SEA ICE RETREAT ALTERS THE BIOGEOGRAPHY OF THE BERING SEA CONTINENTAL SHELF

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Abstract. Seasonal ice cover creates a pool of cold bottom water on the eastern Bering Sea continental shelf each winter. The southern edge of this cold pool, which defines the ecotone between arctic and subarctic communities, has retreated ~230 km northward since the early 1980s. Bottom trawl surveys of fish and invertebrates in the southeastern Bering Sea (1982–2006) show a coincident reorganization in community composition by latitude. Survey catches show community-wide northward distribution shifts, and the area formerly covered by the cold pool has seen increases in total biomass, species richness, and average trophic level as subarctic fauna have colonized newly favorable habitats. Warming climate has immediate management implications, as 57% of variability in commercial snow crab (*Chionoecetes opilio*) catch is explained by winter sea ice extent. Several measures of community distribution and structure show linear relationships with bottom temperature, suggesting warming climate as the primary cause of changing biogeography. However, residual variability in distribution not explained by climate shows a strong temporal trend, suggesting that internal community dynamics also contribute to changing biogeography. Variability among taxa in their response to temperature was not explained by commercial status or life history traits, suggesting that species-specific responses to future warming will be difficult to predict.

Key words: benthic fauna; Bering Sea; biogeography; climate change; cold pool; continental shelf; fisheries; global warming; sea ice.

INTRODUCTION

Global warming has been most dramatic in arctic and subarctic regions (Overpeck et al. 1997), and one of the most obvious effects in these regions has been the poleward retreat of seasonal sea ice cover (Holland et al. 2006). Although the implications of retreating sea ice for marine mammals have received considerable attention (Arctic Climate Impact Assessment 2004), the loss of sea ice also has important potential consequences for demersal (sea floor) fish and invertebrate communities. On boreal continental shelves (e.g., Bering Sea, Barents Sea, Sea of Okhotsk), winter ice cover creates a pool of cold (<2°C) bottom water that is protected from summer mixing by the thermocline, so that winter surface conditions, especially the extent of ice, are the dominant factor controlling summer conditions for demersal taxa (Wyllie-Echeverria and Wooster 1998, Hunt and Stabeno 2002). Because many temperate species, especially groundfish, are intolerant of the low temperatures of ice-associated bottom water, the extent of sea ice determines the boundary between arctic and subarctic demersal communities (Wyllie-Echeverria and Wooster 1998, Grebmeier et al. 2006). Retreat of sea ice

should therefore lead to a northward migration of the arctic–subarctic ecotone on continental shelves, just as warming air temperatures lead to migration of the arctic–subarctic ecotone in terrestrial vegetation communities.

Understanding the community-level implications of the loss of sea ice and migration of the arctic–subarctic ecotone is critical for appropriate management of boreal continental shelf fisheries. In this paper, we document community-level distribution shifts of demersal taxa in the Bering Sea when sea ice and the cold pool retreat northward, whether as a result of decadal-scale trends, as a result of global warming, or both. The continental shelf of the eastern Bering Sea is one of the most productive marine ecosystems in the world, produces average annual landings of approximately 1.3×10^6 metric tons (1 metric ton = 1 Mg) of fish and shellfish (North Pacific Fishery Management Council 2005), and has experienced significant warming and loss of sea ice in recent decades (Stabeno et al. 2001, Grebmeier et al. 2006). Distribution changes in individual taxa have been noted in response to temperature variability (Wyllie-Echeverria and Wooster 1998, Orensanz et al. 2004, Kotwicki et al. 2005, Zheng and Kruse 2006), but a community-wide analysis of distribution changes has not been presented. An important feature of distribution changes in response to warming is variability among species in responses, such that new community combi-

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TABLE 1. Taxa included in analysis of southeastern Bering Sea National Marine Fisheries Service trawl survey data, 1982–2006.

Common name	Scientific name	Max. length (cm)	Trophic level	Habitat	Commercial?	n (total)	With temp.
Arctic taxa							
Alaska plaice	*Pleuronectes quadrituberculatus*	62	3.5	demersal	yes	6465	5980
Arctic cod	*Boreogadus saida*	40	3.6	demersal	no	602	556
Bering flounder	*Hippoglossoides robustus*	52	3.7	demersal	no	1734	1622
Butterfly sculpin	*Hemilepidotus papilio*	37	4.0	demersal	no	613	563
Greenland halibut	*Reinhardtius hippoglossoides*	130	4.6	demersal	yes	1518	1446
Humpy shrimp	*Pandalus goniurus*		2.9	demersal	no	750	705
Marbled eelpout	*Lycodes raridens*	70	3.6	demersal	no	724	680
Snow crab	*Chionoecetes opilio*		3.4	demersal	yes	6617	6193
Wattled eelpout	*Lycodes palearis*	54	3.6	demersal	no	3267	3084
Subarctic taxa							
Arrowtooth flounder†	*Atheresthes* spp.	86	4.3	demersal	yes	4590	4264
Bering poacher	*Occella dodecaedron*	22	4.0	demersal	no	785	738
Bigmouth sculpin	*Hemitripterus bolini*	73	4.0	demersal	no	1491	1413
Blue king crab	*Paralithodes platypus*		3.5	demersal	yes	1129	1030
Capelin	*Mallotus villosus*	25	3.5	pelagic	no	2543	2336
Decorator crab	*Oregonia gracilis*		3.1	demersal	no	1033	964
Eulachon	*Thaleichthys pacificus*	25	3.5	pelagic	no	883	852
Flathead sole	*Hippoglossoides elassodon*	61	3.7	demersal	yes	7140	6642
Helmet crab	*Telmessus cheiragonus*		3.1	demersal	no	857	783
Korean horsehair crab	*Erimacrus isenbeckii*		3.1	demersal	yes	1341	1223
Longhead dab	*Limanda proboscidea*	41	3.6	demersal	no	1876	1718
Pacific cod	*Gadus macrocephalus*	119	4.1	demersal	yes	8754	8134
Pacific halibut	*Hippoglossus stenolepis*	267	4.6	demersal	yes	6051	5602
Pacific herring	*Clupea pallasi*	46	3.5	pelagic	yes	2463	2293
Pacific sand lance	*Ammodytes hexapterus*	28	3.5	pelagic	no	295	275
Pacific sandfish	*Trichodon trichodon*	31	4.5	demersal	no	276	242
Pink shrimp	*Pandalus borealis*		2.9	demersal	no	2071	1968
Pygmy cancer crab	*Cancer oregonensis*		3.1	demersal	no	281	260
Rainbow smelt	*Osmerus mordax*	36	3.5	pelagic	no	141	129
Red king crab	*Paralithodes camtschaticus*		3.5	demersal	yes	2150	1948
Rex sole	*Glyptocephalus zachirus*	59	3.7	demersal	yes	1816	1671
Rock sole	*Lepidopsetta* spp.	69	3.7	demersal	yes	8252	7647
Sablefish	*Anoplopoma fimbria*	120	4.5	demersal	yes	186	174
Saffron cod	*Eleginus gracilis*	55	4.1	demersal	no	431	405
Sawback poacher	*Leptagonus frenatus*	24	4.0	demersal	no	1348	1275
Searcher	*Bathymaster signatus*	38	3.9	demersal	no	1110	1043
Shortfin eelpout	*Lycodes brevipes*	33	3.6	demersal	no	1979	1866
Skates	Rajidae	107	4.2	demersal	yes	6850	6416
Spinyhead sculpin	*Dasycottus setiger*	45	4.0	demersal	no	1084	1019
Starry flounder	*Platichthys stellatus*	91	3.8	demersal	no	1209	1109
Sturgeon poacher	*Podothecus acipenserinus*	31	4.0	demersal	no	5152	4738
Tanner crab	*Chionoecetes bairdi*		3.4	demersal	yes	5765	5345
Tanner-snow hybrid	*Chionoecetes* hybrid		3.4	demersal	yes	1142	1074
Walleye pollock	*Theragra chalcogramma*	91	3.7	pelagic	yes	8851	8231
Whitespotted greenling	*Hexagrammos stelleri*	48	4.2	demersal	no	348	317
Yellow Irish lord	*Hemilepidotus jordani*	50	4.0	demersal	no	2028	1892
Yellowfin sole	*Limanda aspera*	47	3.6	demersal	yes	6529	5999

