

Abstract—Data collected from an annual groundfish survey of the eastern Bering Sea shelf from 1975 to 2002 were used to estimate biomass and biodiversity indexes for two fish guilds: flatfish and roundfish. Biomass estimates indicated that several species of flatfish (particularly rock sole, arrowtooth flounder, and flathead sole), several large sculpins (*Myoxocephalus* spp.), bigmouth (*Hemitripterus bolini*), and skates (*Bathyraja* spp.) had increased. Declining species included several flatfish species and many smaller roundfish species of sculpins, eelpouts (*Lycodes* spp.), and sablefish (*Anoplopoma fimbria*). Biodiversity indexes were calculated by using biomass estimates for both guilds from 1975 through 2002 within three physical domains on the eastern Bering Sea shelf. Biodiversity trends were found to be generally declining within the roundfish guild and generally increasing within the flatfish guild and varied between inner, middle, and outer shelf domains. The trends in biodiversity indexes from this study correlated strongly with the regime shift reported for the late 1970s and 1980s.

Manuscript submitted 25 March 2004
to the Scientific Editor's Office.

Manuscript approved for publication
13 August 2005 by the Scientific Editor.
Fish. Bull. 104:226–237 (2006).

Biodiversity as an index of regime shift in the eastern Bering Sea

Gerald R. Hoff

Alaska Fisheries Science Center
National Marine Fisheries Service
7600 Sand Point Way N.E.
Seattle, Washington 98115
Email address: jerry.hoff@noaa.gov

Environmental and biological events in the North Pacific can indicate regime shifts or reorganizations of the ecosystem at the environmental and biological level (Hare and Mantua, 2000). Measurable climatic events were identified in the mid-1970s, late 1980s (Anderson and Piatt, 1999; Anderson, 2000; Hare and Mantua, 2000; Zhang et al., 2000; Minobe, 2002) and the late 1990s (Hunt and Stabeno, 2002; Minobe, 2002). Regime shifts in the eastern Bering Sea (EBS) have been correlated with several climatic events, including the Pacific Decadal Oscillation, the El Niño Southern Oscillation (Hollowed et al., 2001), sea ice coverage (Stabeno et al., 2001; Hunt et al., 2002; Hunt and Stabeno, 2002), and summer sea surface temperatures (Bond and Adams, 2002; Hunt et al., 2002; Minobe, 2002). The far reaching effects that climate change has on an ecosystem are not well defined, but many studies have shown strong correlations between climate change, fish recruitment, and plankton production in the North Pacific (Brodeur and Ware, 1992; Anderson et al., 1997; Anderson and Piatt, 1999; Brodeur et al., 1999; Clark et al., 1999; Hare and Mantua, 2000; Zhang et al., 2000; Hollowed et al., 2001; Sugimoto et al., 2001; Connors et al., 2002; Hunt et al., 2002; Wilderbuier et al., 2002). During periods of climatic change, some fishes may not be well adapted to dramatic changes over a short time scale (1–10 years), whereas others may proliferate in a more hospitable environment. Key triggers of regime shifts and the extent to which species will respond remain unclear; however, evidence may indicate that species

diversity is correlated with primary production in many systems, and the two may be interdependent (Rosenzweig and Abramsky, 1993; Waide et al., 1999). A biodiversity index can be useful for monitoring the stability, health, and productivity of an ecosystem, as well as for aiding management, by tracking exogenous changes and their far reaching effects on species. In the present study, I used biodiversity indexes, reflecting richness and evenness, as indicators of species composition changes and related these changes to regime shift events for the eastern Bering Sea (EBS) shelf.

Methods

Data were synthesized from a continuous 24-year period of standardized groundfish surveys conducted by the Alaska Fisheries Science Center (AFSC) on the EBS shelf from 1979 through 2002; additional estimates from 1975 were included. Biodiversity indexes (species richness and evenness) were calculated from biomass estimates for two fish guilds, flatfish and roundfish, in each of the inner, middle, and outer domains of the EBS shelf. Biodiversity indexes were plotted for each fish group and domains and examined for changes over the study period. The observed changes were correlated with regime shift and ocean climatic change events for the EBS.

Data collection

Gear, station location, sampling procedures, and time of year of the AFSC

eastern Bering Sea continental shelf survey have been standardized since 1982. Prior to 1982, a 400-mesh eastern trawl (smaller than the current 83-112 trawl) was used (Bakkala, 1993). Although the biomass estimates produced by the two trawls are not directly comparable because of unknown catchability differences between the nets, survey data from 1975 and 1979–81 were included in the present analysis because of the importance in the timing of the 1970s regime shift. The biodiversity indexes are based on the relative proportion of the species and therefore are an indicator of assemblage structure.

Data used for this study were collected by the Resource Assessment and Conservation Engineering (RACE) division of the AFSC, which surveys the EBS shelf each summer (May–August). The survey area extends from the Alaska Peninsula north to Nunivak Island and St. Matthew Island, and west to the 200 m shelf break. Trawl hauls were conducted on a grid of 356 fixed stations (20 nmi by 20 nmi) (Fig. 1) during daylight hours. Hauls were towed for 30 min at 3 knots and ranged in depth from 15 m in Bristol Bay to nearly 200 m near the shelf edge. Most trawling was conducted with the AFSC 83-112 eastern trawl (1982–2002), which is a low-opening two-seam trawl with a 26.5-m headrope and 34.1-m cable footrope wrapped with rubber striping and chain hangings that contact the bottom while the trawl is towed (Rose and Walters, 1990).

Height and width of the net were measured with an acoustic SCANMAR (Scanmar, Asgardstrand, Norway) or NETMIND (Northstar Technical Inc., St. John's, NF, Canada) net mensuration system, or estimated by using a function that relates trawl widths to tow depths from measured hauls. Each haul was measured with GPS or LORAN to record latitude and longitude data at the start and end of the trawl in order to determine distance fished.

Processing of the catch was done entirely in the field at the time of capture. The entire catch was sorted to species, enumerated, and weighed, or a weighed subsample was used for very large catches.

Catch per unit of area (CPUE) was determined for each trawl station completed during each survey. Biomass estimates for each species were then calculated by expanding the average CPUE for each stratum and then summing over all strata of the total survey area to obtain a biomass estimate in metric tons for each species.

