

Community structure of eastern Bering Sea epibenthic invertebrates from summer bottom-trawl surveys 1982 to 2002

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ABSTRACT: Catches of invertebrates from the annual summer bottom-trawl surveys in the eastern Bering Sea between 1982 and 2002 were analyzed to describe the composition and spatial distribution of epibenthic invertebrate communities. A persistent characteristic is distinct inshore and offshore community types separated by the dynamic oceanographic inner front that generally coincides with the 50 m isobath. This typical spatial distribution of the 2 communities corresponds closely with surficial sediment type and previously reported patterns for groundfishes and infaunal invertebrates. The biomass of the inshore assemblage is overwhelmingly dominated by the sea star *Asterias amurensis*, whereas Gastropoda, Paguridae and the snow crab *Chionoecetes opilio* dominate the offshore assemblage. Variations in the typical inshore–offshore pattern occurred in 1982–84, 1987–88, 1998–99 and 2001–02, when there were substantial reductions in the spatial extent of the inshore community, especially in the Bristol Bay area. During these reductions, epibenthos in Bristol Bay shifted from the inshore type to either offshore or an undefined community type. In general, reductions in the inshore domain were correlated with a mean bottom temperature in the survey area that was higher than normal in the preceding summer. Extreme El Niño events coincided with sizable contractions of the inshore community in 1982–84 and 1998–99. Spatial variability in the epibenthic communities may thus reflect the influence of environmental changes on interannual and decadal scales. Evidence suggests that mobile taxa, especially crabs, may be migrating offshore toward cooler waters, thereby rearranging the epibenthic communities.

KEY WORDS: Dominant epibenthos · Indicator taxa · Spatial distribution · Interannual variability · Oceanographic front · El Niño · Environment · Climate shift

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INTRODUCTION

The Bering Sea ecosystem is extremely rich in living resources. The eastern Bering Sea (EBS) continental shelf (see Fig. 1a) within the US Exclusive Economic Zone accounts for more than half of the total US fishery production (NRC 1996). The importance of this ecosystem has prompted several collective works detailing its hydrography, geology, biology and chemistry (e.g. NRC 1996, Loughlin & Ohtani 1999). Effective conservation and management of ecosystem resources require an understanding of the structure and dynamics of its various components. In the EBS, benthic invertebrates function as predators, prey, competitors, and shelters to harvested and managed species (Feder et al. 1985, NRC 1996).

Defining the composition and spatial distribution of their communities is thus fundamental to a better understanding of overall ecosystem structure, dynamics and functions. Furthermore, analysis of spatio-temporal variability in benthic invertebrate communities is one of the principal methods for detecting and monitoring the effects of disturbance on the marine environment (e.g. Warwick & Clarke 1993, McConnaughey et al. 2000, Schratzberger & Jennings 2002, Hermsen et al. 2003, Blyth et al. 2004).

The few existing studies of EBS benthic communities are primarily concerned with inventory, distribution and abundance. Life-history and ecology information for the majority of species are unavailable (Feder et al. 1985). Investigations before 1970 were mostly con-

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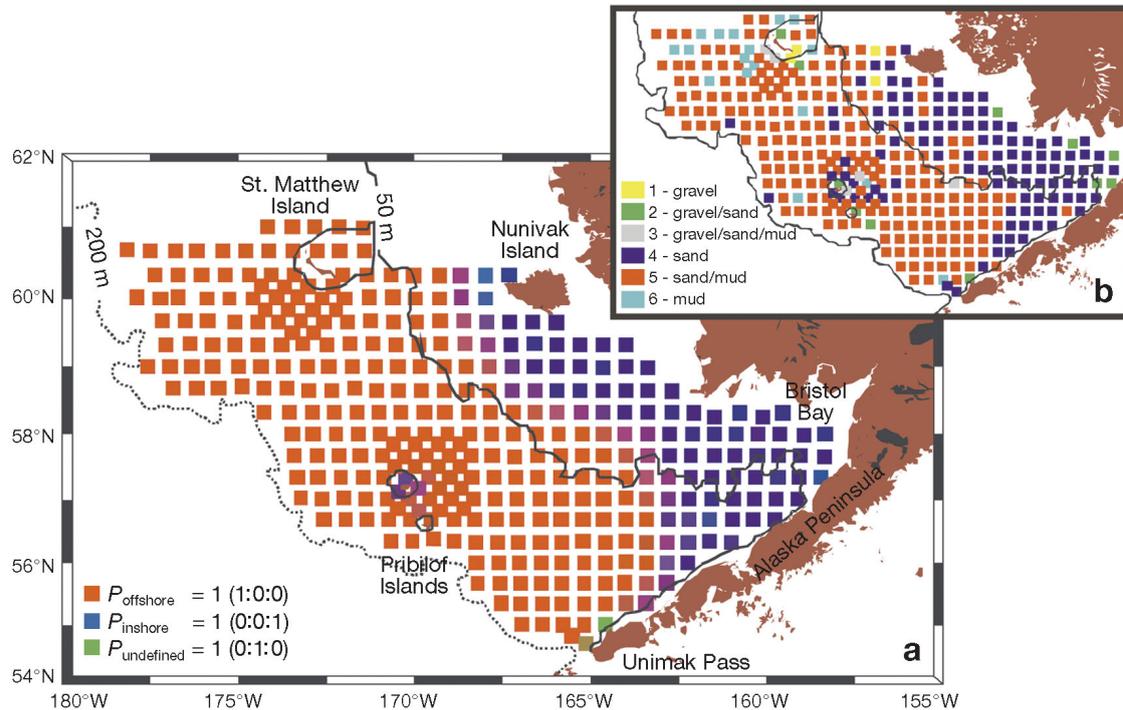


Fig. 1. Bottom-trawl survey area in Eastern Bering Sea, showing (a) probability of cluster membership, and (b) general surficial sediment type of standard survey stations. Squares are centered on station locations. In (a), red:green:blue (RGB) colorscale denotes probabilities of cluster membership, $p_c = n_c/N$, of stations (c = inshore, offshore, or undefined; n_c = number of surveys in which station was classified as c ; and N = total number of surveys in which station was sampled); red (1:0:0): $p_{\text{offshore}} = 1$; blue (0:0:1): $p_{\text{inshore}} = 1$; green (0:1:0): $p_{\text{undefined}} = 1$; e.g. a station with $p_{\text{offshore}} = 0.2$, $p_{\text{undefined}} = 0.5$, and $p_{\text{inshore}} = 0.3$ is represented by a symbol colored with a mix of red, green, and blue in the proportion (0.2:0.5:0.3)

ducted by Soviet scientists working on the western and northern Bering Sea shelf. Stoker (1978) examined the distribution and biomass of benthic infauna on the EBS shelf and Chukchi Sea with van Veen grab and otter-trawl samples collected during 1970 to 1974. His was the first study to assess seasonal and annual fluctuations. The seminal works on EBS benthic communities thus far have stemmed from effort between 1975 and 1976, in which the distribution, abundance and biomass of dominant epifauna (Jewett & Feder 1981, Stoker 1981) and infauna (Haflinger 1981) were surveyed systematically to establish baseline information prior to offshore energy exploration. Benthic infauna in oil-lease areas in the EBS and Chukchi Sea were also surveyed with grab sampling during 2 cruises in 1979 and 1980 (Feder et al. 1985). Since then, little effort has been expended to study the benthic community other than the commercially important crabs. None of the work to date has examined interannual or long-term variability in these communities.

Opportunely, a time series dating back to 1971 exists on the catches of groundfishes and invertebrates (predominantly epifauna) in the annual, summer, bottom-trawl surveys conducted by the Alaska Fisheries Science Center (AFSC) over the EBS shelf. This data set has previously been used in a by-year community

analysis of demersal fishes (groundfishes) and invertebrate taxa from 1971 to 1981 (Walters & McPhail 1982, Walters 1983) and from 1971 to 1994 (Bowerman 1999). The emphasis of these analyses were on the much more abundant groundfishes being targeted by the trawl.

In this paper, we focus on the invertebrate catches to define the structure of the EBS epibenthic community and, for the first time, describe its spatio-temporal variability using 21 yr of standardized and synoptic trawl survey data (1982 to 2002). Clearly, a bottom trawl is not effective for sampling infauna, but it is a satisfactory tool for sampling epifauna, particularly in soft-bottom areas (Stoker 1978, 1981, Jewett & Feder 1981, McConaughy et al. 2000). We therefore confine our analysis to epibenthic macroinvertebrates (epibenthos).

MATERIALS AND METHODS

Data source. The Resource Assessment and Conservation Engineering (RACE) Division of the AFSC has conducted annual summer bottom-trawl surveys of groundfishes and invertebrate populations over the EBS shelf since 1971 (Acuna & Kotwicki 2004). The present configuration of sampling stations, methods and gear was adopted in 1982 under the Bering Sea

Aleutian Islands Groundfish Fishery Management Plan. A total of 356 standard stations are sampled each summer. Standard stations are centered in a 20×20 nautical mile (1372 km^2) grid covering a $460\,000 \text{ km}^2$ survey area between the Alaska Peninsula ($54^\circ 36' \text{ N}$) and St. Matthew Island ($60^\circ 50' \text{ N}$), and cross-shore between the 20 and 200 m isobaths (see Fig. 1a). Grid-cell corners were also sampled near St. Matthew and the Pribilof Islands to better assess red and blue king crab (*Paralithodes camtschaticus* and *P. platypus*) concentrations.

