on the results of NMDS and often produces ordination results that are superior to those based on unstandardized data (Kenkel and Orloci 1986). While Kenkel and Orloci (1986) standardized to site totals, Faith et al. (1987), based on extensive simulations, recommended standardizing to equal species maxima when using the Bray-Curtis or similar measures of dissimilarity with NMDS ordination. Jackson (1997) argued that any standardization may produce artifacts in the patterns that emerge from ordination. In light of these conflicting opinions, I conducted ordinations for standardized and unstandardized data and compared the results from both approaches. However, standardization to equal site totals should probably be limited to cases where the abundances among sites are not comparable (e.g. where sampling effort cannot be quantified), as the standardization entails a considerable loss of information and can greatly distort patterns in the relative abundance of species among sites. Standardization to equal species maxima results in all species receiving approximately equal weight in the ordination. Without standardization, more abundant species contribute more to the dissimilarity index and hence to the ordination. I compared ordinations based on unstandardized data to ordinations based on standardization to equal species maxima (b). Results were generally similar and only results for unstandardized data are presented.

5. Bray-Curtis dissimilarities were computed between each pair of sites from the site-by-species matrix of transformed and standardized or unstandardized abundances.
6. NMDS ordination was performed using Bray-Curtis dissimilarities. Most analysts tend to do the ordination along 2 axes to facilitate visual examination of patterns. However, particularly with a large number of sites, a satisfactory fit may not be obtained in 2 dimensions. Therefore, I chose a criterion for goodness of fit in advance and did the ordination using as many axes as was necessary to achieve the criterion. Goodness of fit was assessed using Kruskal's stress criterion, a measure of discrepancy between the distances in ordination space and the underlying Bray-Curtis dissimilarities. Kruskal (1964) suggests as a rule of thumb that a stress of 10% or smaller results in a fair fit, whereas a stress of 20% is considered a poor fit.
7. The solution was rotated such that the first axis corresponded to the axis of maximum variation because the orientation of NMDS axes is arbitrary. The scores for each site along each rotated ordination axis were then used as indices of species composition. Each index (axis scores) can be interpreted as representing a different, independent aspect of species composition with the first index (Axis 1 scores) representing the major mode of variation in species composition. The indices have no units as they reflect relative distances only.
8. The indices (axis scores) were related back to the underlying species abundances to interpret their biological meaning in terms of the underlying species abundances. To interpret the indices I used scatterplots and rank correlations between each species' CPUE and the ordination axes. Plotting the abundance of a species against each index helps to identify individual species that are strongly related to each index, and to assess the nature of the relationships. Typically, species CPUEs were monotonically related to the ordination axes such that each axis was positively correlated with one group of species and negatively

correlated with another group. I chose indicator species that were strongly associated with axes score based on the magnitude of rank correlations.

9. Finally the indices of species composition, as well as species richness, diversity, and total CPUE were related to appropriate explanatory variables, either in an exploratory sense to identify variables that are most strongly related to species composition, or to test hypotheses regarding species composition. I used a regression approach using general linear models and additive models (McCullagh and Nelder 1989; Hastie and Tibshirani 1990) to model the indices as a function of the independent variables. Additive models were used in addition to standard linear models to allow for the possibility of non-linear relationships. I assumed a normal distribution for the indices of species composition, an assumption that was tested using residual plots and other appropriate regression diagnostics. Errors were typically close to normally distributed and the model fits were generally superior to models based on individual species abundances.

The general statistical approach described here was adapted to the specific objectives and the nature of the environmental data available for each survey. Other exploratory methods such as cluster analysis, and test procedures such as randomization tests, were used where appropriate as described in the Methods sections of the individual chapters.

Chapter 4: Linking community structure of small demersal fishes around Kodiak Island, Alaska, to environmental variables[1]

Franz J. Mueter and Brenda L. Norcross

Abstract

Juveniles and small adults of at least seventy-five species of demersal fishes were identified in trawl catches from the nearshore waters of Kodiak Island 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 five 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

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water group. Non-linear depth effects on most indices suggest relatively rapid changes in species composition in shallow water (0-50 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.

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 and 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 and 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 four most common flatfish species collected around Kodiak Island and found depth 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 and Pearcy 1968, Rowe and 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 factors 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 and Elliott 1998).

The goal of this study is to characterize the community structure of small demersal fishes in relation to environmental variables in a nearshore area of the Gulf of Alaska characterized by relatively deep bays. 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 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

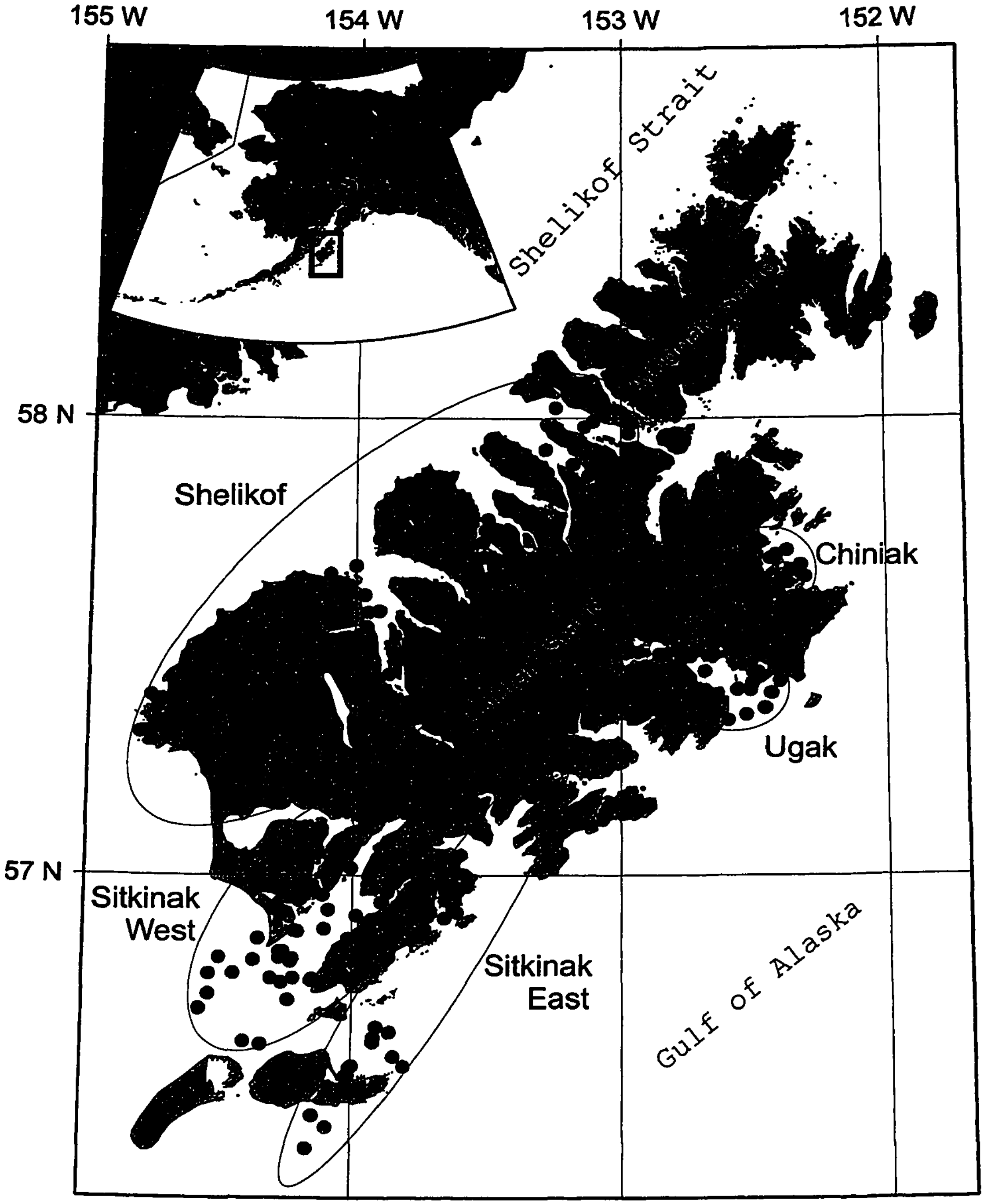

Figure 4.1: Map of Kodiak Island, Alaska, showing sampling locations and five geographical areas used in analysis.

Alitak Bay (Fig. 4.1). 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 m^3 Ponar grab for analysis of grain size. A portable conductivity, temperature, and depth (CTD) probe (Seabird Seacat Profiler SB19) was deployed to within 1-5 m of the bottom to measure temperature and salinity at all except eight 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 stretched mesh and a codend liner of 4 mm bar mesh (Gunderson and Ellis, 1986). The depth to warp ratio was approximately 1:8 for sites less than 10 m, 1:5 at 10 - 20 m sites, and 1:3 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/sec.

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 catch per unit effort (CPUE) as individuals per 1000 m^2. The towing distance was estimated based on GPS positions where available or on the average speed and tow duration. Area swept was computed from the estimated tow distance and effective width of the net (Gunderson and 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 five distinct geographical areas (Fig. 4.1). The areas were Chiniak (84 stations), Ugak Bay (21), Sitkinak East (26), Sitkinak West (44), and Shelikof (36). The 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 two 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 and Wichern 1992).

Indices of community structure

We computed four 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 catch-per-unit-effort 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 possibly species diversity, to be related to the area sampled by the trawl, we included area swept as 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 two 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 catch-per-unit-effort (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 4.1).

Indices of species composition were related to environmental variables using indirect gradient analysis (Gauch 1982, Digby and Kempton 1987, Ter Braak 1995). Specifically, we used non-metric multidimensional scaling (NMDS), which has proven useful in analyzing marine community data (Field et al. 1982, Clarke 1993, Clarke and 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 and Norcross (in review):

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).

Table 4.1: Number of species collected in August 1991 and August 1992 around Kodiak Island, Alaska, by family. * indicates that no fish were identified to the species level.

Family	Number 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
Zaproridae	1
Trichodontidae	1
Ammodytidae	1
Bothidae	1
Scorpaenidae	*
Liparidinae	*

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 and 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 3 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 stepwise procedure based on the Akaike information criterion (Hastie and 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 29,749 bottom fishes belonging to one of 75 identified species from 20 families (Table 4.1). The most abundant species were rock sole (*Pleuronectes bilineatus*), flathead sole (*Hippoglossoides elassodon*), and Pacific cod (*Gadus macrocephalus*) with 9,862 (33%); 2,481 (8.3%); and 2,073 (7.0%) specimens respectively (Table 4.2). Rock sole were captured at more sites than any other species (159 of 211 sites, Table 4.2). 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 individuals per 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. 4.2). 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 variable (DT) 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 two unusually low values (27.1 and 24.0 psu). The percentage of gravel in the sediment

Table 4.2: List of groundfish species and taxa collected in August 1991 and August 1992 around Kodiak Island, Alaska. Sites refers to the number of sites at which each group was captured, number to the total number of specimens caught, and rank refers to the rank order of numerical abundance (Number). Groups shown are those used for analysis.

Family	Scientific name	Common name	Sites	Number	Rank
Gadidae	*Gadus macrocephalus*	Pacific cod	106	2073	3
"	*Theragra chalcogramma*	Walleye pollock	81	786	11
Hexagrammidae	*Hexagrammos* spp.	Greenling	61	367	14
"	*Ophiodon elongatus*	Lingcod	29	111	23
Cottidae	*Dasycottus setiger*	Spinyhead sculpin	21	118	22
"	*Gymnocanthus* spp.	*Gymnocanthus* spp.	72	385	13
"	*Hemilepidotus* spp.	Irish lord	49	173	18
"	*Icelinus borealis*	Northern sculpin	59	940	9
"	*Myoxocephalus* spp.	*Myoxocephalus* spp.	82	1346	6
"	*Radulinus asprellus*	Slim sculpin	17	76	28
"	*Triglops* spp.	*Triglops* spp.	28	154	19
"	*Enophrys* spp.	*Enophrys* spp.	12	30	33
"	*Psychrolutes sigalutes*	Soft sculpin	33	318	16
Agonidae	*Podothecus acipenserinus*	Sturgeon poacher	97	847	10
"	*Pallasina barbata*	Tubenose poacher	48	127	21
"	*Aspidophoroides bartoni*	Aleutian alligatorfish	15	31	32
"	*Bathyagonus* spp.	*Bathyagonus* spp.	59	449	12
"	*Anoplagonus inermis*	Smooth alligatorfish	14	62	29
Liparidinae	*Liparis* spp.	Snailfishes	79	229	17
Bathymasteridae	*Bathymaster* spp.	*Bathymaster* spp.	24	96	26
"	*Ronquilus jordani*	Northern ronquil	28	108	24
Zoarcidae	*Lycodes* spp.	*Lycodes* spp.	27	1152	7
Stichaeidae	*Lumpenus* spp.	*Lumpenus* spp.	134	1980	4
Pholidae	*Pholis* spp.	*Pholis* spp.	21	78	27
Pleuronectidae	*Atheresthes stomias*	Arrowtooth flounder	50	340	15
"	*Hippoglossoides elassodon*	Flathead sole	92	2481	2
"	*Pleuronectes isolepis*	Butter sole	37	143	20
"	*Pleuronectes bilineata*	Rock sole	159	9862	1
"	*Pleuronectes asper*	Yellowfin sole	97	1890	5
"	*Microstomus pacificus*	Dover sole	13	25	34
"	*Pleuronectes vetulus*	English sole	19	42	30
"	*Platichthys stellatus*	Starry flounder	11	34	31
"	*Pleuronectes quadrituberculatus*	Alaska plaice	18	104	25
"	*Psettichthys melanostictus*	Sand sole	12	24	35
"	*Hippoglossus stenolepis*	Pacific halibut	92	1053	8
Other species				1715	
Total				29749	

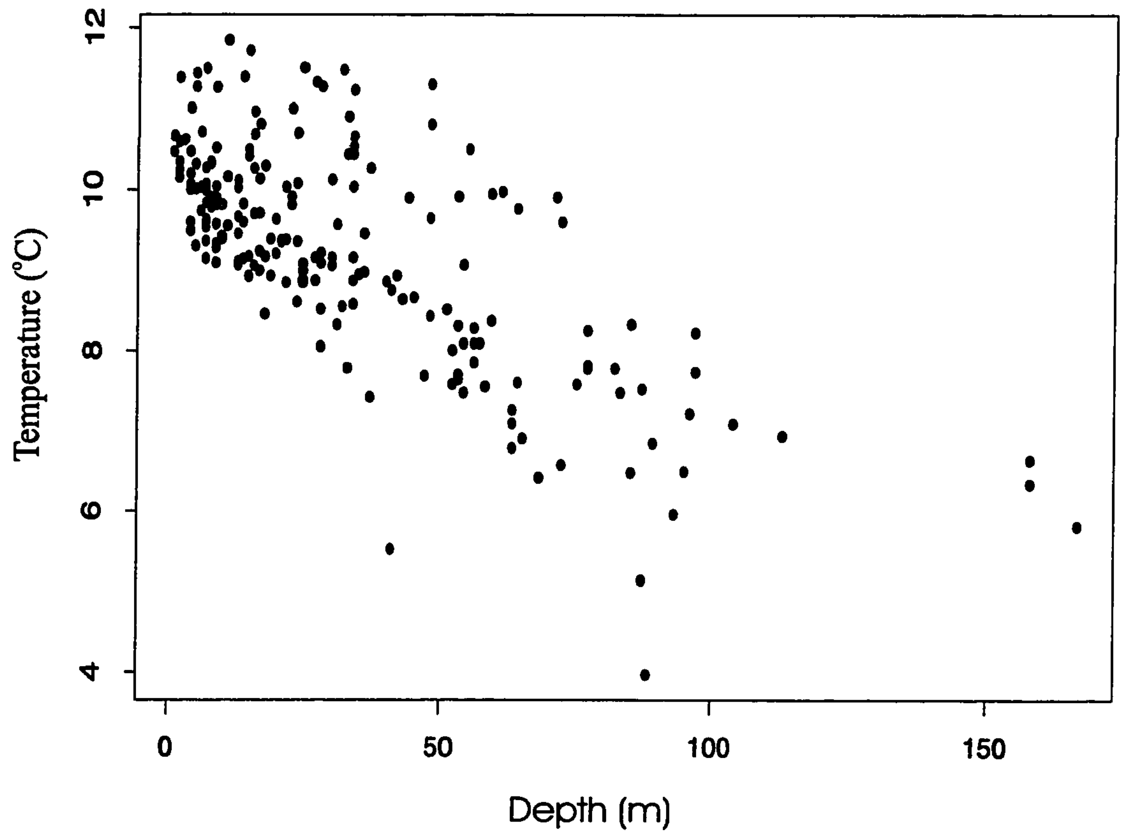

Figure 4.2: Scatterplot of temperature versus depth for all sites sampled in August 1991 and August 1992.

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 two principal 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 primarily 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 one depth-temperature variable (DT), salinity, two sediment variables (S1 and S2), and geographic area. Each regression that included one or both of the sediment variables was also compared to a regression that included a categorical sediment variable with six levels in place of the continuous sediment variables. The six levels were pure gravel (G), sand (S), or mud (M) if the sediment contained at least 95% of one of these sediment types and mixed gravel, mixed sand, or mixed mud if the sediment contained less than 95% of any one 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 summarizing the standardized effect of each covariate on the dependent variable. 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. 4.3, pseudo $R^2 = 0.35$). As expected, the number of species increased with the area sampled, but leveled off at 600-700 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. 4.3). This pattern became more obvious when the categorical sediment variable was substituted for S2 in the regression (Fig. 4.4). 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 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. 4.3). Species richness was significantly higher in area Sitkinak East compared to all other areas. The number of species averaged 12.6 in Sitkinak East, 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. 4.5). 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 m^2. Diversity decreased linearly with salinity over the range of salinities sampled. Like species richness, diversity was highest in area Sitkinak East. Species

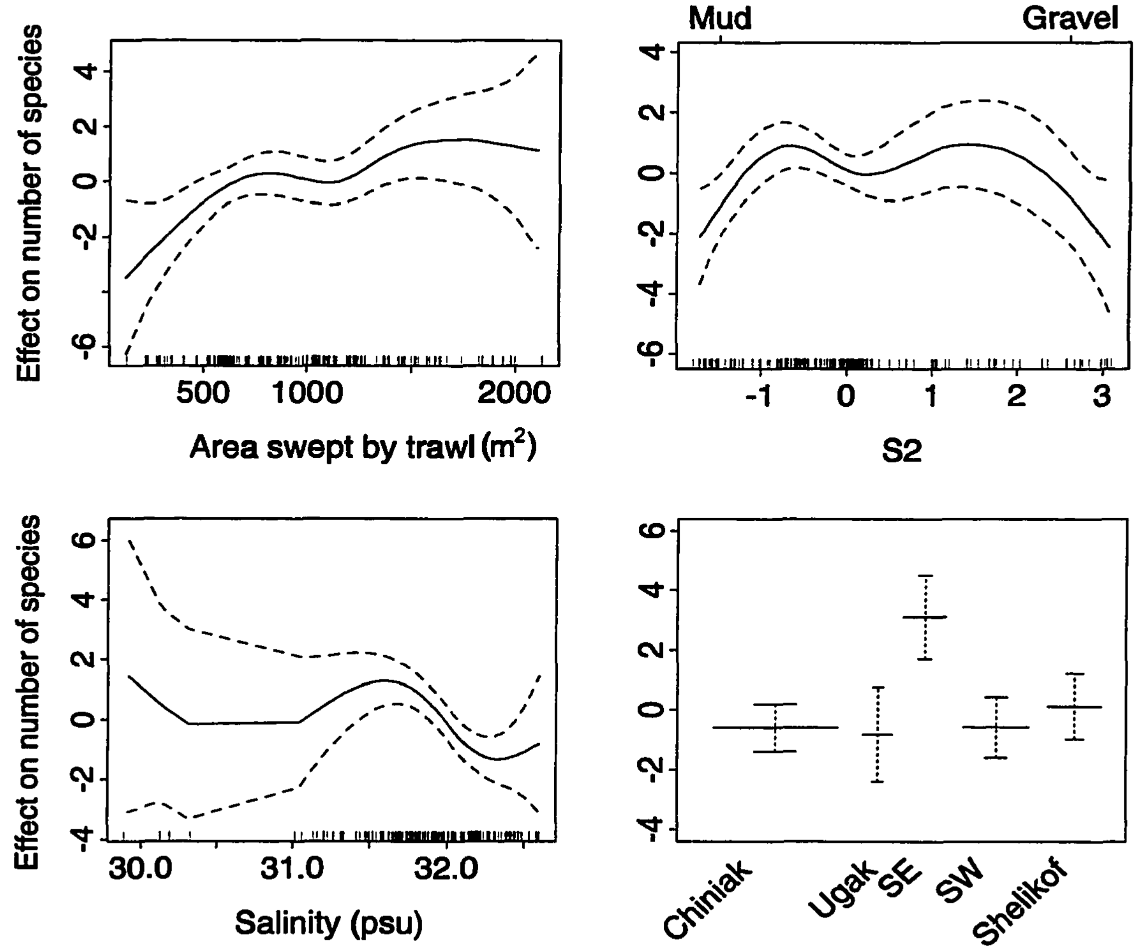

Figure 4.3: Estimated relationship between number of species and significant explanatory variables. Tickmarks along x-axis indicate values of observations. Dashed lines indicate approximate 95% confidence limits of the regression lines. Horizontal lines in lower right plot indicate mean response with 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.

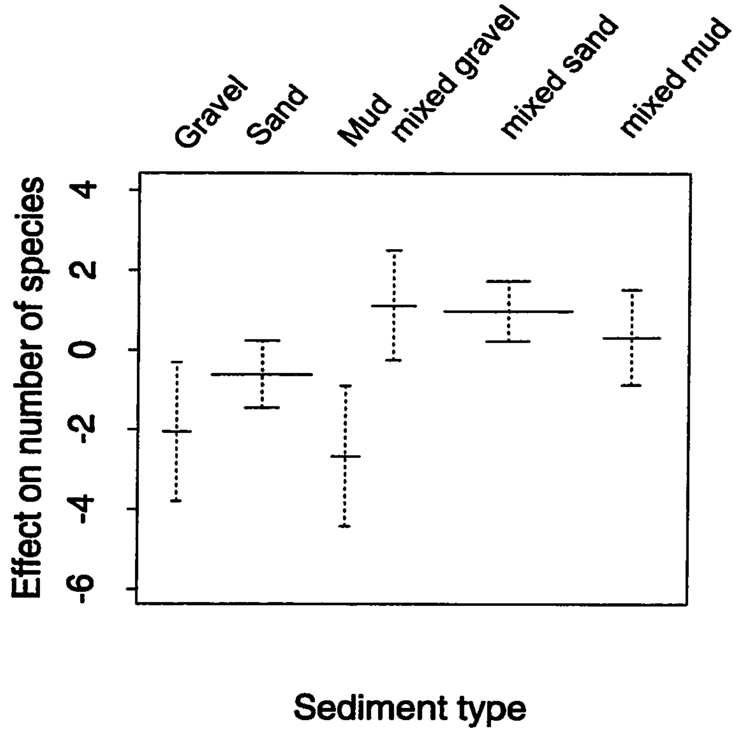

Figure 4.4: Estimated effect of sediment type on the number of species, after accounting for effects of area swept and differences among geographic areas, with 95% pointwise confidence intervals.

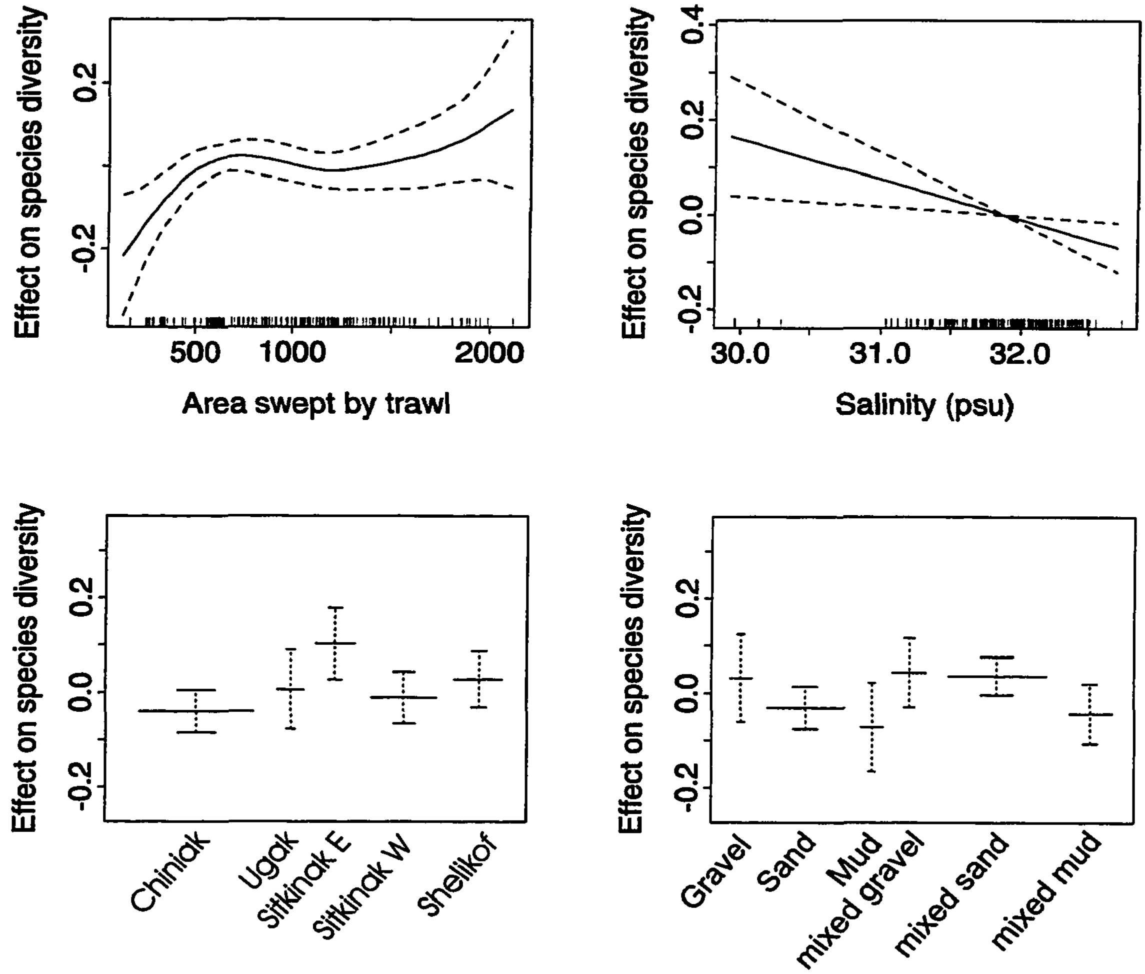

Figure 4.5: Estimated relationship between species diversity and significant explanatory variables. For explanation of plots, see Figure 3.

diversity tended to be significantly lower on pure sand, pure mud, and mixed mud sediments (Fig. 4.5), 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 five geographical areas (Fig. 4.6), 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 six 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 4.3). Among the five areas, highest abundances were observed in areas Sitkinak East and Chiniak Bay (Fig. 4.6).

Table 4.3: Mean CPUE ± 1 SD by sediment type for 208 samples with known sediment type collected in 1991 and 1992.

Sediment type	Mean CPUE {# / (1000 m^2)}	Standard deviation
Gravel	47	34
Sand	156	146
Mud	93	90
Mixed gravel	133	206
Mixed sand	202	195
Mixed mud	156	112

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 six indices was modeled separately as a function of the explanatory variables. The indices will be referred to as

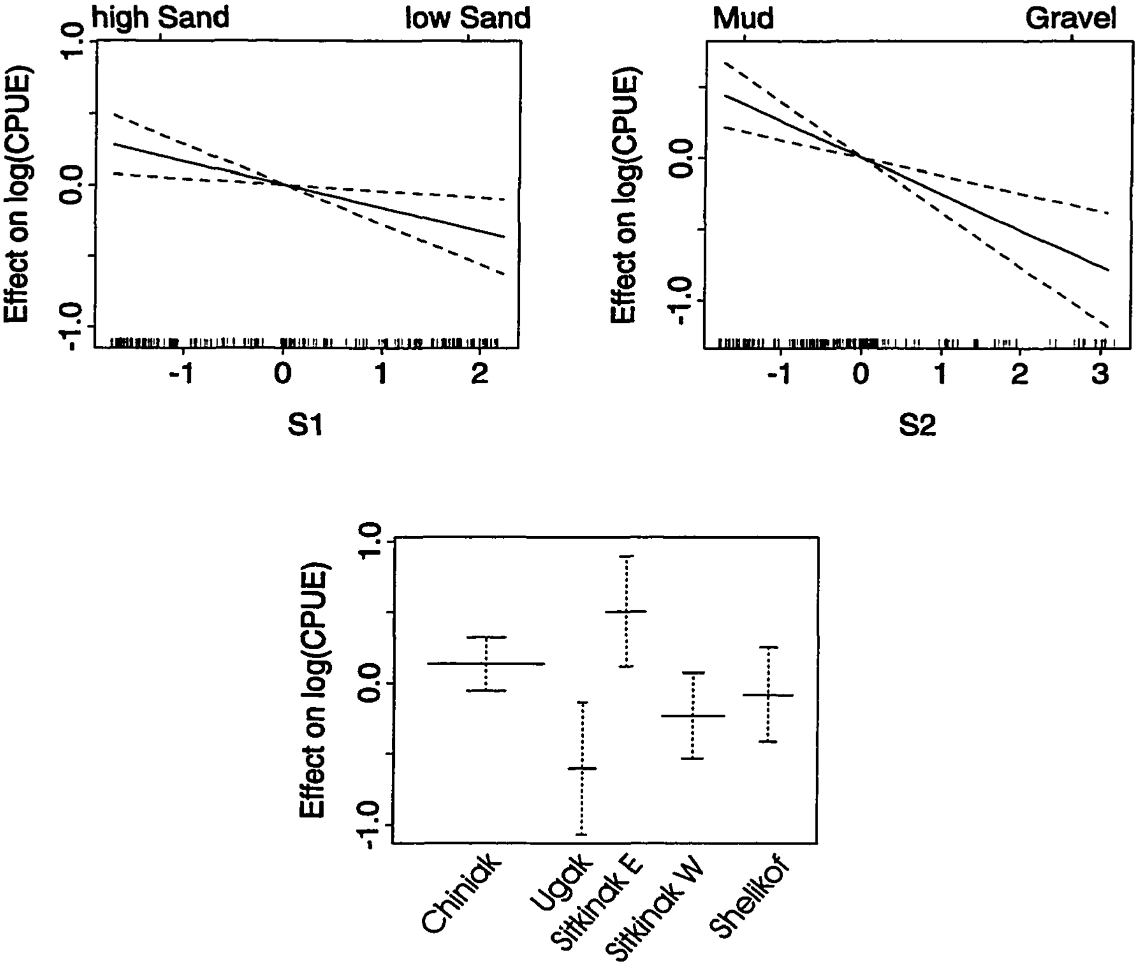

Figure 4.6: Estimated relationship between total abundance (log(CPUE+1)) and significant explanatory variables. For explanation of plots, see Figure 3.

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 two axes accounted for approximately half the variation in the NMDS ordination.

To aid interpretation of the indices we first related each of the six indices to the CPUEs of all species. Scatterplots of individual species CPUEs against Axes 1-6 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 4.4). 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., *Atheresthes stomias*, and *Hippoglossoides elassodon*, and strong negative rank correlations with the CPUE of a group of 9 other species (Table 4.4), thus contrasting these two groups of species.

All variables except salinity explained a significant proportion of the variance of one or more of the indices. The first four indices of species composition were significantly related to the depth-temperature 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 depth-temperature gradient (Fig. 4.7a). The variable DT had by far the largest coefficient of partial determination for Axis 1 (Table 4.5). 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 4.4, Fig. 4.7b). Axis 1 was also weakly associated with area, indicating that the deep water group was more abundant in areas Sitkinak East and Shelikof on the west side of Kodiak island, while the shallow water group was more abundant in areas

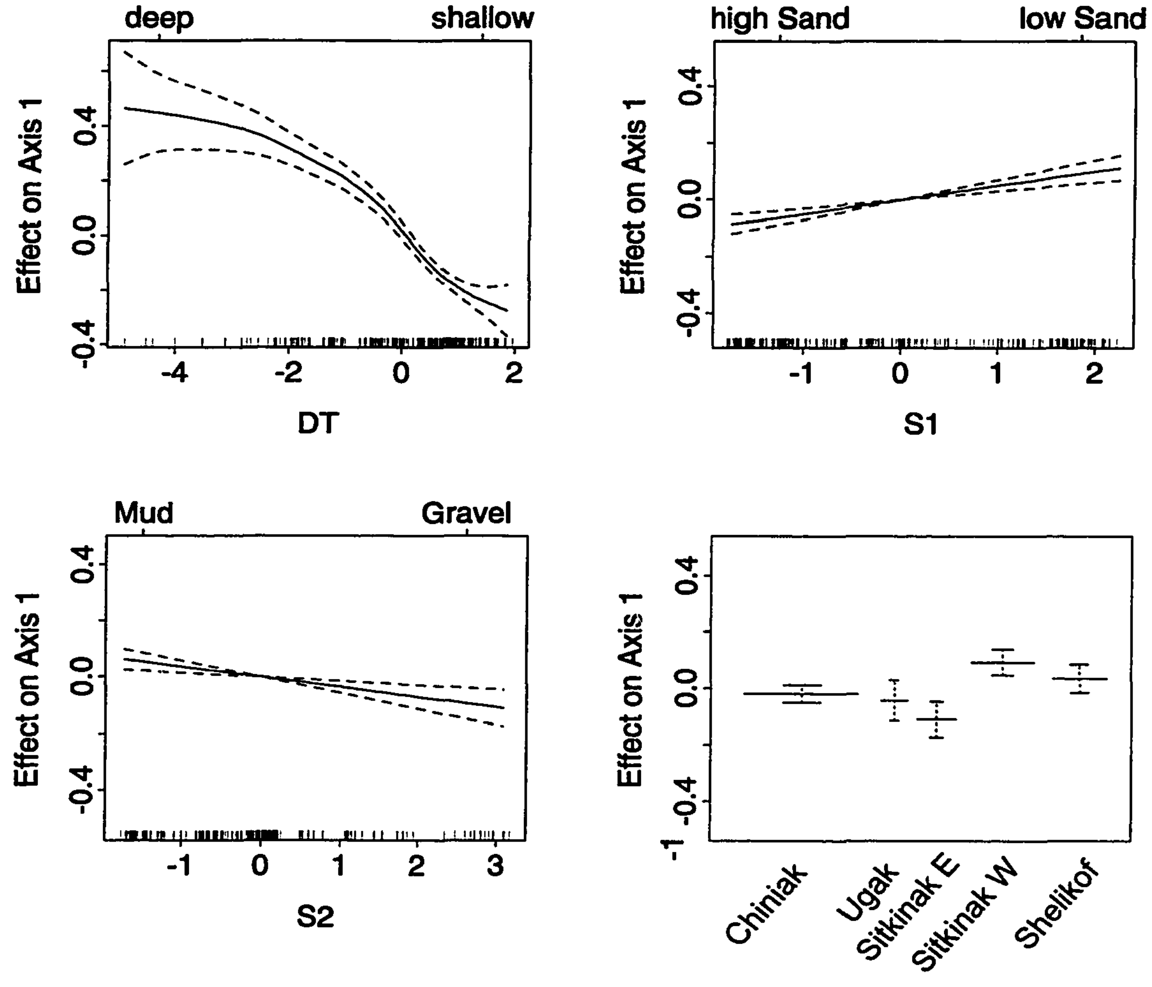

Figure 4.7: (a) Estimated relationship between Axis 1 and environmental variables. For explanation of plots, see Figure 3.

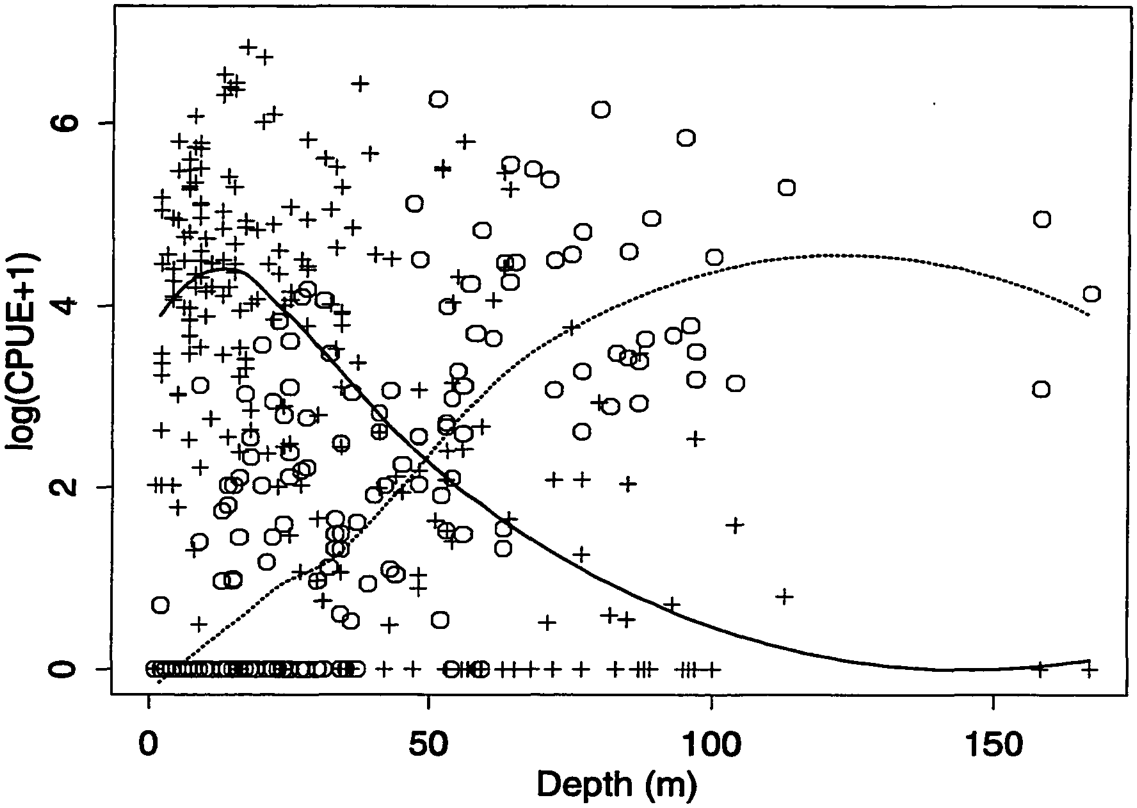

Figure 4.7: (b) Scatterplot of the total abundances of the two species groups defined by Axis 1 against depth. Combined abundance of shallow water group (*G. macrocephalus, Hexagrammos spp., O. elongatus, Myoxocephalus* spp., *P. acipenserinus, P. barbata, P. bilineata*, and *H. stenolepis*) indicated 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 (LOESS).