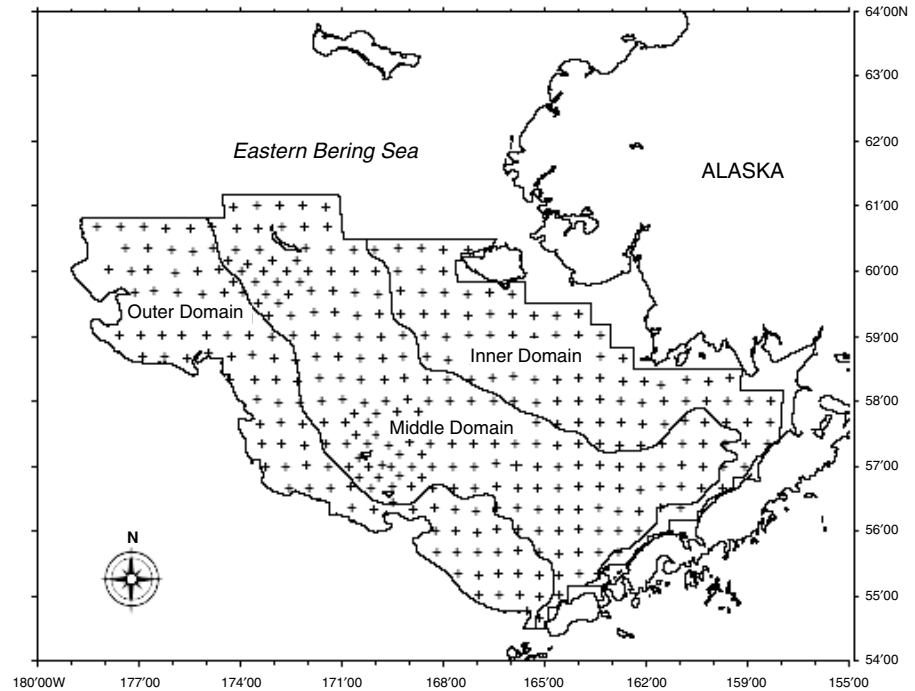


Figure 1

Survey area in the eastern Bering Sea. Crosses represent annual trawl survey stations from 20–200 m. Bathymetry lines delineate the inner, middle and outer domains.

EBS shelf domains and study area

The EBS is composed of three well-defined regions designated as the inner, middle, and outer domains from east to west, respectively, across the shelf (Fig. 1). The three domains are distinct regions characterized by depth, water temperature, current flow, summertime primary production, and species composition (Bakkala, 1993; Schumacher and Stabeno, 1998; Stabeno et al., 2001). Briefly, the inner domain is a relatively shallow (<50 m) and well-mixed warm basin with strong influences from a large coastal area, several major river systems, and a current flow northward along the coast from the Aleutian Islands. The middle domain is a relatively stagnant area of deeper water (50–100 m) that has strong summer water-column stratification and low current flows. The bottom water mass is relatively cold, overlaid by a layer of warmer wind-mixed water. Although characterized as a cold region, the water mass in the middle domain varies from year to year. The outer domain is influenced by the EBS slope region and by upwelling and northward current flow from the Aleutian Islands. This domain is relatively warm when compared to the middle domain (see Hunt et al., 2002, for review). For the purposes of this study the inner domain designation consisted of trawl stations less than 50 m in depth; the middle shelf designation was for trawl stations between 51 and 100 m in depth; and outer domain designation was for trawl stations between 101 and 200 m in depth.

Table 1

Flatfish guild species or species groups used for biodiversity indexes. * indicates the major proportion of the biomass for the group. Superscripts indicate the primary domains where each species occurs during the summertime AFSC survey. I=inner domain, M=middle domain, O=outer domain.

Group name	Scientific name
Pacific halibut	<i>Hippoglossus stenolepis</i> ^{IMO}
Flathead/Bering flounder	* <i>Hippoglossoides elassodon</i> and <i>H. robustus</i> ^{IMO}
Greenland turbot	<i>Reinhardtius hippoglossoides</i> ^O
Arrowtooth/Kamchatka flounders	* <i>Atheresthes stomias</i> and <i>A. evermanni</i> ^{MO}
Starry flounder	<i>Platichthys stellatus</i> ^{IM}
Alaska plaice	<i>Pleuronectes quadrituberculatus</i> ^{IM}
Northern/southern rock sole	* <i>Lepidopsetta polyxystra</i> and <i>L. bilineata</i> ^{IMO}
Longhead dab	<i>Limanda proboscidea</i> ^I
Yellowfin sole	<i>Limanda aspera</i> ^{IM}
Rex sole	<i>Glyptocephalus zachirus</i> ^O
Oher flatfish	* <i>Isopsetta isolepis</i> ^{IM} , * <i>Limanda sakhalinensis</i> ^{MO} , <i>Psettichthys melanostictus</i> , <i>Microstomus pacificus</i>

Fish assemblages differed noticeably among the inner, middle, and outer domains in the EBS; many species (sculpins, poachers, and eelpouts) primarily inhabited a single domain and many flatfishes and skates inhabited all three domains (Kaimmer¹; Kinder and Schumacher, 1981; Smith and Bakkala, 1982: Tables 1 and 2). Because of the distinct domain environments and assemblages, the flatfish and roundfish species groups were analyzed by inner, middle, and outer domains separately and all domains were combined to detect the influence of climate change on each assemblage.

Species groups

The taxonomic level of species identification for the entire survey period (1975–2002) has varied because of an incomplete knowledge of species characters and because of survey time constraints at-sea. Historically, survey goals were to obtain fisheries data on commercially or potentially commercially important species, and limited effort was put forth for identification of other species. However, given more efficient technologies, better identification field guides, and increased focus on noncommercial species, species identification has improved and is approaching the current extent of taxonomic knowledge.

Efforts in recent years (1998–2002) have increased our knowledge of current species distributions in the

EBS shelf region. To assess species-identification confidence over the study period, current species distributions from the AFSC survey and primary literature not associated with AFSC survey data, as well as historical fish collections of selected taxonomic groups (University of Washington Fish Collection, Oregon State University Fish Collection, and Auke Bay Fish Collections) were examined. After this assessment, it was subjectively determined whether species in this study were identified correctly throughout the study period. Species that were determined to be distinguishable and correctly identified were examined as individual species, and species that were possibly misidentified were grouped at a higher taxonomic level for this study. The resulting list of species or species groups includes the greatest number of fish taxa (Tables 1 and 2).

At least 15 flatfish species (within the order Pleuronectiformes) and more than 75 species of fish and elasmobranchs not of the order Pleuronectiformes were recorded during the AFSC summer surveys (1975–2002) on the EBS shelf (20–200 m). Although flatfish make up about 16% of the total number of fish species, they contribute approximately 50% of the biomass of all fish combined (2001 and 2002 AFSC EBS survey estimates). Walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) represent approximately 42% of the survey biomass, and 8% of the biomass that included all other roundfish. Because of the extremely large biomass of walleye pollock and Pacific cod, the biodiversity indexes used are uninformative when walleye pollock and Pacific cod are included owing to the “swamping” effect by their relatively large biomasses when compared to those of other species. To account for this, two species guilds were defined: flatfish and roundfish. The flatfish guild included all Pleuronectiformes recorded from the EBS survey and comprised 11 species or species groups (Table 1). The roundfish

¹ Kaimmer, S. M., J. E. Reeves, D. R., Gunderson, D. R., Smith, G. B., and R. A. Macintosh. 1976. Baseline information from the 1975 OCSEAP survey of the demersal fauna of the eastern Bering Sea. In *Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975* (W. T. Pereyra, J. R. Reeves, and R. G. Bakkala, eds.), p. 157–367. NWAFC Processed Report. Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E. Seattle WA 98115.