Notes: Trophic level estimates were obtained from the Alaska Fisheries Science Center (AFSC) and are computed from diet matrices based on AFSC's fish stomach collection program (Kerim Aydin, *personal communication*). "With temp." refers to the number of hauls that had temperature measurements. T_{50} refers to the temperature below which 50% of total CPUE (catch per unit effort) for a taxon was observed. Arctic taxa are those with $T_{50} \leq 2°C$; subarctic taxa are those with $T_{50} > 2°C$. Northward displacement is calculated from estimated linear trend in the center of distribution over time for taxa with an average of 10 or more positive catches per year. P values test the null hypothesis of no linear trend in the center of distribution over time (P_1) and no distribution response to bottom temperature (P_2). "Slope on bottom temperature" denotes the slopes from simple linear regressions of annual centers of distribution (CPUE-weighted mean latitude) on average annual temperature, weighted by the number of positive catches in each year. Empty cells indicate that no measurements are available.

† Includes Kamchatka flounder; maximum length and trophic level are for arrowtooth flounder.

nations may be caused by warming, instead of existing communities simply shifting poleward (Parmesan et al. 2005). Community-wide studies are therefore necessary for understanding the ecological and economic implications of the loss of sea ice in the Bering Sea and other boreal seas.

We used a time series of trawl surveys conducted in the southeast Bering Sea from 1982 to 2006 to test for shifts in the distribution of demersal fishes and crustaceans in response to recent climate warming. We tested the hypotheses that northward retreat of the cold pool would result in a northward shift in the arctic–

TABLE 1. Extended.

T_{50} (°C)	Northward displacement (km)	P_1	Slope on bottom temperature	P_2
1.8	3	0.832	−0.033	0.434
−1.3	40	0.106	0.002	0.988
0.3	76	0.001	0.276	<0.001
0.3	−7	0.857	−0.003	0.945
1.9	98	0.001	0.028	0.853
1.8	62	0.201	−0.137	0.519
−0.4	27	0.174	0.272	<0.001
1.6	89	0.010	0.173	0.051
2.0	−70	0.263	0.092	0.233
3.6	46	0.008	0.260	<0.001
3.5	66	0.037	0.225	0.065
3.1	60	<0.001	0.084	0.258
2.2	−15	0.551	0.071	0.488
3.6	−38	0.402	0.201	0.086
3.0	−5	0.646	0.211	0.001
3.9	34	0.001	0.110	0.006
3.0	57	0.002	0.181	0.017
4.6	13	0.519	0.051	0.199
3.3	26	0.004	0.010	0.802
3.8	51	0.013	−0.050	0.300
2.7	16	0.704	0.038	0.509
3.6	55	<0.001	0.109	0.037
4.4	39	0.399	0.011	0.953
4.6				
4.7				
2.1	47	0.551	0.340	0.032
2.6	14	0.426	−0.035	0.635
6.4				
3.2	−11	0.794	0.011	0.781
4.0	−10	0.612	0.041	0.328
3.3	76	0.005	0.104	0.034
3.8				
6.7				
3.3	6	0.835	0.193	0.059
3.5	237	<0.001	0.052	0.746
2.2	153	0.010	0.246	0.298
2.9	90	<0.001	0.251	<0.001
3.3	41	0.287	0.178	0.196
4.5	23	0.592	0.229	0.022
3.3	−70	0.307	0.000	0.995
3.3	−2	0.143	0.027	0.518
2.4	−38	0.199	−0.079	0.602
2.8	48	0.108	0.092	0.176
5.8				
3.7	21	0.002	0.045	0.162
3.3	2	0.582	0.002	0.945

subarctic ecotone, and that the area formerly covered by the cold pool would see increased total demersal biomass, increased species diversity, and an increase in the mean trophic level of survey catches as subarctic groundfish colonized newly favorable habitat. We also tested for direct climate control of the commercial catch of snow crab (*Chionoecetes opilio*), commercially the most important taxon of the arctic community, and of the average trophic level of commercial fisheries as the (low trophic level) arctic community retreats, and the (high trophic level) subarctic community advances northward (Grebmeier et al. 2006). Finally, we attempted to relate variability in the magnitude of distribution

shifts among species to commercial status and life history characteristics.

METHODS

Survey data

Biological data for this study are from bottom trawl surveys conducted annually by the U.S. National Marine Fisheries Service during 1982–2006. Sampling occurs on a 20-nautical-mile (37-km) grid over a period of six to eight weeks during summer. Stauffer (2004) describes the trawl survey gear and methods; Lauth and Acuna (2007) provide details on the sampling design. We restricted our analyses to summer hauls south of 61°6′ N, which excluded some northern stations added in later years, and in water ≤200 m deep, which restricted the data set to stations on the continental shelf (9148 hauls, annual mean = 366, range = 337–409). We included 46 fish and invertebrate taxa that were consistently identified throughout the time series in our analyses (Table 1). Commercial catch data for the eastern Bering Sea management area (1982–2005 for snow crab, 1982–2004 for the entire commercial catch) were obtained from the North Pacific Fisheries Management Council (2005).