Stations were sampled during daylight hours with an eastern otter trawl (25.3 m headrope, 34.1 m footrope) towed for 30 min at 1.54 m s^{-1} . Mesh size was 10 cm in the body of the net and 8 cm in the codend. Steel V-doors measuring $1.8 \times 2.7 \text{ m}$ and weighing 816 kg were used. Prior to 1988, the area swept by the net was determined using loran fixes and a standard net width. Since that time, an acoustic net mensuration-system has been used to measure net height and width during fishing. Mean estimated net width for 1982 to 2002 was $16.72 \pm 1.26 \text{ m}$ (mean \pm SD, $n = 7377$), and mean estimated distance fished was $2.74 \pm 0.35 \text{ km}$, resulting in a mean estimated area fished (net width \times distance fished) of 0.046 km^2 .

Invertebrate species were sorted and identified to the lowest possible taxonomic level while at sea. Ambiguities in taxonomic identification resulting from uneven effort and expertise over the years were resolved as best possible. Catch weights (biomass) and numbers (abundance) were recorded by taxon. Weight is our common measure of catch for all invertebrates, since counts for colonial taxa like sponges and corals are impractical. Detailed sampling methods are documented in Acuna & Kotwicki (2004). All survey data are stored in and accessed from the RACEBASE database maintained at the AFSC.

Data analysis. Community analysis was performed on a subset of invertebrate taxa that were dominant across all trawl surveys in terms of biomass and/or frequency of occurrence. Cluster analysis was used to group stations in each survey into distinct communities based on similarity in taxa composition. Indicator taxa that best characterized each station group were identified. Spatio-temporal patterns in epibenthic communities were examined graphically and by multivariate ordination. Lastly, temporal trends in the epibenthic community structure in 1982 to 2002 were examined for possible correlations with annual environmental indices that are commonly associated with ecosystem changes in the Pacific Ocean and the Bering Sea.

Dominant taxa: More than 400 invertebrate taxa have been recorded over all the EBS trawl surveys, classified at taxonomic levels ranging from species to phylum. Many of these taxa are considered rare (<50

occurred at $\geq 6\%$ of the stations in a survey). The dominant (or core) taxa used herein in the community analyses are those which consistently ranked high in occurrence and/or biomass in every survey. The occurrence of a taxon in a survey is the percentage of the total number of stations at which it occurred. The biomass of a taxon in a survey is indexed by the total weight caught divided by the total area trawled (kg ha^{-1}), i.e. catch per unit effort (CPUE). To select the core taxa subset, the top 50 taxa by biomass were first compiled into a rank list for each survey (taxon with highest biomass is ranked 1). Only taxa that were ranked in all 21 surveys were considered herein. The mean rank was then calculated for each of these taxa. The same procedure was repeated based on occurrence. A dominant or core taxon is defined as one ranked among the top 50 taxa in all surveys based on biomass or occurrence.

Spatial structure of benthic communities: Stations in each survey were grouped by the similarity of their assemblage of dominant taxa using hierarchical clustering (MATLAB 2004). The station \times taxon biomass matrix was first 4th root-transformed to reduce the influence of the very heavy taxa (Clarke 1993, Legendre & Legendre 1998), and then converted into a matrix of Bray-Curtis dissimilarity between stations. Hierarchical clustering with average linkage (= UPGMA, unweighted pair-group method using arithmetic averages) was performed on the dissimilarity matrix (Clarke 1993, Legendre & Legendre 1998). A maximum of 5 clusters were retained to facilitate interpretation and display. Above 5 clusters there was usually fragmentation into very small clusters, often with just 1 member. Such clusters are not ecologically meaningful; the chance occurrence of a rare taxon at a station, for example, could isolate the station as a cluster. Although some detail can be lost, this approach is consistent with our objective to identify large-scale patterns in community structure. The resulting clusters were plotted on the survey map to depict the spatial structure of the epibenthic community. Cluster maps for the individual surveys were visually compared and the probability of a station belonging to the same cluster across all surveys was calculated to evaluate the robustness of the spatial pattern.

Indicator taxa: Indicator taxa were identified to characterize each station cluster. The mean biomass per station of a taxon within a cluster is a simple measure of its value as an indicator taxon. The indicator value, or *IndVal* index (Dufrêne & Legendre 1997) is a more sophisticated measure that combines a taxon's relative abundance or biomass with its relative frequency of occurrence in the clusters of stations. Since it is based on within-taxon comparisons, it is not sensitive to the biomass of other taxa. The *IndVal* for each

Taxon i in each Station Cluster j is the product of the specificity (A_{ij} ; the mean biomass of Taxon i in the stations of Cluster j compared to all clusters in the study), and the fidelity (B_{ij} ; the relative frequency of occurrence of Taxon i in the stations of Cluster j): $IndVal_{ij} = A_{ij} \times B_{ij} \times 100$, where, $A_{ij} = \text{biomass}_{ij}/\text{biomass}_i$, $B_{ij} = \text{stations}_{ij}/\text{stations}_j$, and biomass_{ij} = mean biomass of individuals of Taxon i across stations of Cluster j , biomass_i = sum of mean biomass of individuals of Taxon i over all clusters, stations_{ij} = number of stations in Cluster j , where Taxon i is present, stations_j = total number of stations in that cluster.

The *IndVal* analysis was performed on 4th root-transformed biomass to identify indicator taxa. The statistical significance of the indicator values was evaluated with 2 randomization tests that reallocate stations among clusters (999 permutations; Dufrêne & Legendre 1997). The first test calculates the difference between the observed *IndVal* and the mean *IndVal* from the random permutations, weights the difference by the standard deviation of the permuted values, and evaluates this z -statistic under the assumption of approximate normality of the permuted statistic. The second test takes the rank of the observed *IndVal* among the permuted values arranged in decreasing order for a distribution-free probability. At any level of the hierarchical structure, an indicator taxon for a cluster of stations is most characteristic of that cluster, i.e. it is found mostly in that cluster, and is present in the majority of the stations belonging to that cluster. It is defined here as a Taxon i that has: (1) *IndVal* $\geq 25\%$, which supposes that its relative frequency of occurrence in Cluster j (B_{ij}) is $\geq 50\%$ and that its relative mean biomass in that cluster over all clusters (A_{ij}) is $\geq 50\%$, and (2) the *IndVal* is significant at $p \leq 0.05$ for both randomization tests.

Variations in community structure: Non-metric multidimensional scaling (NMDS) was used to identify interannual variability in the biomass distribution of dominant taxa. NMDS ordines objects in a reduced dimensional space by a set of characters so that the distances among objects correspond to the measure of similarity among them (Clarke 1993, Legendre & Legendre 1998, Steyvers 2003). Survey years were ordinated in 2D space by NMDS of the Bray-Curtis dissimilarity matrix derived from the 4th root-transformed year \times taxon–station biomass matrix using all the core taxa and individual indicator taxon, respectively, in the matrix. A missing cell in the biomass matrix was handled by omitting that taxon–station across all years. The starting ordination was constructed from the principal coordinate analysis of the original dissimilarity matrix. The iterative algorithm minimizes the Kruskal stress function, which is a function of the scaled differences between the input distances and those of the

ordination (Legendre & Legendre 1998). The final ordination axes were rotated with principal component analysis and reflected where appropriate to maximize interpretability. The goodness of fit between the observed and fitted dissimilarities was evaluated by the Spearman correlation coefficient (r). The similarity between survey years is inversely related to the distances of the corresponding points on the ordination space.

There are 2 obvious factors that may explain the NMDS ordination of survey years, i.e. the magnitude and spatial distribution of taxon biomass. The correlation between biomass magnitude and NMDS ordination is visually examined by superimposing symbols scaled to the mean annual biomass (per station) onto the NMDS ordination. The concordance between the geographic distribution of the center of biomass over the years and NMDS ordination is examined with a Procrustean randomization test (PROTEST) (Peres-Neto & Jackson 2001) implemented in the R vegan package (Dixon 2003). The procedure returns a correlation-like statistic (m_{12}) that evaluates the concordance of a pair of configurations after symmetrically scaling and rotating them for optimal fit (H_0 : the 2 configurations have no significant common structure). The m_{12} statistic is derived from the sum of squared differences between the rotated configurations, such that a low value indicates good concordance. The signifi-

Table 1. Total number of taxa caught, stations sampled, and frequency of occurrence (% of stations) of most dominant and 50th most dominant taxa by survey from 1982 to 2002

Year	No. of taxa	No. of stations	— Occurrence (%) —	
			Most dominant	50th most dominant
1982	77	329	92.4	1.2
1983	107	353	89.2	2.5
1984	174	355	96.3	5.1
1985	142	353	97.5	4.8
1986	141	354	95.5	3.7
1987	129	342	97.4	4.4
1988	123	353	96.3	4.5
1989	104	353	94.3	2.8
1990	102	351	98.0	3.7
1991	101	351	93.7	3.7
1992	93	336	91.1	3.9
1993	103	355	92.4	3.1
1994	94	355	94.4	4.2
1995	99	356	94.9	2.8
1996	105	355	96.3	4.2
1997	122	356	96.6	3.9
1998	119	355	99.2	3.7
1999	128	353	97.2	4.8
2000	120	352	97.4	5.4
2001	95	355	98.3	5.4
2002	119	355	98.3	5.9

cance of the statistic was tested by running PROTEST 9999 times with random permutations of one of the configurations while the other was unchanged (Peres-Neto & Jackson 2001).

Environmental indices and community variability: Significant changes in the EBS pelagic ecosystem have been linked to decadal climate patterns (Benson & Trites 2002). Variability in the benthic community structure in the 21 yr trawl-survey time series was examined for correspondence with 3 major indices of environmental variability: (1) the mean summer bottom-temperature anomaly in the survey area, (2) the multivariate El Niño-Southern Oscillation (ENSO) index, and (3) the Pacific Decadal Oscillation (PDO) annual index. The mean summer bottom temperature is the overall mean bottom temperature of the EBS trawl-survey stations sampled over a period from early June to early August. Bottom temperature in early summer reflects conditions during the preceding winter and spring (Azumaya & Ohtani 1995), and thus represents inter-annual environmental variability. The anomalies are deviations from the mean value (2.52°C) for 1982 to 2002 period normalized by the standard deviation (0.65°C). The ENSO and PDO are annual indices for oceanographic and climate conditions in the Pacific Ocean and the Bering Sea. The ENSO index describes the oscillation of air masses in the tropical Pacific Ocean. The PDO index is a function of sea surface temperature in the North Pacific. They indicate climate events on the 2 principal time-scales in the North Pacific and Bering Sea: 2 to 7 yr (ENSO) and inter-decadal (PDO) (Hollowed et al. 2001). All 3 variables were obtained from the NOAA Bering Sea Climate website (www.beringclimate.noaa.gov), where they are described in detail. Published works were also used to help interpret and determine the timing of ENSO and PDO events (Hollowed et al. 2001, Benson & Trites 2002, Stabeno et al. 2004).

