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Fluxes, Fins, and Feathers

Relationships Among the Bering, Chukchi, and Beaufort Seas in a Time of Climate Change

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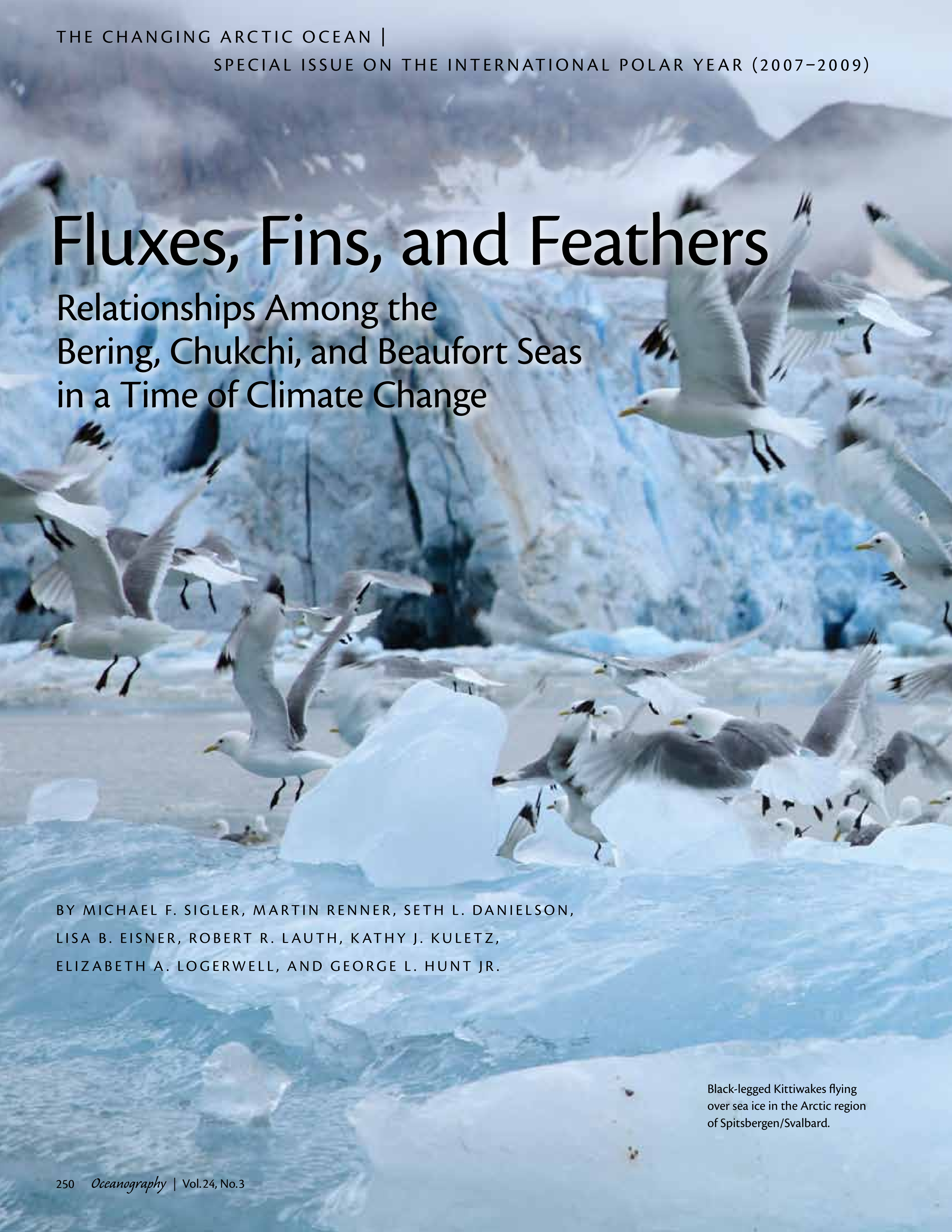

Black-legged Kittiwakes flying over sea ice in the Arctic region of Spitsbergen/Svalbard.