Climate data

We used summer bottom temperatures measured during the trawl survey (±0.1°C, corrected for differences in timing of survey as described in Appendix A, $n = 8497$) as the primary climate parameter for analysis. We also used winter sea-level pressure (SLP), wind stress, wind mixing, and ice cover as measures of climate state. Ice cover relates directly to the formation and breakdown of the cold pool, while winter SLP and summer winds reflect broad changes in Bering Sea climate (Wyllie-Echeverria and Wooster 1998, Grebmeier et al. 2006) that affect the formation and distribution of ice and hence the cold pool (SLP) or modify summer bottom temperatures through mixing and advection (summer winds). In addition to recent climate conditions (1982–2006), corresponding to the survey period, we examined available longer-term climate trends from 1954 to 2006 to provide historical context for recent climate change. Winter SLP data (December–February monthly means for the year corresponding to January) from three areas (55°0′–60°0′ N, 162°30′–175°0′ W; 57°30′–60°0′ N, 160°0′–162°30′ W; 60°0′–62°30′ N, 167°30′–175°0′ W) were obtained from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) reanalysis (Kalnay et al. 1996), with data from different areas combined on an area-weighted basis (data *available online*).[4] Indices of summer (June–July) wind mixing over the middle shelf (57° N, 164° W) and alongshore wind stress over the slope (56° N, 169°

[4] ⟨www.cdc.noaa.gov⟩

W), based on the NCEP/NCAR reanalysis, were obtained from Nicholas Bond (*personal communication*). Annual ice cover index data were obtained from the NOAA Pacific Marine Environmental Laboratory (data *available online*).[5] Winds, SLP, and the ice cover index were smoothed with a three-year running mean before analyzing relationships with biological variables in order to reduce the influence of interannual variability and to better elucidate the effect of changes in the mean climate state.

Analysis

We used a statistical modeling approach to quantify changes in biological response variables over time based on trawl survey data. Response variables included probability of occurrence by taxon (binomial presence–absence variable), catch per unit effort (CPUE, in kg/km^2) by taxon, local species richness (number of taxa per haul), and mean trophic level of the catch (CPUE-weighted mean across taxa, using species-specific trophic level estimates derived from diet data [K. Aydin, *personal communication*]). CPUE was fourth-root transformed before analysis to achieve approximate normality. Although a standardized sampling protocol was used in all surveys, missing stations, differences in the timing of sampling, and subtle gear modifications and vessel differences among years potentially affect our response variables. To quantify spatial patterns and compute annual anomalies in these variables, we estimated smooth spatial trend surfaces in the response variables by latitude and longitude using generalized additive models (GAM; Wood 2006), while accounting for seasonal and gear effects through the use of appropriate covariates (Appendix A).

To compare changes in CPUE and distribution among taxa with different thermal tolerances, we used temperature–abundance relationships to define "arctic" and "subarctic" community groups and to compute the arctic:subarctic biomass ratio in each haul (arcsine square-root transformed for analysis). To define arctic and subarctic taxa, we plotted cumulative catch per unit effort (CPUE) against bottom temperature, and defined a median temperature (T_{50}) as the temperature below which 50% of total cumulative CPUE was observed. Because the cold pool is generally described by the 2°C bottom isotherm (Wyllie-Echeverria and Wooster 1998), we defined taxa with $T_{50} \leq 2$°C as "arctic" taxa, and those with $T_{50} > 2$°C as "subarctic" taxa.

To examine changes in average spatial patterns between the first five years (1982–1986) and the last five years (2002–2006) of the time series, community response variables (combined CPUE, arctic:subarctic biomass ratio, species richness, and mean trophic level) were modeled for each period separately and differences between the two periods were mapped. To examine

changes over time within the cold-pool area, we estimated annual means of each response variable by fitting GAMs to a subset of the data including only stations within the area covered by the cold pool during 1982–1986. Changes over time were then examined graphically and by fitting nonlinear time trends (smoothing splines, degree of smoothing determined by cross-validation) to the annual means.

We used two approaches to quantify and test for changes in spatial distribution over time. First, we calculated centers of distribution for each taxon as the CPUE-weighted mean latitude by year, utilizing a fixed set of stations that were sampled in each survey year ($n = 244$ stations). If a taxon was caught, on average, at fewer than 10 stations per year it was not included. While providing a simple and intuitive measure of average distribution, these calculations ignore many other stations that were sampled in some or most years and do not account for the effect of nuisance variables (which affect responses, but are not of primary interest) on distribution. Therefore, we also estimated linear latitudinal and depth gradients in CPUE and probability of occurrence for each taxon by year, after removing long-term average spatial patterns and the effects of nuisance variables. These gradients (slopes) were compared across years to elucidate changes in spatial distribution over time (Appendix A).

To evaluate effects of climate variability on the demersal community we fit linear or nonlinear regressions of community-level response variables on annual mean bottom temperature. Nonlinear regressions (smoothing splines) were used if a trend was not adequately captured by linear regression (based on approximate F tests [Wood 2006]). To test for effects of changes in mean climate state beyond those explained directly by changing bottom temperature, we also tested for effects of ice cover, alongshore wind stress, wind mixing, and winter SLP on residual variability in the response variables, after accounting for estimated temperature effects.