Table 4.4: Spearman correlations between six indices of species composition (Axis 1 to Axis 6) and CPUE of individual species. Only correlations exceeding 0.3 are shown. For common names of species see Table 4.2.

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

Chiniak, Ugak, and Sitkinak East 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. 4.7a).

Table 4.5: Contribution of each variable to the "best-fit" models for Axes 1-4. 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 refers to the pseudo coefficient of determination for the best model (= 1 - deviance of best model / deviance of null model) and to the pseudo coefficient of partial determination for reduced models (= 1 - deviance of best model / deviance of reduced model). Variables are listed in the order of their contribution to the fit. For further details see methods.

		Model df	Deviance	Pseudo r^2
Axis 1:				
	Null model	1	16.332	
	Best model	11	4.156	0.75
	- f(DT)	7	9.127	0.55
	- area	7	4.771	0.13
	- S1	10	4.751	0.13
	- S2	10	4.420	0.06
Axis 2:				
	Null model	1	8.124	
	Best model	10	5.369	0.34
	- f(S1)	6	6.772	0.21
	- f(DT)	6	6.158	0.13
	- S2	9	5.881	0.09
Axis 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
	- f(DT)	7	4.868	0.06
Axis 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
	- f(S2)	10	3.633	0.12
	- f(S1)	10	3.502	0.08

Axis 2 was primarily related to the first sediment variable (Table 4.5, Fig. 4.8a). Species positively correlated with the index (Table 4.4) 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 depth temperature 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 two groups plotted by depth and percent sand (Fig. 4.8b).

Species that were positively correlated with Axis 3 (Table 4.4) 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 4.5, Fig. 4.9a). 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. 4.9b).

Axis 4 was primarily related to area and depth (Table 4.5). Species that were negatively correlated with the index (Table 4.4) 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. 4.10a). 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. 4.10a). Smoothed abundance trends by depth and S2 (Fig. 4.10b) indicate the presence of interactions between these variables, as the trend in abundance along S2 appeared to depend on depth.

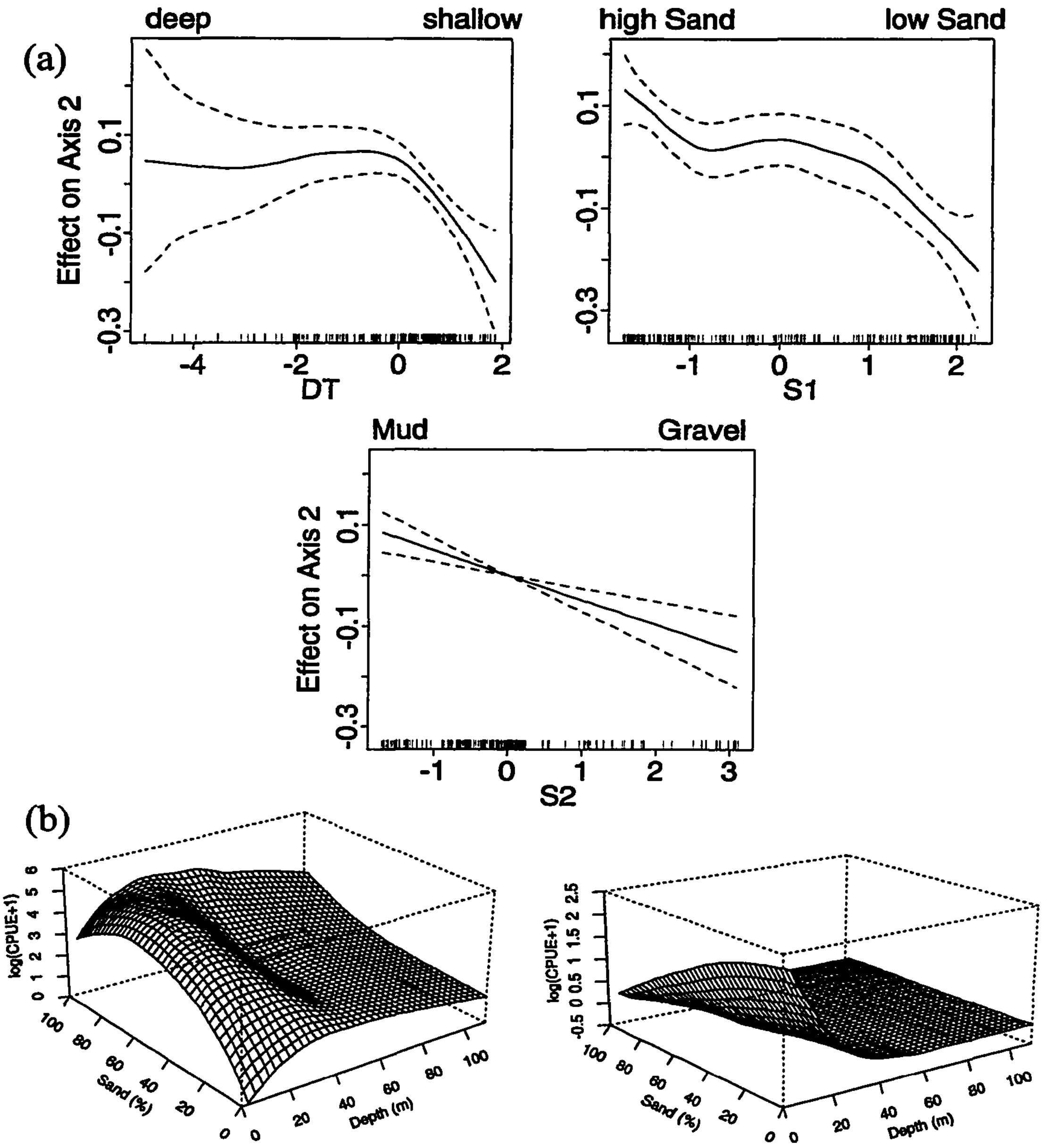

Figure 4.8: (a) Estimated relationship between Axis 2 and environmental variables (for details see Figure 3) and (b) smoothed trend surfaces of abundance for the two species groups defined by Axis 2 as a function of depth and sand. A group that is more abundant at intermediate to deep sites on sediments rich in sand (combined CPUE 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 CPUE of *Hexagrammos* spp., *Hemilepidotus* spp., and *Pholis* spp. shown on right). Smoothed trend surfaces were estimated using a robust, locally weighted smoother (LOESS).

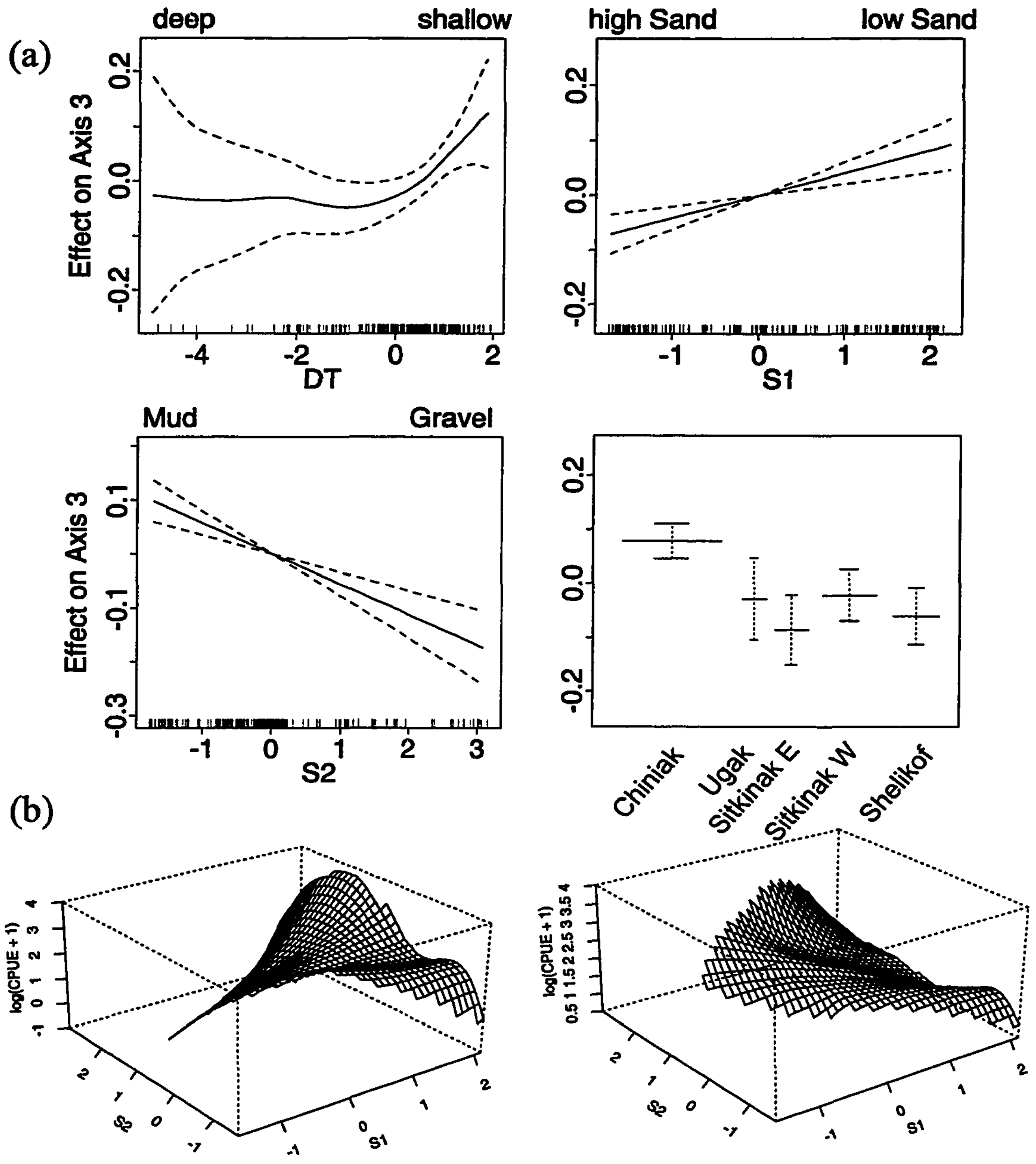

Figure 4.9: (a) Estimated relationship between Axis 2 and environmental variables (for details see Figure 3) and (b) smoothed trend surfaces of abundance (log(CPUE+1)) for the two species groups defined by Axis 3 as a function of sediment variables. Combined abundance of species positively correlated 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 (LOESS).

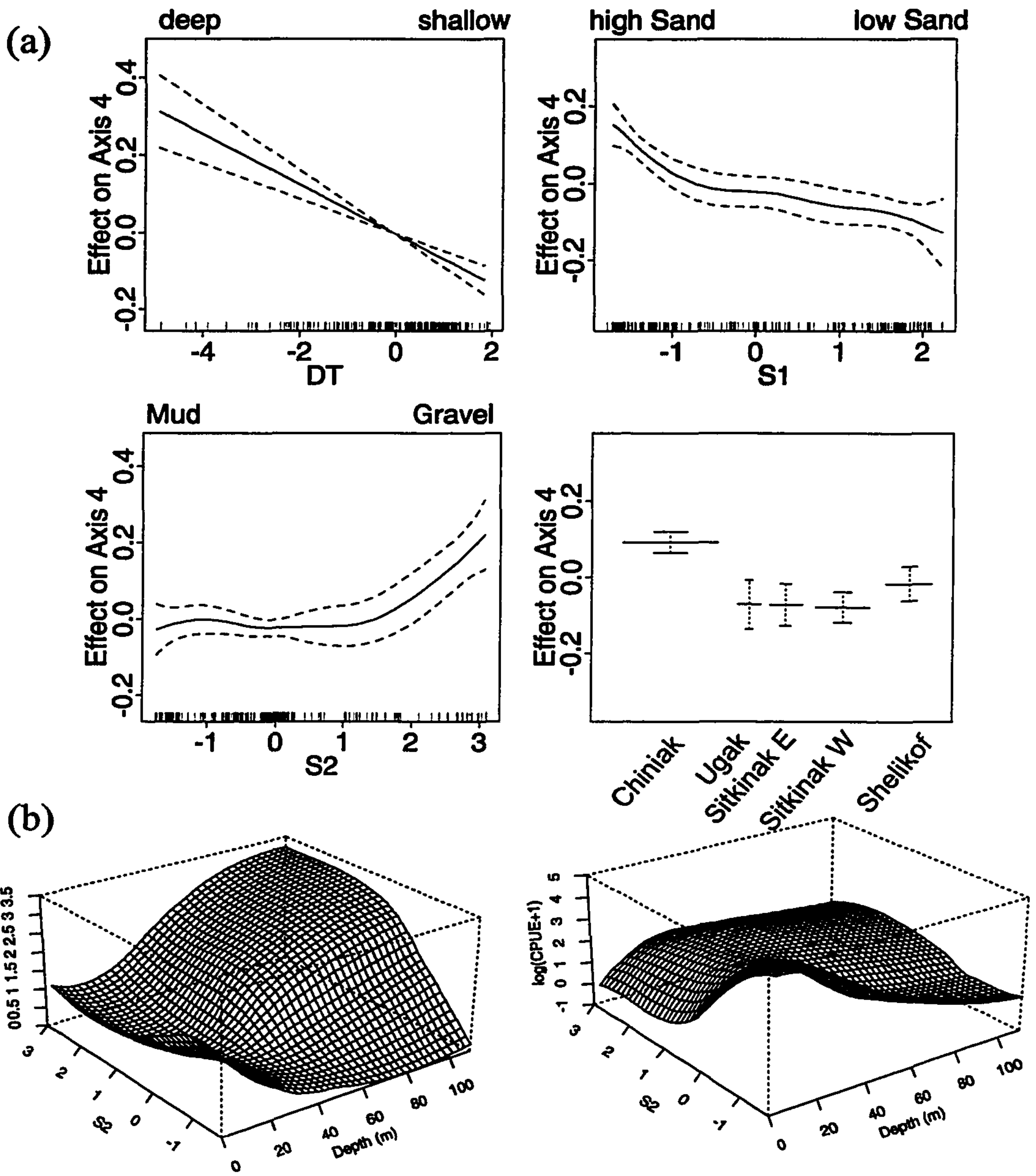

Figure 4.10: (a) Estimated relationship between Axis 4 and environmental variables (for details see Figure 3) and (b) smoothed trend surfaces of abundance (log(CPUE+1)) for the two species groups defined by Axis 4 as a function of depth and S2. Combined abundance of species positively correlated with 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. Smoothed trend surfaces were estimated using a robust, locally weighted smoother (LOESS).

Discussion

Our study suggests that the small demersal fish community in shallow nearshore areas around Kodiak Island was primarily structured along gradients of depth-temperature 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 depth-temperature gradient (Fig.4.7 - 4.10).

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, Bianchi 1992a, Moranta et al. 1998), the continental shelf off Oregon (Day and Pearcy 1968), the abyssal North Atlantic (Haedrich and 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 northeastern United States (Colvocoresses and Musick 1984). Unlike Blaber et al. (1994a) and Colvocoresses and Musick (1984), we found a strong relationship between indices of species composition and sediment variables (Table 4.5). 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 and 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 continental shelf of the Middle Atlantic

Bight using a remotely operated vehicle equipped with video camera. They found strong species-specific relationships between the small-scale distribution of several species and microhabitat 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 and 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 depth-temperature 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 and 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 presence/absence patterns and abundances of four 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 and 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 and 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 depth/temperature 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 4.5), 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 depth-temperature gradient over the observed range. Day and 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 (<200m). The entire depth range sampled in our study fell within the smallest depth stratum examined by Day and 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 (Fig. 4.3, 4.5). 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. 4.4). 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. observations). Spatial heterogeneity is typically associated with a higher diversity of animal species (Begon et al. 1990) and may explain the observed patterns.

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. 4.6), 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, ROV observations seem to confirm that abundances of juvenile fishes are lower on coarse sediments (Norcross and Mueter, 1999).

The four indices of species composition examined in our analysis describe different, independent aspects of community composition. Each index can be interpreted as representing two groups of species that were highly correlated (positively or negatively) with the index (Table 4.4) and each index in turn was related to different aspects of the environment (Table 4.5). 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 two or more indices (Table 4.4). 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 four indices that we examined were significantly related to the depth-temperature 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 depth-temperature 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 and 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 and 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 and Pearcy 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 and Cech 1988). Our analysis suggests strong non-linear effects of depth/temperature on all indices of species composition (Fig. 4.7 - 4.10). The patterns of change along the depth-temperature 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 depth-temperature and secondarily along gradients of sediment type as well as among geographic areas. While the depth-temperature 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.

Acknowledgments

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Chapter 5: Changes in species composition of the demersal fish community in nearshore waters of Kodiak Island, Alaska[1]

Franz J. Mueter and Brenda L. Norcross

Abstract

We examined the species composition of the demersal fish and shellfish community in seven different areas in the nearshore waters of Kodiak Island based on trawl survey data. A major part of the variability in the data set was attributed to trends over time, indicating a significant change in species composition in the early 1980s. Results agree with previous work and show a shift from a community dominated by shrimp and small forage fishes to one dominated by a group of large piscivorous gadid and flatfish species. The shift occurred rather abruptly in most areas between 1980 and 1982, but the pattern of change differed significantly among areas. Correlations between trends in the two groups of species were weak, but were consistent with the hypothesis that the decline in shrimp and forage fishes followed, rather than preceded, the increase in large piscivorous fishes. The results suggest predation as a possible reason for the observed changes.

Introduction

In the late 1970s large-scale climatic and oceanographic changes occurred in the North Pacific, which affected many parts of the marine ecosystem (Brodeur and Ware 1992; Brodeur and Ware 1995; Francis and Hare 1994; Hollowed and Wooster 1995). At the same time, shrimp

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and crab stocks declined precipitously in the Gulf of Alaska as well as the eastern Bering Sea, and most of the fisheries they supported have collapsed since 1980 (Orensanz et al. 1998). Declining shrimp populations in Pavlof Bay and in other nearshore areas in the central Gulf of Alaska were accompanied by declines in capelin and other forage fishes (Piatt and Anderson 1996; Anderson et al. 1997). A decrease in the availability of capelin in the nearshore environment is also evidenced by their reduced frequency of occurrence in the diet of seabirds in the 1980s and 1990s compared to the 1970s (Piatt and Anderson 1996). At the same time the abundance of flatfishes and gadids in the nearshore areas increased (Anderson et al. 1997).

Causes for this apparent shift in species composition are not well understood at present, and may include environmental effects, overfishing, or multiple causes acting simultaneously. Shrimp catches around Kodiak Island peaked in 1971 and began a steady decline into the early 1980s (Orensanz et al. 1998). Fishing effort remained high through most of this period, although fishery independent biomass indices for shrimp around Kodiak Island and in Pavlof Bay showed a strong declining trend (Anderson et al. 1997). While there is evidence that overfishing at least contributed to the decline in shrimp stocks, the influence of large-scale environmental forcing is hard to dismiss (Piatt and Anderson 1996; Orensanz et al. 1998). A marked increase in water temperature in the northern Gulf of Alaska (Royer 1989) may be in part responsible for the observed changes (Piatt and Anderson 1996; Anderson et al. 1997).

Much of the evidence for a shift in species composition is based on abundance data aggregated at the family level because trends in individual species may be obscured by high variability (Anderson et al. 1997). While long-term and large-scale trends are evident in the aggregated data, there has not been an analysis at the species level to test whether the change in species composition was significant, which species were affected, and whether the changes followed the same pattern in different areas. Therefore, the primary goal of our study was to statistically test changes in species composition of the groundfish community in the bays around Kodiak Island. Specifically, we derived multivariate indices that summarize the major patterns of variation in species composition, tested for significant changes in these indices over time, identified species that are primarily responsible for the observed changes, and compared the patterns of change among areas.

Materials and Methods

To test for changes in species composition, we analyzed trawl survey data collected between 1976 and 1995 by the Alaska Department of Fish and Game and the National Marine Fisheries Service in nearshore areas of the central Gulf of Alaska. The survey was conducted using a small-mesh trawl and targeted primarily shrimp (Anderson 1991); however, many groundfish species were caught incidentally. Assuming there were no underlying trends in catchability or in the size structure of fishes over time, the survey provides indices of abundance that reflect true changes in the sampled populations within the area covered by the survey.

We selected seven bays and nearshore areas on the east and south sides of Kodiak Island for our analysis: Marmot Island, Marmot Bay, Chiniak Bay, Ugak Bay, Kiliuda Bay, Twoheaded Gully, and Alitak Bay (Fig. 5.1). Within each of the seven areas between 2 and 5 strata were sampled following a stratified random sampling design (J.E. Blackburn, pers. comm.). We considered only strata that were sampled during at least 4 years of the survey since our primary interest was to detect trends over time in the data. Within a year sampling often extended from early May to early November with few or no samples collected in the month of July. To minimize bias due to seasonal differences we selected only tows collected between August and October. The final data set comprised 1035 hauls from a total of 14 survey years (Table 5.1).

All invertebrates and fish were grouped into 32 taxa (Table 5.2), primarily at the species and genus level. Shrimp were combined because we were primarily interested in the fish community. Fish were grouped at the coarsest level at which specimens were identified. Members of rare families that occurred in less than 1% of the hauls were excluded, as they may distort inferred patterns in species composition (Koch 1987). Catches of all species groups were standardized to catch-per-unit-effort (CPUE, kg per km towed) for analysis. CPUE data were

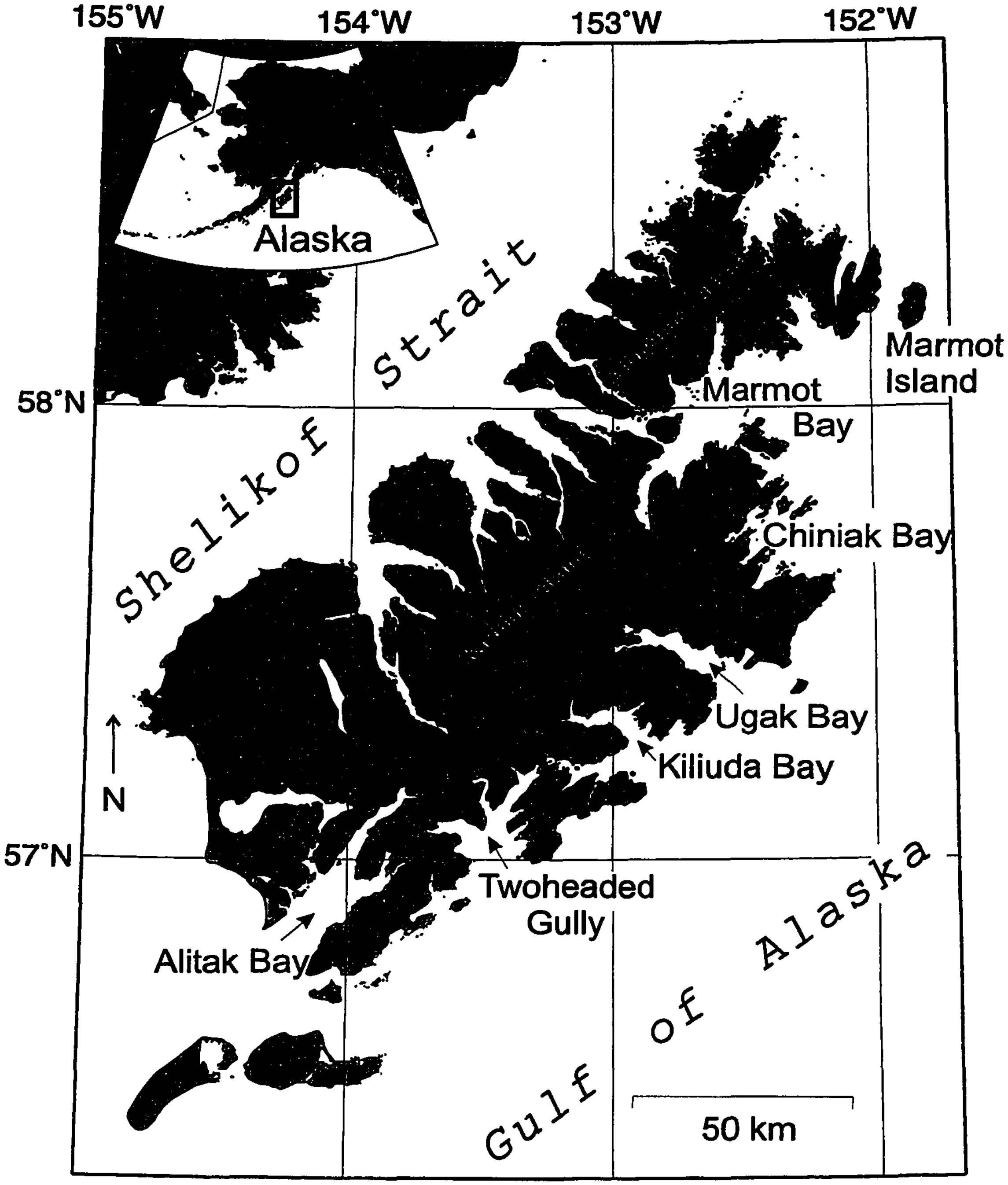

Figure 5.1: Kodiak Island showing 7 sampling areas where shrimp trawl surveys were conducted between 1976 and 1995.

Table 5.1: Number of stations sampled by the Alaska Department of Fish & Game in the September/October sampling period between 1976 and 1995 by area and year.

	76	77	78	79	80	81	82	83	84	85	86	87	89	92	95
Marmot Bay	6	12	12		7	8	8		10	8		9	10	14	16
Marmot Island	22	52	46		4	40	8		6	6		7	6		
Chiniak Bay			4	4	7	10	7	9	5			6	7	3	6
Ugak Bay	19	7	6		11	12	10		5	9	10		10		
Kiliuda Bay	24	10	35	27	18	10	9		10	9	10		10	10	6
Twoheaded Gully		21	16	32	13	13	16		12	10	13		13	8	8
Alitak Bay		10	9	12	16	28	21	9	12	22	12	12	9	7	9

transformed using a fourth-root transformation as recommended by Field et al. (1982). No standardization of species abundances was carried out because all species CPUEs were measured on the same scale and because standardization eliminates information on differences in absolute abundances of species among sites. While some authors advocate some form of standardization (Kenkel and Orloci 1986; Faith et al. 1987), Jackson (1997) argues that any standardization may produce artifacts in the patterns that emerge from compositional data.

To detect and relate patterns in the abundance of a large number of species to environmental or other independent variables, community ecologists have developed a variety of techniques that can be classified into two basic approaches: direct gradient analysis and indirect gradient analysis (Whittaker 1967; Ter Braak and Prentice 1988). Direct gradient analysis incorporates information about the environment directly into the analysis. Regression analysis is a form of direct gradient analysis with a single response variable – for example a regression of the abundance of one species on one or more independent variables (Ter Braak 1995). In the case of multiple species, multivariate direct gradient analysis techniques are needed to detect the main pattern in the relationship between species abundances and independent variables. Commonly used techniques are canonical correlation analysis, redundancy analysis, and canonical correspondence analysis (CCA). Correlation analysis and redundancy analysis assume

Table 5.2: Species and species groups used in analysis and proportion of total catch averaged over all hauls.

Scientific name	Common name	Proportion
Pandalidae \ Crangonidae	Shrimp	39.1%
Theragra chalcogramma	Walleye pollock	24.3%
Hippoglossoides elassodon	Flathead sole	14.6%
Atheresthes stomias	Arrowtooth flounder	6.3%
Gadus macrocephalus	Pacific cod	3.8%
Limanda aspera	Yellowfin sole	1.6%
Cottidae	Sculpin	1.5%
Mallotus villosus	Capelin	1.3%
Hippoglossus stenolepis	Pacific halibut	0.8%
Chionoecetes bairdi	Tanner crab	0.8%
Paralithodes camtschatica	Red king crab	0.7%
Microgadus proximus	Pacific tomcod	0.6%
Trichodon trichodon	Pacific sandfish	0.6%
Anoplopoma fimbria	Sablefish	0.6%
Lepidopsetta spp.	Rock Sole	0.6%
Zoarcidae	Eelpout	0.5%
Clupea pallasi	Pacific herring	0.5%
Thaleichthys pacificus	Eulachon	0.4%
Lumpenella longirostris	Longsnout Prickleback	0.3%
Rajidae	Skates	0.3%
Platichthys stellatus	Starry Flounder	0.2%
Osmeridae	Smelt	0.1%
Sebastes spp.	Rockfish	0.1%
Glyptocephalus zachirus	Rex sole	0.1%
Bathymaster signatus	Searcher	0.1%
Squalus acanthias	Dogfish	0.1%
Microstomus pacificus	Dover Sole	0.1%
Stichaeidae	Prickleback	0.1%
Cyclopteridae (Cyclopterinae)	Snailfish	0.03%
Podothecus acipenserinus	Sturgeon poacher	0.02%
Cancer magister	Dungeness crab	0.02%
Zaprora silenus	Prowfish	0.01%

that species are linearly related to ecological gradients, but CCA allows a non-linear response of the species to underlying variables. A disadvantage of direct gradient analysis is that the set of relevant independent variables needs to be determined a priori. If noisy or irrelevant variables are included, patterns in species composition can be greatly distorted (McCune 1997).

By contrast, indirect gradient analysis is a two-stage approach (Whittaker 1967). In the first step, species abundance data from a potentially large number of species and sites are summarized and sites are arranged in ordination space. Resulting patterns in the ordination of sites are secondarily related to independent variables, for example by regressing site scores from one or more ordination axes on the variables. Commonly used ordination techniques for indirect gradient analysis are principal component analysis (PCA), correspondence analysis (CA), detrended correspondence analysis (DCA), and non-metric multidimensional scaling (NMDS). PCA assumes a linear response between each species and underlying ecological gradients, while CA and DCA allow a unimodal response. No particular response model underlies NMDS, but it has been shown to be robust to a wide variety of potential relationships between individual species abundances and environmental gradients (Minchin 1987).

All ordination techniques are based on a measure of between-site dissimilarities. In the case of PCA, the implicit dissimilarity measure is Euclidean distance, while Chi-square distance is the built-in dissimilarity measure in all forms of correspondence analysis. In contrast, NMDS allows the choice of any dissimilarity measure; thus a measure that is appropriate to the data at hand can be chosen. A confusing variety of dissimilarity measures have been proposed in the literature (e.g. Washington 1984) and few authors agree as to which measure is most appropriate. Trawl data are characterized by the joint absence of many species from a large number of sites, resulting in many zero values in the data matrix. Dissimilarity measures that are not affected by such joint absences are clearly preferable. One such measure, the Bray-Curtis index, has been shown to be a robust measure of ecological distance (dissimilarity) in the presence of joint absences (Field et al. 1982). Based on suitable measure of between-site dissimilarities, NMDS attempts to arrange sites in a low-dimensional space such that distances in the ordination space are close to the underlying between-site dissimilarities (Kruskal 1964).

We used Bray-Curtis dissimilarities between each pair of sites, followed by an NMDS ordination, to summarize patterns in species composition of the groundfish community based on a matrix of transformed abundances consisting of 1035 rows (sites) and 32 columns (taxa). The initial ordination was carried out in 2 dimensions and the number of dimensions was increased until a given goodness-of-fit criterion was achieved. Goodness of fit was assessed using Kruskal's stress criterion, a measure of discrepancy between the Euclidean distances in ordination space and the underlying Bray-Curtis dissimilarities (Kruskal 1964). We accepted the fit if Kruskal's stress was less than 15%. The final configuration from the ordination was rotated such that the first axis corresponded to the axis of maximum variation. The scores for each site along each rotated ordination axis were used as indices of species composition. Each axis can be interpreted as representing a different, independent aspect of species composition, with axis 1 scores representing the major mode of variation in species composition. The axis scores have no units as they reflect relative dissimilarities only.

We estimated and tested trends in species composition over time for significance within each sample stratum using an analysis of covariance of axis scores with depth and date of sampling (Julian day) as covariates:

$$(Axis\ scores)_{ijk} = \alpha + (stratum)_i + (year)_{j(i)} + \beta_1 \cdot depth + \beta_2 \cdot Julian + \varepsilon_{ijk} \qquad \text{(A)}$$

where the subscripts denote strata (*i*), years within strata (*j*) and observations within each stratum / year combination (*k*). Depth was included because species composition is typically strongly related to depth (Mueter and Norcross, in press; Chapter 4). Initially, we assumed that the depth response does not differ among strata. To test this assumption we compared the above model to a model allowing a separate depth response within each stratum. Date of sampling was included as a covariate because species composition may vary over time within the three-month sampling period. Model A was further compared to a model pooling observations over all strata within an area to test whether the trend in axis scores over time differed significantly among strata. To test whether the time trend could be approximated by a polynomial fit we fitted models that included

2^{nd} and 3^{rd} degree polynomials of year, instead of estimating separate means for each year. Models were compared using F-tests.

Scatterplots and rank correlations between axes scores and individual species abundances were used to identify which species were associated with each ordination axis. Plotting the abundance of a species against axis scores helps to identify individual species that are strongly related to an axis, and to assess the nature of the relationship. The use of rank correlations is only appropriate if the relationship between the abundance of a species and the axis scores is at least monotone. While it is not clear what the nature of the relationship should be on theoretical grounds, we found that species were almost always monotonically related to the ordination axes. Based on visual inspection of scatterplots we chose a cut-off point for the magnitude of rank correlations of 0.35 to identify species that were clearly associated with an ordination axis. Correlations between species abundances and axes scores cannot formally be tested for significance at a given significance level, because the scores are based on an ordination of species abundances. Thus they are inherently related.

Results

The NMDS ordination of species abundance data in 5 dimensions achieved a stress of 12.1% and there was a tight relationship between Bray-Curtis dissimilarities and Euclidean distances in the final configuration of the ordination (Spearman's rank correlation = 0.93). Therefore, we considered the fit in 5 dimensions satisfactory. The ordination was repeated with several different starting configurations to minimize the chances of obtaining a solution corresponding to a local minimum in the stress criterion. The first ordination axis accounted for 30% of the overall variation, while axes 2-5 accounted for 22, 20, 16 and 13% of the variance respectively.

The first NMDS axis (Model A fit: $F=19.81$, $p<0.001$, $r^2=0.77$) primarily reflected interannual variation, i.e. there were much stronger differences in axis 1 scores with time than with strata or depth, as indicated by a high coefficient of partial determination for the year effect

($r_{year}^2 = 0.69$). The trend in axis 1 scores over time differed significantly among strata within areas ($F=5.15$, $p<0.001$). When examining each area individually we found that most areas had significant differences among strata ($p<0.005$), except Chiniak Bay ($F=0.42$, $p=0.531$) and Alitak Bay ($F=1.92$, $p=0.110$). Thus we pooled observations over strata within these 2 areas, but estimated separate time trends for each stratum in all other areas (Fig. 5.2). Approximating the time trend by a polynomial fit was inadequate, because residuals were highly autocorrelated and Model A fit significantly better ($F=6.51$, $p<0.001$). Therefore, separate means were estimated for each year. The depth effect appeared to differ among areas ($F=4.93$, $p<0.001$), but not among strata within individual areas ($p> 0.15$ in all cases). Including Julian date as a covariate in model A did not significantly improve the fit ($F=1.414$, $p=0.235$), thus there was no indication that axis 1 scores varied over time within years.

Axes 2 and 3 were primarily related to variations in species composition along the depth gradient and among areas (Model A fits: $F=10.80$, $p< 0.001$, $r^2=0.64$ and $F=8.10$, $p<0.001$, $r^2=.58$). Only a small proportion of the variance in axis 4 and axis 5 scores was explained by model A ($r^2=0.37$ and 0.30 respectively). Most of the variation in these axis scores was related to other, unknown gradients. Because the focus of our paper is on differences in species composition over time, only results for axis 1 are presented.

The estimated means for axis 1 scores declined significantly in most areas between 1980 and 1982 (Fig. 5.2). Although the mean scores differed among strata within most areas, the same sharp drop was evident in all strata. The decline was least evident at Marmot Island and in Chiniak Bay. Alitak Bay was unique in that the decline was much more gradual and the most significant change occurred after 1985 (Fig. 5.2). Furthermore, in those areas that were sampled during 1978 (Marmot I., Kiliuda Bay, Twoheaded Gully, and Alitak Bay), the axis 1 scores were significantly lower in 1978 compared to other years in the 1976-1980 period. This suggests that species composition in 1978, at least in these bays, was more similar to that in later years.