ABSTRACT. Ocean currents, water masses, and seasonal sea ice formation determine linkages among and barriers between the biotas of the Bering, Chukchi, and Beaufort Seas. The Bering Sea communicates with the Chukchi and Beaufort Seas via northward advection of water, nutrients, and plankton through Bering Strait. However, continuity of the ocean's physical properties is modulated by regional differences in heat, salt, and sea ice budgets, in particular, along the meridional gradient. Using summer density data from zooplankton, fish (bottom and surface trawl), and seabird surveys, we define three biogeographic provinces: the Eastern Bering Shelf Province (the eastern Bering Sea shelf south of Saint Lawrence Island), the Chirikov-Chukchi Province (the eastern Bering Sea shelf north of Saint Lawrence Island [Chirikov Basin] and Chukchi Sea), and the Beaufort Sea Province. Regional differences in summer distributions of biota largely reflect the underlying oceanography. Climate warming will reduce the duration and possibly the extent of seasonal ice cover in the Eastern Bering Shelf Province, but this warming may not lead to increased abundance of some subarctic species because seasonal ice cover and cold ($< 2°C$) bottom waters on the Bering shelf form a barrier to the northward migration of subarctic bottom fish species typical of the southeastern Bering Sea. While Arctic species that are dependent upon the summer extent of sea ice face an uncertain future, other Arctic species' resilience to a changing climate will be derived from waters that continue to freeze each winter.

INTRODUCTION

The Bering, Chukchi, and Beaufort Seas lie off the western and northern coasts of Alaska and provide both physical and biological connections between the North Pacific and Arctic Oceans. Ocean currents (relatively warm in summer and fall) flow from the Pacific Ocean across the Bering and Chukchi Sea shelves (Figure 1) en route to the greater Arctic Ocean (Coachman and Aagaard, 1966). The Beaufort shelf shares a common boundary with the Chukchi shelf to the west, and these two shelves communicate via both surface and subsurface flow pathways (Aagaard, 1984; Pickart, 2004; Münchow et al., 2006). These three continental shelves share the characteristic of seasonal sea ice cover, a dominant phenomenon that structures their ecology. Sea ice formation occurs after the water column is homogenized by fall wind mixing and cooled to the freezing point (Pease, 1981). As days shorten, ice growth progresses southward from the northern Chukchi and Beaufort Seas toward Bering Strait and subsequently across the northern Bering Sea (Figure 2). The southern extent of sea ice is determined by a balance between southward advection, air-sea heat fluxes, and melting at the leading edge as the ice encounters warmer water (Pease, 1980; Niebauer et al., 1999).

The upper trophic levels of the southeastern Bering Sea are dominated by subarctic or temperate-zone bottom fish, such as flatfish, walleye pollock, and Pacific cod, and substantial production reaches both the pelagic and benthic communities. Farther to the north, there is a profound change in the fauna, as large fish become relatively scarce (Cui et al., 2009; Norcross et al., 2010; Stevenson and Lauth, provisionally accepted), the benthic community receives more of the production than the pelagic community (Grebmeier and McRoy, 1989), and benthic invertebrates dominate the biomass (Bluhm et al., 2009). Seabirds and marine mammals are abundant in the Bering, Chukchi, and Beaufort Seas; some species migrate between summer and winter feeding grounds.

The Bering, Chukchi, and Beaufort Seas are important for commercial and subsistence harvests, energy reserves, and global thermohaline circulation. The southeastern Bering Sea provides the United States with about 40% of its fish and shellfish landings (Van Vorhees and Lowther, 2010). Coastal subsistence fishers and hunters harvest fish, seabirds, and marine mammals for communities that depend on their catch success (Hovelsrud et al., 2008). Nearshore oil production already occurs on man-made islands in the Beaufort Sea; the Beaufort and Chukchi shelves also host many potential offshore oil and gas development sites. Northward fluxes of freshwater through Bering Strait and from Canada's Mackenzie River play a role in regulating the North Atlantic's deep convection and the associated global thermohaline circulation (Reason and Power, 1994; Goosse et al., 1997).