To evaluate climate effects on the distribution of individual taxa we fit linear regressions of their annual centers of distribution (CPUE-weighted mean latitude) on year and on average annual temperature, weighted by the number of positive catches in each year. Linear regressions on year were also used to estimate the total northward displacement of each taxon from 1982 to 2006. Similar to the community-level responses, we tested for linear effects of other climate variables on the residual centers of distribution, after removing the estimated effect of annual mean bottom temperature (Appendix A). We related variability in species-specific responses (slopes of CPUE-weighted mean latitude on year and bottom temperature) to commercial status (exploited or not exploited), T_{50}, mean adult trophic level, habitat (pelagic or demersal) and, for fishes only, maximum length (Table 1, based on data from Mecklenburg et al. 2002).
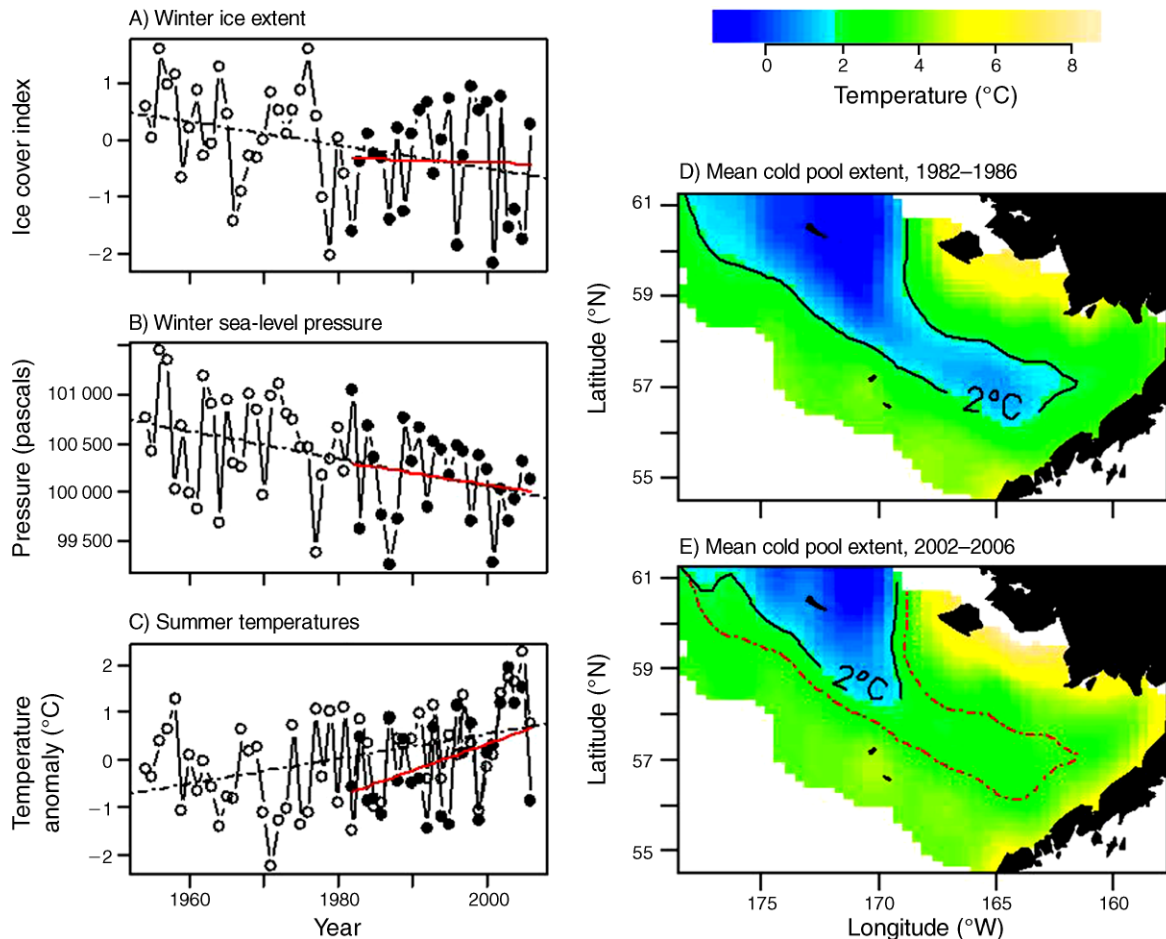
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[5] ⟨www.beringclimate.noaa.gov⟩

FIG. 1. Recent climate change in the southeastern Bering Sea: linear trends from 1954 to 2006 (dashed line) and from 1982 to 2006 (solid red line) in (A) ice cover (see *Methods: Climate data*), (B) winter sea-level pressure (SLP), and (C) summer sea-surface temperature (open circles) or bottom temperature (solid circles); and mean position and extent of the cold pool (summer bottom temperature <2°C) in (D) 1982–1986 and (E) 2002–2006. The dashed line in (E) indicates the average cold-pool position in 1982–1986; the spatial extent of the temperature data corresponds to the area of the bottom trawl survey.

RESULTS

Climate change

The Bering Sea has experienced highly variable climate conditions over recent decades, characterized by interannual and decadal-scale variability superimposed on a long-term climate trend (Fig. 1). Ice cover on the shelf decreased significantly from 1954 to 2006 ($R^2 = 0.11$, $P = 0.015$; Fig. 1A), while showing a weak but nonsignificant trend over the more recent period (1982–2006, $P = 0.794$). Likewise, recent (1982–2006) winter SLP values show no significant trend ($P = 0.355$; Fig. 1B), but continue a long-term declining trend (1954–2006, $R^2 = 0.18$, $P = 0.001$). Average summer bottom temperature, the variable most directly affecting fish distribution, increased significantly from 1982 to 2006 ($R^2 = 0.17$, $P = 0.042$; Fig. 1C). While earlier bottom temperature records are not available, sea-surface temperatures have increased at an average rate of

0.23°C per decade since 1954 ($R^2 = 0.16$, $P = 0.003$; Fig. 1C). In contrast, we found no evidence of linear trends in alongshore wind stress or wind mixing since 1954 ($R^2 = 0.03$, $P = 0.217$ and $R^2 = 0.01$, $P = 0.667$, respectively) or for the 1982–2006 period ($P > 0.5$). The increase in summer bottom temperature was associated with the retreat of the cold pool (defined by the 2°C isotherm) in a northwesterly direction (i.e., perpendicular to the depth gradient) such that the average location of its southern edge was approximately 230 km farther north in the final five years of the survey time series (~58°6′ N; Fig. 1E) than in the first five years (~56°0′ N; Fig. 1D).

Community-wide distribution change

Of the 46 taxa used in the analysis, nine were defined as "arctic" ($T_{50} \leq 2°C$), and 37 were defined as "subarctic" ($T_{50} > 2°C$; Table 1). Forty taxa occurred frequently enough for changes in the center of distribu-
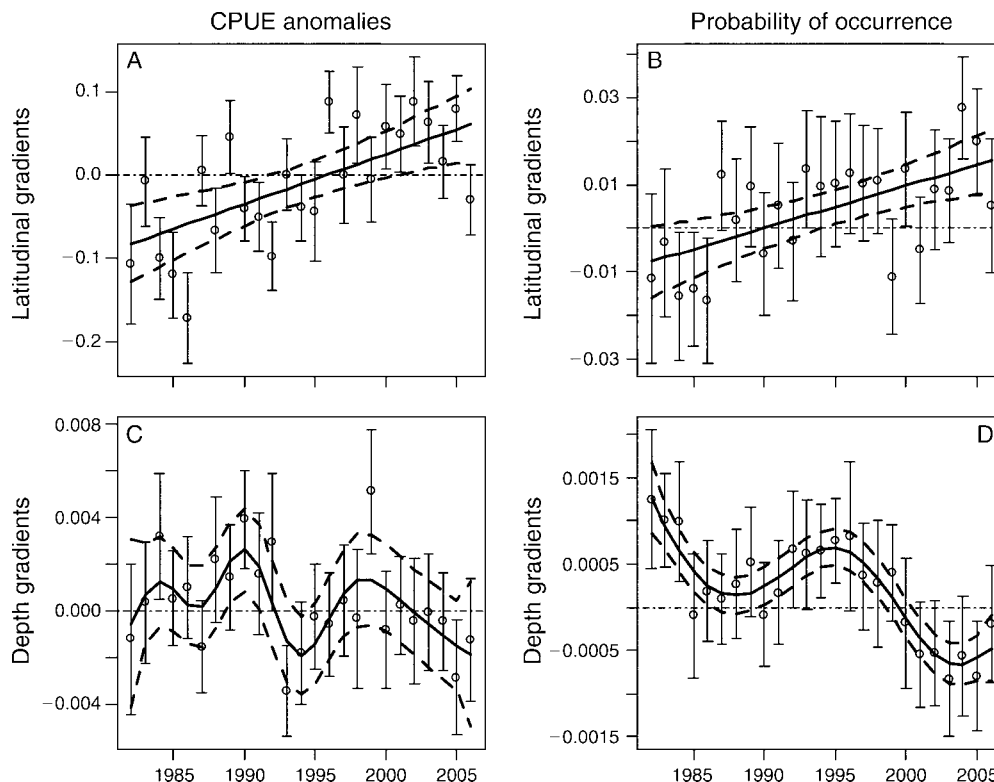
FIG. 2. Community-wide distribution shifts in the southeastern Bering Sea from 1982 to 2006: (A) average latitudinal gradients in catch per unit effort (CPUE) anomalies, (B) average latitudinal gradients in probability of occurrence, (C) average depth gradients in CPUE anomalies, and (D) average depth gradients in probability of occurrence. Each dot represents means across 46 taxa; vertical bars denote 95% confidence intervals for the mean. Positive values indicate more northerly or deeper distribution relative to the long-term average spatial pattern, and negative values indicate more southerly or shallower distribution. Linear or nonlinear time trends (solid lines) with 95% confidence bands (dashed lines) are based on weighted nonparametric regression (the amount of smoothing is determined by cross-validation).