Since seabed characteristics are known to affect the distribution of epifauna, we examined spatial variation of sediment texture in the EBS survey area. Surficial sediment data for the EBS were assembled by Smith & McConnaughey (1999) from all available sources. Their low-resolution scheme classifies samples according to

their gravel-sand-mud composition to achieve the densest spatial coverage with the maximum number of samples, although at some loss of textural detail. Herein, a nearest-neighbor search in that database was conducted in a GIS (ArcGIS™ 9.0) to assign a low-resolution sediment class to each trawl-survey station.

RESULTS

Dominant taxa

An average of 114 invertebrate taxa were recorded per survey, with a minimum of 77 in 1982 and a maximum of 174 in 1984 (Table 1). The most dominant taxon in a survey usually occurred at ≥90% of the sta-

Table 2. Core taxa that were dominant in all surveys by frequency of occurrence and/or by biomass (see 'Materials and methods' for definition). Mean rank of each dominant taxon and total number of surveys (N) in which it was dominant based on occurrence and on biomass are given separately. Most taxa were dominant both by occurrence and by biomass. Those that were dominant either by occurrence or by biomass, but not both, are in bold-face. The 3-letter code assigned to each taxon is used in subsequent tables and in Fig. 3

Code	Taxon	— Occurrence —		— Biomass —	
		Mean rank	N	Mean rank	N
Pag	Paguridae	1.3	21	3.2	21
Meg	Gastropoda ^a	1.9	21	3.5	21
Cho	<i>Chionoecetes opilio</i>	3.4	21	3.2	2
Chb	<i>Chionoecetes bairdi</i>	5.1	21	10.2	2
Asa	<i>Asterias amurensis</i>	6.3	21	1.2	2
Goe	<i>Gorgonocephalus eucnemis</i>	6.6	21	7	21
Hyc	<i>Hyas coarctatus</i>	8.8	21	18.1	21
Act	Actiniaria	9.2	21	10.7	21
Gag	Gastropod eggs	14.1	21	28.6	2
Prc	<i>Paralithodes camtschaticus</i>	16.4	21	9.9	21
Hyl	<i>Hyas lyratus</i>	16.5	21	33.8	2
Por	Porifera	17.1	21	7.7	21
Pnb	<i>Pandalus borealis</i>	18	21	35.4	21
Ech	Echinacea ^b	18.4	21	27.1	2
Bot	<i>Boltenia</i> sp. ^c	19	21	16.4	21
Arg	<i>Argis</i> sp.^d	22.6	21	24	1
Eri	<i>Erimacrus isenbeckii</i>	24.2	21	30	21
Prp	<i>Paralithodes platypus</i>	26.3	21	18.2	21
Crn	<i>Crangon</i> sp.^d	27.7	21	40	1
Asc	compound ascidean	27.7	21	22	20
Ctc	<i>Ctenodiscus crispatus</i>	32.2	21	16.3	21
Nud	<i>Nudibranchia</i>	32.2	21	42.2	15
Org	<i>Oregonia gracilis</i>	32.7	21	44.1	14
Tlc	<i>Telmessus cheiragonus</i>	33.9	21	36	21
Hay	<i>Halocynthia</i> sp.^e	36.5	20	11.4	21
Oph	Ophiuroidea	37.3	20	20	21
Ger	<i>Gersemia</i> sp.^f	18	20	30.2	21

^a mainly whelks and snails

^b mainly sea urchins (Echinoidea)

^c possibly *B. ovifera*

^d may consist of more than one species

^e possibly *H. aurantium*

^f possibly *G. rubiformis*

tions. The subset of 27 core taxa is given in Table 2. Only 8 taxa were not simultaneously dominant by occurrence and by biomass. Core taxa comprise 1 taxon identified to phylum (Porifera), 4 to class (Ascidiacea, Gastropoda, Gastropoda eggs, Ophiuroidea), 2 to order (Actiniaria, Nudibranchia), 1 to superorder (Echinacea), 5 to genus, and the rest (14) to species (Table 2).

Spatial structure of benthic communities

A consistent, interannual pattern of 2 major clusters of stations, generally separated by the 50 m isobath, is evident (from Figs. 1a & 2). With a 5-cluster limit, 3 additional groups besides the inshore and offshore groups are shown, but these are typically small and fragmented, and tend to have variable memberships

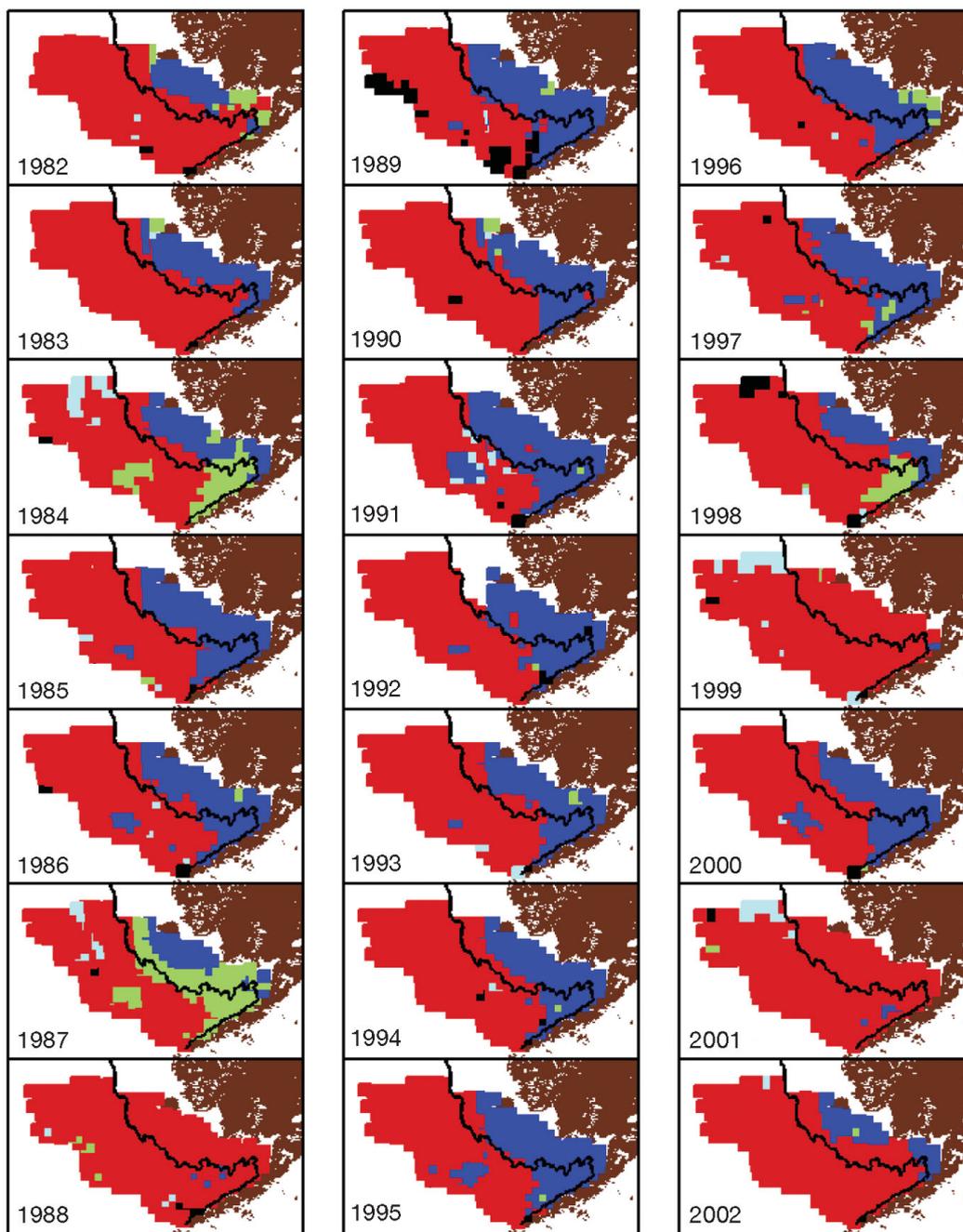


Fig. 2. Stations clustered by similarity of their core-taxa assemblage in each survey; maximum of 5 clusters displayed. The 2 largest clusters are typically inshore (blue) and offshore (red) of 50 m isobath (black line). Colors assigned arbitrarily to remaining clusters, which are typically small, and temporally and spatially variable

interannually. We focus here on the more robust inshore–offshore pattern.

The offshore cluster consists of stations that are mostly >50 m in depth, while stations in the inshore cluster are characteristically <50 m in depth. However, the inshore domain does extend southwest along the coast of the Alaska Peninsula from Bristol Bay to about the 100 m isobath near Unimak Pass. Some stations around the Pribilof Islands are also frequently classified as inshore. The probability of a station belonging to the inshore cluster, offshore cluster, or neither (undefined) is summarized in Fig. 1a. A station in the inshore–offshore transition zone appears as a blend of blue–red, proportional to the relative probability of being classified as inshore or offshore. The few stations that do not have strong affinities with either the inshore or offshore clusters are located near Unimak Pass.