Examination of the underlying species abundances revealed that the decline in axis 1 scores was related to a strong decrease in catch-per-unit-effort of shrimp, as well as small

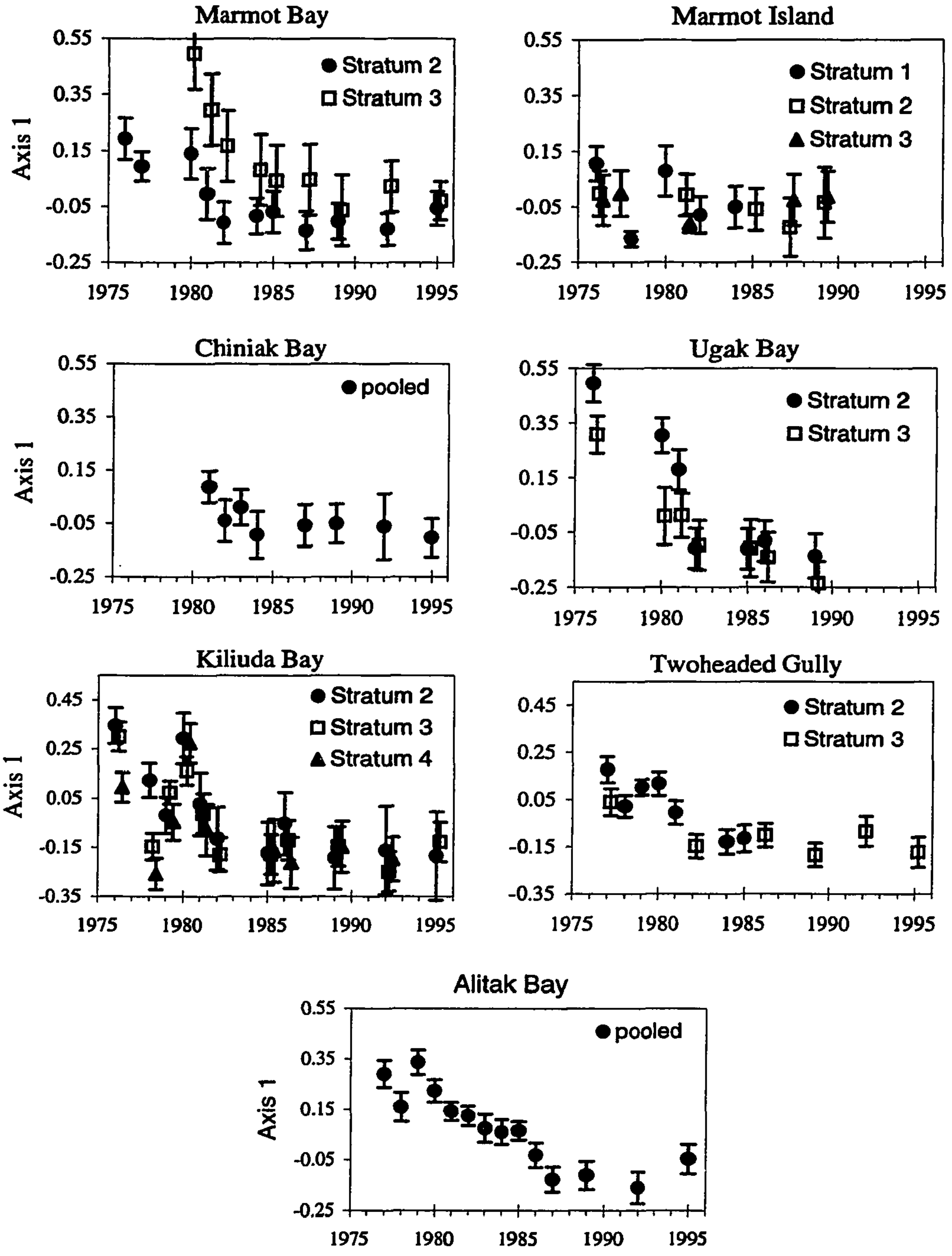

Figure 5.2: Estimated means for the first index of species composition (axis 1 scores) by year and area with 95% pointwise confidence intervals based on model A (see text). Observations in Chiniak Bay and Alitak Bay were pooled across strata.

schooling forage fishes, and a nearly simultaneous increase of several piscivorous flatfish and gadid species. A group of five taxa (shrimp, Pacific herring, capelin, Pacific sandfish, and Pacific tomcod) had a positive association with the axis 1 scores (Group A, Fig. 5.3). A second group consisting of arrowtooth flounder, flathead sole, Pacific cod, and walleye pollock (Group B) was negatively rank correlated with axis 1 scores (Group B, Fig. 5.3). Axis 1 can thus be interpreted as contrasting these two species groups.

Estimates of the combined CPUE of Group A and the combined CPUE of Group B over time for each of the 7 areas suggest a clear shift in community composition in at least four of the seven areas between 1980 and 1982 (Fig. 5.4). CPUE estimates were based on the same model that produced the best fit for axis 1, however we pooled strata within each area to examine overall trends by area. Model fits were poor because there were significant differences among strata in most cases and residuals were skewed due to the presence of zero values. While the fitted means indicated the main trends in the two species groups, confidence intervals are unlikely to be accurate at the stated significance level due to the poor model fits. The CPUE of Group A, consisting of shrimp and small forage fishes, decreased in all areas from 1980 to 1982, but the sharpest decline in Alitak Bay did not occur until after 1984. Catches of Group B, consisting of large piscivorous species, tended to increase during the same time period, although the increase was generally less pronounced (Fig. 5.4). Marmot Bay, Ugak Bay and Twoheaded Gully most clearly showed a shift in community composition between 1980 and 1982.

To examine possible cause and effect relationships between changes in the two groups we examined correlations between the abundances of Group A and Group B species at different lags. Because of the time series nature of the data and strong autocorrelation, we used differences in abundance between consecutive sampling years, rather than the abundances themselves. Differencing is commonly used to remove autocorrelation in time series data (Diggle 1990). Cross-correlations between the differenced trends in Group A and B showed few significant correlations (Table 5.3). Correlations at lag -1 were weak and inconsistent. At lag 0, most correlations were positive, suggesting that in most bays a trend in Group A was accompanied by

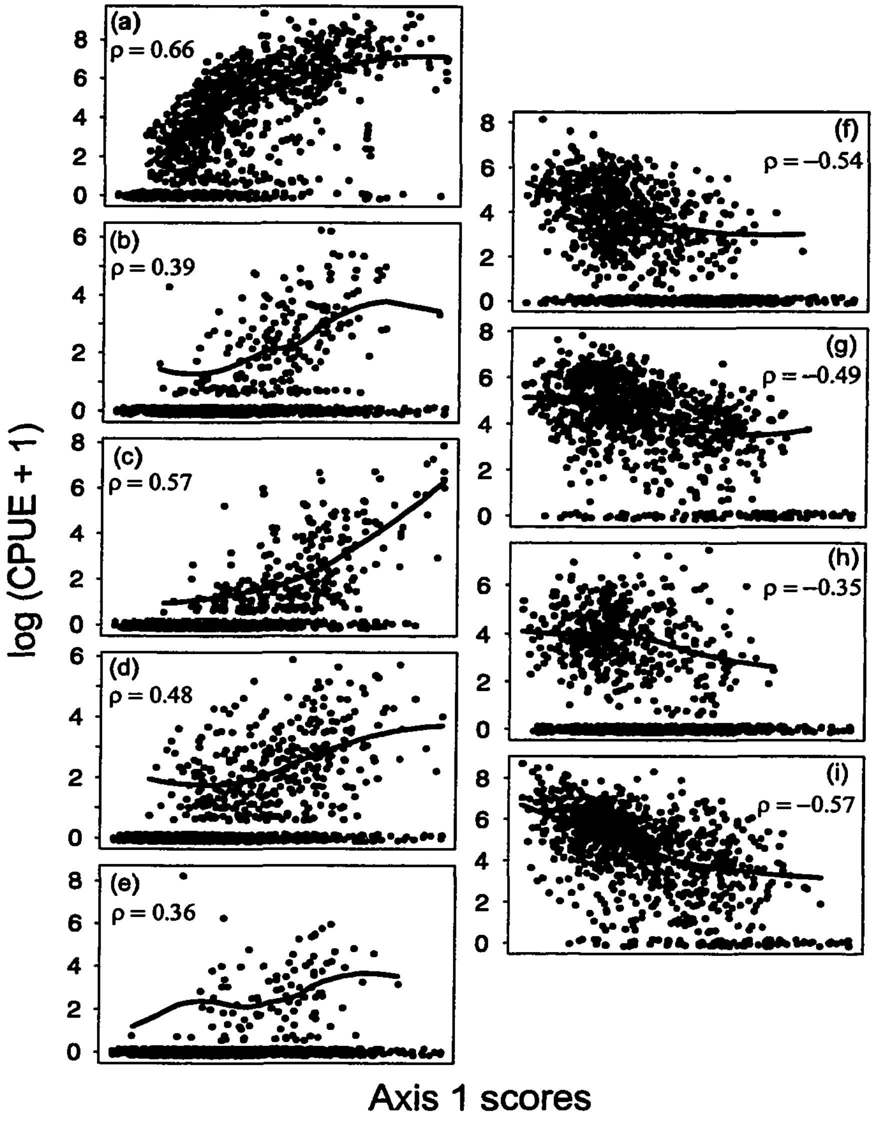

Figure 5.3: Scatterplot of log(CPUE+1) against first index of species composition (axis 1 scores) for five species that were positively rank correlated (ρ) with the index (group A: shrimp (a), Pacific herring (b), capelin (c), Pacific sandfish (d) and Pacific tomcod (e)) and four species that were negatively correlated with the index (group B: arrowtooth flounder (f), flathead sole (g), Pacific cod (h) and walleye pollock (i)). Zero CPUE values were jittered along y-axis by adding a small random component to indicate number of observations. Non-parametric smooth trend (LOESS, heavy line) was fitted to positive CPUEs (excluding zeros).

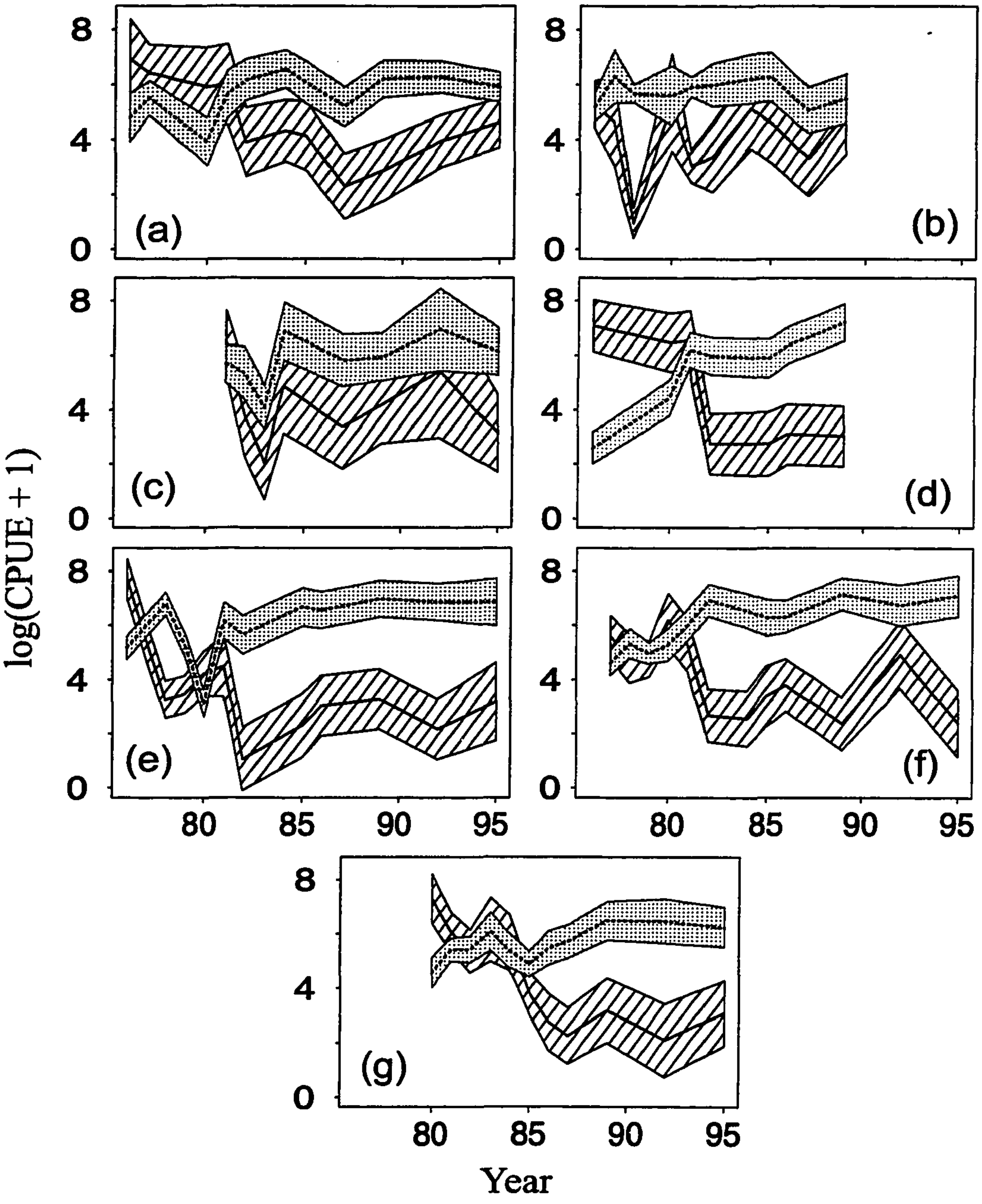

Figure 5.4: Estimated means and 95% confidence intervals for trends over time of the combined CPUE of Group A: shrimp, Pacific herring, capelin, Pacific sandfish, and Pacific tomcod (bars) and the combined CPUE of Group B: arrowtooth flounder, flathead sole, Pacific cod, and walleye pollock (stipples) in Marmot Bay (a), Marmot Island (b), Chiniak Bay (c), Ugak Bay (d), Kiliuda Bay (e), Twoheaded Gully (f) and Alitak Bay (g).

a parallel trend in the piscivorous group (Group B) between consecutive sampling years. However, only one of the positive correlations (Chiniak Bay) was significant. Two correlations at lag 0 were negative, but only one (Twoheaded Gully) was significant. For lag 1, in 5 out of 7 bays an increase in the piscivorous group between 2 sampling events was followed by a decrease in Group A. However, the correlation was significant only at Marmot Island. Positive correlations at lag 0 and negative correlations at lag 1 in four of the bays suggest that the increase in gadids and flatfish species preceded the decline in shrimp and small forage fishes in these bays.

Table 5.3: Summary of cross-correlations between differenced trends in two species groups at 3 different lags by area. Trends were estimated for the combined CPUE of shrimp, Pacific herring, capelin, Pacific sandfish, and Pacific tomcod (Group A) and the combined CPUE of arrowtooth flounder, flathead sole, Pacific cod, and walleye pollock (Group B). Each time series was differenced by taking the difference in estimated CPUE between consecutive sampling periods. Cross-correlations are shown for lag –1 (Group A leading Group B), lag 0, and lag 1 (Group B leading Group A).

Area	Lag : –1	Lag: 0	Lag: 1
Marmot Bay	- 0.26	0.21	- 0.27
Marmot Island	0.16	0.29	- 0.73 *
Chiniak Bay	- 0.29	0.89 *	- 0.55
Ugak Bay	0.24	0.41	- 0.55
Kiliuda Bay	0.14	-0.12	- 0.48
Twoheaded Gully	0.40	-0.73 *	0.05
Alitak Bay	-0.39	0.30	0.004

* significant at α=0.05

We examined changes in Alitak Bay more closely because of differences in the observed time trends between Alitak Bay and the other bays (Fig. 5.5). The CPUE of Pacific cod and walleye pollock increased in Alitak Bay from 1980 to 1983, while flathead sole did not increase over the same time period (Fig. 5.6). Arrowtooth flounder was found in very low abundances in Alitak Bay prior to 1984 and increased strongly between 1984 and 1985. Pacific cod showed a pattern of increasing CPUEs from 1980 to 1985 that was very similar in all areas, including Alitak Bay (Fig. 5.7). Arrowtooth flounder CPUEs, while increasing in all other areas between 1980 and 1981, did not increase in Alitak Bay until 1984, suggesting that the delayed decline in shrimp and forage fishes in Alitak Bay may have been related to the absence of arrowtooth flounder prior to 1984.

Discussion

The nearshore groundfish community around Kodiak Island

Although the patterns of change in our index of species composition (axis 1 scores) differed between Alitak Bay and the other areas, there is likely to be a single underlying cause for the observed shift in species composition, because of the wide geographic extent of the changes (Orensanz et al. 1998). Because the observed changes around Kodiak Island were related to the dynamics of two species groups, changes in the relative abundance of these groups within each area provide a means to examine possible cause and effect relationships. Environmental changes may influence both groups simultaneously or lead to changes in one group, which in turn results in changes in the other group. There was little statistical support for a relationship between the trends in species Groups A and B at the level of individual bays. There was some evidence that increases in the piscivorous were followed by decreases in the shrimp and forage fish group (Table 5.3). One obvious mechanism that is consistent with this pattern is predation of large piscivorous fish on shrimp and small prey fish. All species in Group B are known predators of shrimp (Yang 1993) and there is anecdotal evidence that Pacific cod in the bays around

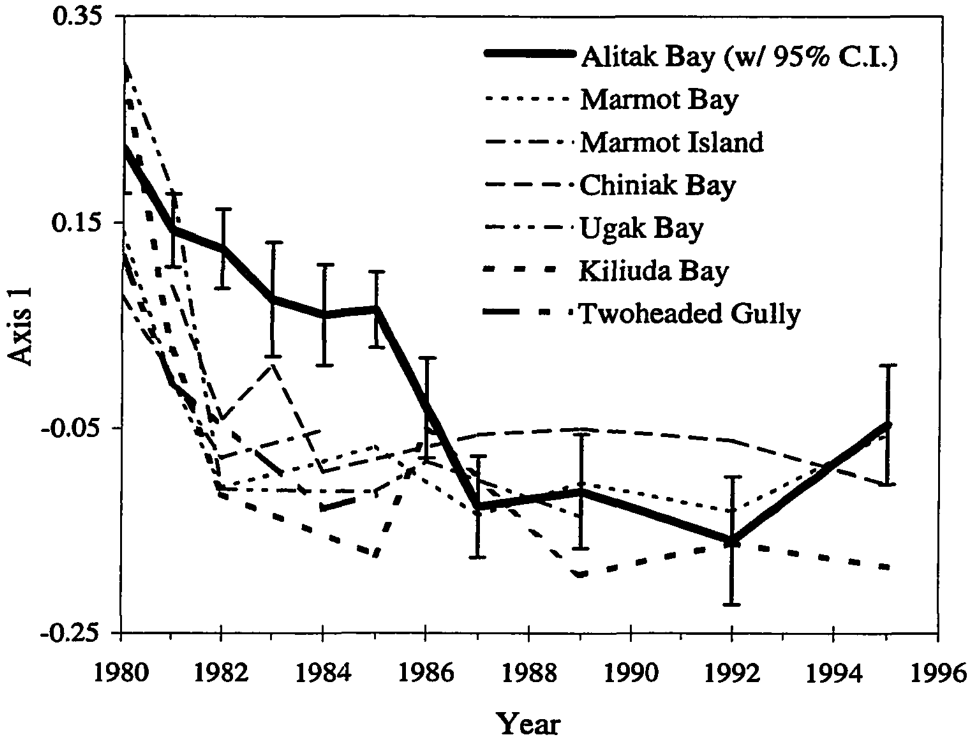

Figure 5.5: Trajectories of the means of the first index of species composition (axis 1) from the 7 areas sampled. Means for Alitak Bay (solid line) include error bars indicating 95% confidence intervals.

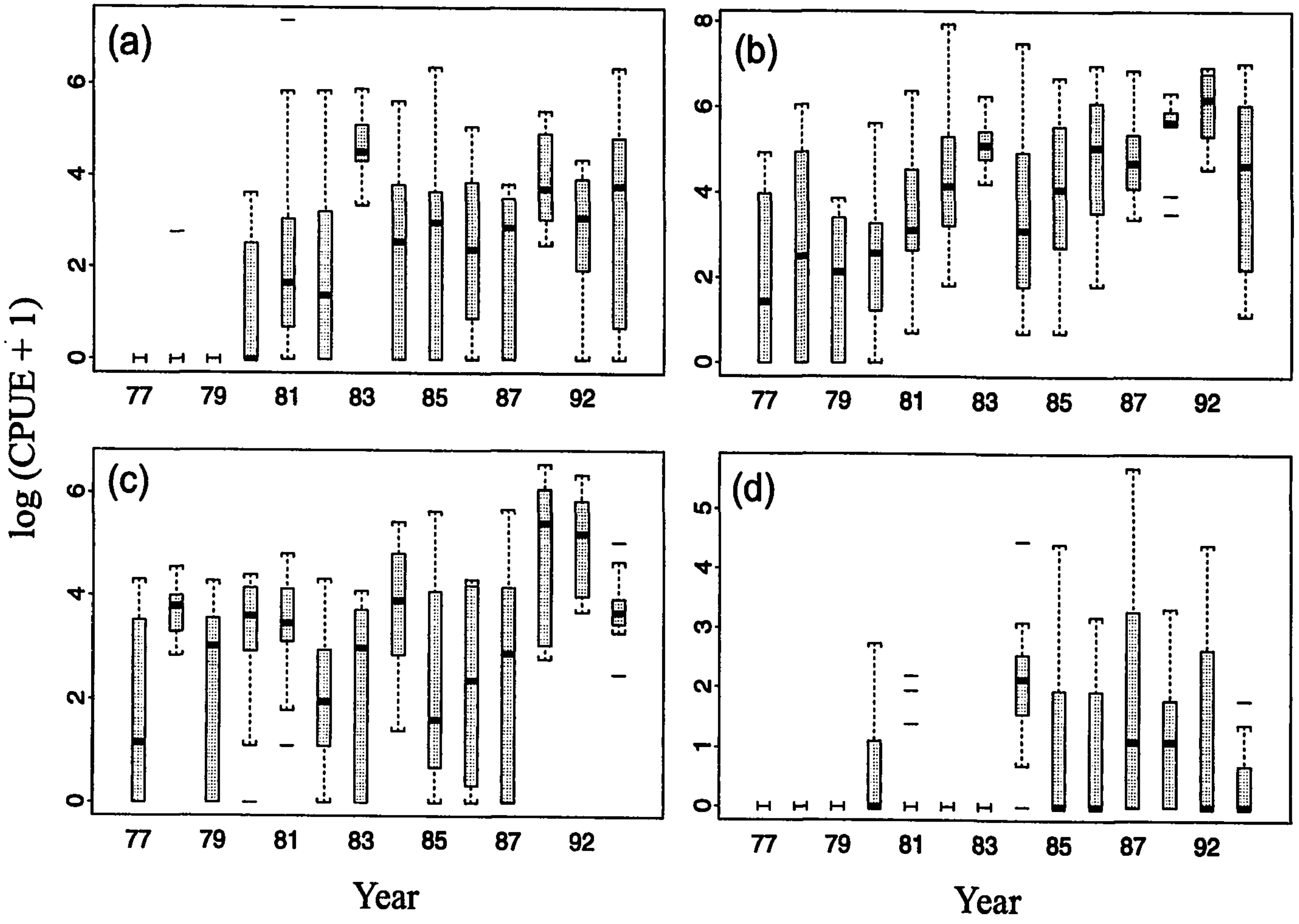

Figure 5.6: Observed abundances (log(CPUE+1)) of Pacific cod (a), walleye pollock (b), flathead sole (c) and arrowtooth flounder (d) in Alitak Bay by sampling year. Boxplots indicate, for each species and year, the median (dark horizontal bar), lower and upper quartiles (stippled box), and range (dotted "whiskers"). Outliers that are more than 1.5 times the interquartile range above the upper or below the lower quartile are shown as individual horizontal bars.

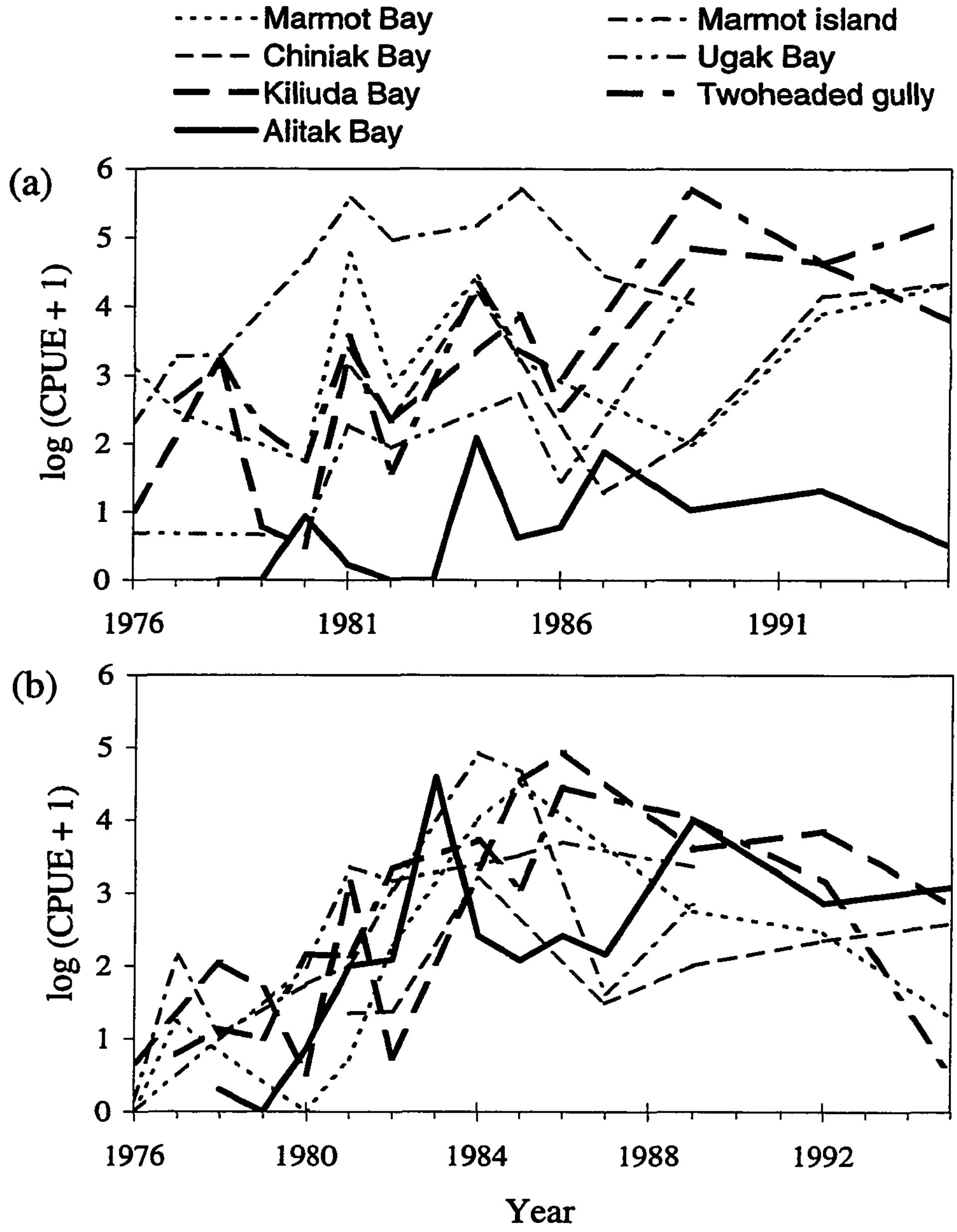

Figure 5.7: Estimated time trends of CPUE for arrowtooth flounder (a) and Pacific cod (b) in seven areas sampled around Kodiak Island between 1976 and 1995.

Kodiak preyed heavily on shrimp during the early 1980s (J.E. Blackburn, pers. comm.). In other areas in south central Alaska, the crash in pink shrimp populations in the 1980s has been attributed to an increase in natural mortality, presumably resulting from predation (Fu et al. in press). Thus there is some support for the hypothesis that the decrease in the abundance of shrimp and small forage fishes in the early 1980s was related to and followed an increase in the abundance of large piscivorous flatfish and gadid species. The hypothesis does not address the ultimate cause responsible for the increase in predatory fishes in the nearshore environment during the early 1980s.

If the ultimate cause of the observed changes was overfishing of shrimp, an increase in the piscivorous group would be expected to follow the decline in shrimp. We found no support for this hypothesis (Table 5.3, lag -1) and overfishing cannot explain the fact that small forage fishes declined simultaneously with the shrimp resource. Furthermore, it would be difficult to explain why large piscivorous fishes would replace shrimp and small forage fishes, because the two groups occupy very different trophic niches.

Alternatively, overfishing and environmental changes could have acted in concert to cause the observed shift in species composition. The most likely scenario is that heavy fishing contributed to the initial decline in shrimp abundance after the fishery peaked in the early 1970s (Orensanz et al. 1998). Possibly as a result of changes in the physical environment, the abundance of large predatory fishes in nearshore areas increased in the early 1980s, which may have led to the rapid demise of already depressed shrimp populations and to a simultaneous decline in abundance of small forage fish species.

Whatever the ultimate cause for the observed shift in species composition, the patterns of change clearly differed among areas spanning a relatively restricted geographical range (Fig. 5.2). Therefore statistical linkages between changes in species composition and large-scale environmental factors will be difficult to establish, as they require the use of aggregate measures of species composition or species abundances. Such measures may be misleading if they average over responses from a number of areas with different trends. When trying to elucidate mechanisms that led to the observed changes, differences among areas may be more important than the average response over a large area. For example, understanding the marked difference in the timing of the observed shift in community composition between Alitak Bay and the other areas sampled (Fig. 5.5) may be more helpful in understanding possible causes for the shift than correlations at larger scales.

One obvious physical difference between Alitak Bay and the other areas is the presence of a relatively shallow sill (~40 m) in Alitak Bay, which may affect water mass characteristics and the distribution of demersal fishes. Bottom temperatures in Alitak Bay indicate that low temperatures (< 4°C) can persist inside Alitak Bay below 70 m, in contrast to comparable depths in other bays and on the shelf outside Alitak Bay (B.L. Norcross, unpublished data). If warm temperatures contributed to the decline of shrimp and small forage fishes (Piatt and Anderson 1996; Anderson et al. 1997), cold temperatures in the deep waters of inner Alitak Bay may have provided a "cold refuge" for these species for several years.

A different hypothesis, relating to predation, is that the shallow sill isolated shrimp in Alitak Bay from shelf species, reducing predation by cod and other piscivores common on the shelf (J.E. Blackburn, pers. comm.). However, Pacific cod catches increased in Alitak Bay after 1980, at the same time as in all other areas (Fig. 5.7). Thus, while the increase in Pacific cod in all areas may have contributed to the decline in shrimp and forage fishes, it cannot explain the delayed decline in Alitak Bay. Unlike Pacific cod, arrowtooth flounder did not show a strong increase in Alitak Bay from 1980 to 1981, although such an increase was observed in all other areas (Fig. 5.7). The CPUE of Group A species remained high in Alitak Bay until 1984, in spite of high abundances of Pacific cod, but collapsed after 1984, simultaneously with a strong increase in arrowtooth flounder CPUE. The biomass of arrowtooth flounder in the Gulf of Alaska has greatly increased from the 1970s to the 1990s (NPFMC 1997), particularly in areas of less than 100 m depth (Mueter and Norcross, unpublished data). In the Gulf of Alaska, shrimp, capelin, and herring, three of the groups that declined sharply around Kodiak Island in the early 1980s, are important components of arrowtooth flounder diets (Yang 1993). Thus increases in the abundance of arrowtooth flounder may have contributed to the decline of shrimp and small forage fishes in the nearshore areas around Kodiak Island.

Modeling changes in species composition

The multivariate approach used here allowed us to directly test for differences in species composition over time, while taking the effects of other covariates and of the sampling design into account. The ordination axes provide indicators of species composition and can be used to identify the most important species that contribute to observed changes. Axes scores were suitable for statistical modeling, as they were close to normally distributed after conditioning on relevant independent variables. Therefore statistical tests based on the normal distribution could be used to test specific hypotheses regarding species composition. Multivariate indices generally are more sensitive to variations in species composition; therefore trends that may not be obvious otherwise can be detected (Austen and Warwick 1989).

A major concern when using any measure of species composition is whether the measure is sensitive to the level of aggregation in the species abundance data or to the inclusion or elimination of certain species or taxa. Of particular concern is whether the observed differences in species composition are primarily due to one or a few abundant species. When shrimp, the dominant species group in our example, was eliminated from the species abundance matrix, the resulting patterns in the first axis over time were virtually identical to the patterns observed with shrimp included (Mueter, unpublished data). The same was true when rare species were included in the analysis, suggesting that the index is highly robust to the subjective choices required in selecting species to include.

Another concern with the approach is the subjectivity required in choosing the number of dimensions in which to conduct the ordination. It is doubtful that the true dimensionality of the data can ever be known, i.e., what proportion of the variance in species composition can be attributed to noise. Kruskal's stress (Kruskal 1964) provides an objective criterion for choosing the number of axes. However, the choice of an acceptable level of stress is arbitrary. We have some evidence that the approach is robust to the number of axes. Whether the ordination was conducted in 5, 6 or 7 dimensions had virtually no effect on the first two axes (Mueter, unpublished data), which might be expected because the first axes typically account for most of the overall variation.

Unlike in other ordination techniques, the orientation of axes in NMDS ordination is arbitrary. Therefore we inserted an additional step in the analysis by rotating the final configuration of the NMDS ordination such that the major axis of variation was chosen as the first axis of species composition. Each further axis was perpendicular to the previous axis and was oriented along the major axis of the remaining variation. As in other indirect ordination techniques, there is no guarantee that the axes are aligned with any of the environmental gradients included in the analysis.

As an alternative to selecting the axis of major variation, the ordination axes may be rotated to maximize the correlation between the first axis and a specific gradient, in order to examine species composition along the chosen gradient. Patterns in species composition along this gradient can thus be examined. However, hypothesis tests involving this gradient would no longer be valid, as the index was chosen a priori to maximize variation along the gradient.

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Chapter 6: Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska[1]

Franz J. Mueter and Brenda L. Norcross

Abstract

We analyzed data from NMFS 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-effort (CPUE) of all groundfish 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. Results are discussed in terms of spatial and temporal patterns in productivity.

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Keywords: biomass, continental shelf, demersal fish, Gulf of Alaska, nonmetric multidimensional scaling, species composition, species diversity, species richness

Introduction

The continental shelf and upper slope of the Gulf of Alaska (Fig. 6.1) support a diverse community of demersal fishes. This community includes many commercial species that support rich demersal trawl and longline fisheries with landings averaging approximately 250,000 metric tons over the past two decades (Low 1993; NPFMC 1997). The most important species during the past decade were 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 this area (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 Gulf of Alaska (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 examining demersal fish assemblages from the GoA shelf and slope.

In order to understand, and eventually to predict, the effects of environmental variations on fish stocks, scientists and managers increasingly advocate ecosystem approaches to research

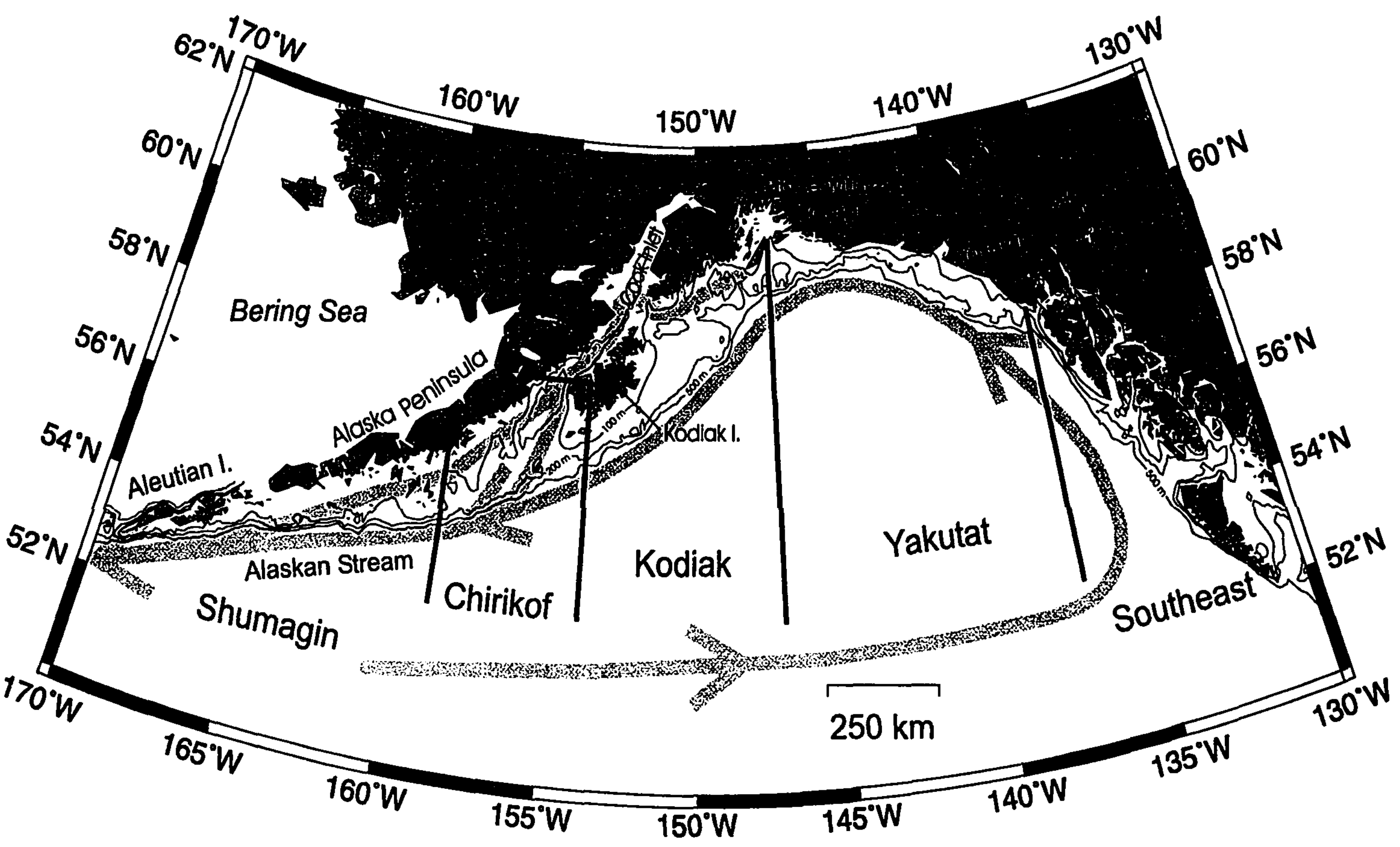

Figure 6.1: Bathymetric and geographic features of the Gulf of Alaska between 130° and 170° W. Heavy lines separate five areas used in survey design and analysis. Thin lines indicate 100 m, 200 m, and 500 m isobaths. Shaded arrows summarize major circulation patterns.

and management (Yaffee *et al.*, 1996; Boreman *et al.*, 1997; 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.