Arctic marine ecosystems are understudied compared to other regions (Wassmann et al., 2011), but recently, the Bering, Chukchi, and Beaufort Seas have been the focus of attention for several medium- and large-sized research programs. Those with both strong physical and biological components include SBI (Shelf-Basin Interaction, 1998–2008), NPCREP (North Pacific Climate Regimes and Ecosystem Productivity, 2004–present), RUSALCA (Russian American

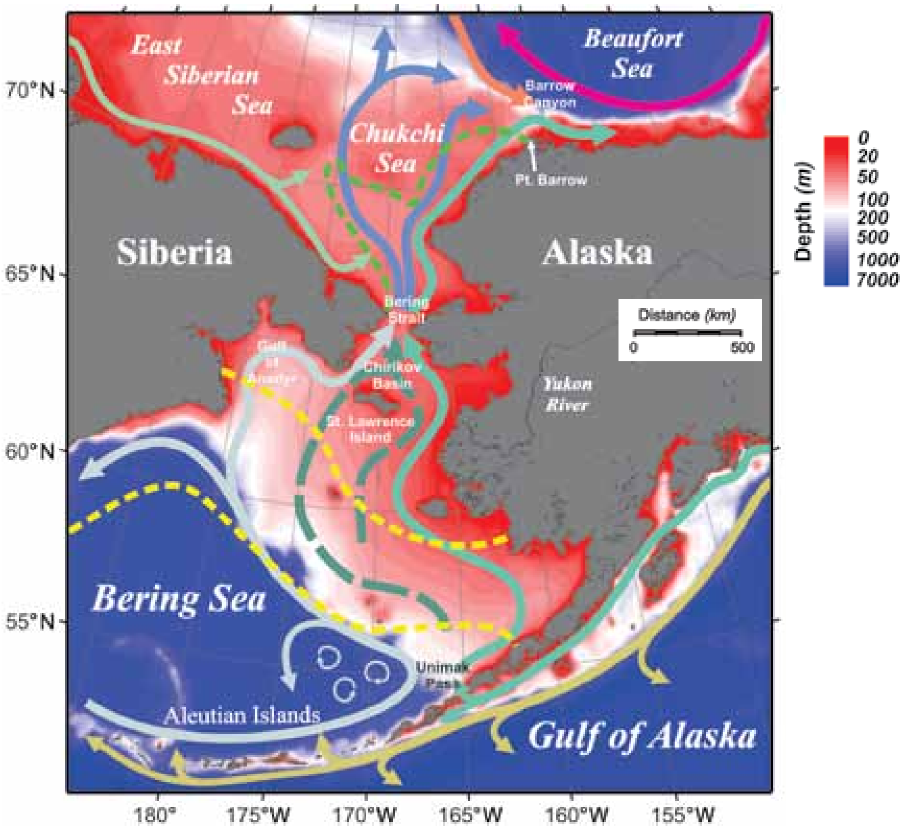

Figure 1. The Bering, Chukchi, and Beaufort Seas form a continuum between the North Pacific Ocean and the Arctic Ocean. This idealized schematic denotes some of the important water masses and currents that impact regional differences in physical habitat characteristics.

Long Term Census of the Arctic, 2004–present), BEST (Bering Ecosystem Study, 2007–present), BSIERP (Bering Sea Integrated Ecosystem Research Program, 2008–present), and BASIS (Bering Aleutian Salmon International Survey, 2002–present). This paper draws upon some recent results of these programs. (See Supplement Table S1 for a larger list of projects undertaken in the eastern Bering, Chukchi, and Beaufort Seas.)