In addition to being delineated by bathymetry, the inshore–offshore cluster pattern (Fig. 1a) also strongly resembles the spatial distribution of surficial sediments (Fig. 1b). The inshore domain, including the inshore Pribilof stations, matches closely with the area classified as sand bottom, and the offshore domain with sand/mud. Less common sediments (mud, gravel/sand) characterize the unique Unimak Pass area.

Real and persistent differences in the 2 epibenthic communities are indicated by the recurring inshore–offshore spatial pattern in the cluster analysis (Fig. 2). Notable deviations from the typical inshore–offshore spatial pattern, generally in the form of a reduction of the inshore domain, only occurred in 1982–84, 1987–88, 1998–99 and 2001–02. Such anomalies seem to last only 2 to 3 yr. The most severe reduction was in 1988, 1999 and 2001, when the inshore domain practically disappeared. Often, as the inshore domain shrinks, the Bristol Bay and Pribilofs areas, which are typically classified as inshore, join the offshore or undefined clusters. This can be seen in 1984, 1987 and 1998, when the Bristol Bay area (and also the Pribilofs area, in 1984 and 1987) formed a cluster that was distinct from the inshore or offshore clusters (Fig. 2).

Indicator taxa for inshore and offshore communities

Based on the CPUE data, a few key crab and non-crab invertebrate taxa distinguished the inshore and offshore EBS communities (Table 3, Fig. 3). The sea star *Asterias amurensis* was overwhelmingly the dominant taxon inshore, with a mean biomass over all surveys (34.9 kg ha⁻¹) that is 10

times greater than that of the second most dominant taxon, the snow crab *Chionoecetes opilio* (3.8 kg ha⁻¹) (Table 3a). *A. amurensis* had the highest biomass inshore of all core taxa in all years except 1982 (0 kg ha⁻¹). However, the group unidentified Asteroidea was unusually abundant in 1982, which leads us to suspect that that group was actually composed of *A. amurensis*. In contrast, *A. amurensis* ranked 4th in mean biomass (8.1 kg ha⁻¹) offshore (Table 3b). *C. opilio* was the most dominant offshore taxon by mean biomass (11.6 kg ha⁻¹). By rank of biomass, *C. opilio*, Paguridae (hermit crabs) and Gastropoda (snails) were dominant both inshore and offshore, but the actual biomass of these taxa was about 2 to 3 times higher offshore.

The red king crab *Paralithodes camtschaticus* also had a relatively high biomass inshore that was about 3 times that of offshore. The tanner crab *Chionoecetes bairdi* was ubiquitous across both domains. Presence of the helmet crab *Telmessus cheiragonus* was only significant inshore, whereas the blue king crab *P. platypus* was more than twice as abundant offshore than inshore. Among dominant non-crab taxa, compound ascideans and *Boltenia* sp. were more indicative of the inshore, whereas *Gorgonocephalus eucnemis*, *Halocynthia* sp. and Ophiuroidea were more indicative of the offshore. *Ctenodiscus crispatus* was only found offshore (Table 3, Fig. 3).

Similar results were obtained from the *IndVal* analysis (Table 4). *IndVal* indicator taxa were consistent over all surveys: Gastropoda, Paguridae and *Chionoecetes opilio* were the primary offshore indicators, with *Gorgonocephalus eucnemis* as a secondary indicator that often displayed significant presence offshore; *Asterias amurensis* was the primary inshore indicator, with *Telmessus cheiragonus*, *Paralithodes camtschaticus*, and *Boltenia* sp. as secondary indicators.

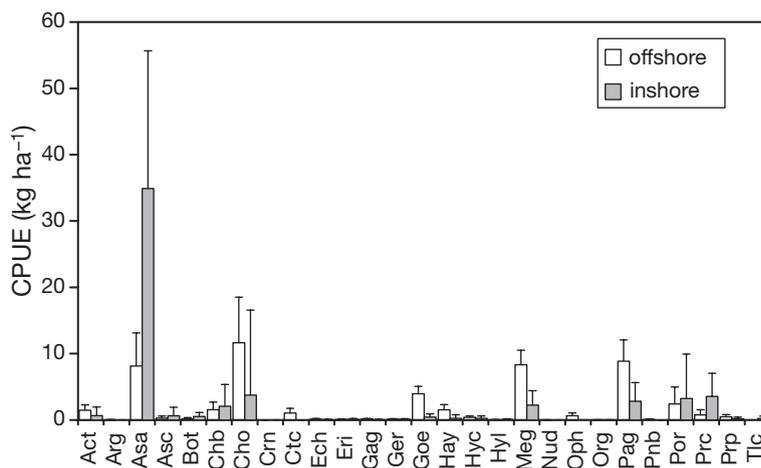


Fig. 3. Overall mean catch per unit effort (CPUE, +SE) of core taxa within inshore and offshore clusters (see Table 3). Taxon codes as in Table 2

Table 3. Mean CPUE (kg ha⁻¹) of core taxa over all stations within (a) inshore and (b) offshore clusters for each survey year (1982 to 2002). Numbers rounded to first decimal place; zero without decimal denotes no catch. Mean = overall mean across years; SE = standard error of overall mean; NStns = number of stations within cluster. Taxa presented in descending order of mean CPUE. Taxon codes as in Table 2