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. 6.1). The total study area is approximately 300,000 km^2, extending over a distance of 2600 km from Southeast Alaska to the eastern Aleutian Islands. The shelf width varies from less than 20 km in the westernmost part to more than 200 km in the Kodiak area and 50-100 km in the eastern GoA. Relatively deep, broad flat banks are separated by numerous troughs, some of which extend from the coastal fjords into deep water (Hampton et al. 1986).

The dominant oceanographic feature along the shelf and slope of the GoA is the Alaskan Stream, which forms the northern limb of the Alaskan Gyre and flows in a westerly direction along the continental slope (Fig. 6.1). The current varies in width from about 300 km off the coast of Southeast Alaska to less than 100 km to the west of Kodiak. Current speeds in the narrow parts can be as high as 100 cm/s (Reed and Schumacher 1986). Inshore of the Alaskan Stream on the shelf the westward Alaska Coastal Current (ACC) is generally present from at least Yakutat to the end of the Alaska Peninsula. This current is influenced by freshwater discharge with a strong seasonal amplitude resulting from a pronounced peak in freshwater input during September (Royer 1998). Seasonal variations are strong in the western GoA but are much less pronounced east of Prince William Sound. The ACC is generally constrained in a very narrow band because of easterly winds that result in onshore Ekman transport and convergence. During the summer when winds are weak or reversed, upwelling may take place locally (Reed and Schumacher 1986; Royer 1998).

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 starting in 1984 (Table 6.1). All surveys were conducted during the summer using 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. 6.1) and 4 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, slope), resulting in a total of 49 strata. Some modifications were made to the stratification scheme after 1987. Our analysis is based on current stratum boundaries. Details of the sampling design, data collection, and sample processing are described in Brown (1986), Stark *et al.* (1988), Martin and Clausen (1995), Stark and Clausen (1995), and Martin (1997). In our analysis we excluded data from the 0-100 m stratum in area Southeast, as it is mostly untrawlable and was not sampled during 3 out of 5 surveys. We further excluded from the analysis 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 (gear type 172, Table 6.1). In addition, an older

Table 6.1: 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.

	1984	1987	1990	1993	1996
Total number of hauls	867	758	705	774	807
(*gear type**: # hauls)	(*160*: 430) (*172*: 133) (*710*: 304)	(*172*: 380) (*717*: 378)	(*160*: 166) (*172*: 539)	(all *172*)	(all *172*)
Starting date	June 3	May 22	June 4	June 6	May 22
Ending date	October 2	September 10	September 9	September 7	July 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

* Gear types are: 160: Nor'eastern trawl; 170: poly-Nor'eastern high opening bottom trawl, 710: Japanese poly trawl; 717: Japanese poly trawl with roller gear.

Nor'eastern trawl (gear type 160) was used during parts of the 1984 and 1990 survey and two different Japanese trawls (gear types 710 and 717, Table 6.1) 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 (172) was used during all surveys, allowing us to estimate gear differences.

Data analysis

Our analysis was based on standardized catch-per-unit-effort of 72 fish taxa collected in the bottom trawl surveys. Catches were standardized to weight per unit area (kg / km^2), where the area swept by the trawl was estimated based on the measured distance trawled and estimates or measurements of the width of the net opening. Taxa to include in the analysis were selected based on the following criteria: 1) All species consistently identified to species level and occurring at least at 1% of the stations were included as species. 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 using fishing power coefficients provided in Tables 28 and 31 in Munro and Hoff (1995). Following standard NMFS methodology, we averaged estimated CPUEs by stratum, weighted the averages by stratum area, and combined them to obtain area-wide averages.

Based on 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. 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 (in review) and in Chapter 3. 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 then was 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 using randomization tests (Manly 1997). The 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, temperature, 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 using the five statistical areas depicted in Fig. 6.1 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 at all stations (Table 6.1), thus all regressions were done both with and without temperature included. Gear type was included as a nuisance variable in all models to account for differences in the indices between gear types. We opted to include gear type directly in our analysis instead 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). Area swept was only included for examining trends in species richness and diversity, since the number of species per haul is expected to increase with the area sampled. All other indices were based on standardized CPUEs. Thus they were already adjusted for area swept.

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 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, homogeneity of variance) and for outliers.

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 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 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 of these species, we used an analysis of covariance model of the following form:

$$\log(CPUE) = area + depth\ stratum + gear + (area \cdot depth\ stratum) + \beta \cdot year$$

Errors were assumed to be normally distributed. Thus CPUEs were 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 and/or depth strata to obtain the most parsimonious model.

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

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

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) 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/km^2) and the highest frequency of occurrence during all surveys (Table 6.2). 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/km^2, Table 6.2). 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 (5-40%), indicating high local abundances and a more restricted spatial distribution.

Species richness, as measured by the number of species per haul, was highly variable (Pseudo-$r^2 = 0.25$). As expected, the average number of species increased with area swept (Fig. 6.2). The number of species tended to peak at intermediate depths (200-300 m) and was highest in the eastern GoA (Table 6.3), decreasing steadily west of Prince William Sound (km 1100, approximately 147°W). Species richness appeared to decrease during the last month of the

Table 6.2: All groundfish taxa included in analysis and their estimated average CPUE (kg/km^2) 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 spp.	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 unident.	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.		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

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

Table 6.2: continued

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
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.		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
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 unident.	0.19	0.19	0.11	1.52	0.53	0.51	4
Triglops spp.		0.37	0.32	0.68	0.40	0.61	0.48	6
Stichaeidae	prickleback unident.	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 unident.	0.25	0.00	0.28	0.08	0.01	0.12	1
Gymnocanthus spp.		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		14786	17286	17436	18400	20662	17714	

survey season and showed some variation across years (Fig. 6.2). There was no consistent trend in species richness along the temperature gradient (not shown). One of the Japanese trawls (gear

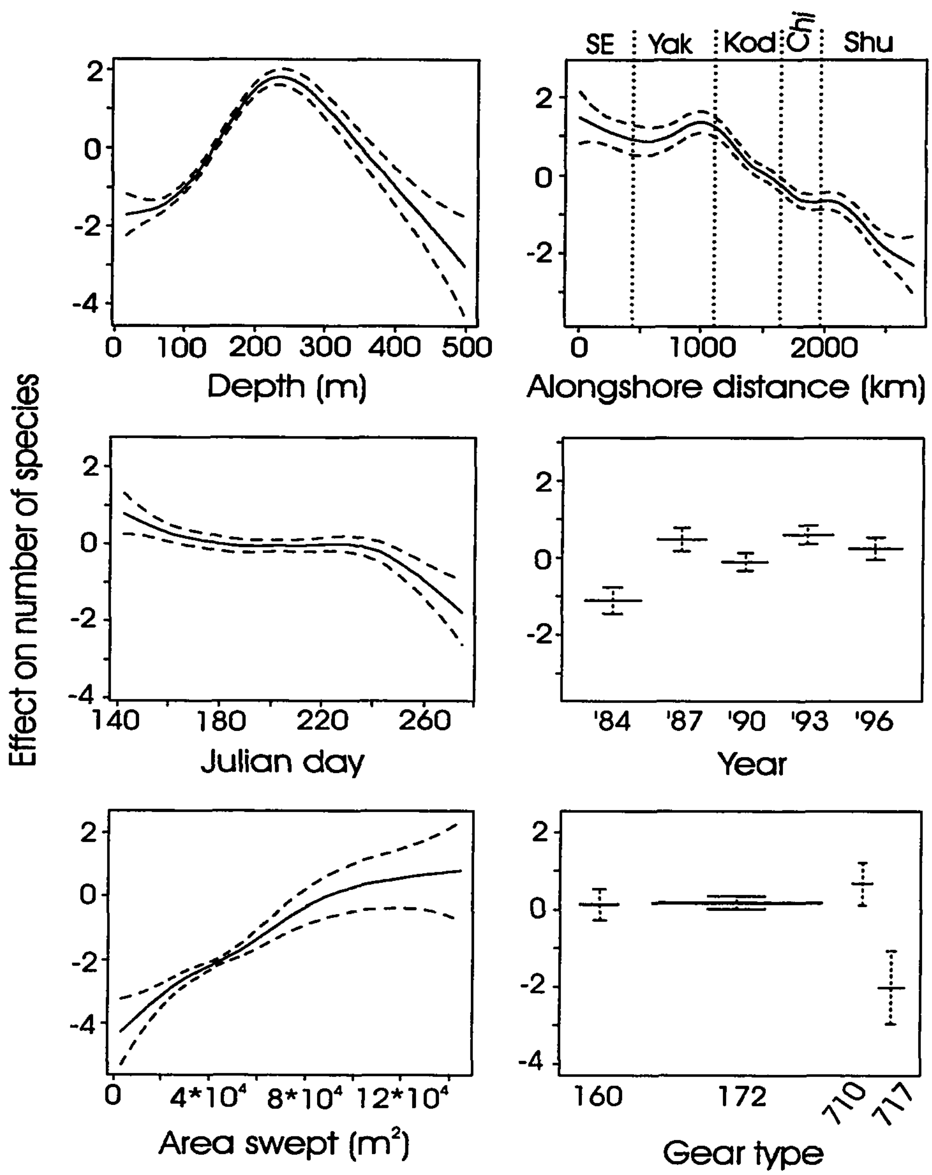

Figure 6.2: Estimated trends in number of species per haul by depth, alongshore distance, Julian day, year, area swept, and gear type. Alongshore distance was measured along the 200 m depth contour from east to west. Major geographic regions from east to west are Southeast (SE), Yakutat (Yak), Kodiak (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 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) 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.

type 717, Fig. 6.2) caught significantly fewer species per haul on average, suggesting a low catchability of this gear for at least some species.

Table 6.3: Average number of groundfish species caught per haul by depth stratum and geographic area, not adjusted for effects of other variables.

Depth stratum	# of species/haul (SE)	Area	# of species /haul (SE)
0 - 100 m	9.5 (0.12)	Shumagin	9.7 (0.11)
100 - 200 m	11.5 (0.08)	Chirikof	10.5 (0.12)
200 - 300 m	13.2 (0.13)	Kodiak	11.6 (0.11)
300 - 500 m	10.9 (0.15)	Yakutat	12.5 (0.14)
		Southeast	12.8 (0.20)

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. 6.3). Diversity generally increased with the number of species, which showed a very similar trend with depth (Fig. 6.2). Diversity was higher in the eastern Gulf and decreased west of Prince William Sound (Fig. 6.3, 6.4). It showed little variation over time, both within the survey period and across years. Area swept and temperature did not enter the best model, suggesting they had no significant effect on species diversity.

Total biomass (CPUE) showed significant trends with depth and alongshore distance (Fig. 6.5), 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 suggest 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. 6.4). Total CPUE appeared to decrease significantly after approximately Julian day 240 (Aug. 28); however, Julian day was confounded with alongshore distance

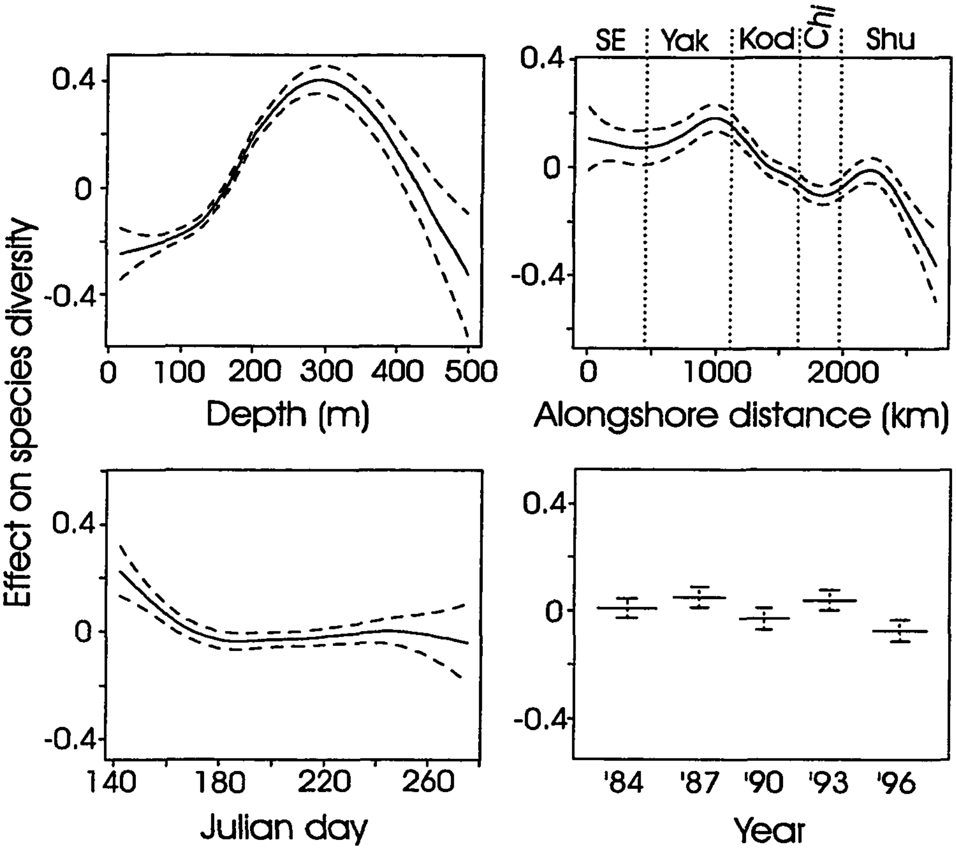

Figure 6.3: Trends in species diversity (Shannon-Wiener index) by depth, alongshore distance, Julian day, and year (area swept and gear type were not significant). For details see Figure 2.

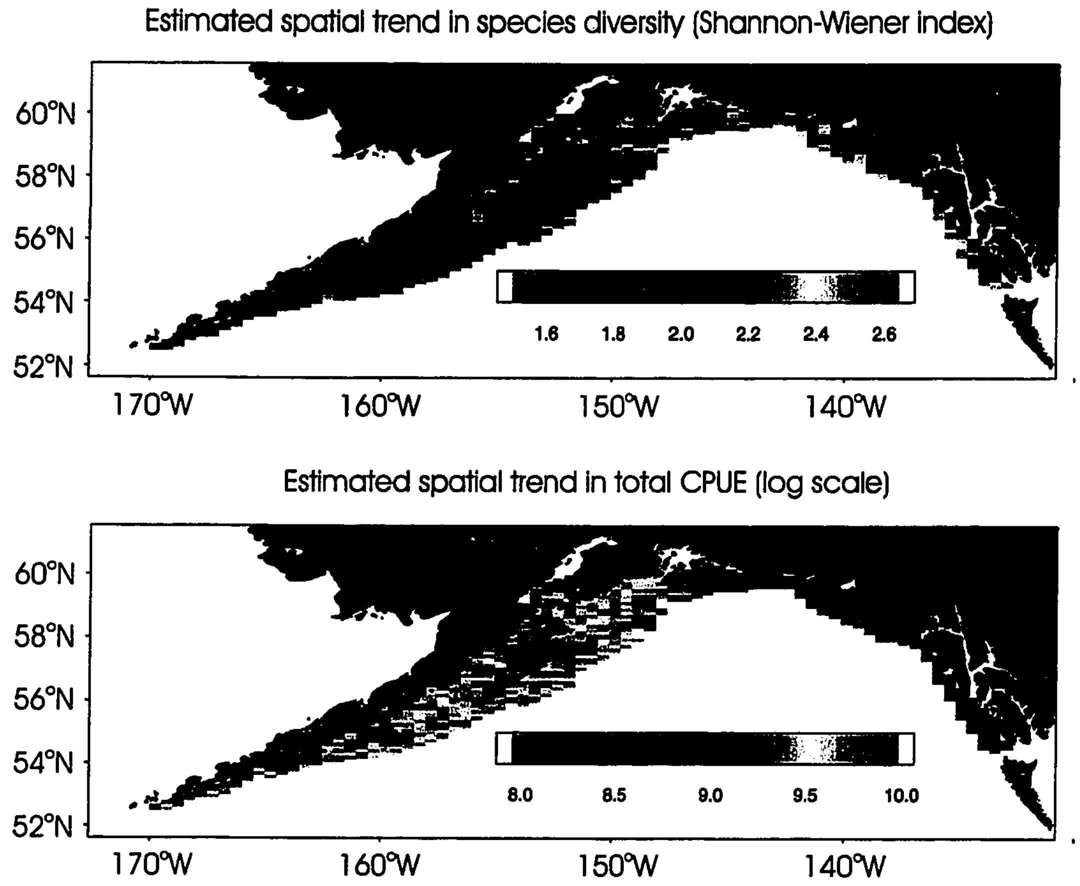

Figure 6.4: Spatial trends in species diversity (Shannon-Wiener index) and total CPUE. Trends are based on predictions from the best regression models for diversity and total CPUE (see Fig. 6.3 and Fig. 6.5).

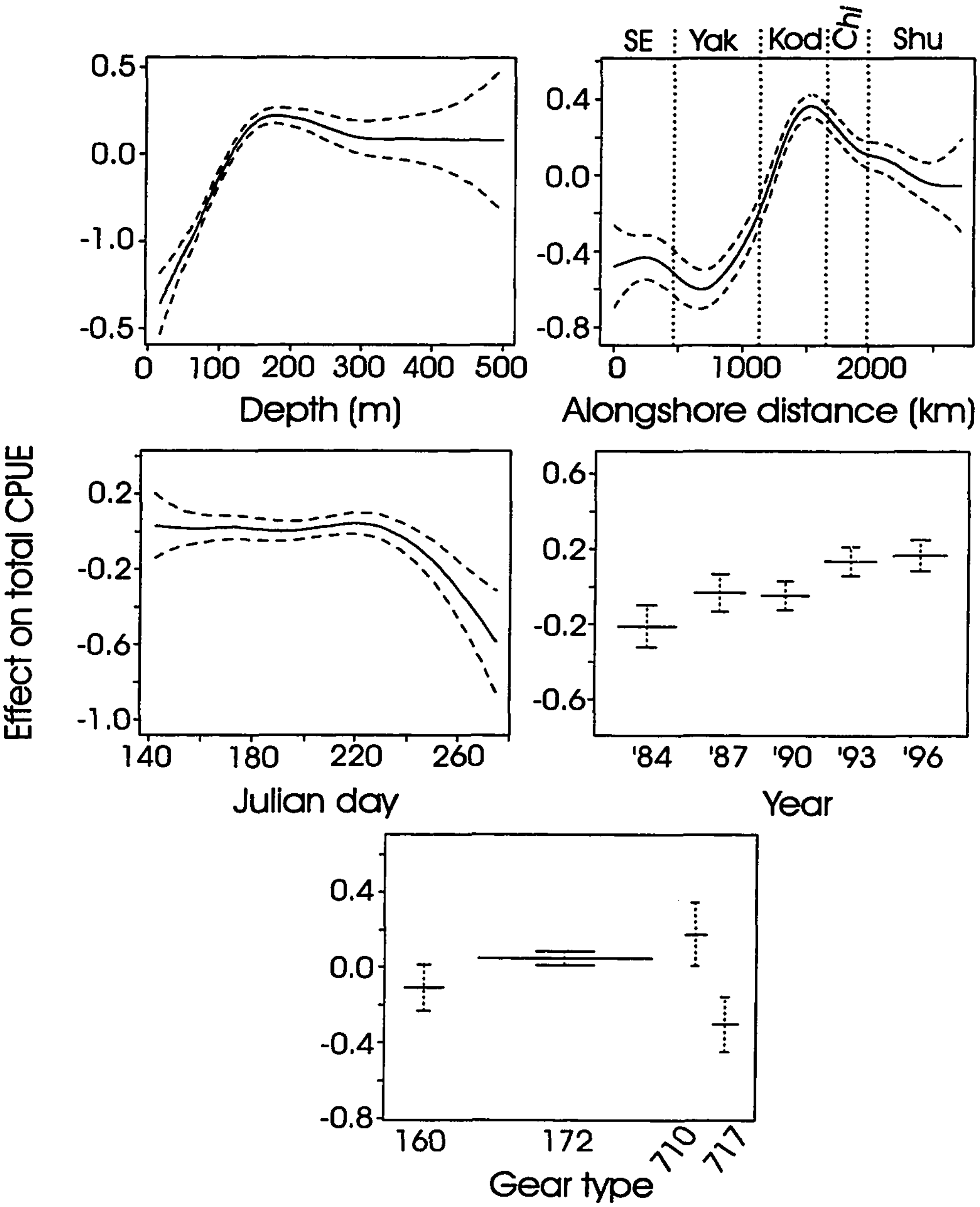

Figure 6.5: Trends in total CPUE by depth, alongshore distance, Julian day, year, and gear type. For details see Figure 2.

(correlation coefficient = -0.38) 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 indicate a lower catch rate for one of the Japanese trawls (gear 717, Fig. 6.5). This and other estimated differences among gear types agree at least qualitatively with results in Munro and Hoff (1995). The estimated time trend (Fig. 6.5) indicates a significant increase in total CPUE between 1984 and 1996. 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 6.2), representing an increase of 40%. No significant effect of temperature on total CPUE was found.

The biomass of 72 groundfish species in 240 stratum/year combinations was effectively summarized by an NMDS ordination in 3 dimensions (stress = 0.085). Our findings suggest that the main gradients along which species composition varied were depth and alongshore distance, while temperature and temporal gradients (within and between years) had relatively minor effects on 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. 6.6). The alongshore gradient was roughly perpendicular to the depth gradient and clearly distinguishes areas Southeast and Yakutat from each other and from the other areas (Fig. 6.6). Kodiak, Chiniak, and Shumagin were similar in species composition, as suggested 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 6.4), suggesting a relatively stable species composition from 1984 to 1996.

Ordinations of individual hauls within a year confirmed that depth and alongshore distance explained much of the variation in species composition within years. The species

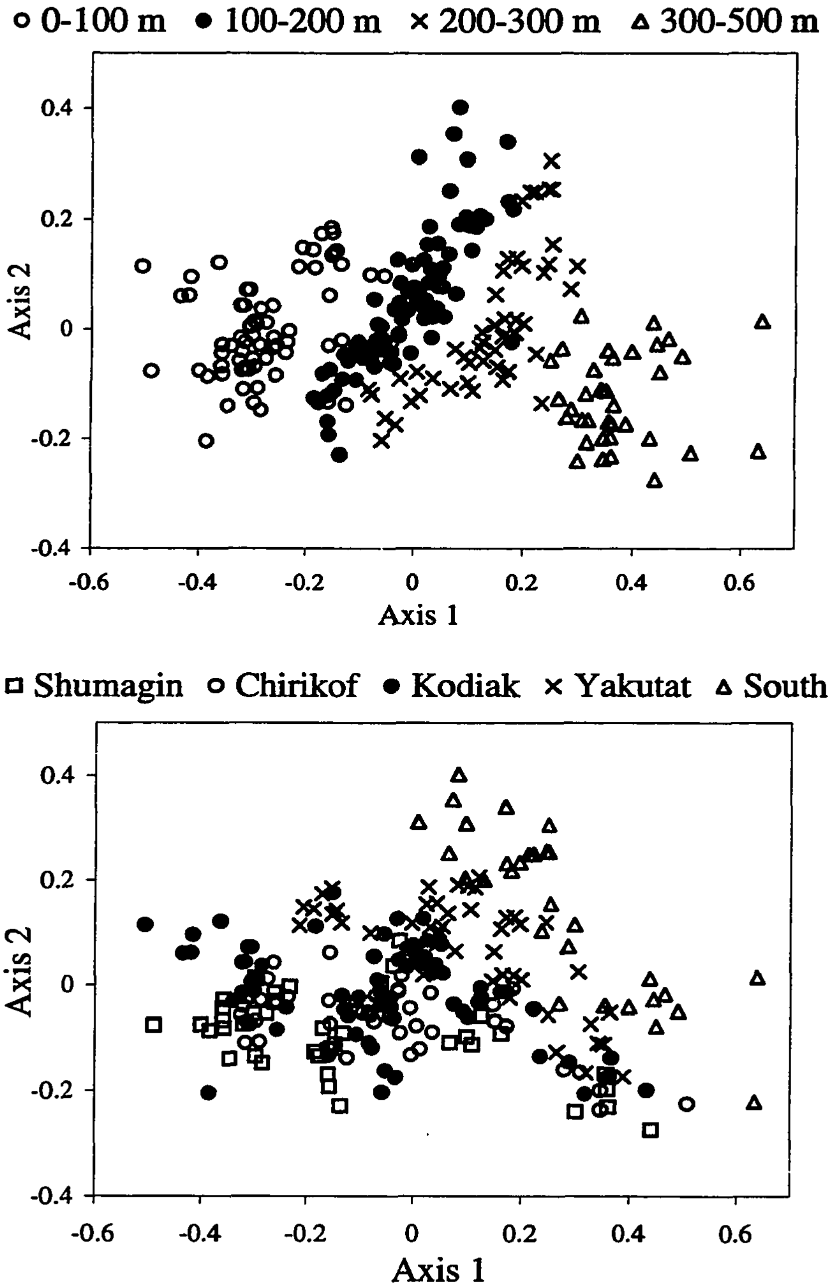

Figure 6.6: Plots of the first two axes from an NMDS ordination of 48 strata sampled during each of 5 years. Distances between 2 points (strata) in the ordination diagram approximately reflect their dissimilarity in terms of species composition. Symbols indicate depth strata (top) and geographic area (bottom).

Table 6.4: Analysis of variance of three axes of species composition by statistical area, depth stratum, and year.

Axis 1

Effect	df	Sum of Squares	Mean Squares	F Value	p Value
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

Effect	df	Sum of Squares	Mean Squares	F Value	p Value
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

Effect	df	Sum of Squares	Mean Squares	F Value	p Value
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		

composition in each year was effectively summarized 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 6.5). 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 (Table 6.5). 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, due to high correlations between Julian day and alongshore distances (correlation coefficients ranging from 0.26 in 1984 to 0.97 in 1996), which were a consequence of sampling from west to east in most years. 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 regressions). 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 6.1). Other years were not examined due to the small number of temperature measurements. The GAM analysis was repeated 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 6.5. 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 3 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

Table 6.5: Results from NMDS ordinations of species CPUEs in 5 dimensions (Axes 1-5) by year, and GAM 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.

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	.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	

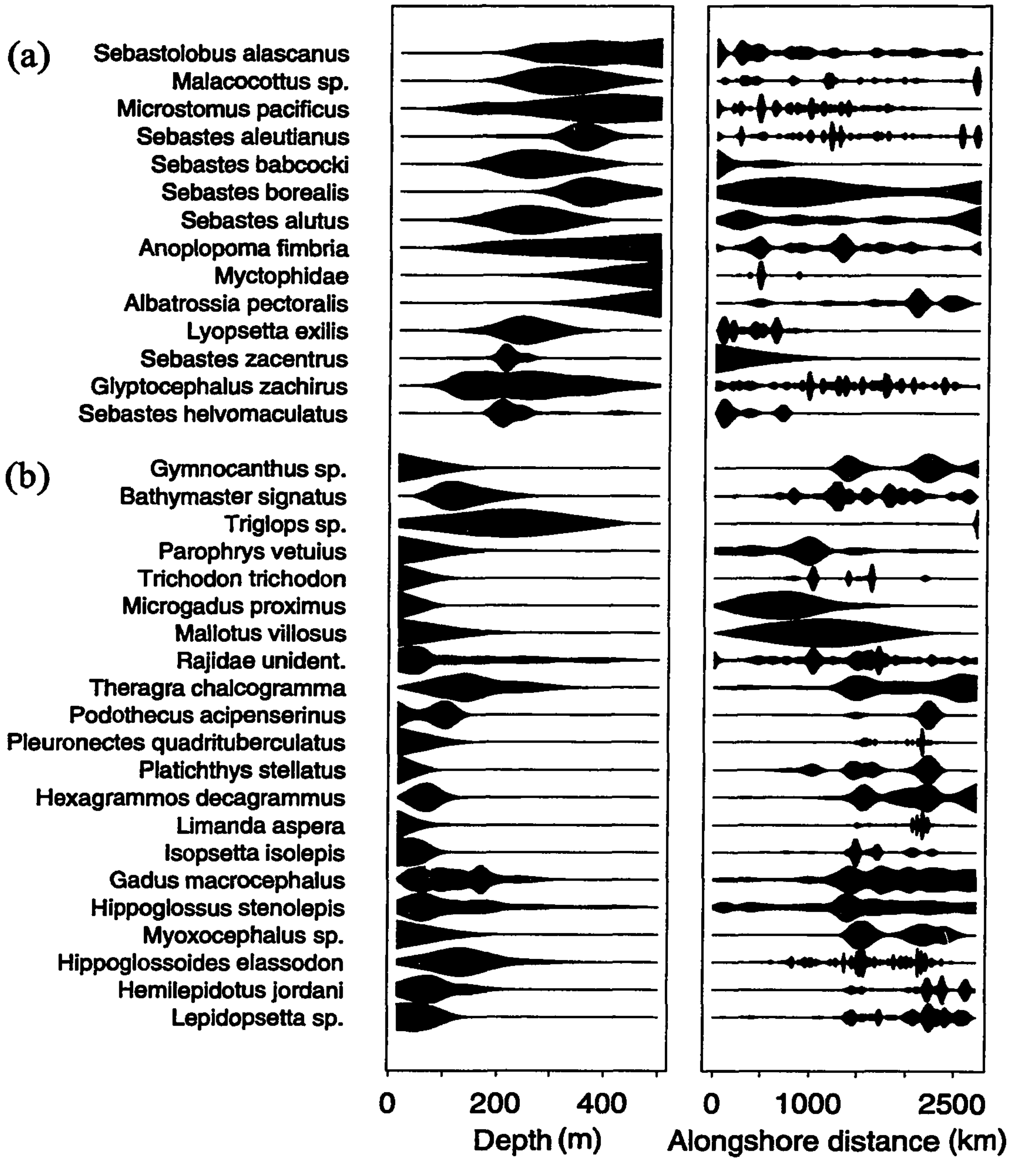

Figure 6.7: Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (a) or negative (b) association with the first index of species composition derived from an NMDS ordination of abundances averaged by strata. Widths of dark bands are proportional to average CPUE of a given species. Average CPUE as a function of depth and alongshore distance was estimated using a scatterplot smoother (cubic smoothing spline). Degree of smoothing was determined by cross-validation.

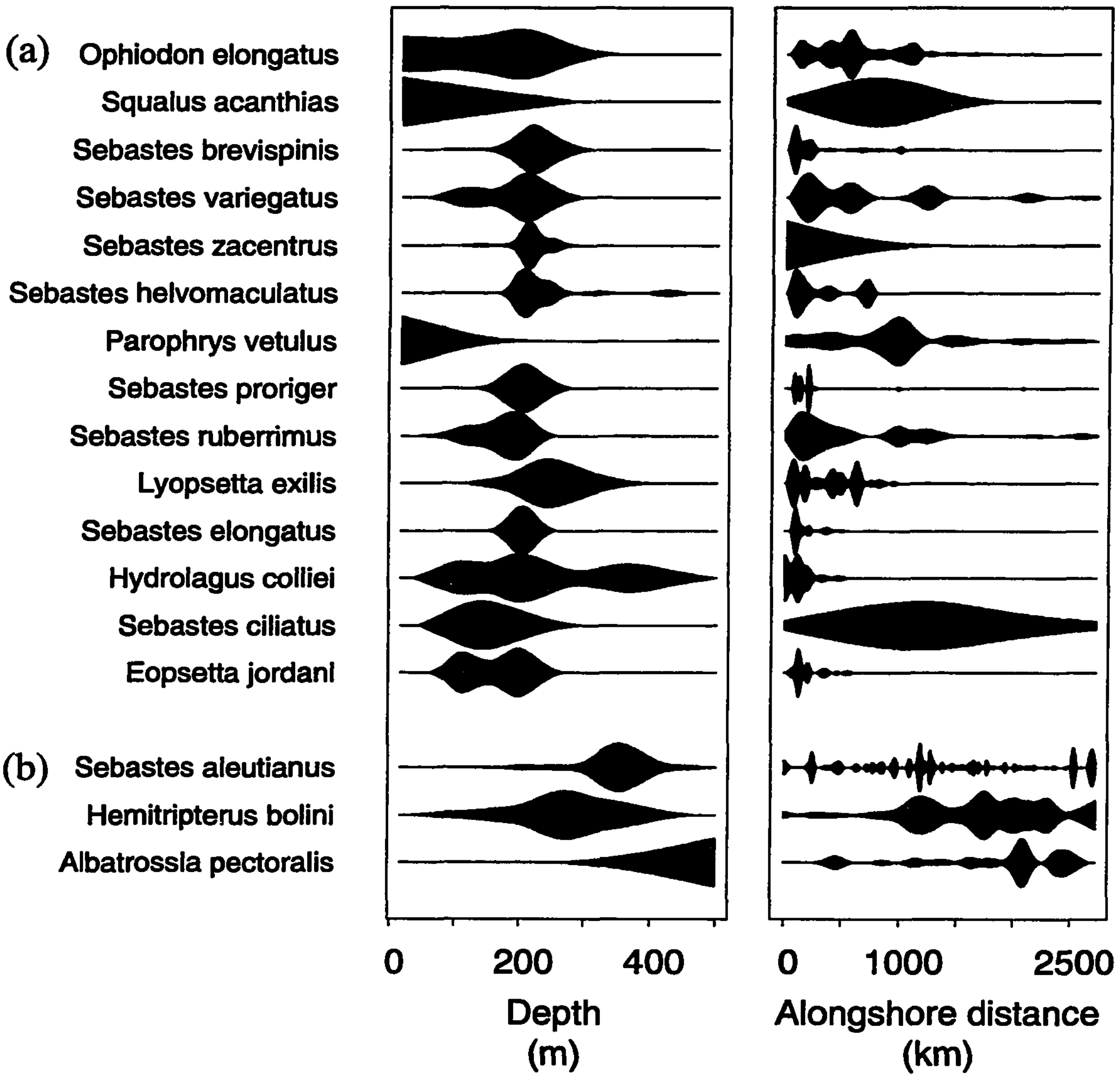

Figure 6.8: Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (a) or negative (b) association with the second index of species composition derived from an NMDS ordination of abundances averaged by strata. For details see Figure 6.7.

gradients of depth and alongshore distance (Fig. 6.7, 6.8). 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). Taxa that were positively correlated with the first axis consisted of a number of deep-water species that were somewhat 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. 6.7).

The second axis was positively correlated with a group of species that can best be described as 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. 6.8). 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.

We examined whether the groundfish species formed identifiable and recurring groups, but a cluster analysis of species showed little evidence of well-defined, discrete species assemblages (Mueter, unpubl. data). Similarly, a cluster analysis of stations did not indicate the presence of well-defined station groups. This suggests that species and stations formed a continuum along ecological gradients, rather than forming distinct station groups or species assemblages.

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. 6.6). Although the indices of species composition were not significantly different among years (Table 6.4), 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. 6.9). Skates were most strongly associated with the index and showed a widespread increase in CPUE and frequency of occurrence, particularly in the Chirikof, Kodiak, and Yakutat areas (Fig. 6.9, 6.10). 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. 6.9). The frequency of occurrence of capelin in the trawl survey increased significantly, while 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. 6.11). Capelin was caught in 14% of all hauls in 1996, compared to only 7% in 1993. Changes in the CPUE of three flatfish species differed among species. While Dover sole increased primarily in the eastern GoA (Yakutat and Southeast), rex sole increased most strongly in the Chirikof area (Fig. 6.9). In contrast, arrowtooth flounder increased in all areas, but only in the 0-100 m depth stratum. While 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 6.2). Both the frequency of occurrence and CPUE-where-present of Pacific Ocean perch increased strongly in the Chirikof area, while frequency of occurrence decreased in the Yakutat area.

Rajidae (skates)

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

Somniosus pacificus

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

Mallotus villosus

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

Thaleichthys pacificus

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

Microstomus pacificus

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

Glyptocephalus zachirus

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

Atheresthes stomias

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

Sebastes alutus

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

Figure 6.9: Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for 8 species that changed 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 '--'. Area / depth stratum combinations where a species was not caught in any of the five survey years are shaded. Significance was tested using generalized linear models including gear effects (see text).

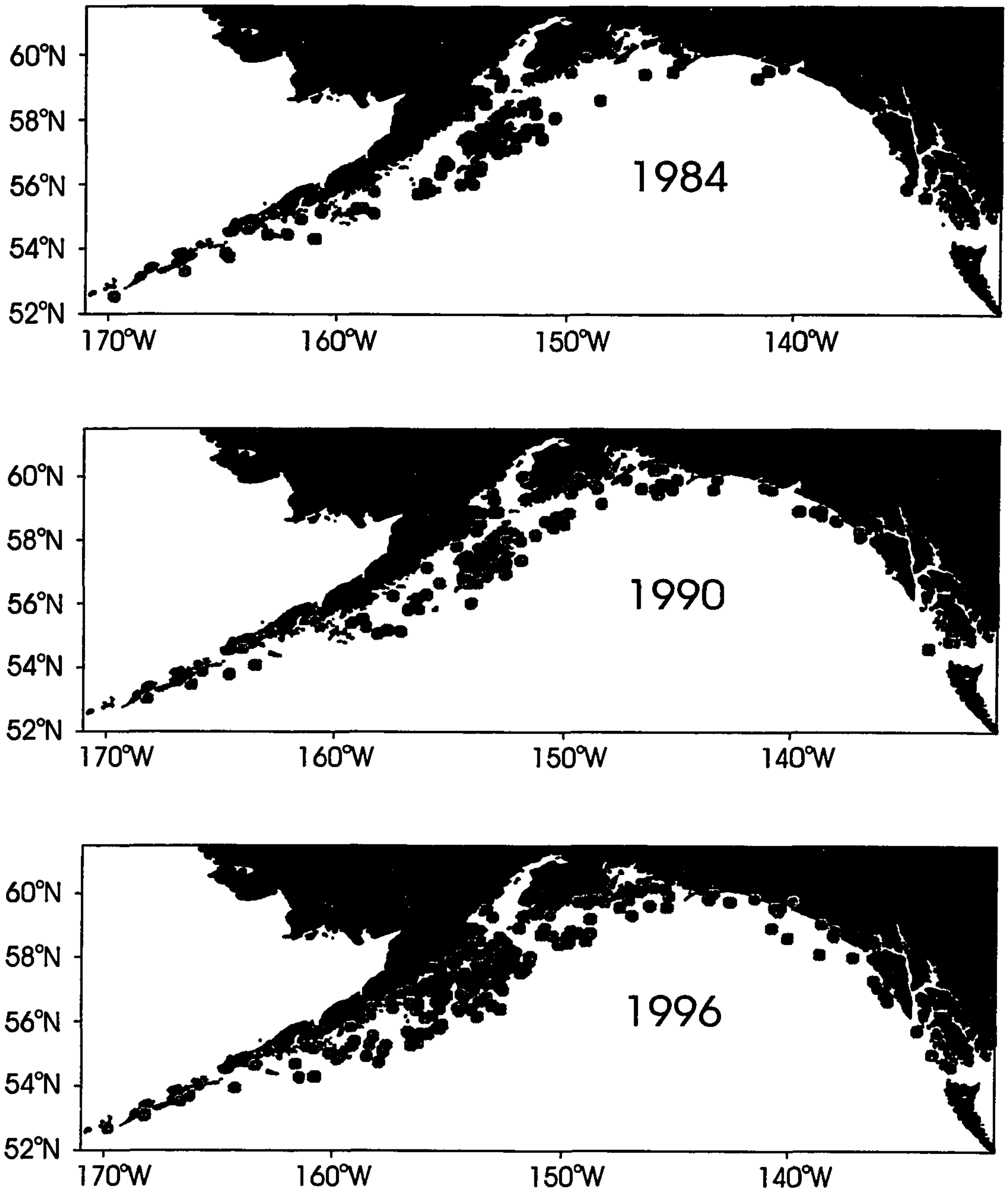

Figure 6.10: All sampling locations where CPUE of skates (Rajidae) exceeded 300 kg/km^2 in 1984, 1990, and 1996.