tion to be calculated, and these had an average northward displacement of 34 ± 56 km (mean ± SD), a community-wide change in average latitude significantly different from 0 (one-sample $t_{39} = 3.84$, two-tailed $P = 0.0004$; Table 1). Linear trends in the center of distribution over time were significant ($P < 0.05$) for 16 taxa, all of which shifted north (Table 1).

The community-wide change in center of distribution was mirrored by a community-wide pattern of changing latitudinal gradients in abundance and probability of occurrence, as well as a shoaling in depth distribution over time (Fig. 2). We found a significant increase in latitudinal gradients over time, averaged across 46 taxa (weighted least-squares [WLS] regression with first-order autoregressive errors [AR1], $R^2 = 0.40$, $P < 0.001$; Fig. 2A). This implies that average CPUE increased in the north relative to the south. Depth gradients of CPUE varied nonlinearly over time, with no obvious trend (GAM fit, $R^2 = 0.43$, $P = 0.044$; Fig. 2C). Probability of occurrence, averaged across all taxa, showed both an increase in average latitudinal gradients (WLS, AR1 linear model, $R^2 = 0.33$, $P = 0.0095$; Fig. 2B) and a nonlinear shoaling in depth gradients (GAM, $R^2 = 0.84$,

$P < 0.0001$; Fig. 2D). These trends imply that, on average, taxa were captured with increasing frequency in the northern part of the survey region, as well as at shallower stations, from 1982 to 2006.

Total biomass (mean CPUE) increased in the northwestern part of the survey area and around the Pribilof Islands (near 57° N, 170° W) relative to other areas (Fig. 3A). Differences between the northern and southern part of the survey area are exemplified by a highly significant increase in average CPUE north of 59° N (weighted least-squares regression with first-order autocorrelated errors [AR1], $R^2 = 0.37$, $P = 0.009$), but no corresponding increase south of 59° N (AR1 linear model, $R^2 = 0.078$, $P = 0.43$). The magnitude of the increase in the northern area was dramatic: in 1982 mean CPUE south of 59° N was 73% greater than mean CPUE north of 59° N, while in 2006 the difference was only 26% (Fig. 4). Changes in community-level metrics within the area initially covered by the cold pool (in 1982–1986) were all consistent with changes expected from a shift from an arctic community to a subarctic community. Total biomass ($CPUE^{0.25}$) within the cold-pool area increased linearly over time ($R^2 = 0.31$, $P =$
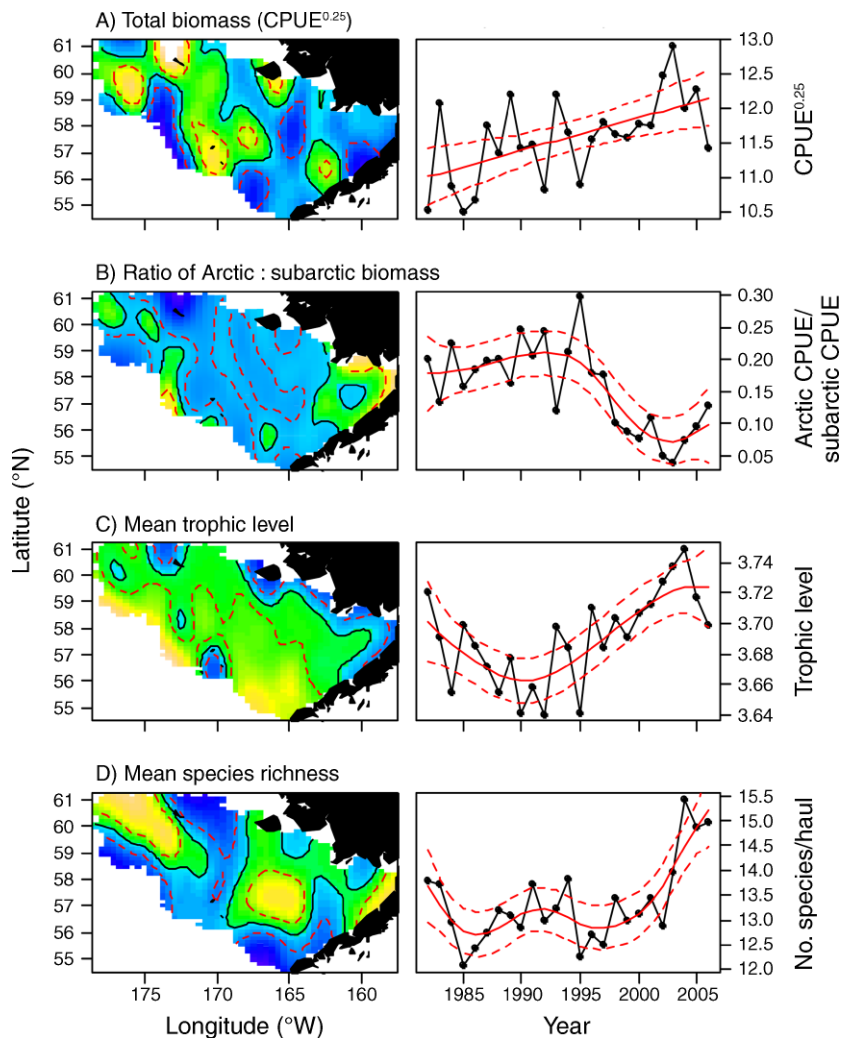
FIG. 3. Changes in the biogeography of the Bering Sea indicated by four community metrics. Left-hand panels show spatial changes between the first five (1982–1986) and last five (2002–2006) years in the bottom-trawl survey time series. Blue indicates declining values; green and yellow indicate increasing values. Black lines indicate no change; values more extreme than those indicated by red dashed lines are significant at $P < 0.05$. The right-hand column shows temporal trends within the area occupied by the cold pool at the start of the time series (i.e., during 1982–1986, denoted by the 2° contour in Fig. 1D). Total catch per unit effort (CPUE; Mg/km^2) of all taxa combined was computed for each individual survey haul as total catch divided by the area swept by the trawl. CPUE was fourth-root transformed (CPUE$^{0.25}$) to normalize values for statistical analyses. Trophic level was computed for each haul as a CPUE-weighted average across all taxa using taxa-specific trophic levels from Table 1. Spatial anomalies of the four community metrics and their annual means in the cold pool were estimated as described in *Methods*.