Taxon	Year																				Mean	SE	
	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00	01			02
(a) Inshore																							
Asa	0	49.7	19.1	27.9	26.8	41.7	0	42.8	47.7	54.9	46.8	57.2	54.4	44.2	42.9	70.6	41.0	0.0	30.1	0.1	35.2	34.9	20.8
Cho	0.0	0.0	1.6	0.1	1.6	3.9	0.1	0.1	0.0	4.5	0.0	0.0	0.0	2.0	0.1	0.2	0.0	5.1	0.3	59.3	0	3.8	12.8
Prc	2.1	1.7	16.5	2.2	1.6	4.2	6.6	3.7	4.8	3.1	3.1	5.6	2.5	3.9	3.1	4.8	0.4	0	4.4	0	0.4	3.6	3.5
Por	0.1	0.5	2.7	1.1	0.4	2.5	0	1.8	1.8	0.4	2.6	6.4	2.3	7.2	6.2	0.8	0.1	0	30.8	0	0.2	3.2	6.7
Pag	0.5	1.1	4.3	1.0	1.4	11.0	0.9	5.8	2.1	8.5	2.3	1.9	1.7	4.9	3.6	3.2	0.7	0.1	3.4	0.1	1.2	2.8	2.8
Meg	0.8	1.2	4.3	1.1	1.7	8.0	2.9	6.7	1.2	4.5	2.6	0.6	1.2	2.5	3.9	2.3	0.1	0.1	1.2	0.0	0.1	2.2	2.2
Chb	0.0	0.1	2.0	0.8	1.5	3.5	14.7	3.6	3.2	5.4	3.6	2.2	0.9	0.6	0.4	0.2	0.0	0.0	0.6	0	0	2.1	3.3
Act	0.0	0.0	6.1	0.0	1.1	1.3	0	0.7	0.2	1.2	0.4	0.4	0.1	0.8	0.1	0.4	0.0	0.0	0.6	0.0	0.4	0.7	1.3
Asc	0.0	0.0	0.5	0.1	0.4	0.8	5.8	0.0	0.1	0.3	0.1	0.4	1.6	1.8	0.7	0.3	0.1	0	0.5	0.0	0.0	0.6	1.3
Bot	0.0	0.2	1.3	1.1	0.8	0	0	0.8	2.1	0.6	0.6	0.7	1.6	0.4	0.0	0.8	0.2	0	0.1	0	0.0	0.5	0.6
Goe	0.0	0	0.3	0.0	0.2	0.6	2.2	0.3	0.3	0.4	0.3	0.2	0.4	0.7	0.5	0.9	0	0.4	0.6	0.5	0.0	0.4	0.5
Hyc	0.1	0.1	0.1	0.1	0.2	1.3	0	0.7	0.3	0.9	0.6	0.1	0.1	0.3	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.3	0.4
Hay	0	0	1.6	0.0	0.0	1.8	0	0	0	0.0	0.0	0	0	0.8	0	0.9	0	0	0.1	0	0	0.3	0.5
Tlc	1.7	0.5	0.1	0.1	0.1	0.0	0	0.1	0.3	0.1	0.2	0.2	0.2	0.3	0.2	0.2	0.3	0	0.1	0	0.2	0.2	0.4
Prp	0.0	0	0.9	0	0.4	0.5	0	0.0	0	0.4	0.0	0.0	0.0	0.7	0.0	0.2	0.0	0.1	0.3	0	0	0.2	0.3
Eri	0.0	0.0	0.4	0.1	0.1	0.2	0.0	0.0	0.1	0.1	0.1	0.2	0.0	0.3	0.1	0.2	0.0	0	0.1	0	0.0	0.1	0.1
Ger	0.0	0.0	0.0	0.1	0.1	0.4	0.3	0.1	0.1	0.3	0.1	0.0	0.0	0.0	0.3	0.1	0.0	0	0.1	0.0	0.0	0.1	0.1
Hyl	0.0	0.0	0.1	0.1	0.2	0.1	0	0.1	0.4	0.0	0.0	0.1	0.3	0.1	0.0	0.1	0.0	0	0.1	0	0.0	0.1	0.1
Ech	0.0	0.0	0.4	0.0	0.0	0.0	0	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Gag	0.0	0	0.0	0.0	0.0	0.1	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Org	0	0.0	0.1	0.0	0.0	0.1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0
Crm	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0
Nud	0	0	0.0	0	0	0.0	0.1	0	0.0	0.0	0	0.0	0	0	0	0.0	0	0	0.0	0	0	0.0	0.0
Oph	0	0	0.0	0.0	0.0	0	0	0.0	0	0.0	0.1	0	0.0	0.0	0	0	0	0	0.0	0.0	0	0.0	0.0
Arg	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0	0	0.0	0.0
Pnb	0	0	0	0.0	0.0	0.0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ctc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0	0	0	0.0	0
NStns	32	55	62	101	98	105	4	110	79	137	97	81	79	122	102	95	38	16	99	10	32	74	39
(b) Offshore																							
Cho	10.7	9.4	7.7	3.5	5.4	20.3	12.1	25.4	21.0	23.3	14.6	10.7	11.3	15.8	16.4	14.5	7.9	2.7	5.8	3.1	2.8	11.6	6.9
Pag	3.8	3.1	8.4	3.1	5.7	9.0	10.0	14.4	13.8	11.4	11.3	11.3	10.0	10.2	8.3	11.9	8.8	6.0	9.3	6.4	9.7	8.9	3.2
Meg	8.0	6.6	11.9	4.0	4.9	8.8	9.4	9.4	11.5	8.6	8.7	7.0	7.4	12.0	7.2	11.3	9.5	5.7	8.6	7.2	6.9	8.3	2.2
Asa	2.5	2.9	4.4	1.7	2.7	2.4	17.3	8.0	5.7	5.2	5.9	10.5	12.3	5.9	7.4	12.0	12.9	13.2	6.4	15.9	16.0	8.1	5.0
Goe	2.5	2.1	4.0	2.3	1.8	4.1	2.9	5.0	4.5	3.9	3.6	3.1	3.4	4.2	4.0	5.4	5.5	5.4	5.1	4.8	4.9	3.9	1.1
Por	1.1	2.5	0.3	0.2	3.2	0.6	3.4	7.1	0.3	0.4	0.7	1.6	2.4	0.2	5.2	0.4	0.3	8.7	2.7	3.1	6.6	2.4	2.5
Chb	3.4	1.6	1.0	0.3	0.3	0.7	2.8	3.3	3.4	3.3	3.2	1.6	1.5	1.3	1.0	0.5	0.5	0.6	0.6	0.9	0.9	1.6	1.1
Hay	1.4	0.6	1.2	1.5	3.5	1.0	1.6	0.6	0.6	2.2	0.7	1.6	1.1	0.9	1.6	1.8	2.1	1.4	2.6	1.4	3.0	1.5	0.8
Act	2.0	1.9	1.1	1.5	0.5	0.9	1.2	2.0	1.3	1.2	2.3	1.5	1.3	4.2	1.9	1.7	1.5	0.6	1.1	0.7	0.8	1.5	0.8
Ctc	1.1	0.4	1.1	0.8	0.5	0.8	1.3	1.4	0.4	0.1	0.6	1.2	0.1	0.3	0.7	0.8	2.2	1.1	2.5	2.2	2.1	1.0	0.7
Prc	3.2	1.0	0.0	0.1	0.8	0.3	1.1	0.2	0.2	1.4	0.0	0.4	0.7	0.3	0.2	0.4	0.7	1.9	0.1	1.5	1.7	0.8	0.8
Oph	0.1	0.1	0.0	0.0	0.1	0.8	0.8	1.0	1.4	1.2	1.5	1.1	0.6	0.7	0.7	0.8	0.6	0.2	0.6	0.7	0.6	0.6	0.4
Prp	1.1	1.2	0.2	0.2	0.1	0.1	0.2	0.7	0.6	0.4	0.7	0.8	0.7	0.2	1.0	0.5	0.5	0.2	0.1	0.2	0.1	0.5	0.3
Hyc	0.3	0.1	0.4	0.1	0.3	0.3	0.5	0.4	0.3	0.5	0.7	0.7	0.8	0.9	0.2	0.4	0.4	0.3	0.4	0.3	0.2	0.4	0.2
Asc	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.0	0.0	0.1	0.1	0.4	0.9	1.0	0.9	0.4	0.3	0.1	0.5	0.2	0.1	0.3	0.3
Gag	0.0	0.0	0.2	0.1	0.1	0.1	0.1	0.2	0.3	0.1	0.1	0.2	0.1	0.2	0.2	0.3	0.3	0.1	0.2	0.1	0.1	0.2	0.1
Bot	0.9	0.2	0.4	0.2	0.2	0	0.2	0.2	0.0	0.2	0.1	0.1	0.1	0.0	0.0	0.0	0.2	0.0	0.1	0	0.0	0.1	0.2
Ech	0.0	0.0	0.1	0.1	0.0	0.1	0.1	0.4	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1
Ger	0.0	0.0	0.1	0.0	0.0	0.1	0.3	0.1	0.2	0.0	0.1	0.1	0.2	0.2	0.2	0.4	0.3	0.1	0.2	0.1	0.1	0.1	0.1
Eri	0.3	0.2	0.0	0.1	0.0	0.0	0.0	0.2	0.1	0.0	0.1	0.1	0.2	0.0	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.1
Pnb	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.2	0.3	0.2	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.1
Hyl	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0
Nud	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Arg	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Org	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tlc	0.0	0.0	0	0	0.0	0	0.1	0	0	0	0.0	0.0	0.0	0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crm	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NStns	281	294	232	247	248	199	341	196	264	199	234	270	271	231	246	250	279	333	250	339	320	263	44

Table 4. Indicator taxa for clusters with >10 member stations in a survey (see Fig. 2) based on the indicator-value index *IndVal* (see 'Materials and methods'). Cluster 1 (the largest) is the offshore cluster in all surveys; Cluster 2 (the second largest) is almost always the inshore cluster. Listed are all taxa that have appeared as indicators for 1 or more surveys. Matrix Values are *IndVal* for indicator taxa for the particular survey-cluster indicated. NStn = number of member stations in cluster; NSvy = number of surveys in which taxon appears as an indicator. Significance of *IndVal* = **bold**, $p \leq 0.01$; *italics*, $p \leq 0.05$; normal print, $p \leq 0.10$; underlining, $p > 0.10$. Taxon codes as in Table 2; -: not applicable

Cluster	NStn	Taxon															
		Meg	Asa	Pag	Cho	Tlc	Prc	Bot	Goe	Asc	Chb	Por	Act	Crn	Eri	Gag	Hyc
1982																	
1	281	45	-	-	87	-	-	-	-	-	-	-	-	-	-	-	-
2	32	-	-	-	-	<i>67</i>	-	-	-	-	-	-	-	-	-	-	-
3	12	-	95	-	-	-	-	-	-	-	-	-	-	33	-	-	-
1983																	
1	294	52	-	-	64	-	-	-	-	-	-	-	-	-	-	-	-
2	55	-	85	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1984																	
1	232	38	-	30	-	-	-	-	-	-	-	-	-	-	-	-	-
2	62	-	-	-	-	-	-	-	-	-	40	<i>68</i>	-	-	-	-	-
3	48	-	51	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	12	-	-	-	49	-	-	-	-	-	-	-	-	-	-	-	-
1985																	
1	247	<i>38</i>	-	53	56	-	-	-	-	-	-	-	-	-	-	-	-
2	101	-	<i>56</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1986																	
1	248	45	-	<i>37</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
2	98	-	<i>48</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1987																	
1	199	34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	105	-	-	<i>34</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
3	29	-	44	-	-	<i>55</i>	-	-	-	-	-	-	-	-	-	-	-
1988																	
1	341	<i>35</i>	66	49	-	-	-	-	-	-	-	-	-	-	-	-	45
1989																	
1	196	39	-	<i>39</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
2	110	-	<i>44</i>	-	-	<i>29</i>	<i>52</i>	-	-	-	-	-	-	-	-	-	-
3	41	-	-	-	-	-	-	-	-	-	<u>33</u>	-	<u>41</u>	-	-	-	-
1990																	
1	264	55	-	-	69	-	-	-	-	-	-	-	-	-	-	-	-
2	79	-	73	-	-	-	-	67	-	-	-	-	-	-	-	-	-
1991																	
1	199	51	-	41	-	-	-	-	-	-	-	-	-	-	-	-	-
2	137	-	52	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	12	-	-	-	<i>41</i>	-	-	-	-	-	-	-	-	-	-	-	-
1992																	
1	234	61	-	62	<i>47</i>	-	-	-	-	-	-	-	-	-	-	-	-
2	97	-	57	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1993																	
1	270	51	-	<i>40</i>	84	-	-	-	-	-	-	-	-	-	-	-	-
2	81	-	<u>36</u>	-	-	<u>32</u>	<u>47</u>	<u>49</u>	-	-	-	-	-	-	-	-	-
1994																	
1	271	54	-	61	-	-	-	-	-	-	-	-	-	-	-	-	-
2	79	-	-	-	-	<u>30</u>	-	<u>47</u>	-	-	-	-	-	-	-	-	-
1995																	
1	234	66	-	-	<i>54</i>	-	-	-	-	-	-	-	-	-	-	-	-
2	122	-	<u>42</u>	-	-	-	-	-	<u>36</u>	-	-	-	-	-	-	-	-
1996																	
1	246	60	-	49	47	-	-	-	-	-	-	-	-	-	-	-	-
2	102	-	<u>34</u>	-	-	<u>28</u>	-	-	<u>26</u>	-	-	-	-	-	-	-	-
1997																	
1	250	42	-	37	-	-	-	-	-	-	-	-	-	-	-	-	-
2	95	-	52	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1998																	
1	279	40	-	33	-	-	-	-	46	-	-	-	-	-	-	27	-
2	38	-	39	-	-	63	-	-	-	-	-	-	-	-	-	-	-
3	27	-	-	-	-	-	76	24	-	-	-	54	-	-	26	-	-
1999																	
1	333	61	-	54	-	-	-	-	49	-	-	-	-	-	-	-	-
2	16	-	-	-	52	-	-	-	-	-	-	-	-	-	-	-	-
2000																	
1	250	49	-	47	42	-	-	-	<i>55</i>	-	-	-	-	-	-	-	-
2	99	-	<u>43</u>	-	-	<u>30</u>	<u>71</u>	-	-	-	-	-	-	-	-	-	-
2001																	
1	339	-	43	48	-	-	-	-	-	-	-	-	-	-	-	-	-
2	10	-	-	-	42	-	-	-	-	-	-	-	-	-	-	-	-
2002																	
1	320	60	-	39	-	-	-	-	66	-	-	-	-	-	-	-	-
2	32	-	<i>49</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-
NSvy		20	19	17	13	8	5	4	4	2	2	2	1	1	1	1	1