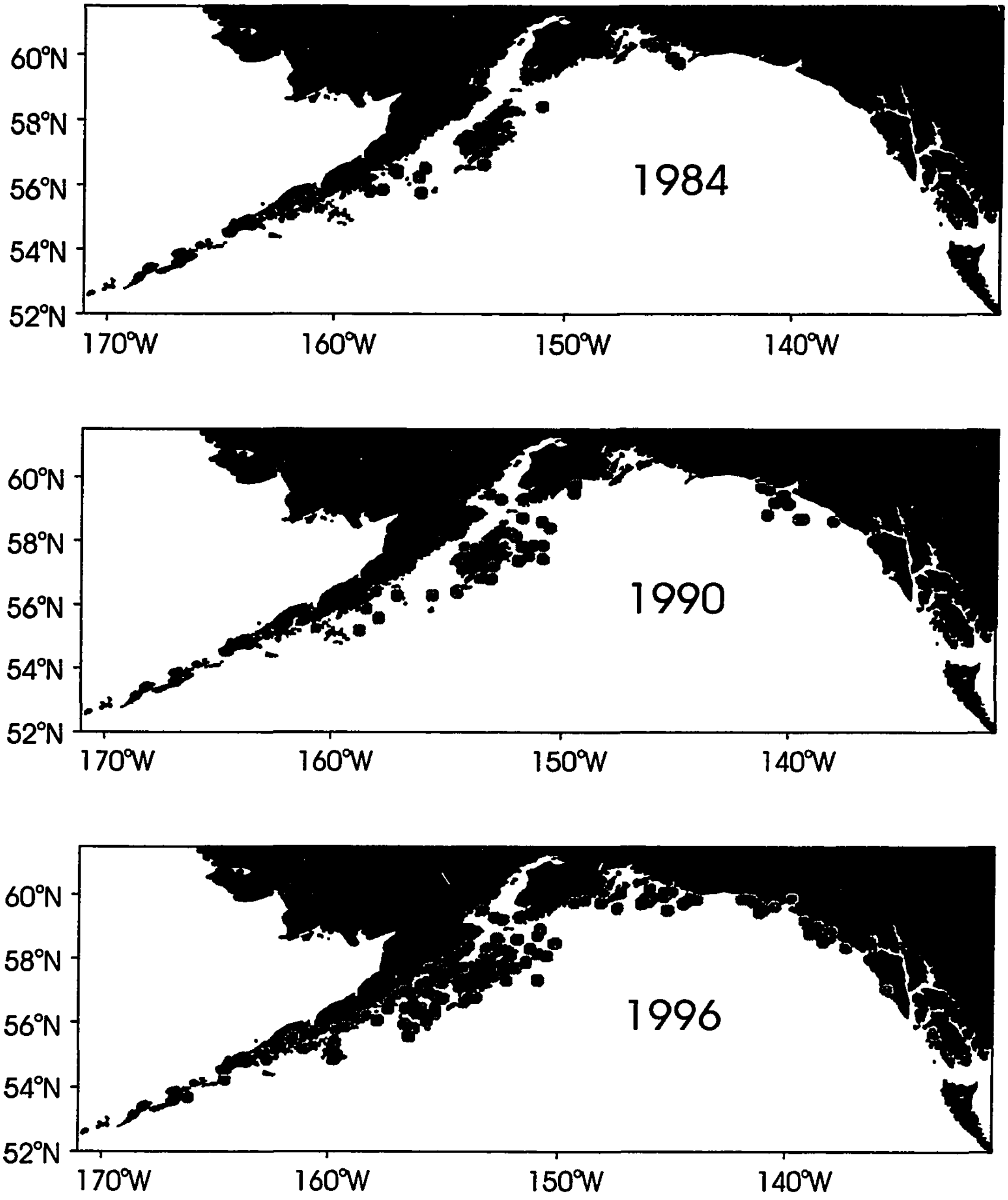

Figure 6.11: All sampling locations where capelin (*Mallotus villosus*) were caught in 1984, 1990, and 1996.

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. 6.12). However, frequency of occurrence decreased significantly for three of the species, particularly for bigmouth sculpin (*Hemitripterus bolini*, Fig. 6.12).

Discussion

Trends in species richness, diversity, and biomass, as well as in the CPUEs of individual species, show that depth is an important gradient structuring the groundfish community in the GoA, and that the shelf break (150-250 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. 6.7) 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 in press) to the abyssal plain (Merrett 1992). As in the terrestrial environment, latitudinal gradients also important in structuring benthic ecosystems on the shelf (Brown and Lomolino 1998).

Species richness and biomass of demersal fish communities are generally higher on the continental shelf than on adjacent slope regions (Day and Pearcy 1968; Colvocoresses and Musick 1984; Farina et al. 1997). These studies did not find peaks in richness or biomass at intermediate depths, possibly because results were typically averaged over large depth ranges. Using individual hauls Fujita *et al.* (1995) found that demersal fish biomass on the continental shelf and upper slope off Japan had a peak in biomass at intermediate depths; however, the peak occurred at 300-400 m, considerably deeper than in the GoA (this study). Unlike in the GoA,

Hemitripterus bolini

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

***Myoxocephalus* spp.**

		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0-100	CPUE				■	■
	FO			-	■	■
100-200	CPUE				■	■
	FO	--	--	--	■	■
200-300	CPUE	■	■	■	■	■
	FO	■	■	■	■	■
300-500	CPUE	■	■	■	■	■
	FO	■	■	■	■	■

***Lepidopsetta* spp.**

		Shumagin	Chirikof	Kodiak	Yakutat	Southeast
0-100	CPUE	++	+			■
	FO				-	■
100-200	CPUE					+
	FO	-	--	-		
200-300	CPUE				■	■
	FO	-		-	■	■
300-500	CPUE			■	■	■
	FO			■	■	■

Figure 6.12: Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for three species that changed 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 '--'. Area / depth stratum combinations where a species was not caught in any of the five survey years are shaded. Significance was tested using generalized linear models including gear effects (see text).

species richness off Japan increased linearly to 500 m and diversity was smallest at intermediate depths (Fujita et al. 1995).

A high biomass of demersal fishes near the shelf break in summer suggests favorable feeding conditions due to 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 (Tom Weingartner, pers. comm.) 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). Increased production in the water column becomes available to the benthos when sinking particles are consumed by infaunal and epifaunal organisms such as shrimp, which are consumed by demersal fish. A region of enhanced benthic productivity near the shelf break is consistent with groundfish biomass being highest just inshore of the shelf break between 150 and 200 m.

Enhanced productivity along the shelf break cannot explain the high biomass of groundfishes observed inside gullies at the same depth range. We hypothesize that topographic effects concentrate suitable prey at this depth range. The most abundant demersal fishes in the GoA feed near or off the bottom on euphausiids, mysids, copepods, shrimps, and fish (Yang 1993). Many euphausiids and mysids feed in the water column at night and migrate into deeper water during the day, where they aggregate in dense layers (Mauchline 1980). When these daytime aggregations are near the bottom they are vulnerable to predation by demersal fishes (Robinson and Gomez-Gutierrez 1998). Associations between euphausiid aggregations and demersal or semidemersal fishes have been observed at the shelf edge off Vancouver Island (Mackas et al. 1997) and around a bank in the Southern California Bight (Genin et al. 1988). Although there is little information on the vertical distribution of euphausiids in the GoA, a similar interaction between euphausiids and demersal predators could explain the large CPUE of demersal fishes observed at 150-200 m in the GoA. We have seen dense euphausiid aggregations during video observations in Marmot Gully near 150 m (Mueter, unpubl. data). Thus euphausiids may serve as an important trophic link between phytoplankton production in the water column and the demersal fish community.

In addition to depth or altitude, 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 (longitudinal) differences in community structure from the eastern GoA to the Aleutian Islands, with the steepest gradient between the Yakutat and Kodiak areas. The gradient was apparent in species richness and diversity (Fig. 6.2, 6.3), total CPUE (Fig. 6.5), and indices of species composition (Fig. 6.6).

Alongshore patterns in CPUE (Fig. 6.4, 6.5) indicate a higher biomass of demersal fishes in the western GoA, particularly in the Kodiak Island area. This is consistent with a higher benthic biomass and productivity of infaunal organisms on the Chirikof and Kodiak shelf, compared to the Yakutat and Southeast areas (Semenov 1965, as cited in Feder and Jewett, 1986). Enhanced primary productivity in the western GoA is evident in estimates from Coastal Zone Color Scanner data and from more recent SeaWifs data (Falkowski *et al.*, 1998, see Web site: http://seawifs.gsfc.nasa.gov/SEAWIFS.html). These differences in productivity across the GoA may be responsible for alongshore differences in species diversity, total biomass, and species composition of the groundfish community. Farina *et al.* (1997) showed that on the continental shelf and upper slope in the Mediterranean Sea, low productivity areas have the greatest species richness, and that upwelling areas with high primary productivity correlate with a high biomass in the upper trophic levels, including demersal species, and low species diversity. Our study suggests that the same general pattern is found on the continental shelf and upper slope of the GoA.

Upwelling, tidal mixing, strong alongshore currents, advection, and nutrient input from major rivers are factors that can contribute to a higher productivity in the western GoA and around Kodiak Island. The east-west gradient in productivity and biomass is consistent with differences in upwelling, which is generally much more pronounced and more frequent in the western GoA (Ingraham Jr. et al. 1976). The presence of strong tidal currents in the vicinity of Kodiak Island (Isaji and Spaulding, 1987; Z. Kowalik, pers. comm.) may further enhance demersal productivity. Phytoplankton production in tidally mixed areas tends to be above average due to increased nutrient flux from the sediment into the water column, although much of it escapes predation by zooplankton and sinks to the bottom (Mann and Lazier 1991). A different mechanism is needed to explain the high groundfish biomass in the deeper areas of Shelikof Strait. Much of the water column production in Shelikof Strait is advected into the region via the Alaska Coastal Current (Napp et al. 1996), originating in lower Cook Inlet or on the shelf northeast of Kodiak Island, two areas of high primary productivity (Sambrotto and Lorenzen 1986). The high groundfish biomass in Shelikof Strait suggests that a large proportion of this production becomes available to the benthic community through sinking particles or through vertical migrations of zooplankton and fish.

The composition of the groundfish community in the GoA and spatial patterns in distribution have remained relatively stable from 1984 through 1996. The composition of groundfish communities over time may change as a result of variations in recruitment due to environmental changes or fishing. Numerous studies 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/Labrador 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)

A lack of strong trends in indices of species composition over time and a visual comparison of the indices mapped by year (not shown) suggest that a large component of the overall variability in species composition displayed spatial patterns that are remarkably stable. A comparison of the estimated centers of distribution (median depth of occurrence and median alongshore distance) for individual species among years confirmed that with one exception all species were distributed over a similar depth range and over a similar range of alongshore distances in all years (Mueter, unpubl. data). The exception was Atka mackerel, which showed a significant eastward expansion into the GoA. The apparent stability of spatial patterns in the GoA contrasts with substantial interannual shifts in the spatial distribution of groundfish species or assemblages on the continental shelf off the U.S. west coast (Jay 1996), and in the northwest Atlantic (Gomes *et al.*, 1995; Mahon *et al.*, 1998). The stability in the spatial distribution of groundfishes in the GoA may simply reflect stability in species composition for the time period of the study, as well as a period of relatively moderate variations in the physical environment and little effect of fishing on species composition.

The recent period of stability 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 (Beamish, 1995; Piatt and Anderson, 1996; Hollowed and Wooster, 1995; Mueter and Norcross, in review). There is evidence of a shift in species composition of at least the nearshore demersal communities during this time period (Piatt and Anderson 1996; Anderson et al. 1997; Mueter and Norcross in review). 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 1997) and historical surveys (Ronholt et al. 1978) suggest that the 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 using 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 differs from the surveys done in the 1980s and 1990s (Ronholt et al. 1978). 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 (Fig. 6.13), 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. The data indicate that walleye pollock became the dominant species in the mid-1970s, 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 abundance since the 1970s. Absolute abundance estimates based on stock assessments of commercial stocks indicate similar trends in abundance (NPFMC 1997), with one notable exception. The proportion of Pacific Ocean perch in the 1961 survey was much smaller than indicated by biomass estimates and commercial catch rates for the 1960s (Heifetz et al. 1997). This may in part be due to differences in catchability and sampling design, which might have led to a severe underestimation of Pacific Ocean perch in the early surveys. 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. 6.13). 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, *Myoxocephalus* spp., see Fig. 6.12, Table 6.2).

The observed increase in overall groundfish biomass in the GoA from the 1980s to the 1990s (Fig. 6.5) is consistent with increases in the productivity of the Northeast Pacific Ocean

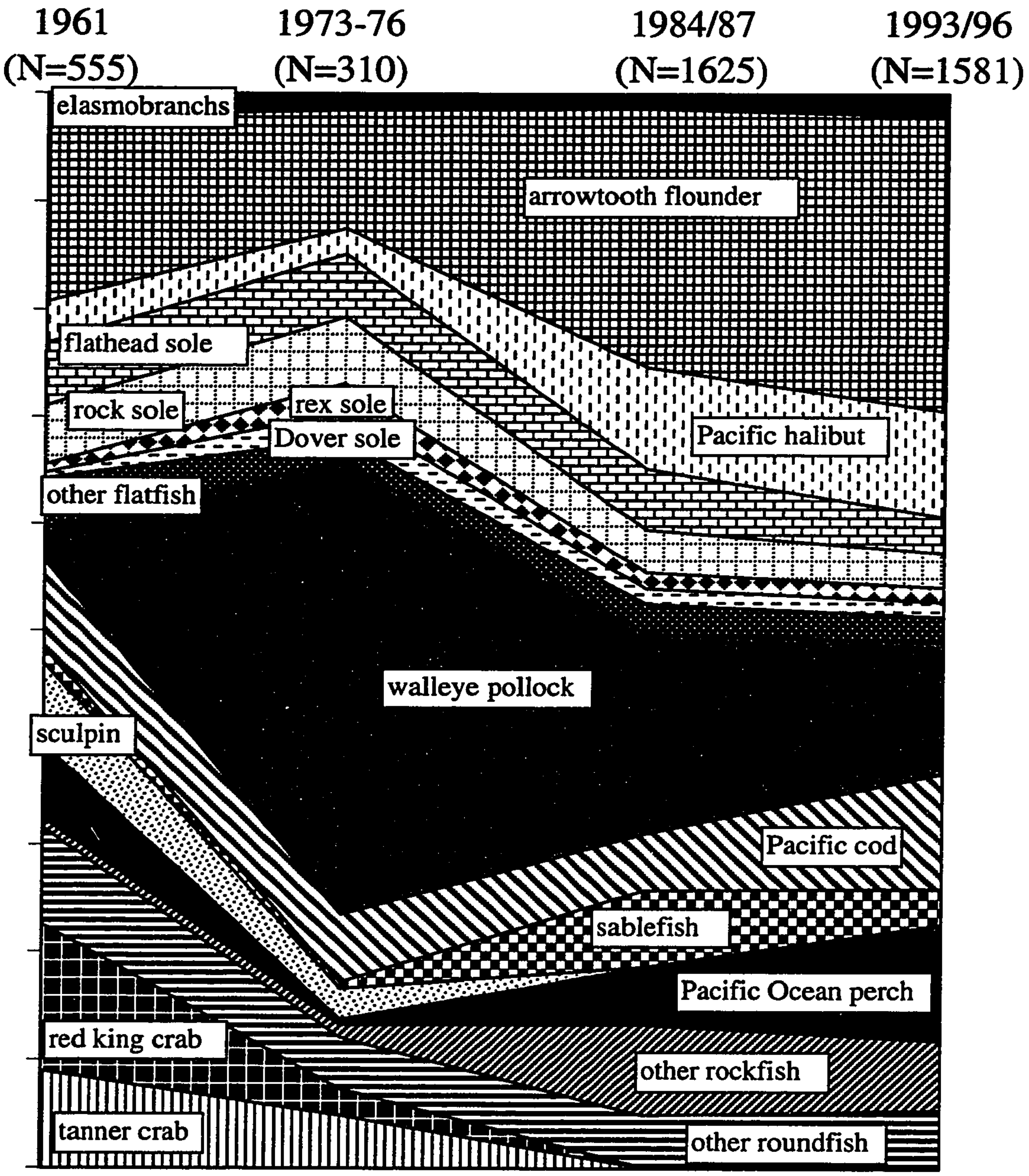

Figure 6.13: Composition of Gulf of Alaska groundfish communities from the 1960s through the 1990s as estimated from bottom trawl surveys. All surveys used similar gear, but sampling in 1961 and 1973-76 was limited to 0-400 m depth. Total number of hauls is indicated below each time period.

between the period of the 1960s/70s and the 1980s/90s. Polovina *et al.* (1995) suggest 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 (Trenberth and Hurrell, 1994). 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.

Implications for management

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 since the catchability of species may change over time due to changes in survey gear, vessel type, spatial distribution, or the length composition of a population. Nevertheless, the survey data used in this study provide the best available indicator of relative changes in species composition and distribution for many species of ecological or commercial interest.

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 (National

Research Council 1995), and Bengtsson *et al.* (1997) suggest including diversity in planning and policy-making. 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 no indication from our study that the number of species or the diversity of the groundfish community in the GoA has decreased over time.

Multivariate techniques that summarize the major variation in species composition using 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.

We found no evidence that any of the commercially important species in the GoA have undergone significant declines between 1984 and 1996. Rather, the increase in productivity of the NE Pacific has apparently allowed a number of groundfish species to increase over the last two decades, with obvious implications for management. Increases in commercially exploitable species allow managers to increase overall harvest levels. However, the species with the largest increases in the GoA were currently noncommercial species such as skates, as well as currently lightly exploited species such as arrowtooth flounder, Pacific Ocean perch, Dover sole, and Rex sole. Should the productivity of the system decline in the future managers need to be vigilant, because heavily exploited species are likely to be the first to decline under unfavorable environmental conditions. In the GoA, walleye pollock are likely to decline first, due to relatively high exploitation rates, a potential for increasing competition with arrowtooth flounder for euphausiid prey, and heavy predation of arrowtooth flounder on walleye pollock (Yang 1993). The increase of arrowtooth flounder in shallow areas (< 100 m, see Fig. 6.9) could have a particularly strong impact on pollock as well as other species, because juvenile stages of many fish species that serve as prey for arrowtooth flounder are most abundant in shallow areas.

Changes in the abundance of skates and other non-commercial 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. As part of an ecosystem approach to management it would be prudent to continue to monitor the abundance of noncommercial species in addition to commercial species. Such monitoring, along with the monitoring of environmental variables, may 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 researches 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/or tested through rigorous research programs and/or 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 to account for species relationships and environmental influences.

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Chapter 7: Effects of environment and fishing on Gulf of Alaska groundfish communities

Abstract

This study examines spatial and temporal patterns in the Gulf of Alaska (GoA) groundfish community in relation to local and large-scale variations in the environment. A strong east-to-west gradient in species richness, total abundance, and species composition coincided with a similar gradient in alongshore wind stress. Summer upwelling in the western GoA appears to support a lower diversity and higher biomass of groundfishes, compared to the eastern GoA, although other east-to-west gradients are likely to contribute to the observed trends. A transition zone occurs between Yakutat and Kodiak Island. An increase in total biomass from 1984 to 1996 and differences in species composition could not be explained by changes in local upwelling or wind mixing over time. Total groundfish biomass increased throughout the Gulf of Alaska, but the increase appeared to be more pronounced in areas where bottom temperatures declined steeply and less pronounced in areas with high commercial fishing effort. The increase in groundfish biomass followed a marked shift in species composition in the nearshore groundfish community in the early 1980s that was significantly correlated with an increase in northward transport in the Alaska Current at a lag of 5 years. Changes in the groundfish community on the GoA shelf and upper slope may be linked to decadal-scale variations in the Northeast Pacific environment through variations of the rate at which water is advected into and around the perimeter of the Gulf of Alaska.

Introduction

The species composition of the GoA groundfish community displays strong spatial and temporal gradients. Observed spatial patterns include strong gradients in species diversity, total abundance, and species composition along the GoA shelf and slope from the eastern to the western GoA (Chapter 6). Temporal patterns include a pronounced shift in species composition of the nearshore groundfish community around Kodiak Island in the early 1980s (Chapter 5), changes in species composition on the GoA shelf and upper slope between 1984 and 1996, and an increase in overall groundfish abundance over the same time period (Chapter 6).

Causes for the observed patterns are poorly understood and may include local oceanographic conditions, large-scale variations in the Northeast Pacific environment, and commercial fishing. Recruitment, abundance, and distribution of Northeast Pacific groundfish species have been related to temperature (Fargo and McKinnell 1989; McFarlane and Beamish 1992; Hollowed and Wooster 1995), winds (Parker 1989; Megrey et al. 1995), or large-scale atmospheric forcing (Hollowed and Wooster 1995; Megrey et al. 1995; Hollowed et al. 1998). At the local scale, conditions that control oceanic variability on the continental shelf include tides, freshwater input, and winds. Local winds promote strong mixing and generally favor downwelling conditions along the coast, but upwelling events are common in the summer, particularly in the western GoA (Reed and Schumacher 1986). Upwelling in other areas has been shown to influence the biomass and species composition of groundfish communities (Mas-Riera et al. 1990; Macpherson and Gordoa 1996; Farina et al. 1997).

Local conditions are linked to large-scale atmospheric forcing, particularly the strength and position of the Aleutian Low Pressure System (see Chapter 2). Large-scale atmospheric patterns further influence oceanographic conditions in the coastal GoA by contributing to variability in the flow of the Alaska Current (Chelton and Davis 1982; Hollowed and Wooster 1992). It has been suggested that variations in the flow of the Alaska Current are related to recruitment variability in GoA groundfish species (Ware and McFarlane 1989), a hypothesis that has not been tested to date.

While most studies of GoA groundfishes have examined environmental effects on individual populations, this study examines effects on the whole groundfish community. Variations in forcing mechanisms at interannual and decadal scales affect different populations in different ways, resulting in changes in the relative species composition of the groundfish community and in overall groundfish abundance. Due to the long life span of many groundfish species there may be considerable lags between changes in the environment and changes in community structure. In contrast, harvesting directly affects the abundance of commercial species and can lead to local, short-term depletion as well as long-term chronic effects on species composition (Goni 1998).

The purpose of this chapter is to examine some possible causes for the observed spatial and temporal patterns in the composition of GoA groundfish communities. Specifically, I examine statistical correlations between indices that summarize patterns in species diversity, abundance and species composition (Chapters 5,6) and indices of local or large-scale atmospheric and oceanographic variability, as well as an index of commercial fishing effort.

Methods

Relationships between the environment, the GoA groundfish community, and commercial fishing effort were examined spatially and temporally. Biotic indices describing spatial and temporal patterns in the groundfish community are based on Chapters 5 and 6 and are briefly summarized below. Indices of environmental variability used in this analysis include bottom temperature, wind stress, upwelling, and indices of large-scale atmospheric and oceanographic forcing, which are described in detail. I limited the number of environmental variables that were examined to minimize the risk of finding spurious correlations (Walters and Collie 1988). Similarly, where monthly indices were available, I decided a priori which months to include in the analysis, rather than examining correlations for multiple months or different combinations of months. As a measure of fishing effort I used estimates of total commercial bottom trawling time based on National Marine Fisheries Survey observer data (Catherine Coon, pers. comm.).

Spatial trends in the GoA groundfish community

Long-term average spatial patterns in species richness, total groundfish abundance and species composition of the groundfish community on the GoA shelf and upper slope in the summer were identified and quantified in Chapter 6. For the current analysis I focused on longitudinal or alongshore trends and examined the following biotic indices:

(a) Alongshore trend in species richness (number of species per haul) adjusted for the effects of depth, date of sampling, year, area swept, and gear type using generalized additive models (Fig. 6.2).
(b) Alongshore trend in total groundfish biomass (CPUE), adjusted for the effects of depth, date of sampling, year, and gear type (Fig. 6.5).
(c) Alongshore trend in species composition. This index summarizes east to west differences in species composition based on an ordination of the average abundance of 72 groundfish species in 48 sampling strata sampled during each of five triennial surveys between 1984 and 1996. For details of the ordination see Chapter 6. Because For this analysis I chose the ordination axis that had the highest correlation with alongshore distance.

The three biotic indices were graphically compared to the following environmental indices:

(a) Alongshore trend in bottom temperatures as estimated from temperature measurements taken in conjunction with bottom trawl surveys. The alongshore trend in bottom temperature was estimated using a generalized additive model to adjust for the effects of depth, date of sampling, and year.
(b) Alongshore trend in wind stress as a proxy for upwelling or downwelling conditions. Monthly wind stress data for the Gulf of Alaska from January 1980 - March 1996 were obtained on a 2x2 degree grid from the National Climatic Data Center (Woodruff et al.

1995). Winds within each 2x2-degree square were rotated to obtain the alongshore component of wind stress. Positive values indicate alongshore winds with the shore to the left, leading to offshore Ekman transport and upwelling. For the analysis of spatial patterns in wind stress (i.e. upwelling) during the summer I averaged monthly wind stress values for April through September within each year, then computed the long-term mean wind stress and its standard error based on April-September means for the years 1980-1995. Mean alongshore wind stress values were computed for each of the 2x2 degree squares shown in Fig. 7.1. The period April - September was chosen because (1) it coincides with the months of peak production and (2) a multivariate analysis of wind patterns indicated that these months were relatively homogenous, whereas winds were highly variable at other times of the year.

(c) Alongshore differences in sediment input and composition, topography, and shelf width. Qualitative differences between the eastern, central, and western GoA are discussed in relation to the observed trends in biotic indices. Descriptions of the geomorphology and sediment composition for different areas in the GoA were obtained from Hampton et al. (1986).

The observed spatial trends in biotic and environmental indices were not compared statistically because of the different time and space scales over which the indices were measured and because of the high degree of autocorrelation induced in the spatial trends of biotic indices by using smoothed trends.

Spatio-temporal trends in the GoA groundfish community

Previously I identified significant changes in the species composition and total biomass of GoA groundfishes from 1984 - 1996 (Fig. 6.5, 6.9). The changes were quantified using an index of species composition over time and estimates of total groundfish CPUE over time as described in Chapter 6. A time series analysis of the observed trends was precluded because only

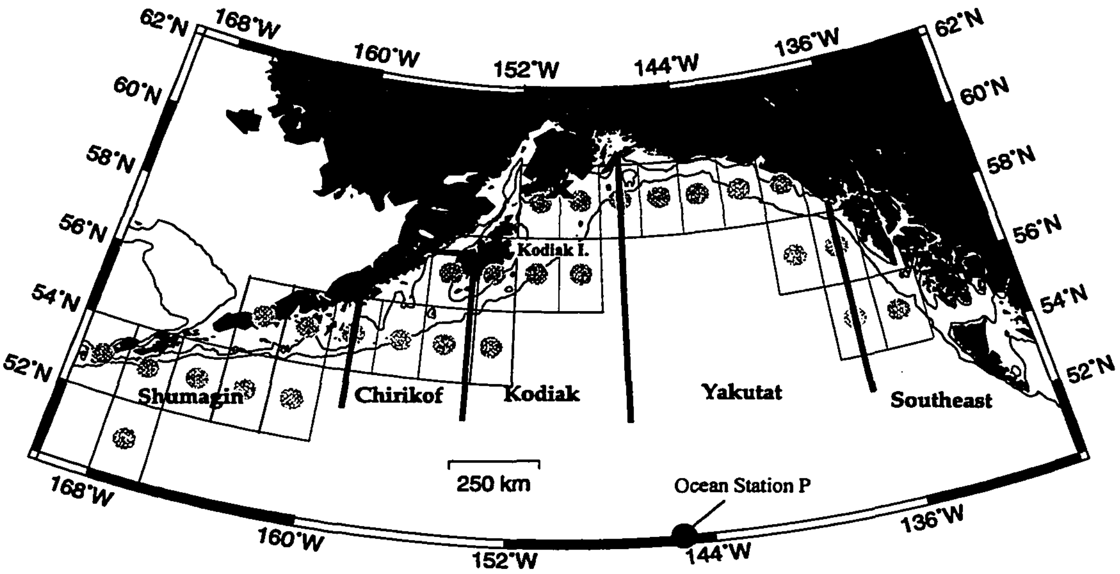

Figure 7.1: Map of the Gulf of Alaska showing selected grid points from a 2x2-degree grid used for analysis of wind stress data. For analysis by area, values from all grid points within the five areas indicated by dark lines were averaged. Symbols indicate locations of temperature station GAK 1 (x), upwelling index (◆), and Ocean Station P (●).

5 years of data were available. Changes in these biotic indices did not occur uniformly throughout the GoA but differed significantly among sampling strata. Spatial variations in the observed trends provide the opportunity to compare trends in species composition or CPUE averaged over appropriate spatial scales to trends in environmental variables or differences in fishing effort on the same spatial scales.

To examine trends in species composition and CPUE, I plotted estimates of the index of species composition and CPUE over time for each of 48 strata sampled during the GoA groundfish surveys. Trends were generally linear or close to linear, thus I quantified the magnitude of the changes in each stratum by computing the slopes of a linear regression of the index of species composition and CPUE on sampling year. The estimated slopes provide a quantitative measure of the magnitude of change in each of the indices from 1984 to 1996.

Trends in the biotic indices were then related to trends in environmental indices or to fishing effort averaged over the same spatial scales. Indices used in the analysis were:

(a) Change in bottom temperature over time. This was estimated similarly to the biotic indices as the slope of a linear regression of temperature on survey year by stratum. Scatterplots of temperature over time indicated that the change in temperature was adequately described by a linear trend.

(b) Annual averages of the alongshore component of (summer) wind stress were obtained as described above and averaged within each of five statistical areas over the 2°x2° grid points shown in Fig. 7.1. Long-term trends in alongshore wind stress within each area from 1980-1995 were estimated by fitting a smoothing spline with approximate 95% confidence intervals to the annual wind stress values. The degree of smoothing was chosen objectively by cross-validation so as to minimize the mean integrated squared error (Venables and Ripley 1994). Trends were qualitatively compared to trends in species composition and CPUE over time averaged over the same areas.

(c) Trends in the absolute magnitude of wind stress from 1980-1995 averaged over the same five areas as in (b) were qualitatively compared to trends in species composition and CPUE.

(d) Fishing effort was estimated for each of the 48 sampling strata based on estimated commercial bottom trawl times, averaged over the years 1990-1996 and standardized to unit area (hours per 1000 km^2 per year).

To test statistically whether changes in the biotic indices were related to changes in temperature or to fishing effort, I regressed the slopes of changes in species composition and CPUE from 1984 to 1996 on the slope of temperature changes and on average commercial trawl fishing effort by stratum.

Long-term changes in species composition

One of the few long-term time series available for the groundfish community in the GoA is based on the catch composition of juvenile and adult fishes caught incidentally in shrimp trawl surveys conducted in the central GoA since the 1970s (Anderson et al. 1997), Chapter 5). To relate long-term changes in species composition to environmental variations I used an index of species composition based on a subset of the shrimp trawl survey data from 1976 to 1995. The index summarizes the major variation in species composition in seven nearshore areas around Kodiak Island and shows a major shift in species composition in the early 1980s (Chapter 5). For this analysis I estimated the average trend in the index of species composition for all Kodiak areas combined using methods described in Chapter 5.

The shrimp trawl survey was not conducted in all years after 1987 and missing values for 1989, 1990/91, and 1993/94 were estimated based on ARIMA time series models fit by maximum likelihood estimation. To handle missing values, parameters of the ARIMA models were estimated using the Kalman filter (Kohn and Ansley 1986). The best-fitting ARIMA model was chosen based on the Akaike Information Criterion and missing values were replaced with their predicted values based on the best model.

To test whether the yearly index of species composition from 1976-1995 was related to variations in local bottom temperatures, upwelling, or large scale atmospheric and oceanographic variability I conducted a correlation analysis using the following indices:

(a) As a proxy for variations in local water temperatures I used water temperatures at 250 m depth at station GAK 1 in the northern GoA (Royer 1993). The station is located within the Alaska Coastal Current upstream from Kodiak Island (59° 50.7' N, 149° 28.0' W) and temperature measurements were taken at irregular intervals between 1 and 20 times per year since 1970. Within-year variability in temperature showed a consistent quadratic trend with reduced temperatures in the summer time resulting from upwelling in the summer. To estimate annual average temperatures at 250 m I fit a model of the following form to the data:

$$temperature = \mu + year + Julian\ day + (Julian\ day)^2 + error$$

Annual means (year effect μ) estimated from this model were used for the analysis. Temperatures at 250 m were used to reduce some of the high frequency variability associated with variations in the Alaska Coastal Current and with surface heating and cooling.

(b) The upwelling index (UI) at 60°N, 149°W (Bakun 1990), which is NE of Kodiak Island, was used as a proxy for upwelling conditions in the Kodiak area. For the analysis I used yearly averages of the April - September monthly means as a measure of upwelling during the summer.

(c) The North Pacific Index (NPI, (Trenberth and Hurrell 1994) was used as a measure of large-scale atmospheric variability. The index is the area-weighted sea level pressure over the region 30°N-65°N, 160°E-140°W and is a measure of the strength of the Aleutian Low Pressure System. For this analysis I used yearly averages of the November - March anomalies (mb). The index was averaged over the winter months following Trenberth and Hurrell (1994) to remove noise resulting from high-frequency weather systems. Variations in the index are associated with changes in surface wind stress and surface layer mixing which affect nutrient availability (Trenberth and Hurrell 1995). The value for a given year corresponds to the period from November of the previous year through March of the current year.

(d) The Papa Trajectory Index (PTI, Ingraham et al. 1998) was used in the analysis as an oceanographic index describing variations in the flow of the Alaska Current. The PTI is the northernmost point of 90-day simulated drift trajectories starting at Ocean Weather Station P (50°N, 145°W) on January 1 of each year.

To test for significant correlations between the Kodiak index of species composition and each of the above indices I computed pairwise correlations among the data series at lags ranging from 0 to 8 (environmental variables leading) and tested for significant correlations. Strong autocorrelation in several of the time series considerably reduced the effective degrees of freedom, thus the test procedure was adjusted for autocorrelation by computing adjusted degrees of freedom using the modified Chelton method of Pyper and Peterman (1998). For each environmental variable I tested the null hypothesis of no correlation at all lags. Although the length of the shortest time series was limited to 20 years (Index of species composition: 1976-1995), all cross-correlations were computed with an overlap of 20 years because all environmental variables were available at least since 1968, except GAK 1 temperatures (1970-1999).

I further examined cross-correlations among the environmental series at lags 0-8. Correlations were tested for significance as described above. The analysis was repeated twice using (1) the period 1970-1995, which was common to all data sets and (2) the period of maximum overlap between each pair of variables.

Results

Spatial trends in the GoA groundfish community

Smoothed trends in the alongshore distribution of species richness, total groundfish CPUE, and species composition coincided with a pronounced trend in alongshore wind stress between the eastern and western GoA (Fig. 7.2). All three biotic indices showed strong east-west differences with the steepest gradient generally occurring between the area east of the Copper River (km 800-1000) and Kodiak Island (km 1500-1600). The steepest part of the gradient in species richness and species composition closely matched the steep increase in average alongshore wind stress, whereas total groundfish CPUE peaked east of the highest (positive) wind stress values. These patterns suggest that differences in upwelling intensity contribute to the observed alongshore trends in the groundfish community from the eastern to the western GoA.

The long-term average summer wind direction (1980-1995) shifted from predominantly westerly winds in the western GoA (positive values of alongshore wind stress component in Shumagin and Chirikof areas) to predominantly easterly winds in the eastern GoA. This suggests that upwelling conditions prevail from April through September in the western GoA, whereas downwelling conditions prevail in the eastern GoA. In general, winds were extremely variable in the western GoA with strong winds out of the North and Northwest, but consistently blew out of the Southeast in the eastern GoA, particularly in the Yakutat area (Fig. 7.3).