0.0043; Fig. 3A). The ratio of arctic : subarctic biomass declined over most of the survey area (Fig. 3B) and the average ratio within the cold pool declined rapidly after about 1995 (GAM, $R^2 = 0.62$, $P = 0.001$; Fig. 3B). Mean trophic level of survey catches increased throughout much of the survey area, except in shallow inshore areas, between the early and late period (Fig. 3C). Within the cold pool, trophic level decreased in the 1980s, followed by a strong increasing trend since the early 1990s (GAM, $R^2 = 0.53$, $P = 0.004$; Fig. 3C). Changes in species richness showed a more complex spatial pattern, with strong increases over much of the middle shelf region and decreases along the slope and in the northeast.

Mean richness in the cold-pool area showed a strongly nonlinear trend over time (GAM, $R^2 = 0.70$, $P = 0.0002$; Fig. 3D), increasing from an average of about 13 species per haul prior to the early 2000s to an average of 15 species per haul in recent years.

Climate–distribution links

Changes in distribution of 11 taxa were significantly related to bottom temperature; in all cases, the center of distribution moved north with warmer temperatures (Table 1). Residual variability in distribution shifts not explained by bottom temperature generally showed
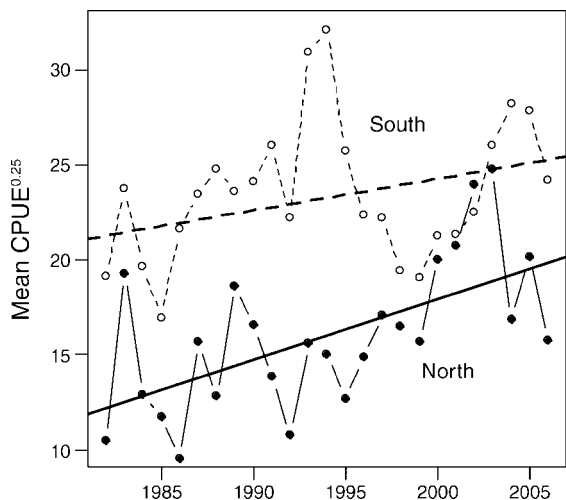
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Fig. 4. Time trends in average annual catch per unit effort (CPUE; sum of all 46 taxa included in analysis, fourth-root transformed) in the northern (>59° N, solid circles) and southern (<59° N, open circles) part of the survey area with lines showing linear time trends (weighted least-squares regression with first-order autocorrelated errors).

weak or no relationships to ice cover, SLP, and wind parameters (Appendix B).

We found similar direct effects of bottom temperature on community-wide distribution patterns. While the biomass ($CPUE^{0.25}$) of subarctic species in the cold pool was strongly related to annual bottom temperature ($R^2 = 0.68$, $P < 0.001$; Fig. 5A), biomass of arctic species within the cold pool showed only weak evidence of a decrease with temperature (GAM, $R^2 = 0.14$, $P = 0.165$). Mean trophic level of survey catches within the cold pool increased linearly with bottom temperature ($R^2 = 0.43$, $P = 0.0004$; Fig. 5B), as did the average center of distribution across all taxa ($R^2 = 0.36$, $P < 0.001$; Fig. 5C).

Even when direct temperature effects were taken into account and removed, residual variability showed a highly significant nonlinear trend in the average center of distribution over time (GAM, $R^2 = 0.73$, $P < 0.001$; Fig. 5D), indicating that a portion of the observed community-wide distribution change was not directly related to warming bottom temperatures. Significant residual time trends ($P < 0.05$, after removing temperature effects) were also evident in subarctic CPUE and mean trophic level within the cold-pool area, as well as in latitudinal CPUE gradients ($R^2 = 0.39$, $P = 0.013$). Variability in any of the residual series was not significantly related to SLP, ice cover, or wind parameters ($P > 0.15$).

We found that commercial catches of snow crab in the eastern Bering Sea significantly increased with the extent of ice cover on the shelf (Fig. 5E), suggesting that climate-related changes have direct implications for this important commercial fishery. More generally, we found that the average trophic level of commercial fisheries

catches decreased with increasing extent of ice cover (Fig. 5F). In both cases, the strongest relationship was found at lag 0, corresponding to ice conditions averaged over the previous three years.

Like the average center of distribution, mean latitudinal gradients in both CPUE where present (Fig. 6A) and probability of occurrence (Fig. 6B) across all 46 taxa showed a strong and linear increasing trend with temperature ($R^2 = 0.65$, $P < 0.001$ and $R^2 = 0.44$, $P < 0.001$, respectively), supporting a direct correlation between warming temperatures and community-wide distribution changes. Depth gradients in CPUE and probability of occurrence (Fig. 6C, D) were inversely related to average bottom temperature ($R^2 = 0.21$, $P = 0.020$ and $R^2 = 0.27$, $P = 0.008$, respectively), implying a shoaling of the average depth distribution with increasing bottom temperature.

Finally, none of the hypotheses that we tested was successful in explaining variability in distribution changes among taxa. Taxon-specific slopes of the annual mean center of distribution on year (long-term trend in distribution) were not significantly related to trophic level ($P = 0.54$), median temperature (T_{50} nested within the arctic/subarctic community, $P = 0.50$), commercial status ($P = 0.85$), habitat ($P = 0.33$), or, for fishes only, maximum length ($P = 0.35$). Similarly, slopes of the annual mean center of distribution on bottom temperature (magnitude of climate effect) could not be predicted by commercial status ($P = 0.53$), trophic level ($P = 0.83$), median temperature (T_{50}, $P = 0.28$), habitat ($P = 0.32$), or, for fishes only, maximum length ($P = 0.63$). Therefore, we were unable to attribute differences in the temperature responses of different species to fishing, environmental factors, or life history characteristics.