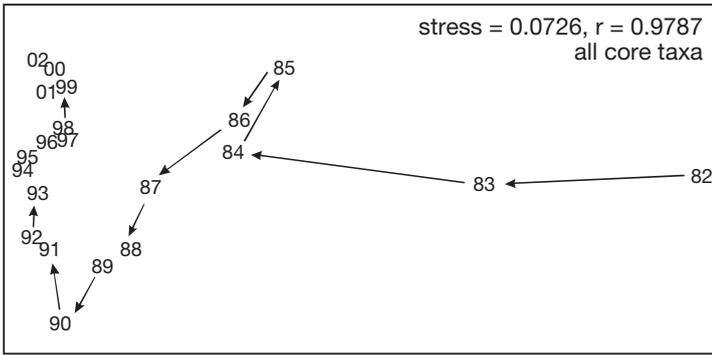


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of the 27 core taxa in surveys from 1982 to 2002: Bray-Curtis dissimilarity based on biomass (CPUE) at each station

Interannual variability in community structure

The distributions of the core-taxa assemblage in 1982 and 1983 apparently differed from those in other years, as these earliest years are distinctly set to the far right of the horizontal axis in the NMDS plot (Fig. 4). In subsequent years there was a progressive shift toward the left, widening the differences between the earliest and the most recent periods in the time series. Differences narrowed from around 1991 to 2002, as inferred from the tighter clustering of these years at the far left of the plot. Generally similar trends are seen when years are ordinated using the biomass

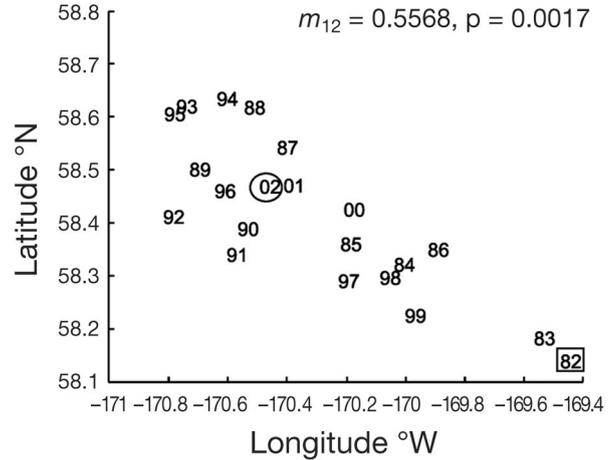
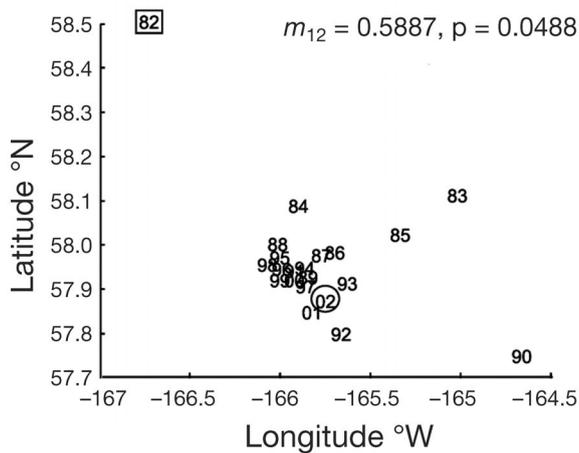
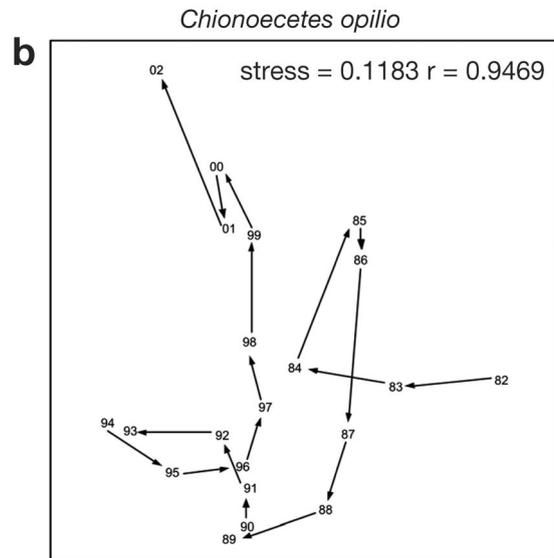
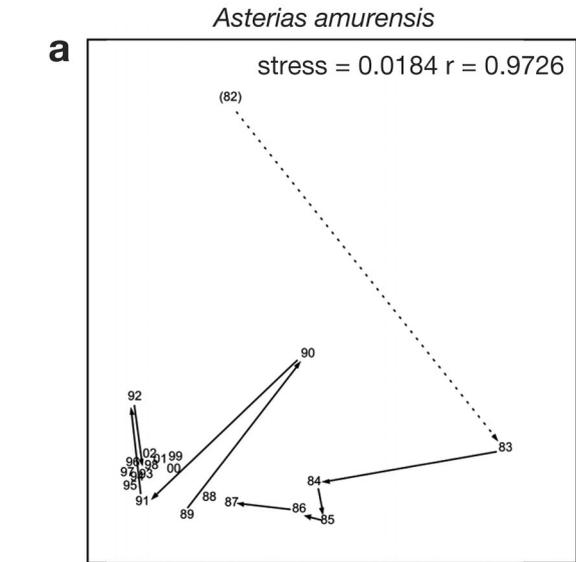
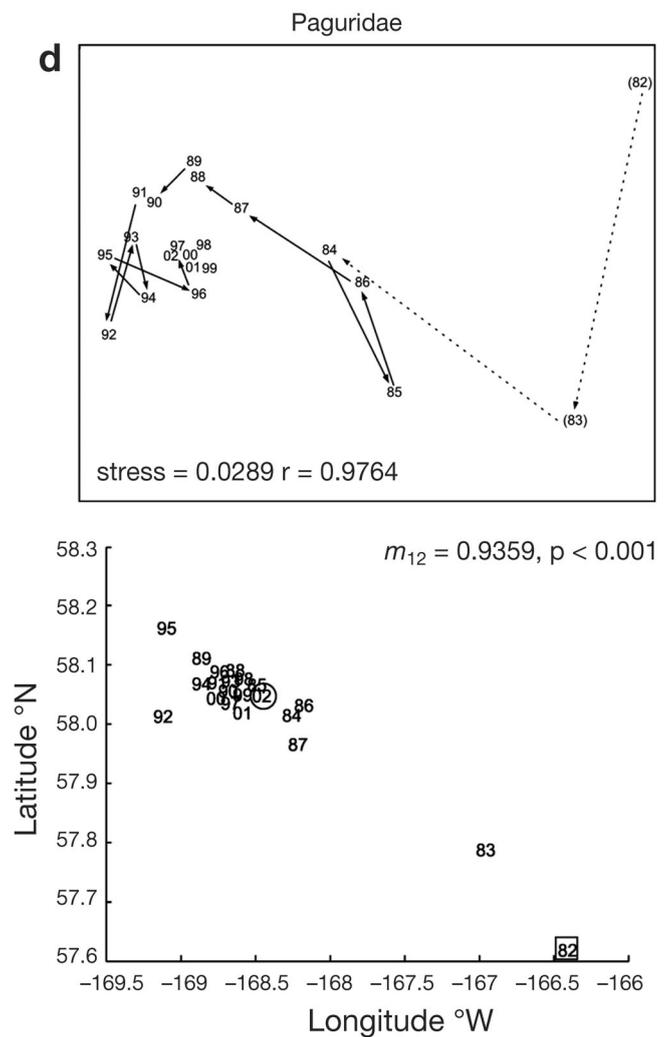
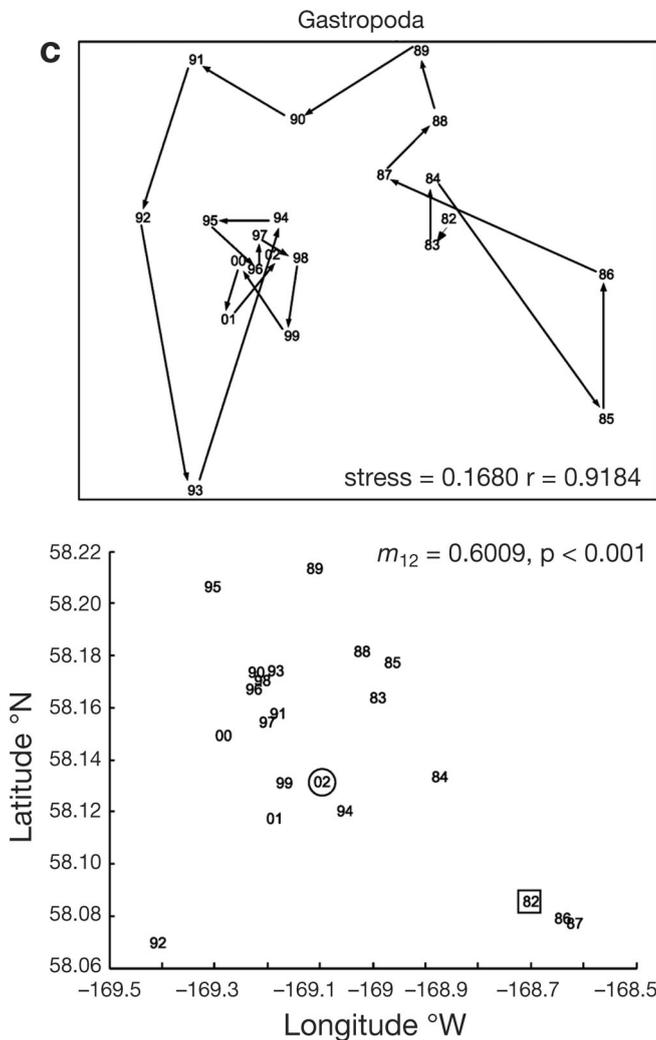