Trends in species richness, CPUE, and species composition showed no apparent relationship with the estimated 1984-1996 average trend in bottom temperature along the shelf (Fig. 7.4). The steepest gradient in temperature occurred west of Kodiak Island and did not correspond to observed trends in any of the biotic indices. Furthermore, the temperature trend was highly variable among years and each year differed significantly from the long-term trend, whereas the alongshore trend in species composition was very consistent among years (Fig. 7.5). The only consistent feature of the alongshore trends in bottom temperatures, after adjusting for

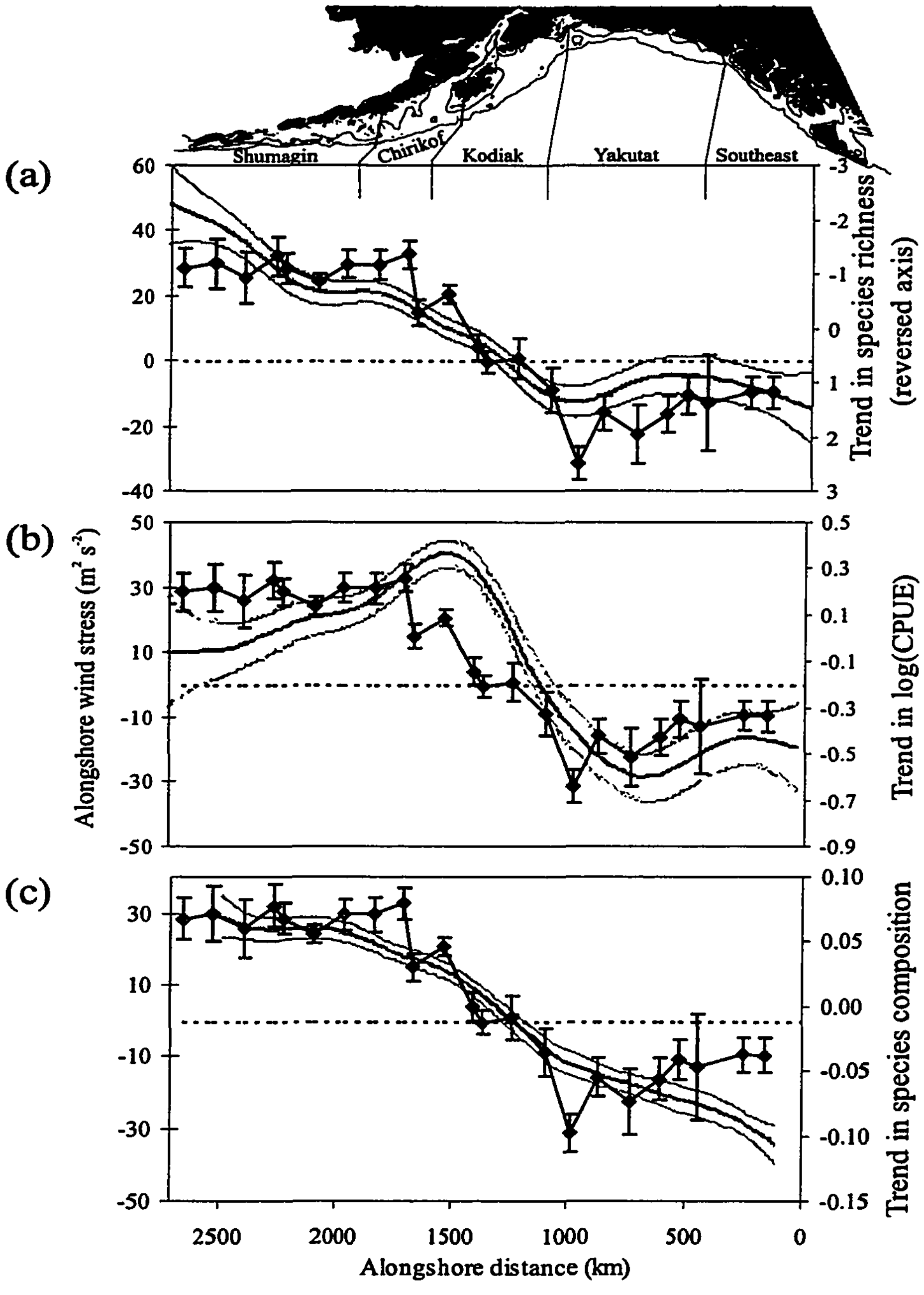

Figure 7.2: April-September alongshore wind stress averaged from 1980-95 for grid points indicated in Fig 7.1 (black) with smooth alongshore trends (light gray) in species richness (a), total groundfish CPUE (b) and index of species composition (c) along the GoA shelf and upper slope. All indices shown with 95% pointwise confidence limits. Dotted zero line separates westerly (positive) and easterly winds (negative).

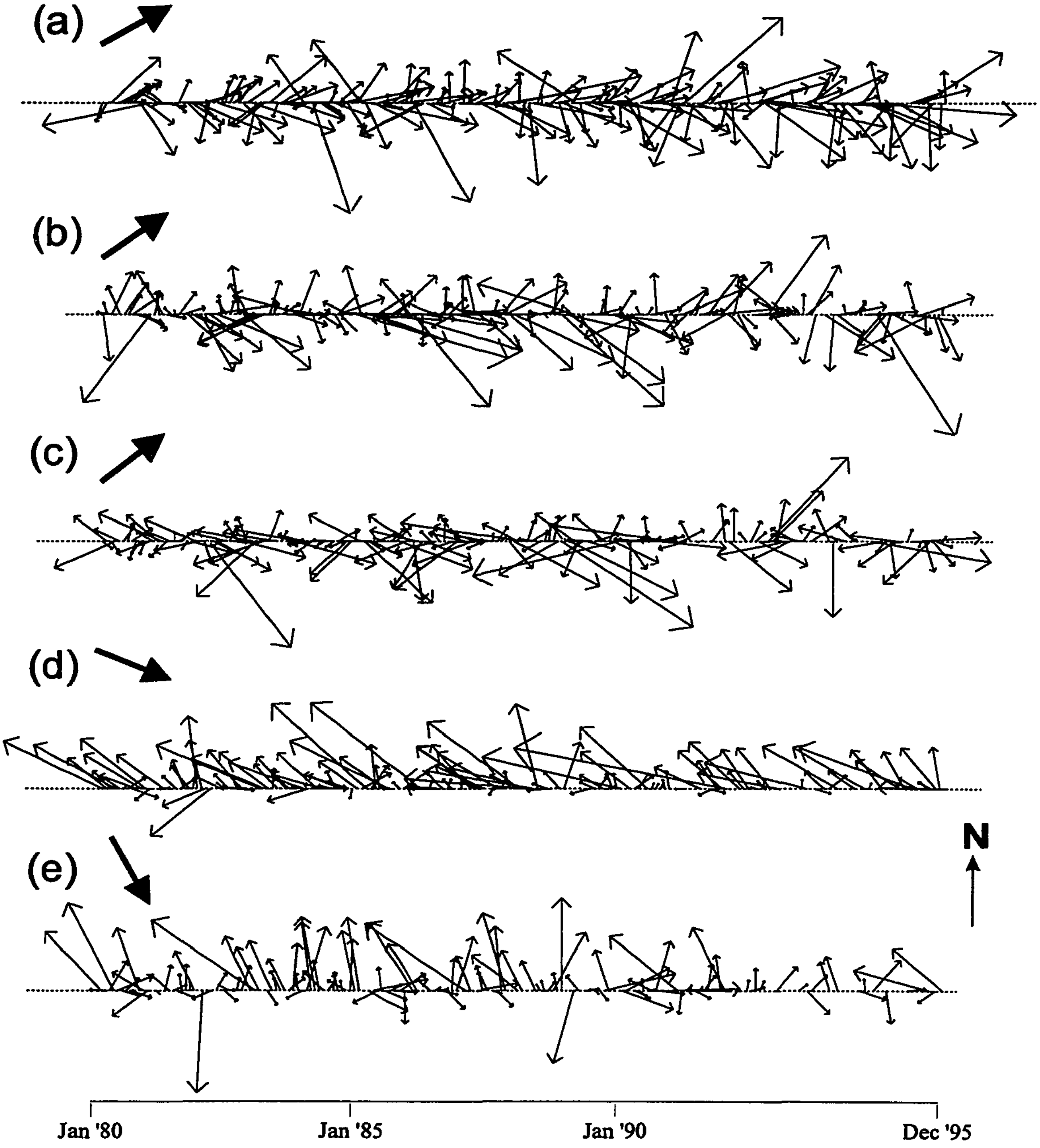

Figure 7.3: Monthly upwelling vectors from January 1980 - December 1995 averaged over 3-8 grid points (see Fig. 7.1) within areas Shumagin (a), Chirikof (b), Kodiak (c), Yakutat (d), and Southeast (e). Heavy arrows indicate average orientation of coastline within each area.

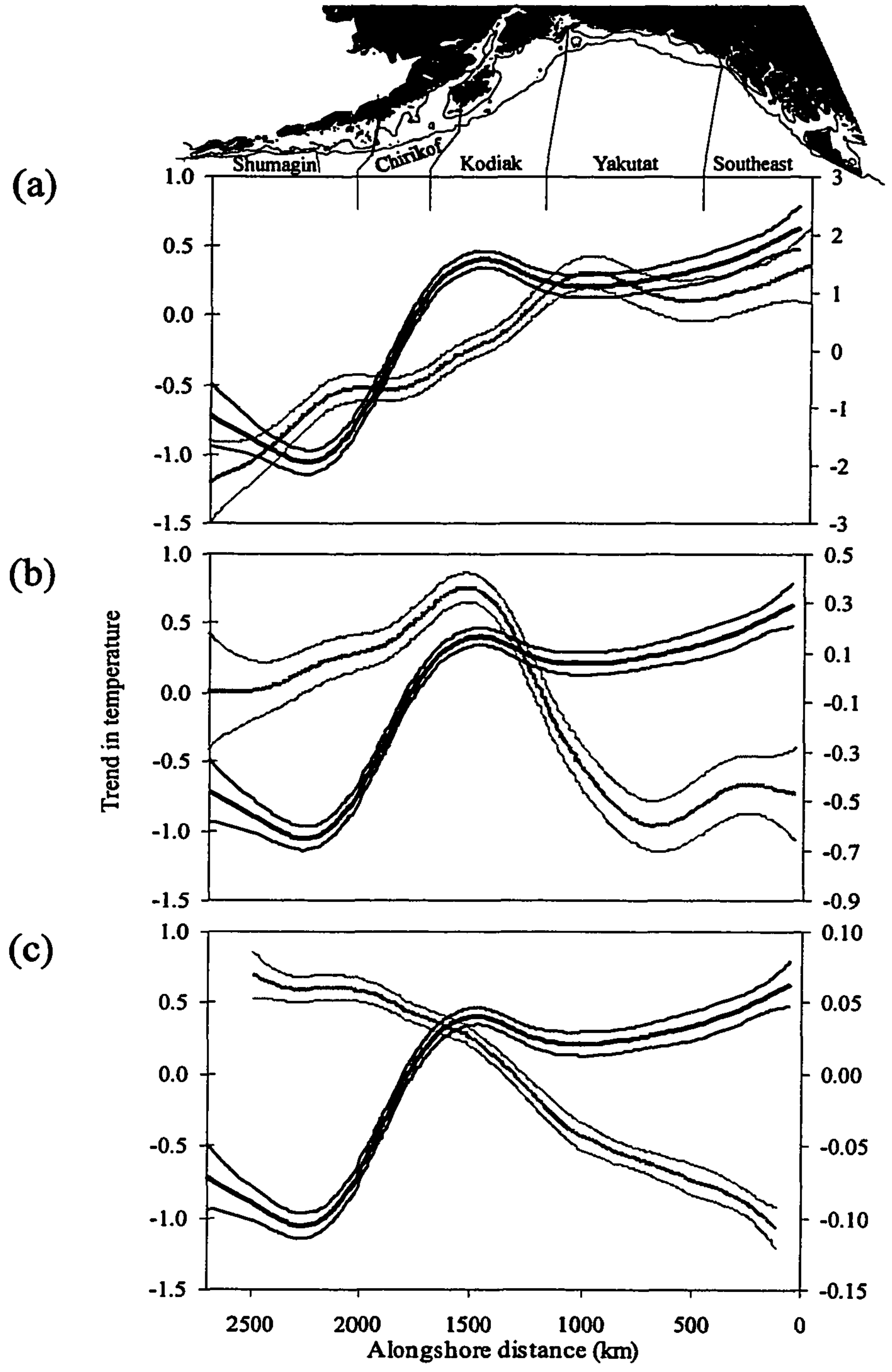

Figure 7.4: Long-term (1984-1996) average alongshore temperature gradient (black line) with smoothed alongshore trends (light gray lines) in species richness (a), total groundfish CPUE (b) and species composition (c) on the Gulf of Alaska shelf and upper slope. All indices shown with 95% pointwise confidence bands.

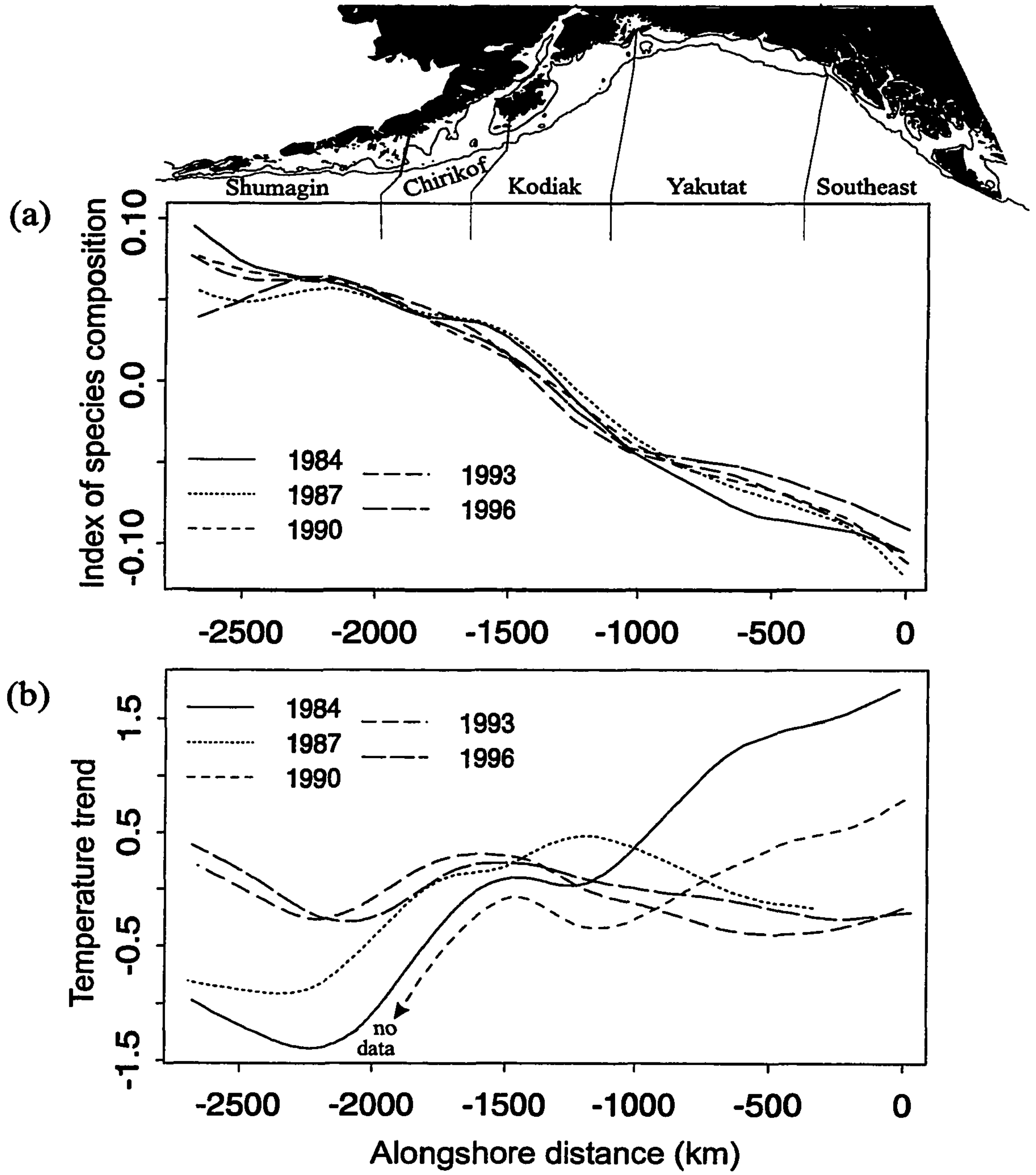

Figure 7.5: Alongshore trends in index of species composition for Gulf of Alaska groundfish community (a) and bottom temperature along Gulf of Alaska shelf (b) for each of five survey years.

depth effects, was a relative maximum in the vicinity of Kodiak Island (Fig. 7.5), suggesting strong vertical mixing in this area.

The increase in average CPUE and other biotic indices west of the Yakutat area coincided with a number of geological trends along the GoA shelf. Sediment input into the GoA increases greatly west of Yakutat due to a number of major rivers and glaciers that empty onto the shelf between Yakutat and Prince William Sound and in upper Cook Inlet (see Chapter 2). As a result bottom sediments are much finer in the central GoA between Yakutat and Kodiak Island (Hampton et al. 1986), compared to areas farther east or west. Finally, the average width of the shelf increases greatly between Yakutat and Kodiak Island, a trend that coincided closely with the increase in CPUE (Fig. 7.6).

Spatio-temporal trends in the GoA groundfish community

The estimated long-term trend in species composition and the increase in total CPUE of the GoA groundfish community from 1984 to 1996 varied in magnitude among strata (Table 7.1). The index of species composition increased in most areas, although the increase was significant in only 12 of 48 strata. Significant increases of the index in the western areas occurred primarily in shallow depth strata, whereas the only significant changes in areas Yakutat and Southeast occurred in the deep strata. Total groundfish CPUE increased significantly in 14 strata, primarily in the shallow strata of the western GoA and in deep strata of the eastern GoA, and decreased significantly in 2 strata (Shumagin Slope, Kodiak Outer Shelf). The index of commercial trawl fishing effort varied from less than 0.05 h 10^{-3} km^{-2} y^{-1} in the Yakutat and Southeast shallow areas (0-200 m) to over 10 h 10^{-3} km^{-2} y^{-1} on the Kodiak slope. Bottom temperatures decreased in all except 2 areas, and the decrease was significant for 35 strata.

Overall, increases in the index of species composition and total CPUE from 1984 to 1996 coincided with decreases in average bottom temperatures over the same period. There was no

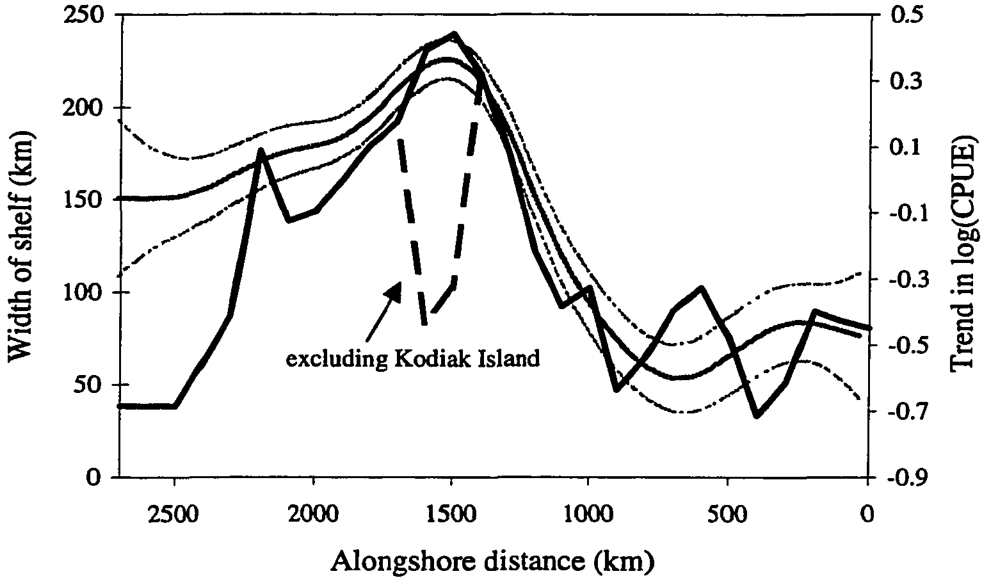

Figure 7.6: Trend in average shelf width (dark heavy line) compared to estimated trend in total groundfish CPUE along the Gulf of Alaska shelf. Shelf width in Kodiak area was measured from coast of the mainland to the shelf break (solid line) or from the east side of Kodiak Island to the shelf break (dashed line).

Table 7.1: Average fishing effort and estimated changes in bottom temperature, species composition and total groundfish CPUE from 1984 to 1996 by sampling stratum. Strata are from (Martin 1997). Fishing effort was measured in hours of commercial trawl fishing time per 1000 km^2 per year. Other values indicate slopes obtained by regressing temperature, an index of species composition over time, and total CPUE on year within each stratum. Sample sizes (total for 5 years) in parentheses. Slope for index of species composition based on single estimates of the index per stratum and year. Slopes that differ significantly from zero at α=0.05 are indicated (*).

			Slopes of linear regressions on year for:			
Area	Depth	Stratum	Species composition	Total CPUE	Bottom temperature	Fishing effort (1990 - 96)
Shumagin	0 - 100	Fox Islands	0.000	0.07 * (119)	-0.07 * (68)	1.13
		Davidson Bank	0.013	0.11 * (185)	-0.14 * (118)	2.50
		Lower Alaska Peninsula	0.007 *	0.05 (81)	-0.09 * (52)	0.15
		Shumagin Bank	0.006	0.10 * (102)	-0.01 (67)	1.23
	100 - 200	Sanak Gully	0.010 *	0.06 * (69)	-0.06 * (50)	1.81
		Shumagin Outer Shelf	0.005	-0.01 (55)	-0.10 * (35)	1.56
		West Shumagin Gully	0.011	-0.04 (122)	-0.03 (75)	1.33
	200 - 300	Shumagin Slope	-0.002	-0.06 * (67)	0.00 (38)	3.06
	300 - 500	Shumagin Slope	0.005	0.02 (152)	-0.01 (81)	3.35
Chirikof	0 - 100	Upper Alaska Peninsula	0.009 *	0.07 * (44)	-0.24 * (35)	0.33
		Semidi Bank	0.010	0.11 * (21)	-0.16 * (16)	1.41
		Chirikof Bank	0.011 *	0.05 * (24)	-0.14 * (15)	0.53
	100 - 200	East Shumagin Gully	0.010 *	0.02 (43)	-0.04 * (37)	1.11
		Shelikof Edge	0.008	0.02 (49)	-0.07 (31)	1.77
		Chirikof Outer Shelf	0.018 *	0.04 (75)	-0.15 * (53)	4.16
	200 - 300	Lower Shelikof Gully	0.006 *	-0.01 (173)	0.00 (92)	0.33
		Chirikof Slope	0.003	0.02 (46)	-0.14 * (28)	7.99
	300 - 500	Chirikof Slope	0.003	0.03 (258)	-0.11 * (121)	5.22
Kodiak	0 - 100	Albatross Shallows	0.004	0.00 (105)	-0.10 * (57)	1.18
		Albatross Banks	0.001	0.06 * (100)	-0.14 * (62)	4.31
		Lower Cook Inlet	0.006	0.03 (175)	-0.15 * (97)	0.98
		Kenai Peninsula	-0.002	0.02 (117)	-0.04 (69)	0.26
		Northern Kodiak Shallows	0.021	0.04 (118)	-0.08 (75)	1.97
	100 - 200	Albatross Gullies	0.004	-0.02 (155)	-0.07 * (84)	8.65
		Portlock Flats	0.007 *	-0.02 (88)	-0.04 (60)	3.88
		Barren Islands	0.005	0.00 (103)	-0.07 * (78)	0.11
		Kenai Flats	0.011	0.05 * (62)	-0.05 * (56)	0.10
		Kodiak Outer Shelf	0.005	-0.07 * (72)	-0.11 * (67)	7.53
	200 - 300	Kenai Gullies	0.013	0.00 (49)	-0.06 * (41)	2.01
		Kodiak Slope	0.009	-0.02 (54)	-0.13 * (50)	12.75

Table 7.1: continued

			Slopes of linear regressions on year for:					
Area	Depth	Stratum	Species composition	Total CPUE		Bottom temperature		Fishing effort (1990 - 96)
		Upper Shelikof Gully	0.016 *	-0.01	(100)	-0.03	(84)	0.07
	300 - 500	Kodiak Slope	0.002	-0.02	(68)	-0.13 *	(41)	10.17
Yakutat	0 - 100	Yakutat Shallows	0.003	-0.06	(101)	-0.06	(61)	0.00
		Middleton Shallows	0.006	0.02	(39)	-0.08	(25)	0.01
	100 - 200	Middleton Shelf	-0.002	-0.04	(88)	-0.07 *	(58)	0.40
		Yakataga Shelf	0.012	-0.01	(34)	-0.07 *	(23)	0.73
		Yakutat Flats	0.009	0.08 *	(28)	-0.04	(18)	0.02
		Fairweather Shelf	0.008	-0.02	(87)	-0.14 *	(86)	0.02
	200 - 300	Yakutat Gullies	0.007 *	0.03	(58)	-0.08 *	(54)	0.43
		Yakutat Slope	0.004	0.04	(48)	-0.10 *	(42)	2.91
	300 - 500	Yakutat Gullies	0.003	0.12 *	(91)	-0.10 *	(76)	1.03
		Yakutat Slope	0.012 *	0.03	(50)	-0.20 *	(33)	3.14
Southeast	100 - 200	Baranof-Chichagof Shelf	0.008	0.00	(38)	-0.11 *	(27)	0.01
		Prince of Wales Shelf	0.011	0.05 *	(53)	-0.09 *	(37)	0.05
	200 - 300	Baranof-Chichagof Slope	0.006	0.01	(44)	-0.12 *	(38)	0.54
		Prince of Wales Slope	0.001	0.12 *	(27)	-0.15 *	(20)	0.49
	300 - 500	Southeastern Deep Gullies	0.013 *	0.09 *	(55)	-0.16 *	(42)	0.94
		Southeastern Slope	0.006	0.05	(10)	-0.24 *	(8)	1.93

evidence at the scale of individual strata that changes in species composition were correlated with decreases in average bottom temperature, whereas the increase in total CPUE was on average more pronounced in strata that showed a steeper decline in bottom temperatures (Table 7.2, Fig. 7.7a). Similarly, there was no significant relationship between the change in species composition and fishing effort, whereas CPUE increased less, and sometimes decreased, in those areas that had higher commercial trawl fishing effort (Table 7.2, Fig. 7.7b). The values for two strata with high fishing effort had unduly high influence on the regression (Cook's distance > 0.1). When these were removed from a multiple linear regression, slopes remained significant for both temperature ($p=0.0005$) and fishing effort ($p=0.033$).

Alongshore wind stress in the three western areas showed no obvious trend over time (Fig. 7.8). There is some indication that the magnitude of alongshore wind stress increased in the Yakutat area after 1990 (i.e. became more negative), suggesting more intense downwelling in this area. Average alongshore wind stress in the Southeast area was highly variable and appeared

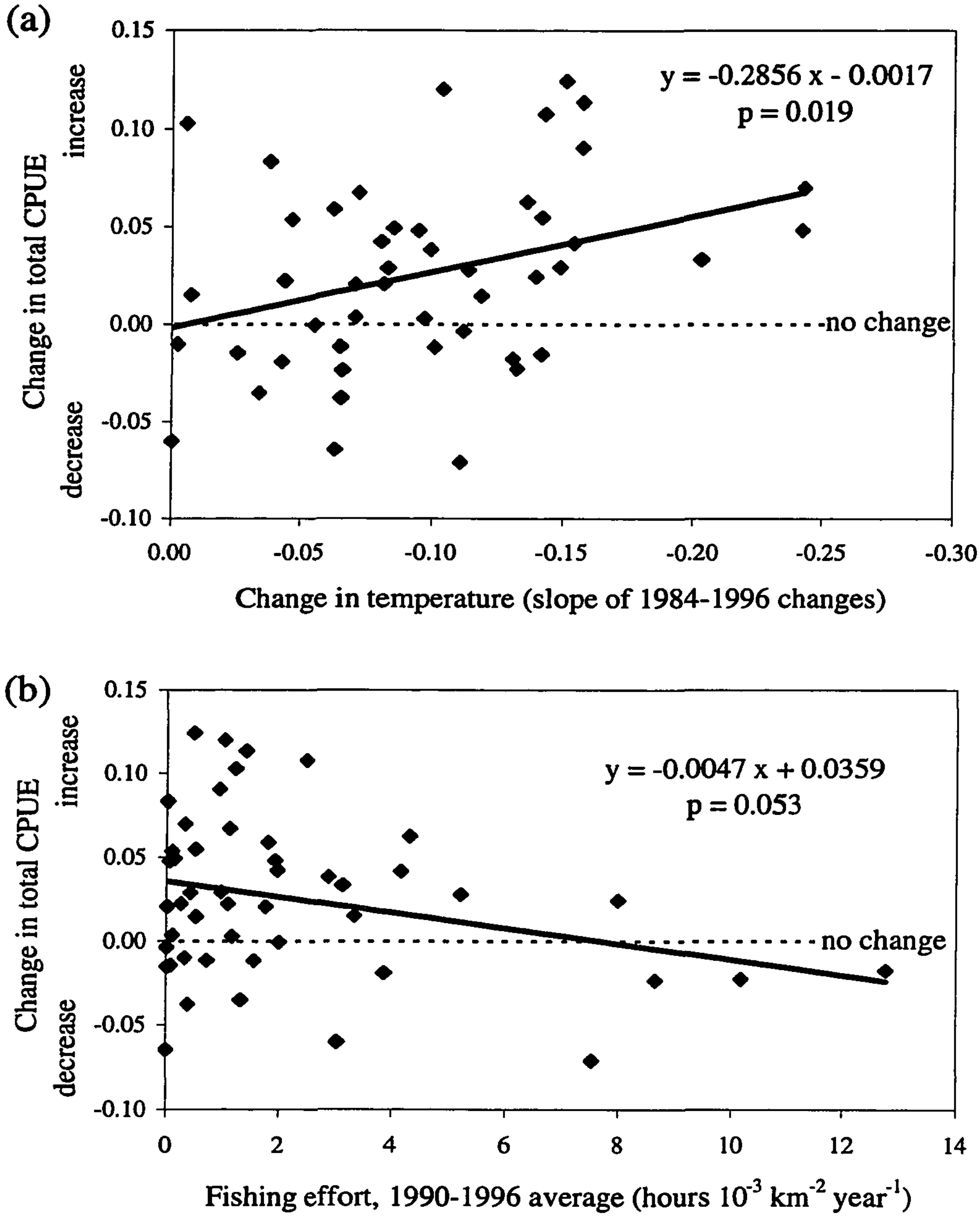

Figure 7.7: Scatterplots of changes in total CPUE over time against temperature change (a) and commercial trawl fishing effort (b) in 48 strata (see Table 8.1). Fitted lines based on simple linear regressions.

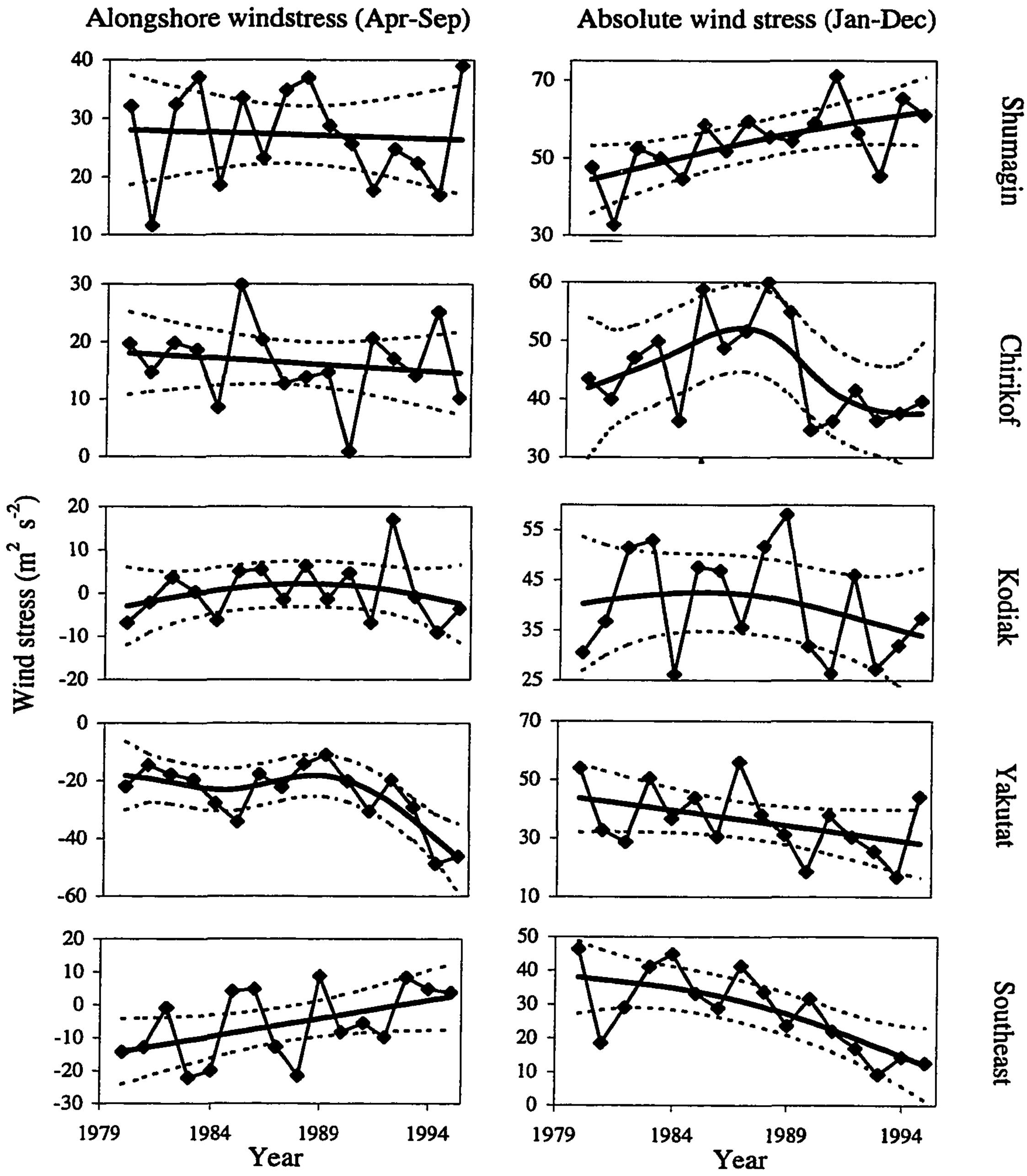

Figure 7.8: Annual averages of alongshore windstress (April - September) and absolute wind stress magnitude for 5 areas in the Gulf of Alaska (see Fig. 7.1) with cubic smoothing spline and approximate 95% confidence band. Degree of smoothing chosen by cross-validation. Note differences in vertical scale.

to decrease in magnitude (i.e., became less negative, implying diminished downwelling), however, a linear regression over time did not suggest a significant trend (F=4.37, p=0.055). In contrast, both the index of species composition and groundfish CPUE increased in all five areas (Table 7.1). Thus there was no indication that changes in species composition and CPUE were related to changes in upwelling or downwelling patterns in the GoA.

Table 7.2: Summary of regression results for regressing changes in index of species composition (Sp Comp) and groundfish CPUE over time on temperature (Temp) and average commercial fishing effort in 48 strata (Table 7.1). P-values refer to tests of the two-sided null-hypothesis that the regression has a slope of zero.

Simple linear regressions: $y = \alpha + \beta x + \varepsilon$

Y	x	Regression results			
		β	Student's t	p-value	R^2
Sp Comp	Temp	- 0.0111	- 0.860	0.394	0.016
CPUE	Temp	- 0.2856	- 2.429	0.019	0.114
Sp Comp	Effort	- 0.0002	- 0.852	0.399	0.016
CPUE	Effort	- 0.0047	- 1.985	0.053	0.079

Multiple linear regressions: $y = \alpha + \beta_1 x_1 + \beta_2 x_2 + \varepsilon$

Y	X	Regression results			
		β	Student's t	p-value	R^2
Sp Comp	x_1: Temp	- 0.0132	- 1.014	0.316	0.038
	x_2: Effort	- 0.0003	- 1.007	0.320	
		(Correlation of β_1 and β_2: 0.164)			
CPUE	x_1: Temp	- 0.3336	- 2.969	0.005	0.230
	x_2: Effort	- 0.0058	- 2.604	0.012	

Changes in absolute wind stress were more pronounced and suggested an increase in annual average wind stress in the western GoA (Shumagin: F=8.55, p=0.011), and a decrease in the eastern GoA (Southeast: F=13.79, p=0.002). No significant linear trends in the other areas were found. Average summer wind stress (April-September) followed a similar pattern; however, only the decrease in the Southeast area was significant (F=16.15, p=0.001).

Long-term changes in species composition

The index of species composition for the nearshore groundfish community of Kodiak Island shows a relatively sharp decline in the early 1980s (Fig. 7.9), which was associated with a decline in shrimp and small forage fishes and an increase in several flatfish and gadid species (Chapter 5). A first order autoregressive model (ARIMA(1,0,0), parameter = 0.826) provided the best fit to the index and was used to predict missing values.

All environmental time series displayed high interannual variability with weak or no autocorrelation, except the GAK 1 temperature series which was significantly autocorrelated at lags 1 ($r = 0.48$) and 2 ($r = 0.37$). The upwelling index was weakly autocorrelated at lags 4 ($r = 0.30$) and 9 ($r = 0.29$), whereas neither the NPI nor the PTI were significantly autocorrelated at any lags. Smooth trends fit to the data series suggest the presence of low-frequency variability in addition to interannual variations. A spectral analysis showed no significant peaks at any frequency for the PTI or NPI series, thus there was no indication of periodicity in the data. The GAK 1 temperature series and upwelling series were too short for a spectral analysis.

I found a significant negative correlation between the Papa Trajectory Index and the index of species composition at a lag of 5 years (Table 7.3). Although none of the other correlations were significant at $\alpha=0.05$, both the North Pacific Index and GAK 1 temperatures were most strongly correlated with the index of species composition at a lag of 5 years. The high negative correlation between GAK 1 temperatures and the index of species composition at lag 5 was not significant ($r = -0.81$, $p = 0.09$) due to the presence of strong positive autocorrelation in both series.