DISCUSSION

Climate-forced distribution shifts are likely to present a major challenge to researchers, fishers, and managers in the Bering Sea and other marginal ice seas in coming decades as they try to understand the dynamics of fish and crustaceans in these systems. We found that warming of the Bering Sea has led to a ~230 km northward retreat in the southern edge of the summer cold pool since the early 1980s (Fig. 1). Subarctic taxa living near the northern limit of their thermal tolerance increasingly occupy the area formerly covered by the cold pool, with resulting changes in community characteristics (Fig. 3) that were predicted for a switch from a relatively depauperate arctic community largely devoid of groundfish to a more diverse subarctic community rich in groundfish. Change within the cold-pool area occurred within a general pattern of northward distribution shifts within the entire survey area. Both centers of distribution (calculated from stations sampled in every year, Table 1) and latitudinal gradients of abundance and probability of occurrence (calculated from all available stations, Fig. 2) showed significant
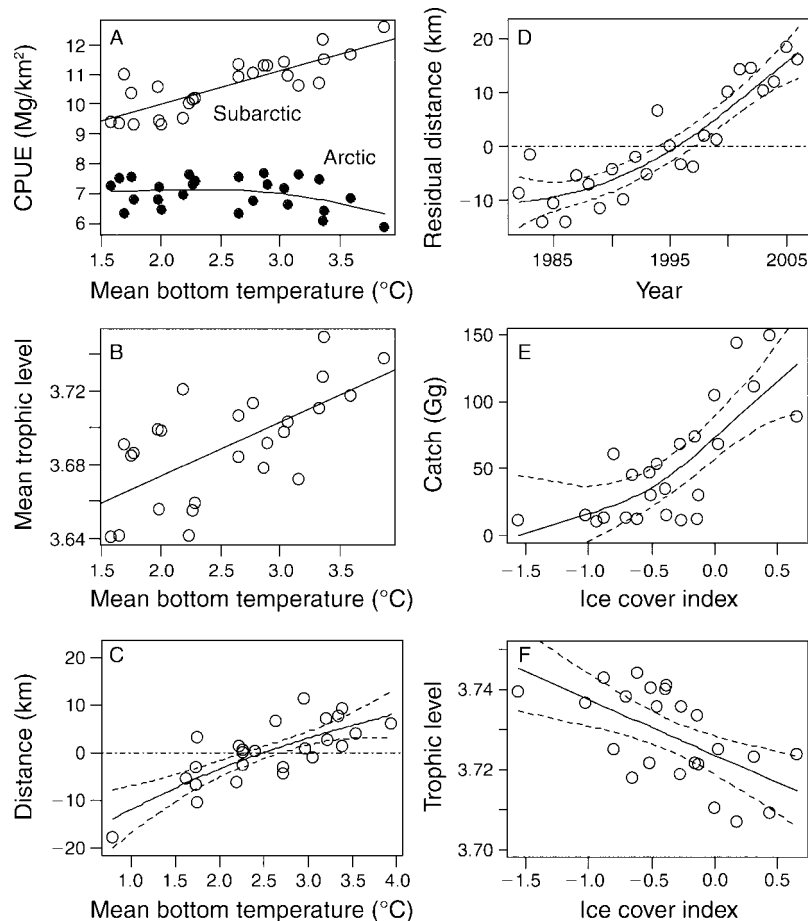
FIG. 5. Direct climate effects on changing biogeography and commercial catches in the southeastern Bering Sea. Effect of bottom temperature on (A) survey biomass of arctic and subarctic communities within the cold pool (fourth-root transformed catch per unit effort [CPUE, Mg/km^2]) and (B) mean cold-pool trophic level of survey catches. Response variables were calculated for the area covered by average extent of the cold pool in 1982–1986; the explanatory variable is average bottom temperature across the entire survey area. (C) Change in the average center of distribution (distance from mean latitude, averaged across 40 taxa) with mean bottom temperature and (D) residual trend in distribution, measured as distance from long-term average, after the direct temperature effect is removed. (E) Effects of ice extent on commercial snow crab catch, and (F) effects of ice extent on mean trophic level of the entire commercial catch. Ice cover index was smoothed with three-year running mean. Fitted lines were based on best-fit linear or nonparametric regression, and the degree of smoothing was determined by generalized cross-validation. Dashed lines show 95% CI. All fitted lines except for arctic CPUE were significant ($P < 0.05$).

northward distribution shifts and significant shoaling when averaged across all taxa in the analysis, providing evidence that these shifts are a community-level phenomenon, and not simply the result of shifts by one or two taxa that dominate catch biomass.

Removal of predatory groundfish by overfishing and climate changes in the North Atlantic has resulted in widespread increases in the abundance of decapod crustaceans, including snow crab, and this pattern has been interpreted as evidence that groundfish predation structures boreal continental shelf ecosystems (Worm and Myers 2003, Frank et al. 2005). The increase in mean trophic level of catches throughout most of the survey area (Fig. 3C) is therefore potentially one of the most significant ecological changes to accompany warming of the Bering Sea, as it suggests increased

top-down control of the ecosystem. Collapses in crustacean stocks in the Gulf of Alaska may have been caused by similar groundfish invasions after the 1976–1977 Pacific Decadal Oscillation (PDO) regime shift resulted in warming of nearshore waters (Albers and Anderson 1985; Litzow and Ciannelli 2007), and it has been suggested that snow crab abundance in the Bering Sea is similarly affected by groundfish colonization of the former cold pool (Orensanz et al. 2004, Zheng and Kruse 2006). The increase in mean trophic level of survey catches suggests that predation pressure on lower trophic level organisms will continue to increase if the cold pool continues to retreat. Climate-forced changes in "leverage species," such as high trophic level predators, have the potential to reorganize community structure, and thereby create emergent patterns that exceed the
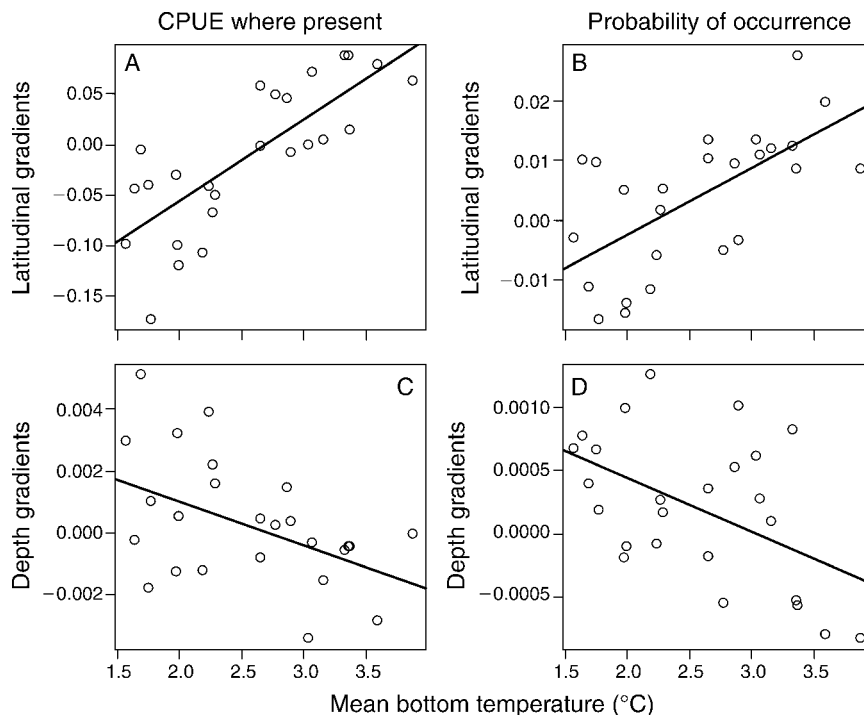
Fɪɢ. 6. Effects of bottom temperature on latitudinal and depth gradients. (A) Average latitudinal gradient in catch per unit effort (CPUE) where present across 46 taxa, (B) average latitudinal gradient in probability of occurrence, (C) average depth gradient in CPUE where present, and (D) average depth gradient in probability of occurrence against mean summer bottom temperature.