Table 2

Roundfish guild species or species groups used for biodiversity indexes. * indicates the major proportion of the biomass for the group. Superscripts indicate the primary domains where each species occurs during the summertime AFSC survey. I=inner domain, M=middle domain, O=outer domain. IMO=inner, middle, and outer domains.

Group name	Scientific name
Lamprey	<i>Lampetra tridentata</i>
Skate	* <i>Bathyraja parmifera</i> ^{IMO} , * <i>B. interrupta</i> ^O , <i>B. aleutica</i> , <i>B. taranetzi</i> , <i>Raja binoculata</i>
Shark	* <i>Somniosus pacificus</i> ^O , <i>Squalus acanthias</i> , <i>Lamna ditropis</i>
Other poachers	* <i>Aspidophoroides bartoni</i> ^O , <i>Bathyagonus alascanus</i> , <i>Leptagonus leptorhynchus</i> , <i>Pallasina barbata</i> , <i>Percis japonicus</i>
Sawback poacher	<i>Sarritor frenatus</i> ^{MO}
Sturgeon poacher	<i>Agonus acipenserinus</i> ^{IM}
Bering poacher	<i>Ocellus dodecaedron</i> ^I
Bering wolffish and wolfeel	<i>Anarhichas orientalis</i> and <i>Anarrhichthys ocellatus</i>
Searcher	<i>Bathymaster signatus</i> ^O
Other sculpins	<i>Arteidiellus pacificus</i> , <i>Leptocottus armatus</i> , <i>Enophrys</i> spp., <i>Psychrolutes paradoxus</i> , <i>Blepsias bilobus</i> , <i>Nautichthys pribilovius</i> , <i>Icelinus</i> spp.
Staghorn sculpin	* <i>Gymnocanthus pistilliger</i> ^I , * <i>G. galeatus</i> ^O , <i>G. detrisus</i>
Darkfin sculpin	<i>Malacocottus zonurus</i> ^O
Yellow Irish lord	<i>Hemilepidotus jordani</i> ^I
Butterfly sculpin	<i>Hemilepidotus papilio</i> ^M
<i>Triglops</i> sculpins	* <i>Triglops scepticus</i> ^O , * <i>T. pingeli</i> ^{IM} , <i>T. macellus</i> , <i>T. forficatus</i>
<i>Myoxocephalus</i> sculpins	* <i>Myoxocephalus jaok</i> ^I , * <i>M. polyacanthocephalus</i> ^{MO} , <i>M. verrucosus</i> ^M
Spinyhead sculpin	<i>Dasycottus setiger</i> ^O
Bigmouth sculpin	<i>Hemitripterus bolini</i> ^O
<i>Icelus</i> sculpins	* <i>Icelus spiniger</i> ^O and * <i>I. spatula</i> ^{IM}
Pacific sandfish	<i>Trichodon trichodon</i> ^I
White-spotted greenling	<i>Hexagrammos stelleri</i> ^I
Snailfish	* <i>Liparis gibbus</i> ^{MO} , * <i>Careproctus rastrinus</i> ^{MO} , <i>C. cyclospilus</i>
Smooth lumpsucker	* <i>Aptocyclus ventricosus</i> ^O , <i>Eumicrotremus orbis</i>
Pricklebacks	* <i>Lumpenus maculata</i> ^{IMO} , * <i>L. sagittae</i> ^{IMO} , <i>L. fabricii</i> , <i>L. medius</i> , <i>Poroclinus rothrocki</i>
Other eelpouts	* <i>Lycodes</i> spp. and <i>Gymnelus</i> spp.
Marbled eelpout	<i>Lycodes raridens</i> ^I
Wattled eelpout	<i>Lycodes palearis</i> ^{MO}
Shortfin eelpout	<i>Lycodes brevipes</i> ^O
Pacific tomcod	<i>Microgadus proximus</i>
Saffron cod	<i>Eleginus gracilis</i> ^I
Arctic cod	<i>Boreogadus saida</i> ^M
Pacific sand lance	<i>Ammodytes hexapterus</i>
Pacific herring	<i>Clupea pallasii</i> ^{IM}
Eulachon	<i>Thaleichthys pacificus</i> ^O
Capelin	<i>Mallotus villosus</i> ^I
Rainbow smelt	<i>Osmerus mordax</i> ^{IMO}
Salmon	<i>Oncorhynchus</i> spp.
Sablefish	<i>Anoplopoma fimbria</i> ^O
Atka mackerel	<i>Pleurogrammus monopterygius</i>
Prowfish	<i>Zaprora silenus</i> ^O
Rockfish	* <i>Sebastes alutus</i> ^O , <i>S. polyspinis</i> , <i>S. ciliatus</i>

guild included 40 species or species groups and excluded walleye pollock and Pacific cod (Table 2). The two guilds devised were subjective; however, owing to their distinctive biomass and life history trends, the members of the flatfish guild were examined separately from all other species.

Biodiversity indexes

Biodiversity measures were calculated by using Ludwig and Reynolds's (1988) recommendations for species richness and evenness. Richness and evenness are considered robust measures and allow one to use biomass proportions for biodiversity estimations. The richness index used was as follows:

$$\text{Richness index} = e^H$$

$$\text{where } H' = \sum_{i=1}^S \left[\left(\frac{n_i}{n} \right) \ln \left(\frac{n_i}{n} \right) \right]$$

and n_i = the biomass of individuals belonging to the i th of S species in the sample; and
 n = the total summed biomass for the entire guild for a given year (Ludwig and Reynolds, 1988).

The evenness index is the "modified Hill's ratio" (Alatalo, 1981) which is

$$\text{Evenness} = \frac{\left(\frac{1}{\lambda} \right) - 1}{e^{H'} - 1},$$

where $\lambda = \frac{\sum_{i=1}^S p_i^2}{\sum_{i=1}^S p_i}$, where $p_i = \frac{n_i}{N}$ and n_i is the biomass of the i th species and N is the total biomass of all S (species) in the guild (Ludwig and Reynolds, 1988).

Biomass estimates obtained from the surveys were used to calculate biodiversity values for both flatfish and roundfish guilds on an annual basis. Biodiversity values calculated were used as an index of the relative proportion of species in each guild and allowed a direct comparison from year to year of the most abundant species. Species richness indicated the effective number of species that are influencing the index (Hill, 1973; Ludwig and Reynolds, 1988). A higher index indicates a larger number of predominant species in the assemblage (i.e., higher diversity). The evenness index determines the distribution of the biomass proportions of the more abundant species among the species in the guild. As the evenness index approaches zero, the biomass proportion of a single species dominates the guild; as the evenness index approaches one, there is less of a single dominant species and the biomass proportions are shared more equally among many species in the guild (Hill, 1973; Ludwig and Reynolds, 1988).