In this article, we examine the physical and biological components of these connected regions and suggest a set of biogeographic boundaries. We hypothesize that some of these boundaries may resist climate warming and that, in spite of future warming, there may be less of a northward shift in some faunal elements than has been suggested previously (e.g., Beaugrand et al., 2002; Perry et al., 2005; Grebmeier et al., 2006a; Wassmann et al., 2011). Our examination focuses on meridional differences because we are interested in how ice from the north and warmer water from the south balance and influence biogeography. East-west differences also exist; they are described but not analyzed. For analysis, summer data on zooplankton, fish, and seabirds are initially classified into five regions; cluster analyses are completed on regional-scale data to determine whether regions could be associated into biogeographic provinces. The five initial regions are southern, central, and northern Bering Sea, Chukchi Sea, and Beaufort Sea (Figure 2). The southern-central Bering Sea boundary lies at 60°N, which is the approximate location of the March minimum ice extent; the central-northern Bering Sea boundary is placed at Saint Lawrence Island, where flows around the island accelerate as they converge toward Bering Strait; the northern Bering Sea-Chukchi Sea boundary is Bering Strait; and the Chukchi Sea-Beaufort Sea boundary is

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located at the longitude of Point Barrow. We examine density data from summer (June–September) zooplankton, fish (bottom and surface trawl), and at-sea seabird surveys. The surveys were broad-scale (e.g., entire southeastern Bering Sea shelf) and many prominent species were sampled, but coastal areas (water depths < 20 m) and benthic invertebrates were not included in our examination. The surveys also were not completed at the same time, so that our results are subject to annual and seasonal differences in community structure. Nevertheless, the available data provide a broad-brush examination of relationships among biota during summer. Zooplankton samples were collected with small (150 µm) and large (335 or 505 µm) mesh nets deployed side by side; species were classified based on mean weight into small zooplankton (mean weight per individual < 0.3 mg blotted wet weight from the 150 µm net) and large zooplankton (mean weight ≥ 0.3 mg from the 335 or 505 µm nets). Fish data were collected with bottom trawls that sampled the bottom 3 m and surface trawls that sampled the top 15 m. These trawls were deployed on separate surveys. Fish caught by bottom trawl hereafter are termed "bottom fish" and those caught by surface trawl are termed "surface fish." Some species were caught in both surveys, indicating utilization of both near-bottom and near-surface habitats. Diet data were used to classify species of fish (Ivonne Ortiz and Ed Farley, NOAA Alaska Fisheries Science Center, *pers. comm.*, 2011) and seabirds (Hunt et al., 1981, 2000) into foraging guilds. Seabird sighting data were collected during 300-m strip transect surveys from vessels of opportunity including fish survey vessels. For each survey, average densities were scaled from zero to the maximum value in each region, and scarce species were excluded from the cluster analysis. The data were analyzed using hierarchical cluster analysis with Ward's minimum variance method (Legendre and Legendre, 1998). A previous examination of the biogeography of the Bering, Chukchi, and Beaufort Seas used presence-absence information (Carleton and Hayden, 1993), whereas we use information on animal density.