sum of direct climate effects on individual species (Harley et al. 2006). Our finding that cold-pool abundance of subarctic taxa was directly related to average bottom temperature, but that the abundance of arctic taxa was not (Fig. 5A) is consistent with a hypothesis of direct climate effects on the distribution of subarctic taxa, but indirect effects, through mechanisms such as predation or competition, on arctic taxa. Several important community metrics (arctic : subarctic biomass ratio, species richness, mean trophic level; Fig. 3), showed complex (nonlinear) responses to generally linear patterns of climate change during the survey period (Fig. 1). Understanding the biological interactions producing these nonlinear community responses to climate change must be a fundamental research goal for successful management of Bering Sea fisheries during a period of rapid climate change.

Because community-wide centers of distribution (Fig. 5C), latitudinal gradients, and depth gradients were directly related to bottom temperature, and centers of distribution for 11 of the 40 taxa examined showed linear responses to changing bottom temperature (Table 1), we conclude that warming of the Bering Sea is likely the primary cause of the distribution changes that have occurred over the past two decades. Other climate variables explained little of the residual variance not explained by bottom temperature, which supports the view that bottom temperature is the dominant climate parameter for determining demersal community com-

position in marginal ice seas (Hunt and Stabeno 2002, Grebmeier et al. 2006). Other factors that affect summer distributions include changes in abundance (through density-dependent habitat selection), changes in phenology (e.g., timing of seasonal migration), and fishing. Expanding populations of skates and flatfishes in the Eastern Bering Sea have affected their centers of distribution (McConnaughey 1995; Paul Spencer, *personal communication*), but across the species examined here, such effects were, on average, smaller than temperature effects (F. J. Mueter, *unpublished data*). Temperature changes may also alter the timing of seasonal migrations of highly mobile species, which may explain some of the observed distribution shifts. Unfortunately, the available data are inadequate to resolve seasonal patterns. Fishing may explain distribution shifts if it is concentrated in more southern areas, but differences in displacement were not explained by commercial status (fished vs. non-fished). Nevertheless, fishing effects deserve more detailed examination (e.g., spatially explicit comparisons of catch, climate, and distribution) before their effects on distribution are ruled out of hand. Specifically, shifts in the spatial distribution of fishing effort (Cathy Coon, *personal communication*) and changes in exploitation rate could have affected the distribution of some commercial species. Finally, we cannot rule out the possibility that temperature-dependent changes in the behavior of some species may

modify their availability to the gear (e.g., burial at cold temperatures).

A nonlinear, accelerating time trend in northward displacement (Fig. 5D), unrelated to temperature or any other climate parameter we tested (at any lag), suggests that mechanisms besides climate must be contributing to distribution shifts in the Bering Sea. External climate forcing may trigger internal dynamics such as changes in species interactions that have the potential to create a nonlinear ecosystem response (Scheffer et al. 2001). Distribution changes in other temperate continental shelf ecosystems have been related to size, trophic level, and life span (Murawski 1993, Perry et al. 2005). However, our analysis failed to replicate this result, as shifts in distribution were unrelated to trophic level, habitat, temperature preference (T_{50}), or maximum length (which is correlated with a suite of important life history characteristics). A better understanding of species-specific responses to warming and emergent patterns of ecological reorganization beyond direct climate effects is fundamental to an ecosystem-based management approach for Bering Sea fisheries. The failure of our exploratory attempts to explain variability among species underlines the difficulties of this research problem.

Climate-forced changes in Bering Sea biogeography are likely to present major challenges to managers in the Bering Sea. The most striking immediate management implication is the effect of declining sea ice on catches of the most important commercial arctic taxon, snow crab (Fig. 5E), although correlations between ice cover and the average trophic level of the entire fishery (Fig. 5F) suggests that climate change may affect all fisheries in the region. Crustacean fisheries in Alaska suffered widespread collapse following the 1976–1977 PDO regime shift (Orensanz et al. 1998). Northward retreat of Bering Sea snow crab (Orensanz et al. 2004; Table 1), and the apparent sensitivity of blue (*Paralithodes platypus*) and red king crab (*P. camtschaticus*) to sea ice cover (Appendix B) suggest that continued warming will bring further disruptions to those fisheries. Northward shifts in distribution beyond the current survey boundary will also affect the availability of some northern species to the trawl survey, with important effects on estimates of stock biomass.

The southeastern Bering Sea is a model of generally sustainable fisheries management and, with the exception of some crustaceans, most exploited stocks are healthy (North Pacific Fishery Management Council 2005). However, the community-wide responses to climate change that we have documented suggest the possibility of highly disruptive responses to continued warming of the Bering Sea. Although accurate prediction of future warming is difficult, and further cooling periods are possible (Overpeck et al. 1997), arctic warming is expected to intensify (IPCC 2001). Some aspects of this change may be beneficial to commercial fisheries in the Bering Sea, such as possible increases in primary production (Richardson and Schoeman 2004) and further increases in total biomass in the cold-pool area (Fig. 3A). However, considerable uncertainty over the nature of climate-forced ecological change in the Bering Sea remains, and ecological transitions can be economically and socially devastating to fishing communities, even when they result in the establishment of productive new fisheries (Hamilton et al. 2004). Physical variability in the Bering Sea is extremely complex (Stabeno et al. 2001), and our concentration on warming and north–south distribution shifts (ignoring within-species variability in distribution [Ernst et al. 2005, Kotwicki et al. 2005]) is merely a first-order look at an extremely complex problem. Nevertheless, the community-wide patterns of change that we observed with northward displacement of the arctic–subarctic ecotone suggest that consideration of distribution shifts needs to become a focus of management and research in marginal ice seas. Management of Bering Sea stocks is typically not spatially explicit, with, for instance, the quota for snow crabs based on population estimates for the entire eastern Bering Sea, but fishing concentrated on the southern (declining) portion of the stock (Ernst et al. 2005). Spatially explicit fishing quotas may be more appropriate for stocks with changing distributions. Extensive research will also be needed to understand the community-wide patterns that we have demonstrated here. That research must be conducted within a community-level framework, as the synergistic effects of climate change, biotic interactions, and fishing will likely frustrate attempts to understand climate effects on a species-specific basis (Harley et al. 2006).

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APPENDIX A

Quantifying spatial patterns in community characteristics and estimating latitudinal and depth gradients in catch per unit effort (CPUE) and probability of occurrence using generalized additive models (*Ecological Archives* A018-008-A1).

APPENDIX B

Evaluating climate effects on distribution of individual taxa (*Ecological Archives* A018-008-A2).