A piecewise linear model (Neter et al., 1996) was applied to the biodiversity indexes using S-Plus (vers. 6.1, Insightful Corporation, Seattle, WA) to determine distinct breaks or inflection points in the linear data trends. The piecewise model finds a "knot," or inflection point, that breaks the data set into two periods by using the least sum of squared residuals and the highest R^2 for the two-line model to determine the best fit lines to the data. Linear regression models were then applied to the data sets by using the recommended inflection point as the breaking point for the two lines. The years covered for each best fit line, as well as the accompanying linear statistics for the individual lines and the piecewise linear model for the best-fit model are presented in Table 3. The indexes calculated for survey year 1975 are included for reference (denoted as an X on the diversity index graphs) but were not included in the linear regression models because of the time gap from 1975 to 1979 and the lack of confidence in the standardization of the 1975 survey compared with later surveys (Bakkala, 1993).

Results

Flatfish biomass

Biomass estimates for the flatfish guild showed an increase from the late 1970s until the early 1990s, and then an overall slight decline between 1999 and 2002 for all domains (Fig. 2). Species that represented a large portion that showed an increase in biomass estimates over the study period included northern and southern rock sole (*Lepidopsetta polyxystra* and *L. bilineata*, spp. undetermined), arrowtooth and Kamchatka flounder (*Atheresthes stomias* and *A. evermanni*, spp. undetermined), flathead sole and Bering flounder (*Hippoglossoides elassodon* and *H. robustus*, spp. undetermined), and Pacific halibut (*Hippoglossus stenolepis*). Flatfish species with declining biomass estimates included the yellowfin sole (*Limanda aspera*) and Greenland turbot (*Reinhardtius hippoglossoides*), and a decline in lesser abundant species such as longhead dab (*Limanda proboscidea*) and Alaska plaice (*Pleuronectes quadrituberculatus*). The inner and middle domains were dominated by northern rock sole, yellowfin sole, Alaska plaice, and flathead sole and Bering flounder (spp. undetermined), whereas main portions of the outer shelf comprised arrowtooth and Kamchatka flounder (spp. undetermined), flathead sole and Bering flounder (spp. undetermined), Pacific halibut, and northern and southern rock sole (spp. undetermined).

Roundfish biomass

Roundfish biomass increased from the 1970s to the 1980s and then declined steadily from the early 1990s through 2002 for all domains combined (Fig. 2). Among roundfish species there has been a decline since the 1970s and 1980s in many middle domain species, such as yellow Irish lord (*Hemilepidotus jordani*), butterfly sculpin (*H. papilio*),

Table 3

Statistics of the linear regression models of biodiversity indexes for flatfish and roundfish guilds for the eastern Bering Sea shelf domains. The years encompassing each time period and the piecewise model r^2 for the two-line model are included.

Domain	Index	Years	n	Intercept	Slope	P -value	r^2	Standard error of estimate	r^2 of piecewise model
Flatfish guild									
Inner	Richness	1979–1993	15	-112.9280	0.0579	0.0000	0.8797	0.0993	0.8850
		1994–2002	9	3.9168	-0.0008	0.9645	0.0303	0.1270	
Middle	Richness	1979–1988	10	-358.4240	0.1821	0.0001	0.8829	0.2130	0.8640
		1989–2002	14	7.8482	-0.0020	0.9171	0.0940	0.2887	
Outer	Richness	1979–2002	24	-2.8281	0.0030	0.6875	0.7493	0.2533	0.9350
Combined	Richness	1979–1989	11	-327.9090	0.1666	0.0000	0.8740	0.2212	
			1990–2002	13	6.1232	-0.0012	0.8866	0.1932	0.1150
Inner	Evenness	1979–1990	12	-48.3712	0.0247	0.0000	0.9291	0.0258	0.9610
		1991–2002	12	-0.0349	0.0005	0.6927	0.0163	0.0161	
Middle	Evenness	1979–1987	9	-61.6390	0.0314	0.0003	0.8663	0.0361	0.8660
		1988–2002	15	3.7805	-0.0015	0.5159	3.3171	0.0375	
Outer	Evenness	1979–2002	24	1.8798	-0.0006	0.6184	0.0115	0.0392	0.9630
Combined	Evenness	1979–1988	10	-59.8421	0.0305	0.0000	0.9318	0.0265	
			1989–2002	14	2.0678	-0.0007	0.4732	0.0437	0.0136
Roundfish guild									
Inner	Richness	1979–2002	24	-5.0326	0.0040	0.8287	0.2175	0.6197	0.9040
Middle	Richness	1979–1986	8	865.6880	-0.4338	0.0119	0.6789	0.7895	
		1987–2002	16	203.6660	-0.1006	0.0000	0.7196	0.3095	
Outer	Richness	1979–1986	8	908.1290	-0.4564	0.0011	0.8511	0.5051	0.8690
		1987–2002	16	-65.9678	0.0340	0.0762	0.2075	0.3276	
Combined	Richness	1979–1986	8	1535.3000	-0.7713	0.0003	0.9072	0.6527	0.9410
		1987–2002	16	81.4226	-0.0394	0.1204	0.1634	0.4390	
Inner	Evenness	1979–1990	12	-14.9002	0.0078	0.3003	0.1066	0.0853	0.5620
		1991–2002	12	-32.0753	0.0164	0.0057	0.5504	0.0561	
Middle	Evenness	1979–1990	12	51.5981	-0.0257	0.0001	0.7779	0.0518	0.9210
		1991–2002	12	20.3337	-0.0099	0.0002	0.7694	0.0206	
Outer	Evenness	1979–1987	9	66.1545	-0.0331	0.0024	0.7550	0.0552	0.7150
		1988–2002	15	-16.5892	0.0085	0.0110	0.4028	0.0482	
Combined	Evenness	1979–1989	11	46.7485	-0.0233	0.0003	0.7782	0.0434	0.8630
		1990–2002	13	1.1549	-0.0003	0.8818	0.0021	0.0306	

armorhead sculpin (*Gymnocanthus galeatus*), snailfishes (*Liparis gibbus* and *Careproctus rastrinus*), marbled eelpout (*Lycodes raridens*), and wattled eelpout (*Lycodes palearis*), and in outer domain species such, as shortfin eelpout (*Lycodes brevipes*) and sablefish (*Anoplopoma fimbria*). There has been an increase in large sculpins, including the bigmouth sculpin (*Hemitripterus bolini*) and the great sculpin (*Myoxocephalus polyacanthocephalus*), in the outer domain. The biomass of skates predominantly the Alaska skate (*Bathyraja parmifera*), increased considerably from 1979 through 1990, followed by a prolonged period of little change from 1990 through 2002.