Most cross-correlations among the four environmental time series at lag zero were significant at $\alpha=0.05$, although the Upwelling Index was not significantly correlated with NPI or PTI (Table 7.4). With the exception of a negative correlation between the upwelling index and

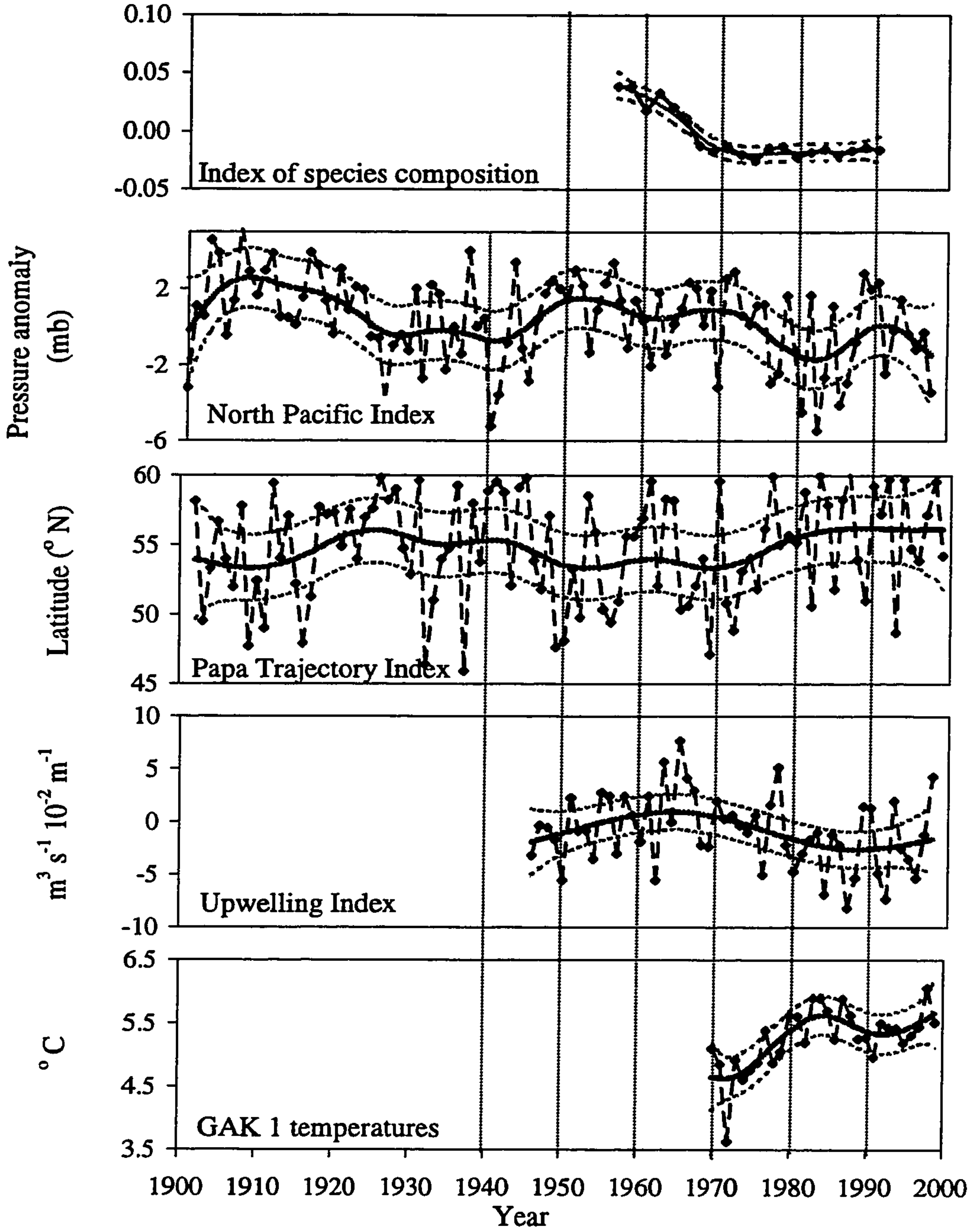

Figure 7.9: Time trends in index of species composition (no units) and four environmental variables from 1900 through 1999 with cubic smoothing spline and approximate 95% confidence bands.

Table 7.3: Cross-correlations between index of demersal species composition and four environmental time series at lags up to 8 years. Environmental indices are North Pacific Index (NPI), Papa Trajectory Index (PTI), Upwelling Index at 60°N, 149°W (UI), and temperatures at station GAK 1 (59° 50.7' N, 149° 28.0' W). The null-hypothesis of no significant correlation at any lag was tested after adjusting degrees of freedom for autocorrelation in the time series.

Lag	NPI	PTI	UI	GAK1
0	- 0.04	0.12	0.14	- 0.36
1	0.05	- 0.06	0.31	- 0.63
2	0.14	- 0.13	0.42	- 0.74
3	0.20	- 0.22	0.30	- 0.68
4	0.30	- 0.35	0.26	- 0.70
5	0.52	- 0.57*	0.30	- 0.81
6	0.34	- 0.34	0.40	- 0.60
7	0.33	- 0.42	0.32	- 0.59
8	0.47	- 0.54	0.19	- 0.53

* denotes significance at $\alpha = 0.05$

GAK 1 temperatures at lag 1 (UI leading, r = - 0.46), there were no significant cross-correlations at lags 1-8 among the environmental time series. Clearly, the patterns of correlations among the five data series are driven by a the presence of a relatively strong trend in all environmental indices in the early to mid-1970s, which was followed by a strong trend in the index of species composition from approximately 1979 to 1982 (Fig. 7.9).

Table 7.4: Cross-correlations among North Pacific Index (NPI), Papa Trajectory Index (PTI), Upwelling Index at 60°N, 149°W (UI), and temperatures at station GAK 1. Correlations for the period 1970-1995 are shown below the diagonal. Values above diagonal refer to correlations of time series for the maximum period of (pairwise) overlap. Total available length of each time series is indicated. The null-hypothesis of no significant correlation at any lag was tested after adjusting degrees of freedom for autocorrelation in the time series.

	NPI (1900-98)	PTI (1902-99)	UI (1946-98)	GAK 1 (1970-98)
NPI		- 0.68*	0.12	- 0.60*
PTI	- 0.63*		- 0.13	0.52*
UI	0.18	- 0.36		- 0.28
GAK 1	- 0.55*	0.49*	- 0.44*	

* denotes significance at $\alpha = 0.05$

Discussion

Spatial trends in the GoA groundfish community

Spatial trends in species richness, total abundance and species composition along the GoA shelf and upper slope are strongly related to marked differences in the physical environment between the eastern and western GoA. Because many of the alongshore patterns are confounded it is difficult to determine what maintains the stable spatial patterns in the groundfish communities, which showed little variation among the five surveys spanning 13 years (Fig. 7.5a and similar patterns for species diversity and total CPUE). Differences in substrate undoubtedly contribute to differences in species composition, as many groundfish species display specific substrate preferences (Scott 1982; Bromley and Watson 1994; Clus et al. 1996). The higher abundance of many rockfish species in the Southeast area is likely to be related to the availability of suitable rockfish habitat characterized by steep bathymetry and coarse substrate (Stein et al. 1992; Scott 1995). Similarly, many flatfish species prefer fine-grained sediments (Scott 1982; Clus et al. 1996) which are more prevalent on the wide shelf in the central Gulf of Alaska, downstream from the Copper River and Cook Inlet. Lack of information on substrate types on most of the GoA shelf currently prohibits a more detailed analysis of fish distribution in relation to substrate type.

Other differences in species composition between the eastern and western GoA are due to species occurring at the limits of their geographical range, which may in part be a function of temperature. Examples are Atka mackerel in the western GoA, which is the eastern limit of their distributional range, and several species of *Sebastes* that are limited to the eastern GoA and more southern waters. Limits of distribution are often determined by the thermal range of a species (Wootton 1990; Mahon et al. 1998). Temperature effects are often confounded with latitude, but in the GoA the main spatial gradient is across longitudes. Temperatures in the western GoA are colder than in the east during most years and may limit the westward extent of warm-water species. However, a stable alongshore pattern in species composition in spite of large interannual fluctuation in temperature (Fig. 7.5) suggests that temperature is not a major determinant of the summer-time distribution of most species in the GoA.

The similarity between gradients in biotic indices and the pattern of variation in alongshore wind stress (Fig. 7.2) suggest that alongshore differences in wind induced upwelling contribute to the observed patterns. Specifically, upwelling may be related to the high groundfish biomass in the western GoA, which presumably reflects higher productivity, and to differences in species richness and species composition. A similar connection has been reported for the groundfish community off the coast of Spain (Farina et al. 1997) and in the Benguela upwelling system (Macpherson and Gordoa 1996). The discrepancy between the trends in upwelling and groundfish CPUE at the longitude of Kodiak Island (Fig. 7.2) suggests that upwelling is an insufficient explanation for the alongshore peak in CPUE. Another factor that may contribute to high productivity in this region is vigorous vertical mixing due to strong tidal currents (see Chapter 6).

The remarkable overlap between a sharp increase in total CPUE and an increase in the width of the shelf (Fig. 7.6) is more difficult to interpret. It is conceivable that the width of the shelf itself enhances benthic productivity because water column production has a higher likelihood of reaching the bottom rather than being advected offshore. Furthermore, the size of the available habitat increases with the width of the shelf, which may have a positive effect on densities. However, the shelf narrows dramatically in the Shumagin area, whereas CPUE does not show a corresponding decline, thus the apparent relationship between shelf width and CPUE in the eastern and central GoA may be coincidental.

The preceding discussion assumes that CPUE patterns reflect differences in overall productivity between the eastern and western GoA. However, at least two other explanations for the trend in CPUE are possible. First, the higher groundfish CPUEs in the western GoA could be the result of tighter coupling between pelagic production and benthic communities on the broad shelf in the western GoA. In contrast, pelagic-benthic coupling in the eastern GoA may be weaker, resulting in low groundfish CPUE. There are higher abundances of herring, coho, and Chinook salmon in the eastern GoA (Ware and McFarlane 1989), but data are insufficient to evaluate the relative biomass in the pelagic and benthic fish communities. Second, the species found in the eastern GoA may generally have a lower catchability than species occurring primarily in the western GoA and the CPUE used here may be a poor index of abundance.

Spatio-temporal trends in the GoA groundfish community

If gradual trends in total groundfish CPUE or species composition result from conditions during early life stages of the component species, there may be a considerable lag between these conditions and changes at the community level, because of the relative longevity of many of the major species in the GoA groundfish community (gadids, flatfishes, rockfishes). Therefore my analysis of long-term average trends in the biotic indices and temperature are unlikely to reveal relationships resulting from mechanisms acting during early life.

The apparent relationship between high CPUE values and upwelling in the spatial dimension suggests that increases in upwelling over time could be invoked to explain the observed increase in the biomass of groundfishes in the GoA from 1984 to 1996. However, there was no evidence that alongshore wind stress and associated upwelling has increased since 1980 (Fig. 7.8), thus increases in CPUE and presumably productivity cannot be explained by increases in local upwelling. Changes in the magnitude of wind stress differed among areas, and it is unlikely that changes in local wind mixing can explain the widespread increase in CPUE throughout the eastern and western GoA.

Recruitment of many groundfish species in the Northeast Pacific is enhanced during warm years, and a number of strong year classes for several GoA groundfish stocks were observed in the late 1970s and early 1980s (Hollowed and Wooster 1995), a period of increased temperatures in the GoA (Fig. 7.9). This included some of the most abundant species that make up a large portion of the GoA groundfish community (walleye pollock, Pacific halibut, sablefish, Pacific Ocean perch). An increase in groundfish abundance associated with warm temperatures appears to contradict my results that increases in CPUE after 1984 were more pronounced in areas where the temperature decline was greater and that wide-spread increases in CPUE were associated with a decline in temperatures throughout the GoA (Table 7.1). However, in spite of a decline after the mid-1980s, temperatures throughout the 80s and 90s were consistently higher than in the 1970s (Fig. 7.9). Furthermore, enhanced recruitment in the late 1970s and early 1980s resulted in increased biomass over an extended period of time for species with moderate to high longevity.

The effect of declining temperatures on CPUE implied by results in Fig. 7.7 and Table 7.2 may reflect an effect of temperature on the distribution of some of the highly mobile groundfish species. The observed effect was weak and even a small redistribution of one or more abundant species with a preference for colder water, such as walleye pollock, may explain the observed relationship.

Although CPUE increased on most of the shelf and upper slope, the increase appeared to be less pronounced in areas subject to intense commercial fishing. Clearly, fishing can remove large portions of the biomass on a local scale and in the short term, but the results suggest that fishing may have reduced the long-term average CPUE in heavily fished areas, relative to lightly fished or unfished areas. The effect was small and fishing effort may be confounded with other variables, but the relationship deserves attention because of potential implications for the fishery. If a long-term increase in CPUE was indeed limited by fishing in heavily trawled areas, during a period of decreasing abundances the same level of fishing effort may have detrimental effects on the groundfish community.

Results regarding species composition are difficult to interpret. The observed trend in species composition from 1984 to 1996 was a minor component of the overall variability in species composition (Chapter 6), and when examined by strata the index changed significantly in only 12 strata (Table 7.1). A change in species composition within a stratum may be poorly quantified by the slope of the index. Although the index can be readily interpreted in terms of overall increases or decreases in several species (Chapter 6), it is much more difficult to interpret the index, much less changes in the index over time, within individual strata. Although the index was chosen specifically to represent changes in species composition over time, variability of the index within individual strata, arising from differences in depth distribution or other variables, may mask variations over time. Thus a lack of a relationship between fishing effort or temperature changes and changes in the index of species composition cannot be taken as evidence that there is no relationship.

Significant correlations between CPUE and fishing effort or temperature changes should be interpreted cautiously because of the potential for spatial autocorrelation in the data. If trends in CPUE, temperature changes, and fishing effort have similar scales of spatial autocorrelation, the effective degrees of freedom will be reduced considerably and the chances of finding spurious relationships greatly increases.

Long-term changes in species composition

The observed correlation between the PTI and changes in species composition of the nearshore groundfish community around Kodiak Island provides statistical support for a link between broad-scale environmental changes in the Northeast Pacific in the 1970s and changes in the groundfish community. Unlike other biological indicators of the regime shift (Ebbesmeyer et al. 1991) the abrupt shift in the nearshore groundfish community appeared to lag changes in the atmosphere and ocean by 5 years. If a causal relationship exists, the delayed response may be explained by the relatively slow growth of those species that showed a strong increase associated with the shift (arrowtooth flounder, flathead sole, walleye pollock, and Pacific cod). Species that declined during the shift in species composition (shrimp and small forage fishes) have much shorter generation times and would be expected to respond to a physical regime shift with a lag time that is shorter than the 5 years suggested by this study. This lends support to the hypothesis that changes in the environment precipitated a change in gadid and flatfish species which was followed by a decline in shrimp and forage fishes, possibly as a result of increased predation (see Chapter 5). To elucidate the mechanisms responsible for the shift and separate effects at different life stages of different species an age-structured analysis of the survey data is warranted.

Correlation patterns among the environmental indices support a connection between an intensification of the Aleutian Low and northward flow in the Alaska current. This connection was described by Chelton and Davis (1982) and has been termed Type B circulation (Hollowed and Wooster 1992). The "spin-up" of the Alaska Gyre in response to a strong low in winter is confirmed in my results showing a negative correlation between November-March sea-level pressures (NPI) and simulated drifter trajectories originating at Ocean Station Papa on January 1 (PTI). Results in Table 7.4 suggest that Type B circulation is not only associated with warm sea surface temperatures (Hollowed and Wooster 1992) but affects bottom temperatures to a depth of at least 250 m (Table 7.4). This suggests that long-term trends in bottom temperatures on the shelf are at least in part determined by changes in the amount of water advected into the region from the South.

The increase in northward transport in the Alaska Current (PTI) from the early 1970s to the early 1980s (Fig. 7.9) was associated with a shift in species composition at Kodiak Island approximately 5 years later, possibly a result of a positive impact of increased advection on the growth and survival of the early stages of gadid and flatfish species. Gadid and flatfish populations, as well as a number of other species, continued to increase into the 1990s (Hollowed et al. 1998), Chapter 6). Table 7.1 indicates the increase occurred throughout most of the GoA shelf and upper slope region. A broad-scale increase in the biomass of numerous groundfish species implies an overall increase in productivity of the benthic system. While there are no independent data to confirm a change in benthic productivity, a large-scale increase in several components of the pelagic system has been well-established and suggests a higher carrying capacity of the Northeast Pacific pelagic system in the 1980s compared to earlier periods. Changes in pelagic species include a widespread increase in zooplankton biomass (Brodeur and Ware 1992) and increases in a number of pelagic fish species (Beamish and Bouillon 1993; Brodeur and Ware 1995).

Several mechanisms have been proposed to explain the observed increases in pelagic productivity in the Northeast Pacific, largely focusing on decadal-scale processes that affect the entire Northeast Pacific (Brodeur and Ware 1992; Polovina et al. 1995; Francis et al. 1998), rather than processes acting in coastal areas such as upwelling or local wind mixing. Although local conditions were likely responsible for spatial patterns in the groundfish community, as discussed in the previous section, temporal changes in the groundfish community, like changes in the pelagic system, appeared to be linked to decadal-scale variations in atmospheric circulation and advection in the Alaska Current.

The Alaska Current is an extension of the Subarctic Current, the southern limb of the Alaska Gyre, after its bifurcation into the Alaska and California Currents. These currents advect water masses originating offshore northward along the GoA shelf and southward along the US West Coast. Variations in the proportion of the flow turning southward have been associated with interannual variation in zooplankton in the California Current, where zooplankton abundances increase during years of strong southward transport (Wickett 1969, McGowan et al. 1998). Whereas McGowan (1998) found no evidence for decadal-scale variations in transport in the California Current, variations in advection of the Alaska Current appear to be an important source of decadal-scale variability on the GoA shelf (Fig. 7.9). Variations in the Alaska Current influence conditions on the GoA shelf and upper slope through variations in the rate at which nutrients, phytoplankton, and zooplankton, as well as physical water mass characteristics (e.g. temperature) are advected around the perimeter of the Gulf of Alaska.

The relationship between southward transport and zooplankton biomass in the California Current and an inverse relationship between zooplankton at Ocean Station Papa and in the California Current region (Brodeur et al. 1996) suggest that increased northward transport contributed to the high zooplankton biomass observed in the 1980s around the perimeter of the GoA (Brodeur and Ware 1992). Increases in zooplankton biomass on the shelf should improve feeding conditions for pelagic species on the shelf (Brodeur et al. 1996) and are likely to improve feeding conditions for groundfishes, resulting in an overall increase in groundfish biomass. Species that feed primarily off-bottom on euphausiids and other zooplankton benefit directly from increases in zooplankton biomass, whereas bottom feeders benefit indirectly through an increased flux of organic material to the bottom.

Other possible explanations for a relationship between PTI and changes in the groundfish community include effects of increases in coastal temperatures and changes in wind mixing and upwelling associated with changes in atmospheric and oceanographic circulation. The strong correlation between GAK 1 temperatures and a shift in community composition of the nearshore community 5 years later, although not significant because of strong autocorrelation in both time series, may reflect a causal relationship between warm years and groundfish year-class strength (Hollowed and Wooster 1992). Because of strong correlation between large-scale atmospheric variability and coastal temperatures in the GoA, which show a clear decadal-scale signal (Fig 7.9), causal relationships cannot be clarified unless correlations between the environmental variables break down as longer time series become available, or detailed process studies are undertaken.

Changes in local winds, and associated changes in upwelling and vertical mixing, can probably be discarded as reasons for the observed shift in species composition and long-term increase in groundfish biomass for several reasons. Firstly, upwelling just upstream from Kodiak Island was poorly correlated with changes in species composition and with the other environmental variables. Secondly, the long-term decrease in upwelling at 60°N, 149°W from the mid 1960s to at least the late 1980s is unlikely to be related to an increase in overall productivity, because spatial patterns suggest a positive relationship between upwelling and groundfish biomass (Fig. 7.2). Finally, wind stress data for 1980-1995 do not indicate consistent trends in wind stress magnitude. Patterns in both year-round and summertime wind stress differ among different areas of the GoA (Fig. 7.8), whereas CPUE increased throughout the GoA (Table 7.1). Therefore, while changes in atmospheric circulation at a large scale (NPI) appear to be correlated with changes in groundfish communities on the shelf (Table 7.3), the mechanisms responsible for the relationship are unlikely to be acting through local changes in wind mixing and upwelling.

In summary, I hypothesize the following chain of events to explain changes in the GoA groundfish community from the mid-1970s to the present. The 1976/77 regime shift was associated with an intensification of the Aleutian Low Pressure System, which caused an increase in northward transport in the Alaska Current. This, and other changes associated with the regime shift, resulted in a substantial increase in zooplankton biomass in the coastal GoA, improving feeding conditions for juvenile and adult groundfishes on the shelf and slope. Recruitment success of flatfish and gadid species increased. Total groundfish biomass increased, resulting in increased predation on shrimp and forage fishes in the nearshore areas, which (along with heavy fishing pressure on shrimp) led to a sharp decline in their abundance, hence the "regime shift" in the nearshore groundfish community. Total groundfish biomass continued to increase throughout the 1980s and into the 1990s, particularly in the case of currently unfished or little-fished species such as arrowtooth flounder.

The increase in total groundfish biomass from 1984 to 1996 suggests an increase in carrying capacity of the benthic system similar to the increase in the carrying capacity of the pelagic system. Whether the increase was related to or was triggered by the regime shift observed in the nearshore groundfish community is not clear, but both may have been related to increased northward transport in the Alaska Current. Total CPUE leveled off after 1993 (Fig. 6.5), suggesting that groundfish biomass was approaching the current limits of the benthic system. Ingraham et al. (1998) show that the most recent phase of strong northward transport was one of the longest on record for the period 1902-1999 and suggest that a reversal may be imminent. If the relationship between decadal-scale variations in circulation around the GoA and the groundfish community on the shelf and upper slope is as I have proposed, reduced northward transport in the Alaska Current is likely to result in a long-term decline in groundfish abundances with important implications for management.

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Chapter 8: Comparison of juvenile and adult groundfish communities

Introduction

In previous chapters I examined patterns in community structure of the juvenile/small adult groundfish community around Kodiak Island and the adult groundfish community on the GoA shelf and upper slope. It is of both ecological and practical importance to compare the factors that determine structure of juvenile and adult groundfish communities. Under provisions of the Magnuson-Stevens Fishery Conservation and Management Act, the NPFMC needs to describe and consider "essential fish habitat" by life stage for all commercially important species. A comparison of juvenile and adult stages in terms of proximate factors is an important first step. This chapter compares patterns in species richness, diversity, and species composition between the juvenile and adult groundfish communities. My goals are to examine whether similar ecological gradients characterize the juvenile and adult community and whether species that share a similar distribution as juveniles maintain their association as adults.

Methods

The following comparison is based on results from chapters 4 and 6, as well as on an ordination of taxa common to both surveys. For the ordination and for a comparison of patterns in species richness, diversity, and total CPUE I extended the juvenile groundfish survey data to include tows from all nearshore areas sampled between 1991 and 1996 in the central GoA during the summer, for a total of 969 tows (Fig. 8.1). I repeated the analysis described in Chapter 4 using the extended data set. The extended data set was used to test whether patterns described in Chapter 6 with respect to environmental variables for 1991 and 1992 were similar to patterns in other years and in other geographic areas. For the adult groundfish community I used data from all survey years and form all areas combined (Chapter 6), rather than limiting it to the Kodiak area, because trends were very similar in all areas. The comparison of trends in species richness,

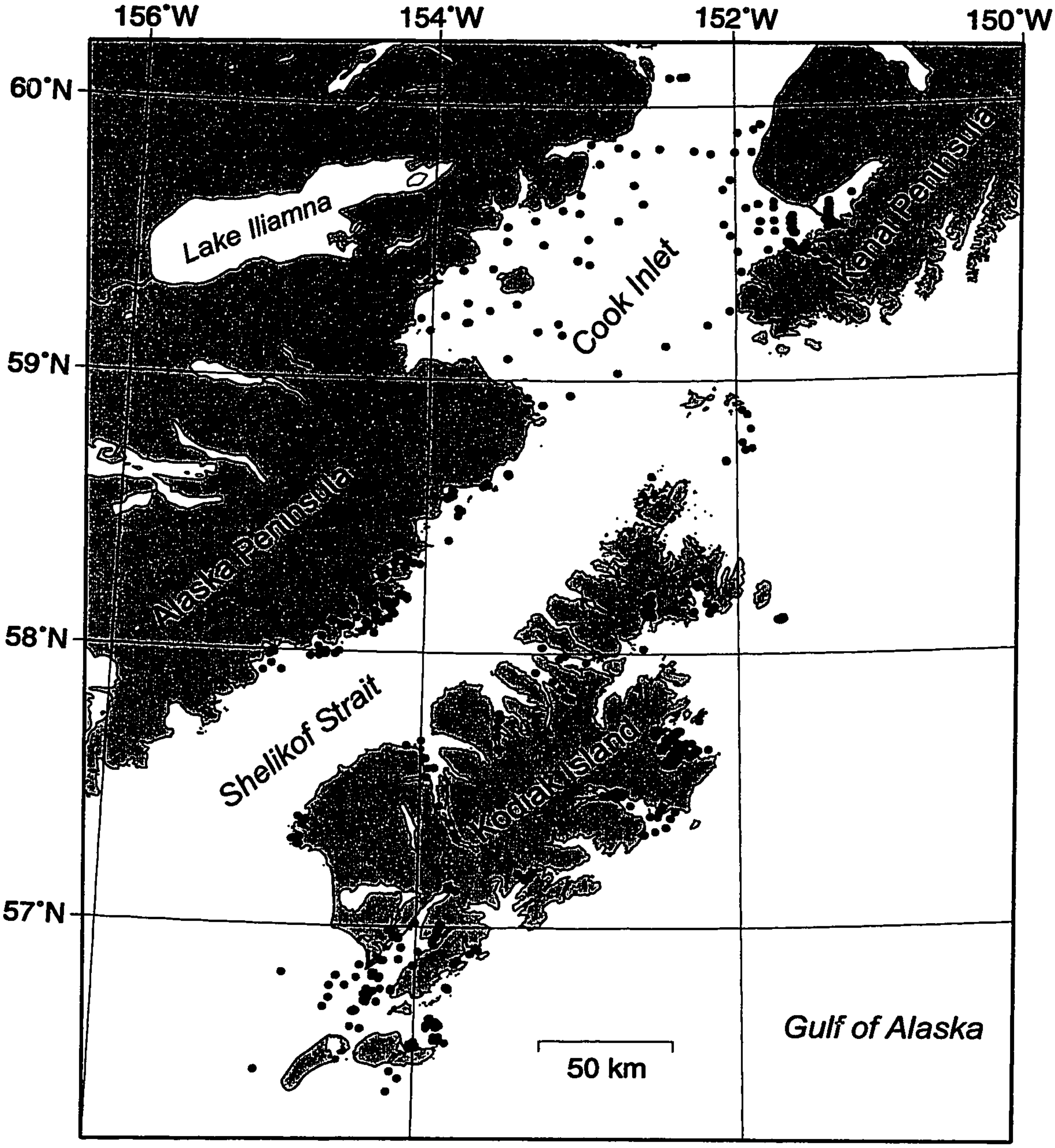

Figure 8.1: All locations sampled during juvenile groundfish surveys between 1991 and 1996 in the central Gulf of Alaska.

diversity, and total CPUE only examines patterns along the depth gradient because depth was the most important gradient among the three variables that were available for both surveys (depth, temperature, and Julian day). Comparisons between the two surveys have to be interpreted with care because different measures of abundance were used (numbers per unit area for juvenile survey, weights per unit area for adult survey), different independent variables were included in the analyses, and the spatial extent of the surveys differed greatly.

To compare patterns in species composition between the juvenile and adult communities I analyzed 23 taxa common to the juvenile and adult surveys. The 23 taxa for analysis were obtained by applying the selection criteria listed in Chapter 6 to reduce the set of species that were common to both surveys. Taxa were further aggregated if necessary, such that the same taxonomic levels were used for both data sets. Based on a matrix of Bray-Curtis dissimilarities between each pair of taxa I conducted a cluster analysis to group taxa using average linkage clustering (Johnson and Wichern 1992) and an ordination of taxa using NMDS (R-mode analysis, (Ter Braak 1995). Groupings of taxa and patterns in similarities among taxa were compared visually between the juvenile and adult communities. In the R-mode analysis, the ordination plot arranges species in ordination space such that taxa that tend to co-occur are close to each other, whereas taxa that tend to differ in distribution are separated.

The ordination diagram was interpreted in terms of the available environmental variables by relating the ordination axes to the average conditions at which each species occurred. "Average" conditions were determined for each taxon by identifying the median value of each environmental variable at which the taxon occurred. To obtain, for example, the median depth of occurrence of a given taxon I fitted a non-parametric smoothing spline to a scatterplot of CPUE against depth. The median depth at which the taxon occurs (i.e., 50% of specimens occur below this depth) was then estimated by integrating under the smoothed curve and computing the depth corresponding to the mid-point of the integral. This procedure was used rather than simply averaging environmental variables over all stations because sampling effort was not distributed evenly or randomly along environmental gradients. The median values obtained for each taxon were related to the ordination axis using multiple regression to determine the direction and magnitude of the correlation between the environmental variable and ordination axes as described in Ter Braak (1995). This allowed me to identify the main gradients responsible for dissimilarities in distribution among species. The gradients were indicated in the ordination diagram by arrows indicating the direction and magnitude of the correlation (biplot).

Results and Discussion

Species richness, diversity, and total CPUE of the juvenile groundfish community decreased significantly with depth over the observed depth range, whereas the adult groundfish community had a strong peak in all three indices at intermediate depths, below the range sampled during juvenile surveys (Fig. 8.2). The depth range for the juvenile data set was limited to the upper 170 m, with few observations at depths below 120 m. Observed species richness and CPUE were lowest below 120 m, but are not indicated in Figure 8.2 because of the large confidence intervals. Many species appeared to be restricted in distribution to the upper 100 m or less (Fig. 8.3). Although there were no observations in deeper water, I assumed that total abundance did not increase with depth below the observed depth range, based on what is known about the distribution of juveniles of many of the common species. The observed patterns indicate a strong partitioning of the available shelf and upper slope demersal habitat between the juvenile and adult groundfish community based on depth. Juvenile groundfishes were most abundant in shallow water where the abundances of adults were at a minimum, thereby minimizing the spatial overlap between small juvenile fishes and adults of the same or other species. This is consistent with the hypothesis that juveniles use the nearshore environment as nursery areas to escape predation, whether incidental or targeted, by large fishes.

As shown in Chapters 4 and 6, the species composition of both the juvenile and adult groundfish communities changed most strongly along the depth gradient. For the juvenile survey, depth and temperature effects were difficult to separate because of the high correlation between

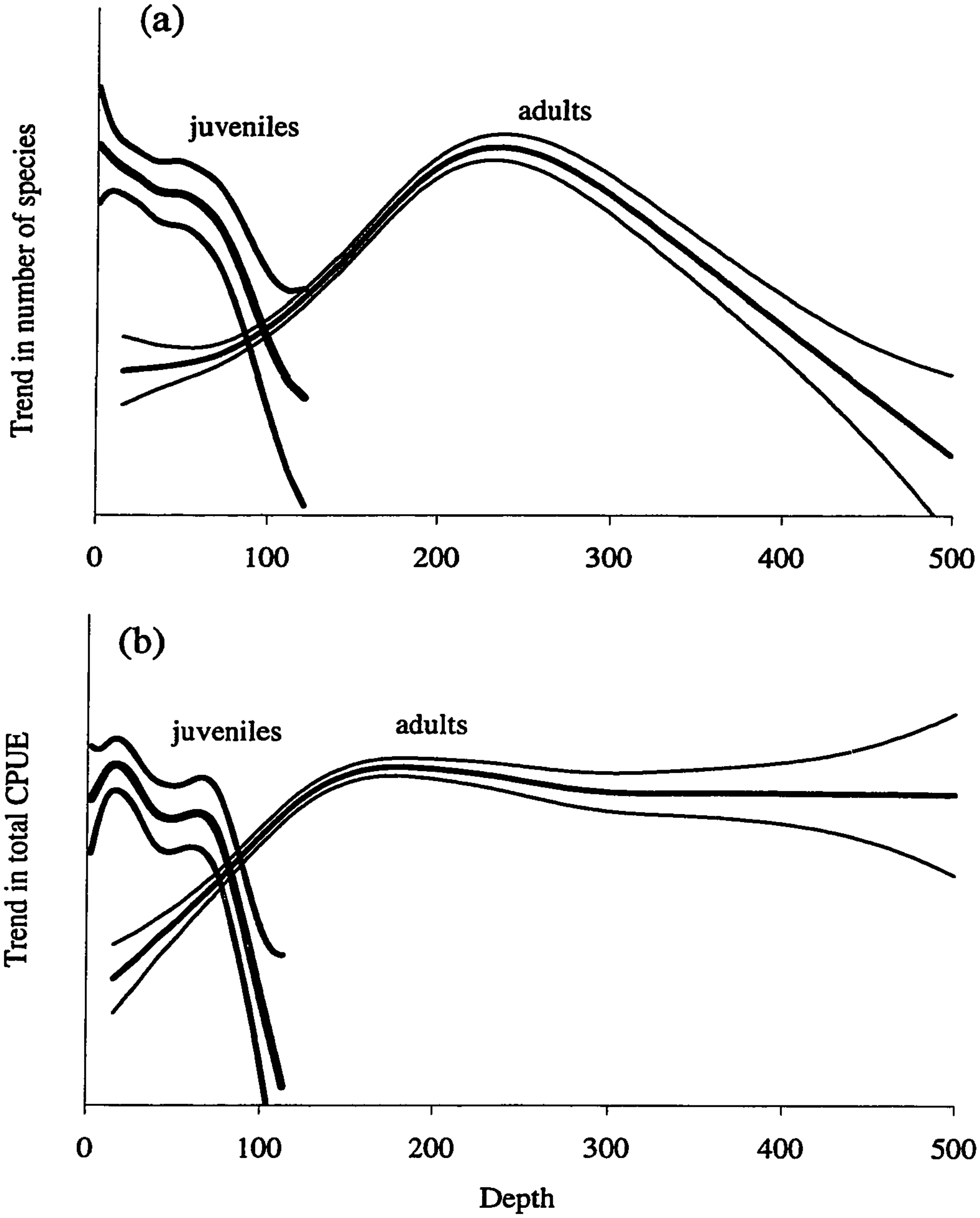

Figure 8.2: Trends in number of species per haul (a) and total CPUE (b) of the juvenile groundfish community in the central Gulf of Alaska (see Fig. 8.1) and adult groundfish community on the Gulf of Alaska shelf and upper slope.

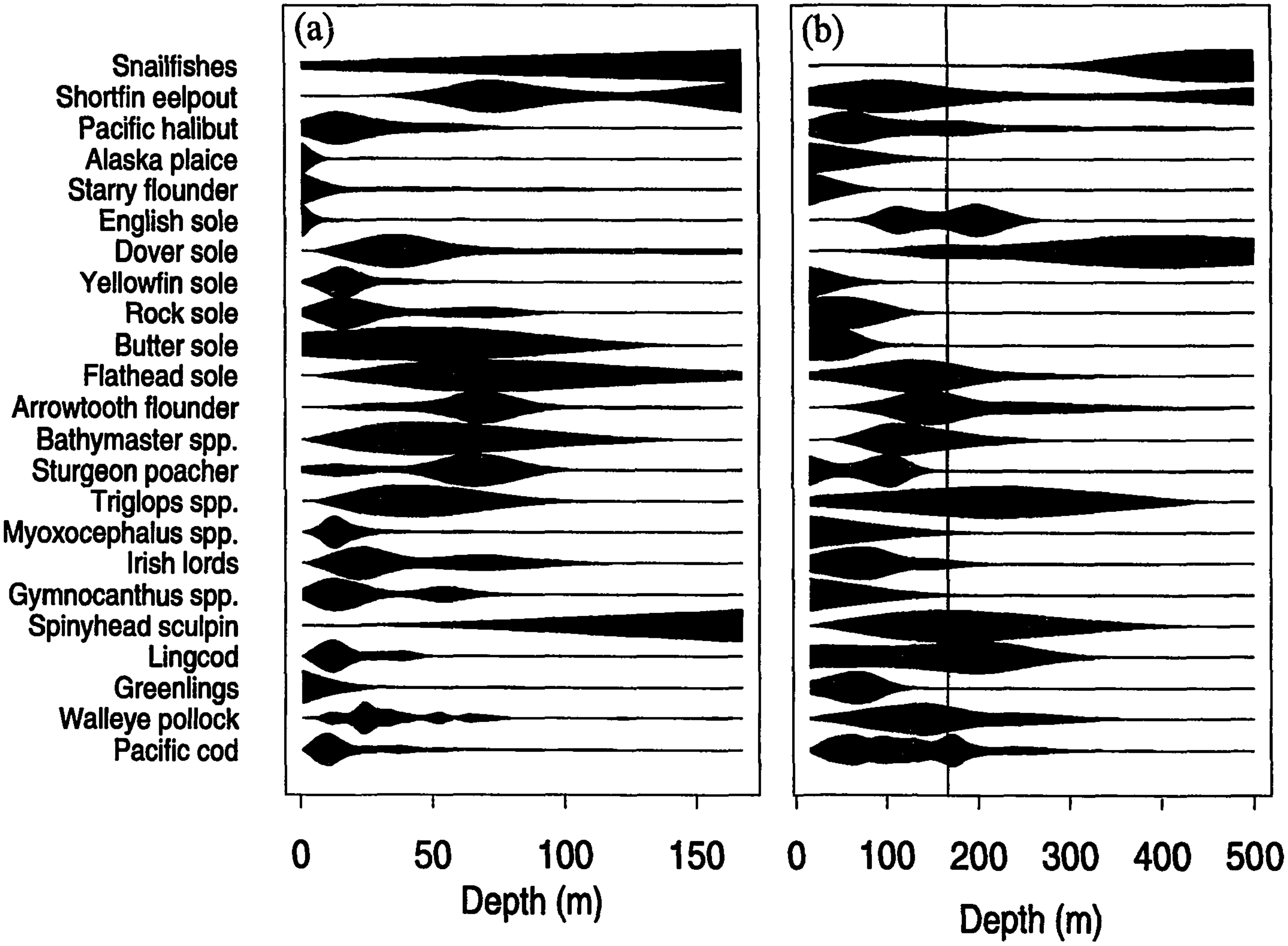

Figure 8.3: Estimated depth distribution of 23 taxa common to juvenile (a) and adult (b) surveys. Width of bands at a given depth is proportional to estimated mean CPUE. Note difference in scale on x-axis. Maximum depth sampled during juvenile survey indicated by vertical line in (b).

these variables. Depth and temperature in the adult groundfish surveys were less strongly correlated, and the analysis indicated that depth was the gradient that was more strongly related to community structure (Table 6.5). Many fish species are physiologically adapted to limited depth (or pressure) ranges (e.g. Ribbink and Hill, 1979) and are highly sensitive even to small variations in pressure. The consistent selection of a preferred depth range presumably reflects evolutionary adaptations to the environment that provides the best conditions for a species' survival. Suitable conditions are related to the physical, chemical and biological characteristics prevailing at a given depth. Physical and chemical factors that determine the distribution of a species include light, temperature, currents, sediment type, salinity, and oxygen (Moyle and Cech 1988; Wootton 1990). Biological factors include predation, which may in part explain the preference of juvenile fishes for shallow nearshore areas, and the availability of food, which may be an important factor in the distribution of species that have a pronounced maximum in abundance near the shelf break (see Chapter 6).