Fig. 5. NMDS ordination of surveys from 1982 to 2002 (Bray-Curtis dissimilarity) of distribution of biomass (upper graphs) compared to plot of locations of geographic center of biomass for those surveys (lower graphs) for (a) *Asterias amurensis*, (b) *Chionoecetes opilio*, (c) Gastropoda and (d) Paguridae. In the NMDS plots (upper graphs), axes were rotated and/or reflected where appropriate for a best match of NMDS trajectory with geospatial shift in the center of biomass over time (lower graphs); dotted

distribution of individual indicator-taxon dominant in the core assemblage (*Asterias amurensis*, *Chionocetes opilio*, Paguridae and Gastropoda) (Fig. 5: upper plots). The 1982 survey emerged as the outlier for all but the NMDS plot for Gastropoda. The 2D NMDS-fitted solutions are highly correlated with the original distances (Bray-Curtis dissimilarity) among survey years ($r > 0.9$), and the low stress values (0.0184 to 0.1680) indicate good to excellent ordinations in 2 dimensions. Higher-dimension solutions in these cases are unlikely to significantly increase information on the overall structure (Clarke 1993).

The observed interannual variability is better explained by spatial biomass distribution than by biomass magnitude. For each of the 4 taxa, symbols scaled to mean annual biomass superimposed onto NMDS

configurations (results not shown) revealed no visual pattern indicating that distances among years are related to interannual differences in biomass magnitude. However, there is visual correspondence between the NMDS ordination and the interannual geographic distribution of the center of biomass of each indicator taxon. For *Asterias amurensis*, the landmark features of correspondence are the separation of 1982 from 1983, the deviation of 1990, and the tight clustering of years from 1991 to 2002; the outlier of 1982 aside, the summary trend of the series as defined by the shift of the geographic center of biomass from 1983 to 2002 is southwestward (Fig. 5a). PROTEST shows that there is significant concordance between the NMDS and center of biomass of *A. amurensis* ($m_{12} = 0.5887$, $p = 0.0488$).



line scales down actual distance of an extreme outlier; Kruskal stress of NMDS configuration and Spearman correlation (r) between configuration and input dissimilarities are given. In plots of geographic center of biomass (lower graphs), the beginning year (1982) is framed and the end year (2002) encircled to highlight eventual distance over the time series; PROTEST (procrustean randomization test) m_{12} statistic and significance value (p) for the difference between NMDS and the geospatial configurations are given

The most recognizable correspondence between the center of biomass and NMDS plots of *Chionoecetes opilio* lies in the overall diagonal shift northward (+y) and westward (-x) from 1982 to 2002 ($m_{12} = 0.5568$, $p = 0.0017$) (Fig. 5b). The correspondence between the center of biomass and NMDS plots for Gastropoda lies mainly in their similar paths northward from 1982 to 1989, and then returning south to end in 2002 ($m_{12} = 0.6009$, $p < 0.001$) (Fig. 5c); the net shift from 1982 to 2002 is thus relatively small, and to the northwest. For Paguridae, both the NMDS and center of biomass plots show 1982 and 1983 as outliers; the trend thereafter is mainly westward, culminating in a tight clustering of the years from 1988 onward to 2002; 1992 and 1995 appear to deviate from that cluster in both plots ($m_{12} = 0.9359$, $p < 0.001$). The main trends of the NMDS and geographic center of biomass are similar for each of the 4 taxa. However, the high PROTEST m_{12} value for Paguridae compared to that for the other taxa indicates a weaker correspondence (Fig. 5).

These results suggest a possible shift in the biomass distribution of the 4 indicator taxa offshore (west) over the years. The centers of biomass of these taxa shifted in relatively greater magnitude along the latitudinal (cross-shore) axis than along the longitudinal (along-shore) axis. The denser clustering of years in the recent decade on both NMDS and geographic plots of *Asterias amurensis*, Paguridae and Gastropoda (Fig. 5) suggests reduced variability in their biomass distribution for that period.

Correlation with environmental variability

The proportion of stations classified as inshore declined sharply during periods with atypical spatial dis-

tribution of the epibenthic communities. The normalized proportion of inshore stations (inshore proportion) over the years (mean = 0.2101, SD = 0.1112) is plotted in Fig. 6. Spatial reduction in the inshore communities in 1982–84 and 1998–99 coincided with the extreme El Niño events of 1982–83 and 1997–98, during which the sea-surface temperature anomaly was $>+3.0^{\circ}\text{C}$, compared to an average El Niño anomaly of $+1.5^{\circ}\text{C}$ (Hollowed et al. 2001). Within our study period, there have also been environmental regime shifts in the Bering Sea ecosystem attributed to the PDO in 1989 and possibly 1998 (Hollowed et al. 2001, Benson & Trites 2002, Stabeno et al. 2004), the latter coinciding with an extreme El Niño. There are, however, no obvious climate events coinciding with the other 2 periods of reduction in inshore proportion in 1987–88 and 2001–02 (Fig. 6).

The reduction of the inshore domain is apparently associated with thermal conditions, particularly over the preceding winter and spring. The mean bottom-temperature anomaly in summer is plotted in Fig. 6 for comparison with the inshore proportion series (note reverse y-axis for bottom temperature). The anomaly fluctuated randomly within ± 1 SD of the mean, with the exception of 1999, when it dropped >-2 SD below the mean, possibly in association with the extreme El Niño and regime shift during that time (Hollowed et al. 2001, Benson & Trites 2002, Stabeno et al. 2004). Significant linear correlations ($p < 0.1$) were found when the bottom-temperature series led the inshore proportion series by 1 yr ($r = -0.4066$, $p = 0.0752$, $n = 20$), 2 yr ($r = 0.4203$, $p = 0.0732$, $n = 19$), 6 yr ($r = -0.4840$, $p = 0.0575$, $n = 15$) and 18 yr ($r = 0.9711$, $p = 0.0289$, $n = 2$). Obviously, the 18 yr correlation comprises too few observations. The visual correlation is best when bottom temperature leads inshore propor-

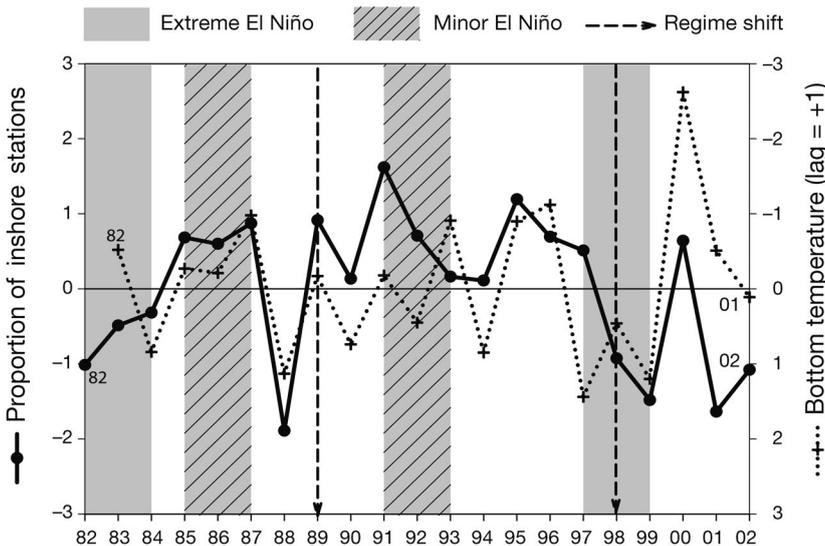


Fig. 6. Time series of (solid line) proportion of stations classified as inshore in survey as a measure of interannual variability in inshore-offshore benthic assemblages, and of (dotted line) mean summer bottom temperature from trawl surveys leading the former time series by 1 yr (i.e. 1982 temperature plotted with 1983 inshore proportion, etc.). Both series are normalized anomalies. Note: y-axis direction for temperature series is reversed to highlight negative correlation between the 2 series. Approximate periods of extreme (gray, unhatched) and minor (gray, hatched) El Niño events are indicated. Dashed vertical lines mark approximate years that the eastern Bering Sea underwent regime shift associated with the Pacific Decadal Oscillation

tion by 1 yr (lag = +1) (Fig. 6). Since the correlation is a negative one (high bottom-temperature correlates with low inshore proportion), the *y*-axis of the bottom temperature in Fig. 6 is reversed to highlight the visual match between the 2 series. There is also a significant positive correlation (low bottom-temperature correlates with low inshore proportion) when bottom temperature leads inshore proportion by 2 yr (lag = +2). This sequential switch in correlation from positive (lag = +2) to negative (lag = +1) suggests that a recent shift from cold to warm conditions may have affected the distribution of epifauna communities.

DISCUSSION

Despite the ecological importance of benthic communities in the EBS, there have been relatively few studies focused on the non-commercial species. One result is a critical lack of biological information to support assessments of natural and anthropogenic impact on the ecosystem (NMFS 2004). The AFSC time series of bottom-trawl surveys allowed us to characterize the epibenthic communities in the EBS and, for the first time, to quantitatively describe a robust long-term trend in taxonomic composition and spatial distribution. Our analyses suggest that variations in these patterns are associated with environmental fluctuations on interannual to decadal scales. From a bottom-up perspective, these findings can have significant implications for the ecosystem, given well-known trophic and habitat linkages with keystone fish and marine mammals stocks (Alton 1974, NRC 1996). Moreover, persistent spatial community patterns could provide a basis for the systematic study of anthropogenic disturbances. Taking community patterns into account in experimental design can reduce the natural variability among experimental sites that confounds true anthropogenic impact.