Flatfish biodiversity

Eleven species or species groups were used for biodiversity indexes for the flatfish guild (Table 1). All 11 species are rarely found together, and within each shelf

domain the major portion of the assemblage comprises 3–5 species. Figure 3 shows the change in biodiversity indexes from 1975 to 2002 for each domain separately and all domains combined. The piecewise model shows a period of inflection for evenness and richness indexes for flatfish in the inner and middle domains that occurred between 1987 and 1993, with the average year of inflection being 1990 (Fig. 3, Table 3). The outer domain for flatfish showed little change in evenness and richness throughout the 24-year study period. Three species dominated the entire period, with somewhat evenly distributed biomass proportions.

Roundfish biodiversity

Forty-one species or species groups were used in the roundfish biodiversity analysis (Table 2). The evenness and species richness index for the roundfish group

Flatfish guild

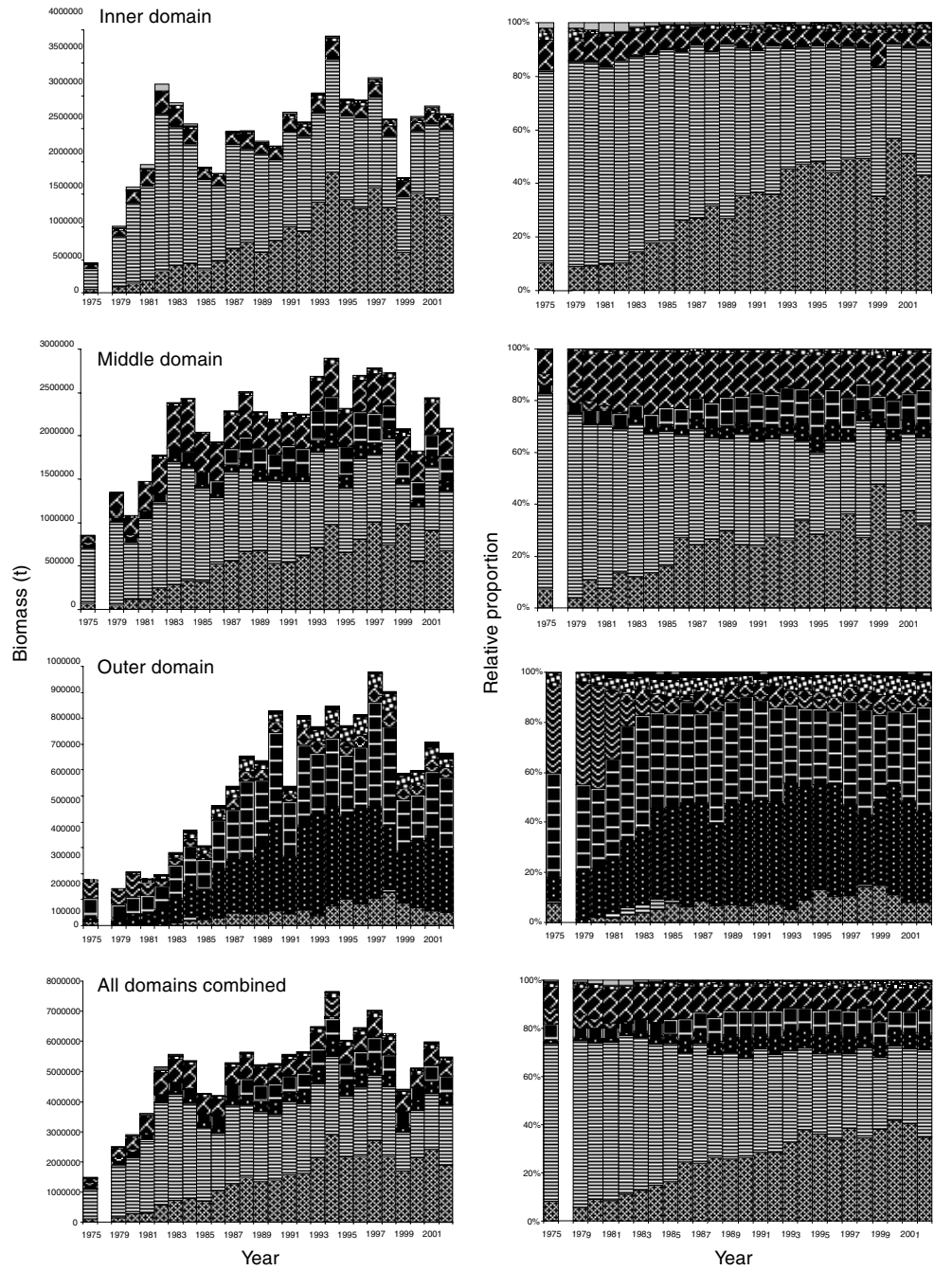
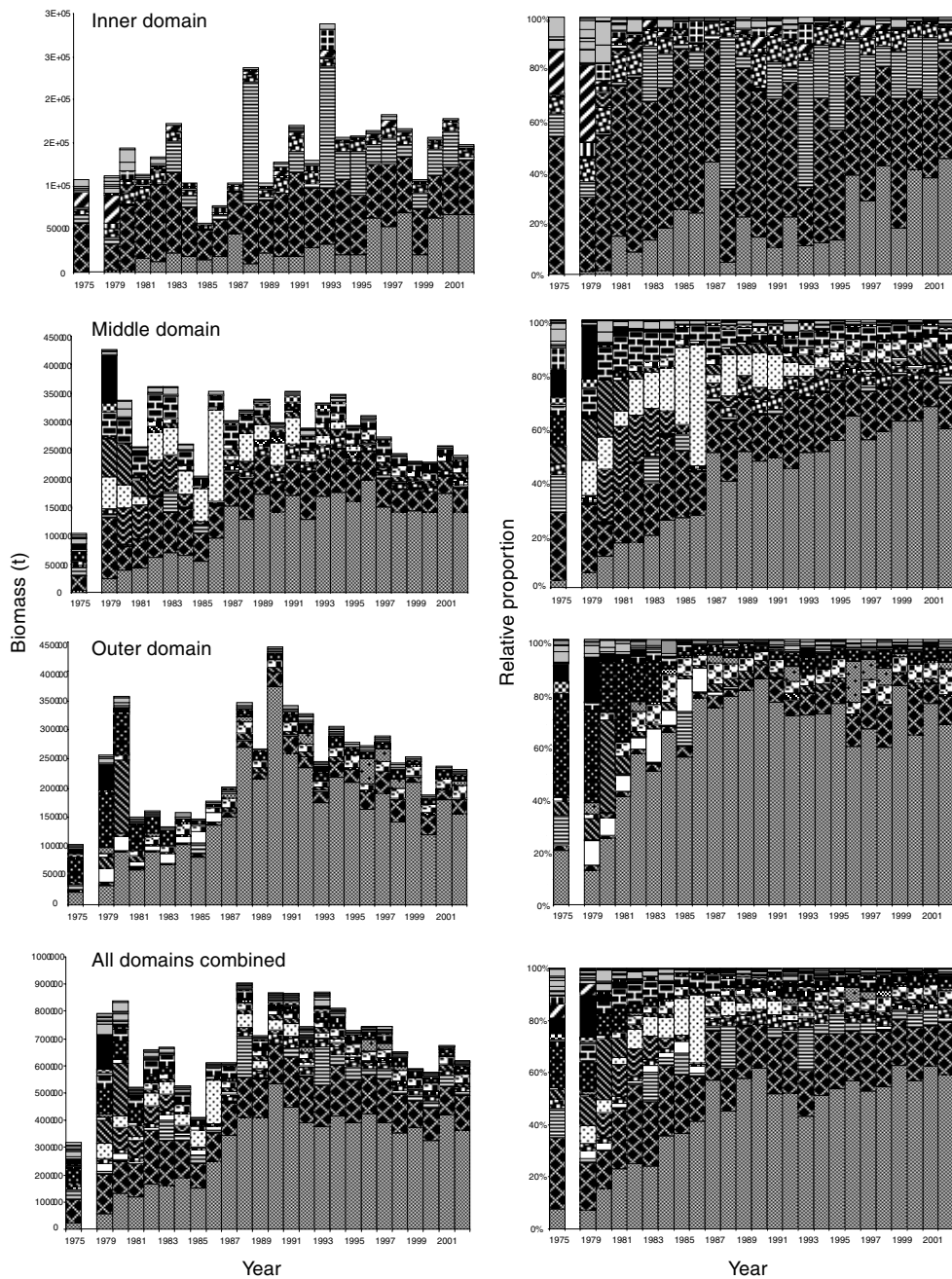