Species composition varied greatly between the two surveys due to difference in the size range sampled by the survey gears and differences in the geographical ranges covered by each survey. The juvenile and adult surveys identified a total of 102 and 138 species respectively with 64 species caught in both surveys (Table 8.1). Species that were common to both surveys included most flatfish species (Pleuronectidae), gadids, several skates, and a number of poachers and sculpin species. The juvenile survey did not catch species that are typically limited to deeper water (e.g. giant grenadier, *Albatrossia pectoralis*, blackfin poacher, *Bathyagonus nigripinnis*), that have pelagic juveniles (e.g. *Sebastes* species), or whose geographic range is limited to the eastern (e.g. petrale sole, *Eopsetta jordani*, slender sole, *Lyopsetta exilis*) or western (e.g. Atka mackerel, *Pleurogrammus monopterygius*) part of the study area. Species in the juvenile survey that were not caught in the adult survey include a number of poachers (Agonidae), sculpins (Cottidae), gunnels (Pholidae), and pricklebacks (Stichaeidae). Most of these species are limited to nearshore, shallow areas and are typically too small to be retained in the relatively large-mesh nets used for adult groundfish surveys.

Table 8.1: All species caught in the juvenile survey around Kodiak Island and in five years of bottom trawl surveys on the Gulf of Alaska shelf and upper slope.

Family	Scientific names	Common names	Adult survey	Juvenile survey
Lamnidae	*Lamna ditropis*	salmon shark	X	
Squalidae	*Squalus acanthias*	spiny dogfish	X	
"	*Somniosus pacificus*	Pacific sleeper shark	X	
Rajidae	*Raja binoculata*	big skate	X	X
"	*Raja kincaidi*	black skate		X
"	*Raja rhina*	longnose skate	X	X
"	*Bathyraja interrupta*	Bering skate	X	
"	*Bathyraja trachura*	black skate	X	
"	*Bathyraja parmifera*	Alaska skate	X	X
"	*Bathyraja aleutica*	Aleutian skate	X	
Chimaeridae	*Hydrolagus colliei*	spotted ratfish	X	
Bothidae	*Citharichthys sordidus*	Pacific sanddab	X	
Pleuronectidae	*Atheresthes stomias*	arrowtooth flounder	X	X
"	*Atheresthes evermanni*	Kamchatka flounder	X	
"	*Hippoglossus stenolepis*	Pacific halibut	X	X
"	*Hippoglossoides elassodon*	flathead sole	X	X
"	*Lyopsetta exilis*	slender sole	X	
"	*Eopsetta jordani*	petrale sole	X	
"	*Parophrys vetulus*	english sole	X	X
"	*Microstomus pacificus*	Dover sole	X	X
"	*Glyptocephalus zachirus*	rex sole	X	X
"	*Limanda aspera*	yellowfin sole	X	X
"	*Platichthys stellatus*	starry flounder	X	X
"	*Psettichthys melanostictus*	sand sole	X	X
"	*Lepidopsetta peracuata*	northern rock sole	X	X
"	*Lepidopsetta bilineata*	southern rock sole	X	X
"	*Isopsetta isolepis*	butter sole	X	X
"	*Pleuronectes quadrituberculatus*	Alaska plaice	X	X
Agonidae	*Pallasina barbata*	tubenose poacher		X
"	*Sarritor frenatus*	sawback poacher	X	X
"	*Xeneretmus leiops*	smootheye poacher	X	
"	*Bathyagonus alascanus*	gay starsnout		X
"	*Bathyagonus infraspinata*	spinycheek starsnout		X
"	*Bathyagonus pentacanthus*	bigeye poacher	X	
"	*Bathyagonus nigripinnis*	blackfin poacher	X	
"	*Podothecus acipenserinus*	sturgeon poacher	X	X
"	*Aspidophoroides bartoni*	Aleutian alligatorfish	X	X
"	*Anoplagonus inermis*	smooth alligatorfish		X

Table 8.1: continued

Family	Scientific names	Common names	Adult survey	Juvenile survey
"	*Occella dodecaedron*	Bering poacher		X
"	*Occella verrucosa*	warty poacher		X
"	*Hypsagonus quadricornis*	fourhorn poacher	X	X
Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	X	X
Anarhichadidae	*Anarrhichthys ocellatus*	wolf-eel	X	
Anoplopomatidae	*Anoplopoma fimbria*	sablefish	X	
Argentinidae	*Nansenia candida*	bluethroat argentine	X	
Bathylagidae		unidentified deepsea smelt	X	X
"	*Leuroglossus schmidti*	northern smoothtongue	X	
Bathymasteridae	*Ronquilus jordani*	northern ronquil	X	X
"	*Bathymaster caeruleofasciatus*	Alaskan ronquil	X	
"	*Bathymaster signatus*	searcher	X	X
"	*Bathymaster leurolepis*	small mouth ronquil		X
Chauliodontidae	*Chauliodus macouni*	Pacific viperfish	X	
Clupeidae	*Clupea pallasi*	Pacific herring	X	X
Macrouridae	*Albatrossia pectoralis*	giant grenadier	X	
Cottidae	*Thyriscus anoplus*	sponge sculpin	X	
"	*Icelinus borealis*	northern sculpin	X	X
"	*Icelinus tenuis*	spotfin sculpin	X	
"	*Gymnocanthus pistilliger*	threaded sculpin	X	X
"	*Gymnocanthus galeatus*	armorhead sculpin	X	X
"	*Radulinus asprellus*	slim sculpin		X
"	*Clinocottus acuticeps*	sharpnose sculpin		X
"	*Artediellus* sp.		X	
"	*Artediellus pacificus*	Pacific hookear sculpin		X
"	*Malacocottus zonurus*	darkfin sculpin	X	X
"	*Hemilepidotus spinosus*	brown irish lord		X
"	*Hemilepidotus hemilepidotus*	red Irish lord	X	X
"	*Hemilepidotus jordani*	yellow Irish lord	X	X
"	*Hemilepidotus papilio*	butterfly sculpin	X	
"	*Hemitripterus villosus*	shaggy sea raven		X
"	*Triglops forficata*	scissortail sculpin	X	X
"	*Triglops pingeli*	ribbed sculpin	X	X
"	*Triglops macellus*	roughspine sculpin	X	X
"	*Triglops scepticus*	spectacled sculpin	X	
"	*Artedius fenestralis*	padded sculpin		X
"	*Myoxocephalus polyacanthocephalus*	great sculpin	X	X
"	*Myoxocephalus jaok*	plain sculpin	X	
"	*Myoxocephalus quadricornis*	fourhorn sculpin		X
"	*Leptocottus armatus*	Pacific staghorn sculpin		X

Table 8.1: continued

Family	Scientific names	Common names	Adult survey	Juvenile survey
"	*Enophrys bison*	buffalo sculpin		X
"	*Enophrys lucasi*	Leister sculpin		X
"	*Dasycottus setiger*	spinyhead sculpin	X	X
"	*Psychrolutes paradoxus*	tadpole sculpin	X	X
"	*Blepsias bilobus*	crested sculpin		X
"	*Blepsias cirrhosus*	silverspotted sculpin		X
"	*Nautichthys oculofasciatus*	sailfin sculpin		X
"	*Nautichthys pribilovius*	eyeshade sculpin	X	X
"	*Nautichthys robustus*	shortmast sculpin		X
"	*Rhamphocottus richardsoni*	grunt sculpin	X	X
"	*Hemitripterus bolini*	bigmouth sculpin	X	X
"	*Eurymen gyrinus*	smoothcheek sculpin	X	X
"	*Icelus spatula*	spatulate sculpin		X
"	*Icelus spiniger*	thorny sculpin	X	X
"	*Asemichthys taylori*	spinynose sculpin		X
"	*Synchirus gilli*	manacled sculpin		X
Trichodontidae	*Trichodon trichodon*	Pacific sandfish	X	X
Gadidae	*Microgadus proximus*	Pacific tomcod	X	X
"	*Gadus macrocephalus*	Pacific cod	X	X
"	*Theragra chalcogramma*	walleye pollock	X	X
"	*Eleginus gracilis*	saffron cod		X
Hexagrammidae	*Ophiodon elongatus*	lingcod	X	X
"	*Pleurogrammus monopterygius*	Atka mackerel	X	
"	*Hexagrammos octogrammus*	masked greenling	X	X
"	*Hexagrammos stelleri*	whitespotted greenling	X	X
"	*Hexagrammos decagrammus*	kelp greenling	X	X
Cyclopteridae	*Aptocyclus ventricosus*	smooth lumpsucker	X	X
"	*Eumicrotremus birulai*	round lumpsucker	X	
"	*Eumicrotremus orbis*	Pacific spiny lumpsucker	X	X
"	*Careproctus melanurus*	blacktail snailfish	X	
"	*Paraliparis* sp.		X	
"	Liparidinae	unidentified snailfish	X	X
Melamphaeidae	*Poromitra crassiceps*	crested bigscale	X	
Melanostomiidae	*Tactostoma macropus*	longfin dragonfish	X	
Merluccidae	*Merluccius productus*	Pacific hake	X	
Myctophidae	*Stenobrachius leucopsarus*	northern lampfish	X	
"	*Lampanyctus ritteri*	broadfin lanternfish	X	
"	*Lampanyctus jordani*	brokenline lampfish	X	
Paralepidae	*Paralepis atlantica*	duckbill barracudina	X	
Osmeridae	*Thaleichthys pacificus*	eulachon	X	X
"	*Hypomesus pretiosus*	surf smelt	X	
"	*Mallotus villosus*	capelin	X	X

Table 8.1: continued

Family	Scientific names	Common names	Adult survey	Juvenile survey
"	*Spirinchus thaleichthys*	longfin smelt	X	
Salmonidae	*Oncorhynchus tshawytscha*	chinook salmon	X	
"	*Oncorhynchus kisutch*	coho salmon	X	
"	*Oncorhynchus gorbuscha*	pink salmon	X	
"	*Oncorhynchus keta*	chum salmon	X	
"	*Oncorhynchus nerka*	sockeye salmon	X	
"	*Salvelinus malma*	dolly varden	X	
Cryptacanthodidae	*Cryptacanthodes giganteus*	giant wrymouth	X	X
"	*Cryptacanthodes aleutensis*	Dwarf wrymouth		X
Stichaeidae	*Lumpenus fabricii*	slender eelblenny		X
"	*Lumpenus maculatus*	daubed shanny	X	X
"	*Lumpenus medius*	stout eelblenny		X
"	*Lumpenus sagitta*	snake prickleback	X	X
"	*Stichaeus punctatus*	Arctic shanny		X
"	*Lumpenella longirostris*	longsnout prickleback	X	X
"	*Poroclinus rothrocki*	whitebarred prickleback	X	X
"	*Alectridium aurantiacum*	lesser prickleback		X
"	*Xiphister* sp.			X
Chirolophidae	*Chirolophis decoratus*	decorated warbonnet	X	X
"	*Chirolophis snyderi*	Wendell's warbonnet		X
"	*Anoplarchus insignis*	slender cockscomb		X
Pholidae	*Pholis clemensi*	longfin gunnel		X
"	*Pholis laeta*	crescent gunnel		X
Ptilichthyidae	*Ptilichthys goodei*	quillfish		X
Zaproridae	*Zaprora silenus*	prowfish	X	X
Zoarcidae	*Bothrocara pusillum*	Alaska eelpout	X	
"	*Lycodes palearis*	wattled eelpout	X	X
"	*Lycodes brevipes*	shortfin eelpout	X	X
"	*Lycodes diapterus*	black eelpout	X	
"	*Lycodes pacificus*	blackbelly eelpout	X	
"	*Lycodapus* sp.		X	
Scorpaenidae	*Sebastolobus alascanus*	shortspine thornyhead	X	
"	*Sebastes aleutianus*	rougheye rockfish	X	
"	*Sebastes alutus*	Pacific Ocean perch	X	
"	*Sebastes brevispinis*	silvergray rockfish	X	
"	*Sebastes ciliatus*	dusky rockfish	X	
"	*Sebastes crameri*	darkblotched rockfish	X	
"	*Sebastes diploproa*	splitnose rockfish	X	
"	*Sebastes elongatus*	greenstriped rockfish	X	
"	*Sebastes entomelas*	widow rockfish	X	
"	*Sebastes flavidus*	yellowtail rockfish	X	
"	*Sebastes helvomaculatus*	rosethorn rockfish	X	
"	*Sebastes maliger*	quillback rockfish	X	

Table 8.1: continued

Family	Scientific names	Common names	Adult survey	Juvenile survey
"	*Sebastes melanops*	black rockfish	X	
"	*Sebastes paucispinis*	bocaccio	X	
"	*Sebastes pinniger*	canary rockfish	X	
"	*Sebastes polyspinis*	northern rockfish	X	
"	*Sebastes proriger*	redstripe rockfish	X	
"	*Sebastes ruberrimus*	yelloweye rockfish	X	
"	*Sebastes babcocki*	redbanded rockfish	X	
"	*Sebastes variegatus*	harlequin rockfish	X	
"	*Sebastes wilsoni*	pygmy rockfish	X	
"	*Sebastes zacentrus*	sharpchin rockfish	X	
"	*Sebastes borealis*	shortraker rockfish	X	
"	*Sebastes reedi*	yellowmouth rockfish	X	
"	*Sebastes* spp.			X

A cluster analysis of the taxa based on Bray-Curtis dissimilarities indicated that neither the juvenile nor the adult groundfish communities formed distinct species groups. Thus species structure was more appropriately summarized in an ordination diagram (Fig. 8.4). The NMDS ordinations of 23 taxa indicated some similarity in the species structure of the juvenile and adult communities. In both cases taxa were primarily aligned along the depth gradient and the relative distribution of taxa along the depth gradient was similar in the juvenile and adult communities. Taxa that tended to prefer shallow depths as juveniles (left side in Fig. 8.4a, Fig. 8.3), were also likely to prefer relatively shallow areas as adults (upper left in Figure 8.4b, Fig. 8.3). The similarity in depth distribution was tested by correlating the mean depth of occurrence at the juvenile stage with the mean depth of occurrence at the adult stage, which was moderate but significant ($r = 0.52$, $p=0.012$). Examples of species that maintain a relatively shallow (summertime) distribution throughout life are Alaska plaice, starry flounder, yellowfin sole, rock sole, *Myoxocephalus* spp., and greenling, whereas spinyhead sculpin and shortfin eelpout occur deeper than the other species both as juveniles and adults. However, the distribution of adults was generally deeper than that of juveniles and the relative depth range of some taxa changed between the juvenile and adult stages. For example, English sole have a very shallow distribution

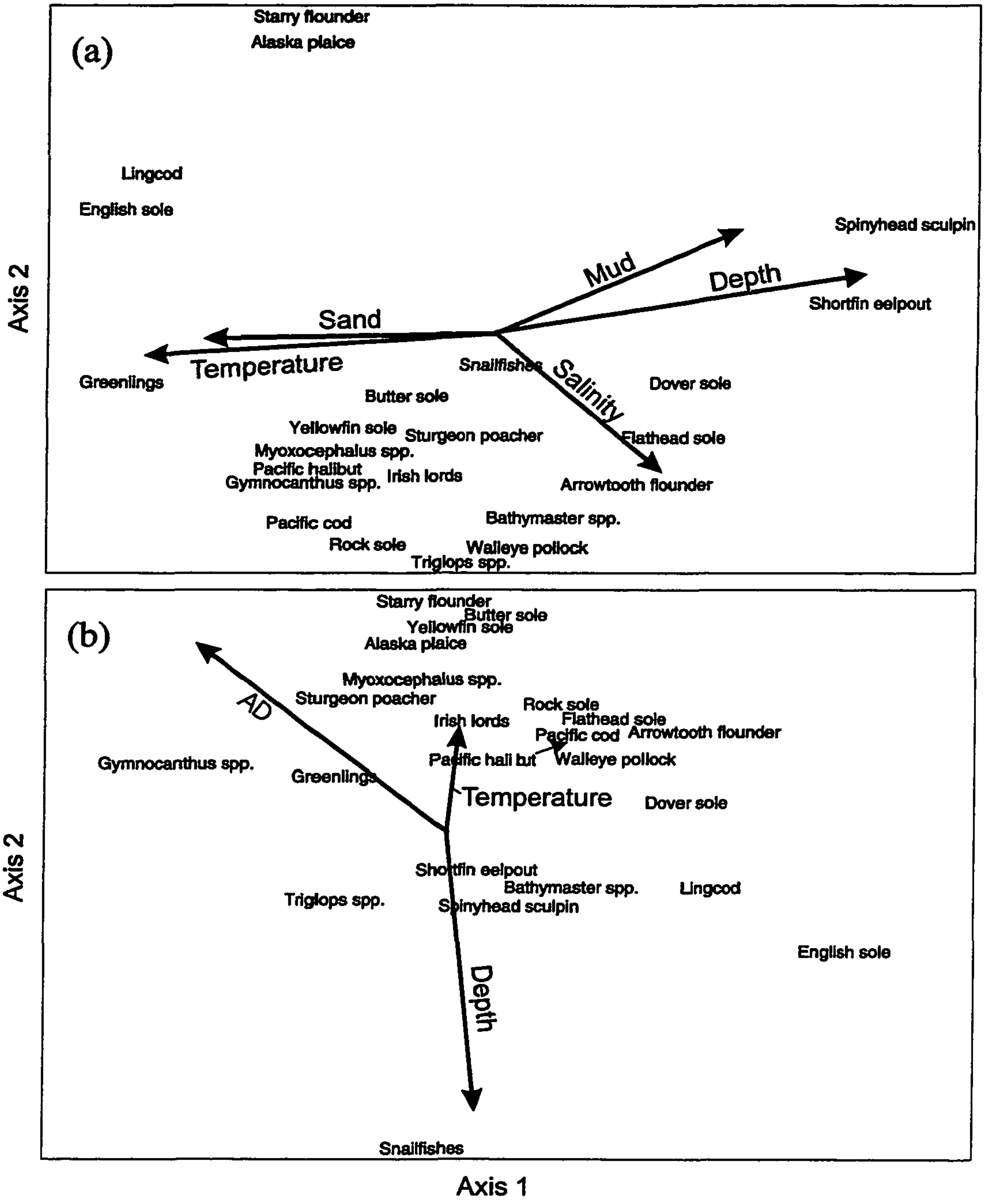

Figure 8.4: Biplots for juvenile (a) and adult (b) groundfish species based on NMDS ordination of Bray-Curtis dissimilarities among 23 taxa. Length and direction of arrows based on regression of environmental variables on axes scores. Values of environmental variables associated with each species were estimates of the median value at which each species occurred (see text). AD denotes alongshore distance.

as juveniles, but tend to occur deeper than most other taxa as adults. Lingcod exhibit a similar pattern as indicated by their position in the ordination plots (Fig. 8.4), as well as their smoothed depth distribution (Fig. 8.3). Snailfishes in the juvenile survey occur at all depths, but were only caught at the deepest stations in the adult surveys, well below the depths sampled during the juvenile survey. The difference in depth distribution may be primarily due to differences in the actual species of snailfishes caught, rather than shifts in depth distribution, as the snailfish family includes a wide variety of different species.

Salinity was another important gradient along which the juvenile community was structured. Low salinity species included starry flounder, Alaska plaice, lingcod, and English sole (Fig. 8.4a, upper left), whereas *Bathymaster* spp. tended to occur at high salinities. No salinity data were available for the adult survey, but the same species that were aligned along the salinity gradients as juveniles were strongly aligned with the depth gradient as adults. Salinity effects at the adult stage may in part be confounded with depth effects as bottom salinities on the GoA shelf are positively correlated with depth. Sediment gradients appeared to be less important (Chapter 4), but were also confounded with depth. This can be seen in the biplot (Fig. 8.4a), which shows that the arrows for sand, mud, and depth are nearly aligned (implying high positive or negative correlations).

Differences between the juvenile and adult communities in the ordination diagram are partly a result of the relatively strong alongshore gradient in the adult community (Fig. 8.4b). This gradient is lacking in the juvenile community because the juvenile survey was restricted to a narrow geographic range. For example, the ordination based on adult surveys contrasts lingcod and English sole, which were more abundant in the eastern GoA, with Alaska plaice and starry flounder, which among other species were more abundant in the western GoA. In contrast, all four species appear in a similar location in the juvenile ordination diagram (upper left in Fig. 8.4a), suggesting a common preference for low salinities at the juvenile stage. Nevertheless there was a clear separation between lingcod/English sole and starry flounder/Alaska plaice in the juvenile community along the depth and/or mud gradient.

One group of species that had a high similarity in distribution at the adult stage comprised rock sole, flathead sole, arrowtooth flounder, Pacific halibut, Pacific cod, and walleye pollock (Fig. 8.4b). These species showed less similarity as juveniles, resulting from a deeper distribution of flathead sole and arrowtooth flounder compared to the other species (Chapter 4). At the adult stage these species (except rock sole in some years) consistently grouped together in a cluster analysis of 72 taxa for each year of the survey. Furthermore, four of the species in this group were associated with the shift in species composition described in Chapter 5, suggesting that the group consists of ecologically similar species that respond similarly to environmental gradients.

Chapter 9: Summary, Conclusions, and Recommendations

Summary

- Species richness and diversity of the juvenile groundfish community around Kodiak Island were significantly higher on mixed sand sediments than on relatively homogenous sediments with high percentages of mud or gravel. The average number of species and species diversity increased with salinity over a relatively narrow range of salinities and decreased with depth from the surface to 100 m.
- The total numerical abundance of juvenile groundfishes was lower on gravel substrate than on sandy and muddy sediments. Catch-per-unit-effort was highest in shallow water and strongly decreased with depth below about 80 m.
- The east side of Kodiak Island had a higher species diversity and CPUE than the Shelikof Strait side, possibly reflecting the settlement of larger numbers of juvenile groundfishes, particularly flatfishes, in the relatively open areas on the east side of Kodiak Island like Sitkinak Strait and Chiniak Bay.
- Species composition of the juvenile groundfish community varied primarily along the depth-temperature gradient with a group of shallow/warm water species consisting of Pacific cod, greenling (*Hexagrammos* spp.), lingcod, *Myoxocephalus* spp., sturgeon poacher, tubenose poacher, rock sole, and Pacific halibut, which can be contrasted with a deep/cold water group consisting of spinyhead sculpin, *Psychrolutes* spp., *Bathyagonus* spp., *Lycodes* spp., arrowtooth flounder, and flathead sole. Secondarily, species composition varied among substrate types and geographic areas, which together explained less of the variation in species composition than the depth gradient.
- A time series of trawl survey data going back to 1976 revealed a pronounced shift in species composition in the nearshore areas of Kodiak Island from a community dominated by shrimp and small forage fishes to one dominated by a group of large piscivorous gadid and flatfish

species. The shift occurred rather abruptly in most areas between 1980 and 1982, but the pattern of change differed significantly among geographical areas.

- Comparing the timing of the changes in the two groups of species provides evidence that the decline in shrimp and forage fishes followed the increase in large piscivorous fishes, suggesting that predation contributed to the observed shift in species composition.
- The groundfish community on the GoA shelf and upper slope showed spatial patterns in species richness, diversity, and total abundance that remained stable over a 13 year period from 1984 to 1996. The number of species per haul, as well as estimates of species diversity, varied strongly with depth and along the shelf, with a significant peak at 200-300 m and a significantly higher species richness and diversity in the eastern GoA. Average CPUE (in weight per unit area) of 72 groundfish species combined increased with depth and had a significant peak near the shelf break at 150-200m. CPUE was on average twice as high in the western 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 indicate a 40% increase in total groundfish biomass between 1984 and 1996.
- Species composition varied along the depth gradient and from the eastern to the western GoA. Most species occurred over a limited depth range but had a relatively broad alongshore distribution, often with numerous local maxima.
- A cluster analysis of species did not indicate the presence of well-defined species assemblages on the GoA shelf and upper slope.
- There was a weak but significant trend in species composition over time from 1984 to 1996. The trend was associated with a decrease in the frequency of occurrence of two sculpin species and increases in the frequency of occurrence and CPUE of at least eight taxa, including skates (Rajidae), Pacific sleeper shark (*Somniosus pacificus*), capelin (*Mallotus villosus*), eulachon (*Thaleichthys pacificus*), three flatfish species, and Pacific Ocean perch.

- A comparison of patterns in species richness and total abundance between the juvenile and adult groundfish communities suggests a strong partitioning of the depth gradient. Juvenile groundfishes had high species richness and high abundances in the upper 80-100 m, whereas the abundance of adult groundfishes was lowest in this depth range.
- The east-to-west gradient in species richness, diversity, total CPUE, and species composition of the adult groundfish community coincided with differences in alongshore wind stress (i.e. upwelling) between the eastern and western GoA. High CPUEs and a low species diversity in the western GoA appear to be related to summer upwelling, although other east-to-west gradients are likely to contribute to the observed trends in the groundfish community.
- In contrast to spatial trends, the observed trend in species composition and the increase in CPUE over time could not be explained by changes in local upwelling or wind mixing. Increases in total groundfish CPUE over time appeared to be more pronounced in areas where bottom temperatures declined more steeply and in areas with high commercial fishing effort.
- The marked shift in species composition in the nearshore groundfish community in the early 1980s was correlated with an increase in northward transport in the Alaska Current five years earlier, which in turn was correlated with sea level pressures in the preceding winter and with bottom temperatures at station GAK 1 during the same year.
- Based on these results I hypothesize the following chain of events to explain changes in the GoA groundfish community from the mid-1970s to the present (Fig. 9.1). The 1976/77 regime shift was associated with an intensification of the Aleutian Low Pressure System, which caused an increase in northward transport in the Alaska Current. This, and other changes associated with the regime shift, resulted in a substantial increase in zooplankton biomass in the coastal GoA, improving feeding conditions for juvenile and adult groundfishes on the shelf and slope. Recruitment success of a number of groundfish species increased, particularly for flatfish and gadid species. Total groundfish biomass increased, resulting in increased predation on shrimp and forage fishes in the nearshore areas, which

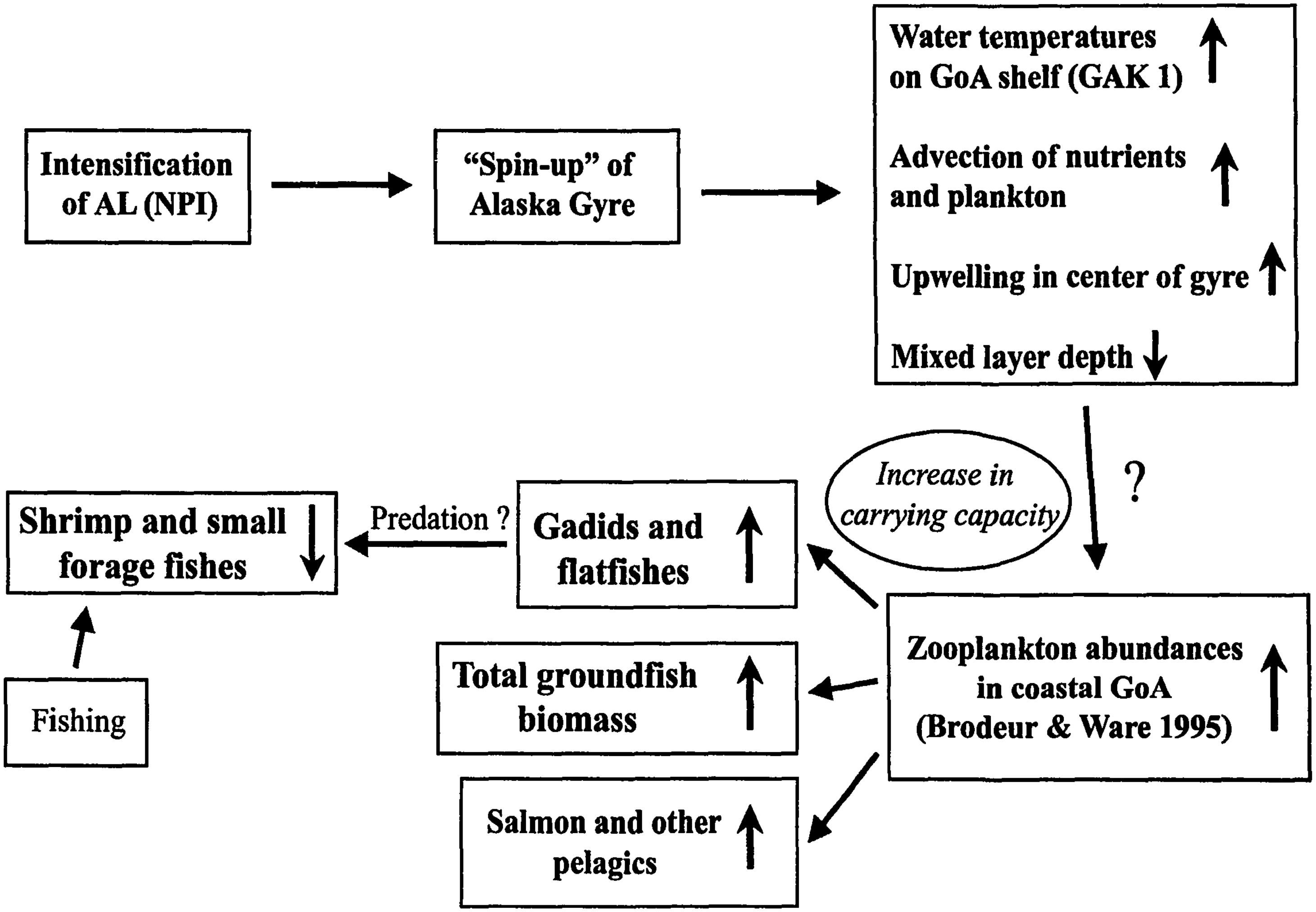

Figure 9.1: Flow chart of proposed trends in environmental and biological indicators following the 1976/77 regime shift in the Northeast Pacific ocean.

(along with heavy fishing pressure on shrimp) led to a sharp decline in their abundance, hence the "regime shift" in the nearshore groundfish community. Total groundfish biomass continued to increase throughout the 1980s and into the 1990s, particularly in the case of unfished or little-fished species such as arrowtooth flounder. The increase reflects a higher carrying capacity of the benthic system after the regime shift and is likely to continue until the new carrying capacity is reached, fishing mortality is increased, or the carrying capacity decreases as a result of changes in the atmosphere and ocean.

Conclusions and Recommendations

Groundfish communities in the GoA display quantifiable spatial and temporal trends. Information contained in these trends can be used to improve the management of groundfish resources. Management relies on stock assessment to provide estimates of abundance and its variability. Scientific research can contribute to improving management by reducing the uncertainty about estimates of abundance and by providing qualitative information useful to management.

First I will discuss some ways in which information gained from this study can be used to improve abundance estimates. Spatial patterns in survey CPUE and species composition observed in the groundfish community appear to be stable over time, and hence predictable. In spite of large variability in total CPUE and in the CPUE of individual species around average trends, the spatial patterns account for a significant proportion of the overall variability in survey CPUE, beyond that accounted for by the stratified sampling design. The additional information contained in such trends can be used to improve survey estimates of abundance. For example, spatial or environmental gradients that are strongly correlated with species abundances can be included as auxiliary variables (covariates) in the estimation using regression estimators instead of simple estimators for stratified sampling (Thompson 1992). An example of using spatial information (latitude and longitude) as well as trends along environmental variables to improve estimates of abundance can be found in Swartzman et al. (1992). They showed that incorporating depth and temperature trends resulted in lower variability of abundance estimates for five flatfish species.

For the GoA groundfish community, environmental variables that have some potential as useful covariates are depth and sediment composition. Depth may be used instead of, or in addition to, the currently used depth strata, as there are strong gradients even within each depth stratum (e.g. a strong gradient in total CPUE within the 0-100 m stratum). Sediment composition explained a significant proportion of variability in the juvenile groundfish community and it should be examined if sediments similarly explain some of the spatial patterns in the adult groundfish community. Currently, there is little quantitative information regarding sediment distribution on the Gulf of Alaska shelf and slope. A pilot study to map sediments in a limited area would be useful in assessing the potential of sediment information to account for variability in groundfish abundances. Improvements in abundance estimates are likely to be moderate given that sediment accounted for a much smaller proportion of variability in abundance than depth, at least in the juvenile groundfish community. Any potential gains from using sediment information obviously have to be weighed against the costs of obtaining such information.

In addition to using environmental or spatial gradients, variability in abundance estimates of individual species can be reduced using information from other co-occurring species. Currently, survey estimates of abundance are obtained for each species separately, thus ignoring much of the information contained in the full matrix of abundances of all species caught in the survey. If the information resulting from covariation among species can be properly quantified it can be used much like spatial or environmental variables to improve abundance estimates. Multivariate indices of species composition provide a means to summarize and quantify the covariation among all species.

The information contained in such indices can be illustrated by the following example. Over 80% of the overall spatial variability in 1996 arrowtooth flounder CPUEs could be accounted for by 5 indices of species composition derived from an ordination of all other species (excluding arrowtooth flounder). The same was true for 15 other species. Moreover, indices of species composition from 1993 were highly correlated with those from 1996, and 1993 indices could account for a high proportion of variability in 1996 abundances (>50% for 21 species, 82% for rock sole). For these comparisons the abundances of individual species and indices of species composition were interpolated onto the same regular grid for both 1993 and 1996 to allow comparisons among years that sampled different stations.

Regression estimators will be more successful for some species than others in reducing the variance of abundance estimates, just as any given stratification scheme will be more useful for some species than others. Simulation studies should be used to assess whether including auxiliary information in the form of biotic or environmental variable reduces uncertainty in abundance estimates sufficiently to warrant their use. The presence of strong spatial patterns further suggests that spatial modeling could play a useful role in estimating species abundances.

The indices of community structure used in this study may also be used as indicators of the status of the groundfish community in the context of "ecosystem-based" management. The North Pacific Fisheries Management Council each year prepares a chapter on "Ecosystem Considerations" as part of the Stock Assessment and Fishery Evaluation Report to facilitate linking ecosystem research to the management process. The chapter is meant to provide a more complete and standardized assessment of ecosystem status and one of the goals is to incorporate a variety of ecosystem, multispecies, or community indicators. I suggest including the following indices based on an analysis of community composition following each triennial survey: (1) the number of species per haul, (2) the total number of species (3) a measure of species diversity (4) an estimate of total groundfish biomass, and (5) multivariate indices of species composition based on an ordination of species abundances. Each index would be averaged by stratum or over the entire survey region. The indices could then be related to environmental variables and examined for apparent changes over time.

Stable spatial patterns in species composition seem to imply the presence of well-defined assemblages in the groundfish community. However, I found little evidence that the groundfishes on the GoA shelf and slope form distinct species groups, suggesting that management based on single species rather than management of species groups or assemblages may be appropriate. The contradiction between stable patterns in species composition and the lack of well-defined species groups can be explained by considering the different ways in which indices based on ordination and species groups based on a cluster analysis summarize the variation in a matrix of abundances. Cluster analysis emphasizes the similarity among groups of species and is appropriate if some species display a high degree of similarity, but are clearly separated from other species. The reason I found few well-defined groups is that any two species typically showed little similarity in distribution, and pairwise scatterplots or rank correlations of species abundances showed little evidence of covariation between most species pairs. Nevertheless, some species are more similar to each other in distribution and abundance than others, forming more or less continuous ecological gradients. Given such gradients each species alone contributes little information to the abundance of any other species, but indices that summarize the covariation patterns among a large number of species may be able to predict the abundance of another species with high precision. This implies that any multispecies stock assessment or management for the GoA groundfish community should consider as many species as possible to take full advantage of multispecies relationships.

In addition to strong spatial gradients, I identified temporal changes in the groundfish community that appear to be associated with large-scale changes in the Northeast Pacific environment. Although the available time series are short, this provides evidence that groundfishes respond to decadal-scale changes in the environment as do pelagic species such as Pacific salmon (Beamish and Bouillon 1993; Hare and Francis 1995). Long-term trends in abundance provide a special challenge for stock assessment and fisheries management. A decadal-scale shift in community composition results from long-term changes in the average recruitment or growth of a number of species. Such long-term changes imply a similar trend in the underlying population parameters that govern recruitment, growth, and survival. Most currently used stock assessment methods assume that population parameters such as stock-recruitment parameters, growth parameters, and natural mortality do not vary over time (Quinn and Deriso 1999). If trends in parameters are not accounted for, biased estimates of abundance may result. Thus some of the challenges for stock assessment and management are to monitor physical and biological variables in order to detect shifts in the environment that may lead to changes in population parameters as early as possible, and to develop new and improved models that allow for time-varying parameters.

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