EBS benthic community structure

Our data revealed a clear and persistent division of the EBS epibenthos into inshore and offshore communities approximately separated by the 50 m isobath. This separation held for the most part in areas parallel to the coast, except in the south, where the inshore community typically extends westward along the coast of the Alaska Peninsula from Bristol Bay up to about the 100 m isobath near Unimak Pass. The offshore community forms a contiguous band seaward of the inshore community to the offshore limit of the trawl survey area at the edge of the continental shelf (200 m) (Fig. 1). A similar inshore-offshore organization is ap-

parent in EBS infauna, based on community studies in the 1970s (Haflinger 1981, Stoker 1981) and on groundfish studies in the 1980s and 1990s (Walters & McPhail 1982, Walters 1983, Bowerman 1999). Haflinger (1981) studied the faunal zonation and community boundaries of infauna in the EBS and concluded that there is an abrupt faunal transition at ~50 m. Similarly, MacIntosh & Somerton (1981) identified 3 thermal regions in the EBS (coastal, central, outer shelf) and found distinct assemblages of large gastropod species in each. In general, a pattern of relatively few (2 to 3), large, and contiguous faunal communities aligned with the isobaths seems to be characteristic of the EBS. In our case, these patterns are robust, based on examination of long-term, systematic data. In other cases, the stability of the pattern is less certain, based on shorter time series (Stoker 1978, Haflinger 1981).

The spatial distributions of epifauna, infauna and groundfish communities in the EBS are closely tied to depth-associated oceanographic domains. During summer, the EBS shelf waters are differentiated into 3 domains (inner, middle and outer) separated by oceanographic fronts associated with the 50, 100 and 200 m isobaths, respectively (Hunt et al. 2002). The inner front separates the well-mixed waters inshore from the 2-layered system offshore. Its position varies depending on wind and tides, but typically originates near Unimak Pass, continuing around the perimeter of Bristol Bay and northwestward past Nunivak Island (Fig. 1). At the spatial resolution of the trawl-survey data, the inner front and the transition zone between the inshore and offshore communities correspond almost exactly. A feature similar to the inner front exists at the 50 m isobath around the Pribilof Islands (Kachel et al. 2002) and, coincidentally, the benthic community around the Pribilof Islands is of the inshore type (Fig. 1). Interestingly, there is a small area at the outer edge of the shelf near Unimak Pass where the epifauna community seems distinct from the inshore and offshore types, probably due to unique local currents conditions and associated water-mass properties (Kachel et al. 2002).

The general inshore-offshore pattern of epibenthic invertebrate communities also corresponds closely with spatial patterns of surficial sediments on the EBS shelf (Fig. 1). Other studies have also found the distribution, abundance and biomass of EBS benthic community to coincide with physical characteristics of the shelf (Haflinger 1981), particularly sediment particle-size (Stoker 1981). Hydrography, an important factor in community organization in its own right, is also strongly connected with sediment transport, deposition and composition—the last, especially, is a major determinant of benthic community structure (Grebmeier et al. 1989).

Composition of EBS epibenthic invertebrate community

The dominant macroinvertebrate epifauna in our data are consistent with those in previous studies. In the 1975–76 surveys of EBS invertebrates, polychaetes and bivalves were the major classes of benthic invertebrate infauna (Stoker 1981), while crabs and sea stars dominated the benthic macroinvertebrate epifauna (Jewett & Feder 1981); 4 crabs (*Paralithodes camtschaticus*, *P. platypus*, *Chionoecetes opilio* and *C. bairdi*) and 4 sea stars (*Asterias amurensis*, *Evasterias echinosoma*, *Leptasterias polaris* and *Lethasterias nanimensis*) accounted for nearly 70% of the epifaunal biomass of the entire EBS shelf in 1975–76. Mollusks, decapods and echinoderms constituted the bulk of benthic biomass. *Neptunea* spp. and *Pagurus trigonochirus* were among the dominant species. The tunicates *Styela rustica* and *Halocynthia* sp., the anemones Actiniaria (*Metridium senile*) and the sponges Porifera were the major sessile epifauna, but accounted for a relatively small percentage of the catch. The match in taxa composition between our trawl data and previous results is good to the species level for crabs and sea stars, and to the family level or higher for groups such as Paguridae, Gastropoda and Actiniaria, which were not as finely resolved taxonomically in the EBS trawl data. These consistencies with results from studies using other gear types (e.g. grabs, dredges) support the use of trawl-survey methods for shelf-scale characterization of epifauna in soft-bottom areas.

Spatio-temporal variability

The notable deviations from the typical inshore-offshore pattern of the EBS benthic community over the 21 yr time series appear to be related to shifts in the biomass distribution of 1 or more of the core taxa. Geographic centers of biomass for the major indicator taxa, *Chionoecetes opilio*, *Asterias amurensis*, Paguridae and Gastropoda show a common general trend toward the offshore (west). Shifts in the biomass distribution of these mobile taxa suggest cumulative directed movement over the long term. On preliminary examination, this movement may be related to changes in bottom temperature. Stoker (1981) had predicted that summer bottom-temperature would be another major factor influencing benthic distribution besides sediment grain size. On the interannual time scale, temperature is probably the most obvious source of variability impacting the physiology, reproduction, trophic dynamics, distribution and, thus, the community organization of benthos.

Mobile benthos, especially crabs, can respond relatively quickly to changes in temperature regimes.

Zheng & Kruse (2000) suggested that the year-class strength of the Bristol Bay red king crab stock is negatively correlated with warmer ocean temperature and ENSO events. The shift in the distribution of ovigerous females in this stock appears to be related specifically to the geographic extent of the cold pool (Loher & Armstrong 2005)—cold bottom-water generated during sea-ice formation (Azumaya & Ohtani 1995). In particular, the distributions in the years 1981–83 were notably different from those in most years, and little qualitative change occurred over the past 12 to 15 yr (Loher & Armstrong 2005)—trends that are similar to our results for *Asterias amurensis*, Paguridae, and Gastropoda. We also see Bristol Bay, a major red king crab habitat, as one of the key areas of variation in the spatial pattern of the EBS epibenthic community. Ernst et al. (2005) hypothesized that mature, female snow crabs track bottom-temperature gradients during ontogenetic migrations. They noticed a pronounced shift to the north and west between 1978 and 1985 of the females, which continued more gradually thereafter. This trend is consistent with the NMDS trend of the core taxa (Fig. 4) in general and with the NMDS and center of biomass trends of *Chionoecetes opilio* specifically (Fig. 5b). Short- and long-term temperature shifts can thus alter spatial patterns of epibenthic communities through their effects on the dominant crabs alone.

Extreme climate events such as the El Niño may also modify epibenthic communities in the EBS. A shift in benthic biomass and community structure in the early to mid 1980s at 3 sites in the EBS has been attributed to the PDO regime shift from cold to warm in 1977 (Connors et al. 2002). Another shift of lesser effect from warm to cool occurred in 1989 (Hare & Mantua 2000, Bond & Adams 2002) with associated widespread alterations in food-web dynamics (NRC 1996, Connors et al. 2002, Hunt et al. 2002). The most recent shift to a warm phase began between 1997 and 1999 (Hollowed et al. 2001, Hunt et al. 2002, Stabeno et al. 2004). Prominent weather and hydrographic anomalies were recorded in the Bering Sea in 1997 and 1998 (Napp & Hunt 2001, Minobe 2002)—the inner front on the SE Bering Sea shelf was well inshore of its normal position of the 50 m isobath, and nutrient transport onto the shelf decreased as a result of weaker winds and higher sea-surface temperature (Napp & Hunt 2001). Recent evidence has shown that El Niño/La Niña can affect benthic communities even in the deep ocean (Ruhl & Smith 2004). In the NE Pacific, mobile epibenthos (ophiuroids, echnoids and holothuroids) underwent a major shift in abundance between 1989–98 and 2001–02, which correlates with El Niño/La Niña indices and the regime shift in the North Pacific, with a time lag of generally <1 yr.

Environmental factors such as hydrodynamic regime, depositional environment, water temperature, wind, primary production and ice cover are inter-correlated, and operate on interannual to climate scales. It is widely acknowledged that these factors affect the distribution of major taxa of benthic invertebrates (Haflinger 1981, Jewett & Feder 1981, Stoker 1981), but the dynamics are unclear. The effects of climate-induced variations in food supply on the recruitment, migration and mortality of epibenthos can vary among taxa (Ruhl & Smith 2004). Variability in the spatial structure of the EBS benthic community may be the manifestation of subtle changes, e.g. in species/developmental stage composition (including infauna), ranking, or distribution (driven by complex environment-species and interspecific relationships). Insofar as interspecific interactions that define communities are also poorly understood, what is described as communities is less a biological than a geographic entity, allied by similar environmental requirements (Stoker 1978). Knowledge of distribution and abundance has yet to be translated into larval recruitment dynamics, habitat preference, physiological requirements, and intraspecific and interspecific interactions.

The veracity of the changes in the benthic community, their precise nature, the driving forces, and the ecosystem effects are all areas that require further investigation. The recent regime shift marks the onset of unprecedented, persistent, warm ocean temperatures (Stabeno et al. 2004). Sea surface temperature in May of 2003 was the highest since 1981 (www.bering-climate.noaa.gov). It will be interesting to see how, if at all, the spatial distribution of the epibenthic communities will shift. Changes in the benthic community distribution, whether natural or anthropogenic, will impact the ecosystem. To predict these impacts and move towards an ecosystem-based management of resources, we will first have to identify these changes through long-term and broad-scale monitoring efforts, and clarify the underlying processes.

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