Figure 2

Biomass estimates for flatfish guild and roundfish guild (left panel), and relative proportion of each species (right panel) for inner, middle, outer, and all three domains combined, respectively.

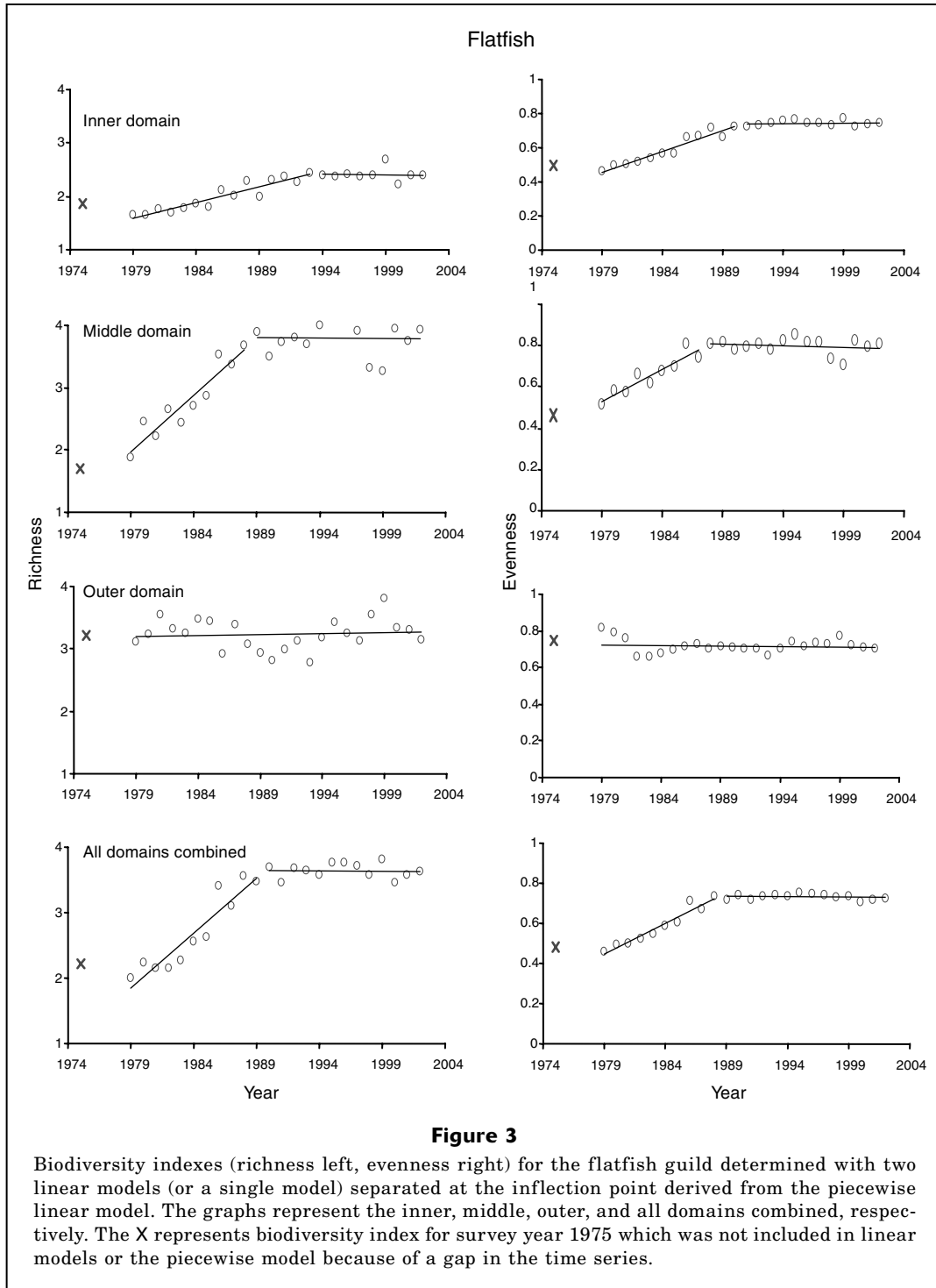
Roundfish guild



Roundfish guild

- | | | | | |
|----------------------|--------------------------|-----------------------------|-------------------------|-------------------------------|
| Atka mackerel | eulachon | armorhead sculpin | saffron cod | wattled eelpout |
| prowfish | Pacific sand lace | Bering wolffish and wolfeel | other eelpouts | butterfly sculpin |
| pricklebacks | Pacific sandfish | Bering poacher | snailfishes | marbled eelpout |
| salmon | other sculpins | sawback poacher | white spotted greenling | sturgeon poacher |
| hagfish and lampreys | <i>Icelus</i> sculpins | other poachers | yellow Irish lord | sablefish |
| sharks | spinyheaded sculpin | searcher | shortfin eelpout | Pacific herring |
| arctic cod | <i>Triglops</i> sculpins | lumpsuckers | rockfish | <i>Myoxocephalus</i> sculpins |
| Pacific tomcod | darkfin sculpin | capelin | bigmouth sculpin | skates |
| rainbow smelt | | | | |

Figure 2 (continued)



is plotted for each shelf domain and for all domains combined. The inner domain richness index revealed a steady level of approximately 2–3 dominant species or species groups (*Myoxocephalus* sculpins, skates, and Pacific herring) over the 24-year period. The gradual increase in skates and slight decline in the plain sculpin caused an increase in the evenness index to somewhat even proportions of the three dominant species in the

inner domain, from 7 to 2 dominant species over the 24-year period, and evenness declined by about one-half (Fig. 4). The increase in skates and decline of many inner domain species from 1975 through the early 1990s resulted in an assemblage dominated by two species groups, *Myoxocephalus* sculpins and skates (Fig. 2).

The outer domain showed a dramatic decline in richness and evenness from 1975 to the mid-1980s and

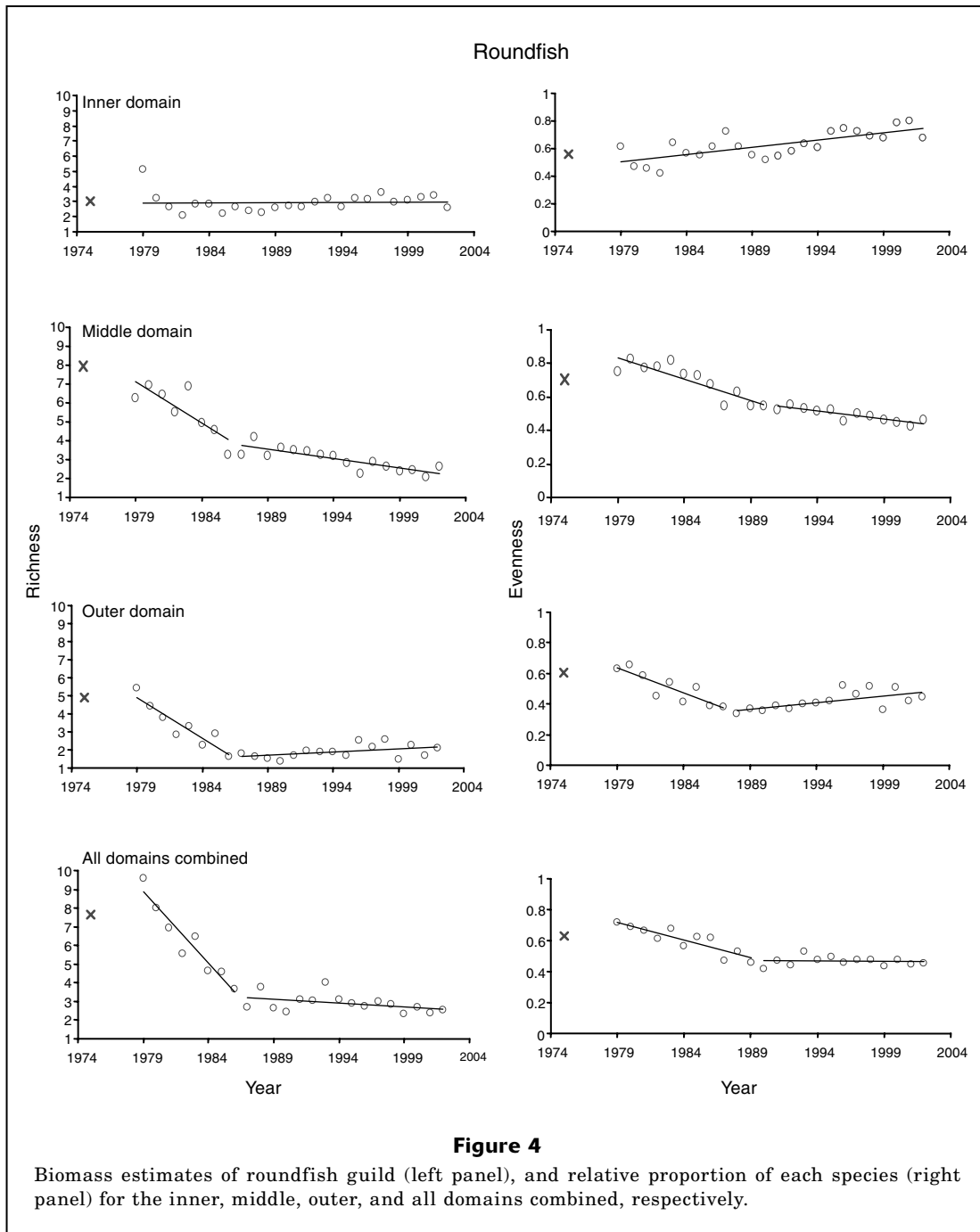


Figure 4
 Biomass estimates of roundfish guild (left panel), and relative proportion of each species (right panel) for the inner, middle, outer, and all domains combined, respectively.

then a slight increase through 2002. A decrease in the number of dominant species, such as sablefish, wattled and shortfin eelpouts from 1979 to 1986, and a large increase of skate biomass from 20% in 1975 to approximately 75% of the total biomass by 1986, explain the index decline during this same period as the skate biomass dominated. After 1986 the skate populations stabilized somewhat to a slight decline which accounts for the slight increase in evenness and richness as other species gained a larger percentage of the total biomass.

All indexes for the roundfish guild, except for inner domain richness, indicated two distinct linear periods. Inflection points ranged from 1986 to 1990 and 1988 was an average inflection year for the roundfish guild.

Discussion

Periods of climatic change have been shown to instill long-term changes in the North Pacific ecosystem (Hare

and Mantua, 2000). Biodiversity indexes are a robust measure for large ecosystem monitoring and possible indicators of resulting regime shift phenomenon from climatic change based on an assemblage's long-term responses. Hare and Mantua (2000) summarized over 100 studies from the eastern North Pacific identifying two distinct periods of change or "regime shifts" in 1977 and 1989. Recently, Stabeno et al. (2001) and Hunt and Stabeno (2002) suggested the possibility of a third period of significant climatic change in the late 1990s for the northeastern Pacific. Although environmental changes may be readily identified, the ecosystem fauna may respond more slowly, or in ways not immediately obvious; however the changes may be persistent and far reaching. According to survey data, the last 20 years have proven to be a very hospitable environment for many flatfish species in the EBS, where populations such as northern rock sole and arrowtooth and Kamchatka flounder have rapidly expanded since the late 1970s. Biodiversity indexes are significantly higher than they were 20 years ago for flatfish as a group and have remained high and unchanged. The biodiversity indexes for flatfish guild corroborate the timing of the strong regime shift reported in the late 1980s. An inflection around 1990 is the strongest evidence of a regime shift from the biodiversity indexes. It would be expected that a purely biological response to a climatic event may lag by a time period, perhaps accounting for a later year than previously reported.

Survey data indicate that many roundfish species have not fared as well as flatfish species and biodiversity indexes are significantly lower now than 20 years ago. The roundfish guild has undergone a significant reorganization in which a large group of species have declined and a single species has become dominant, causing biodiversity to be suppressed. The regime shift is reflected in the roundfish biodiversity around 1988, which agrees with the results of other reported studies.

Although EBS productivity has increased through the 1970s and 1980s and remained high through the 1990s, the trend in the ecosystem is towards fewer or single dominant species. The decline of many nonexploited species in the EBS is difficult to explain with the current regime shift theories. Unfortunately, a lack of information on the life history of the large number of species, such as poachers, sculpins, eelpouts, and skates in the EBS hinders a complete understanding of recruitment success or failure.

Acknowledgments

I thank all the dedicated scientists, vessel skippers, and crew for their hard work over the years collecting data and G. Walters and M. Martin for assistance with data analysis. Also I thank the reviewers for their contributions in improving this manuscript. The reviewers were D. Somerton, G. Walters, J. Orr, S. Kotwicki, G. Stauffer, A. Hollowed, and an unknown journal reviewer. Thank you all.

Literature cited

- Alatalo, R. V.
1981. Problems in the measurement of evenness in ecology. *Oikos* 37:199–204.
- Anderson, P. J.
2000. Pandalid shrimp as indicators of ecosystem regime shift. *J. Northw. Atl. Fish. Sci.* vol. 27:1–10.
- Anderson, P. J., J. E. Blackburn, and B. A. Johnson.
1997. Declines of forage species in the Gulf of Alaska, 1972–1995, as an indicator of regime shift. *In* Proceedings of the international symposium on the role of forage fishes in marine ecosystems, p. 531–543. Univ. Alaska Sea Grant College Program Report AK-SG-97-01, Anchorage, AK.
- Anderson, P. J., and J. F. Piatt
1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Progr. Ser.* 189:117–123.
- Bakkala, R. G.
1993. Structure and historical changes in the groundfish complex of the eastern Bering Sea. NOAA Tech. Rep. NMFS 114, 91 p.
- Bond, N. A., and J. M. Adams.
2002. Atmospheric forcing of the southeast Bering Sea shelf during 1995–99 in the context of a 40-year historical record. *Deep-Sea Res.* 11 49:5869–5887.
- Brodeur, R. D., M. T. Wilson, G. E. Walters, and I. V. Melnikov.
1999. Forage fishes in the Bering Sea: Distribution, species associations, and biomass trends. *In* Dynamics of the Bering Sea: a summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea (T. R. Loughlin and K. Ohtani, eds.), p. 509–356. Univ. Alaska Sea Grant AK-SG-99-03, Anchorage, AK.
- Brodeur, R. D., and D. Ware.
1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* 1:32–38.
- Clark, W. G., S. Hare, A. M. Parma, P. J. Sullivan, and R. J. Trumble.
1999. Decadal changes in growth and recruitment of Pacific halibut (*Hippoglossus stenolepis*). *Can. J. Fish. Aquat. Sci.* 56:242–252.
- Connors, M. E., A. B. Hollowed, and E. Brown.
2002. Retrospective analysis of Bering Sea bottom trawl surveys: regime shift and ecosystem reorganization. *Progr. Oceanogr.* 55:209–222.
- Hare, S. R., and N. J. Mantua.
2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progr. Oceanogr.* 47:103–146.
- Hill, M. O.
1973. Diversity and evenness. A unifying notation and its consequences. *Ecology* 54:427–432.
- Hollowed, A. B., S. R. Hare, and W. S. Wooster.
2001. Pacific basin climate variability and patterns of northeast Pacific marine fish production. *Prog. Oceanogr.* 49:257–282.
- Hunt, G. L. Jr., and P. J. Stabeno.
2002. Climate change and the control of energy flow in the southeastern Bering Sea. *Prog. Oceanogr.* 55:5–22.
- Hunt, G. L., P. Stabeno, G. Walters, E. Sinclair, R. D. Brodeur, J. M. Napp, and N. A. Bond.
2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. II* 49:5821–5853.

- Kinder, T. H., and J. D. Schumacher.
1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. *In* The eastern Bering Sea shelf: oceanography and resources, vol. 1 (D. W. Hood and J. A. Calder, eds.), p. 31–52. U.S. Government Printing Office, Washington D.C.
- Ludwig, J. A., and J. F. Reynolds.
1988. Statistical ecology: a primer on methods and computing, 337 p. John Wiley and Sons, New York, NY.
- Minobe, S.
2002. Interannual to interdecadal changes in the Bering Sea and concurrent 1998/99 changes over the North Pacific. *Progr. Oceanogr.* 55:45–64.
- Neter, J., M. Kutner, C. J. Nachtsheim, and W. Wasserman.
1996. Applied linear regression models, 3rd ed., 720 p. McGraw-Hill Com, Chicago, IL.
- Rose, C. S., and G. E. Walters.
1990. Trawl width variation during bottom trawl surveys: causes and consequences. *In* Proceedings of the symposium on application of stock assessment techniques to gadids (L-L. Low ed.), p. 57–67. *Int. North Pac. Fish. Comm. Bull.* 50.
- Rosenzweig, M. L., and Z. Abramsky.
1993. How are diversity and productivity related? *In* Species diversity in ecological communities historical and geographical perspectives (R.E. Rickles and D. Schuller, eds.), p. 52–65. Univ. Chicago Press, Chicago, IL.
- Schumacher, J. D., and J. P. Stabeno.
1998. Continental shelf of the Bering Sea. *In* The sea, vol. XI, The global coastal ocean: regional studies and synthesis (A.R. Robinson and K.H. Brink, eds.), p. 789–822. John Wiley, Inc., New York, NY.
- Smith, G. B., and R. G. Bakkala.
1982. Demersal fish resources of the eastern Bering Sea: spring 1976. NOAA Tech. Rep. NMFS SSRF-754, 129 p.
- Stabeno, P. J., N. A. Bond, N. B. Kachel, S. A. Salo, and J. D. Schumacher.
2001. On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fish. Oceanogr.* 10(1):81–98.
- Sugimoto T., S. Kimura, and K. Tadokora.
2001. Impact of El Niño events and climate regime shift on living resources in the western North Pacific. *Progr. Oceanogr.* 49:113–127.
- Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter.
1999. The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30:257–300.
- Wilderbuer, T. K., A. B. Hollowed, W. J. Ingraham Jr., P. O. Spencer, M. E. Conners, N. A. Bond, and G. E. Walters.
2002. Flatfish recruitment response to decadal climatic variability and ocean condition in the eastern Bering Sea. *Progr. Oceanogr.* 55:235–247.
- Zhang, C. I., J. B. Lee, S. Kim, and J. H. Oh.
2000. Climatic regime shifts and their impacts on marine ecosystem and fisheries resources in Korean waters. *Progr. Oceanogr.* 47:171–190.