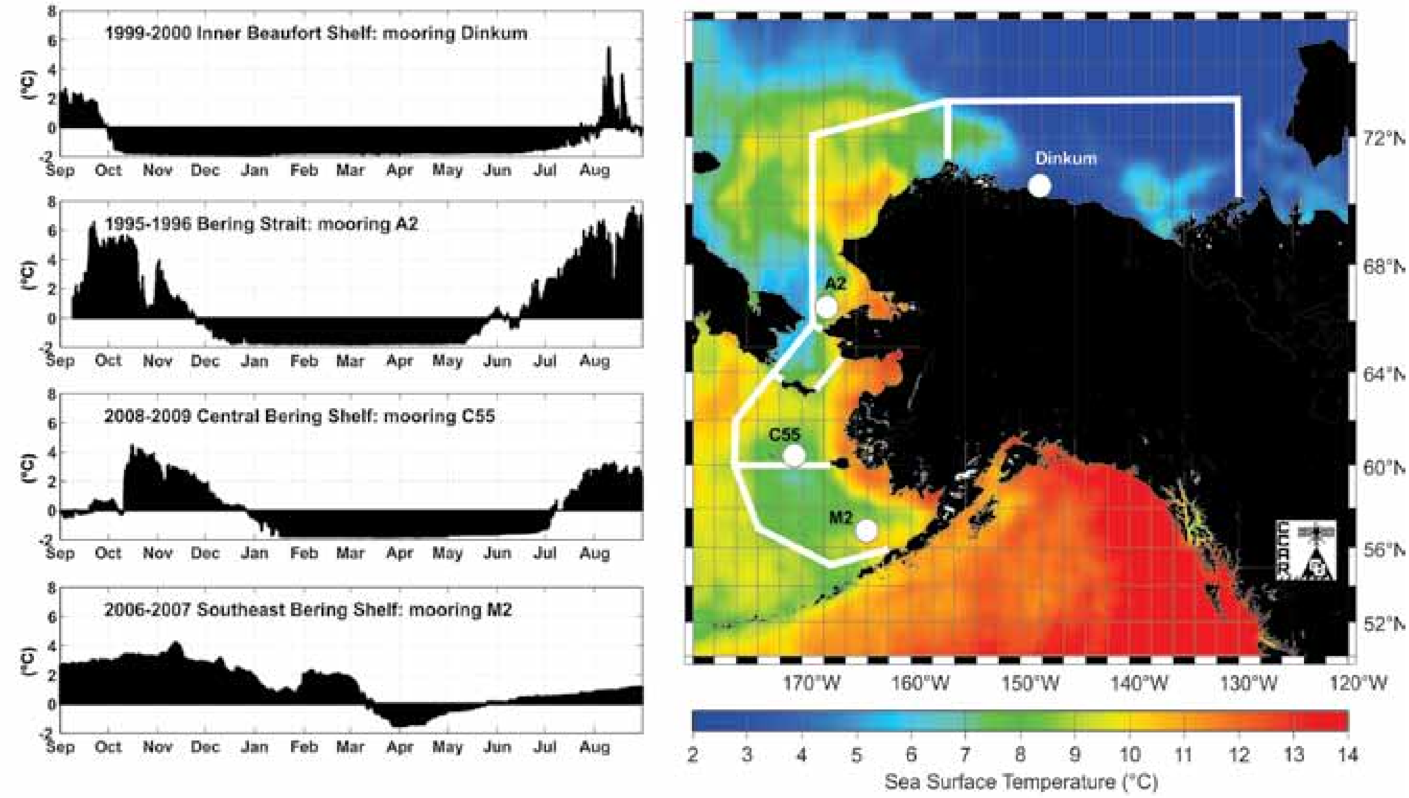

Figure 2. (left) Annual cycle of temperatures recorded at the four mooring sites denoted on the map. Data are courtesy of T. Weingartner (Dinkum and A2), K. Aagaard (C55), and P. Stabeno (M2). (right) Surface temperature (°C) for mid-September derived from satellite observation using GHRSST (Global Ocean Data Assimilation Experiment [GODAE] high-resolution sea surface temperature data [http://argo.colorado.edu/~realtime/global-sst]). White lines indicate region boundaries. From south to north, the regions are: southern, central, and northern Bering Sea (eastern shelf); Chukchi Sea; and Beaufort Sea.

OCEANOGRAPHY

A sea level height difference of approximately 0.5 m between the North Pacific Ocean and the North Atlantic Ocean (Stigebrandt, 1984) forces water northward through Bering Strait (and by continuity, across the Bering and Chukchi shelves) with a flux of about 0.8 Sv (1 Sv = 1 x 10^6 m^3 s^{-1}; Coachman and Barnes, 1961; Roach et al., 1995). Three distinct water masses comprise this flow (Figure 1): Alaskan Coastal Water (ACW), Anadyr Water (AW), and Bering Shelf Water (BSW). Each reflects the culmination of numerous processes and geographic origins spanning the Bering Sea and Gulf of Alaska.

The Alaska Coastal Current (ACC) carries ACW northward through eastern Bering Strait (Coachman et al., 1975; Woodgate et al., 2005, 2006). ACW is formed by summer freshening and solar heating of cold, low-salinity inner Bering shelf water (Coachman et al., 1975) and is depauperate in macronutrients (Kachel et al., 2002) and large crustacean zooplankton (e.g., large copepods, euphausiids, and amphipods; Hunt and Harrison, 1990; Coyle et al., 2011). The ACC forms a nearly continuous low-salinity corridor along the Alaskan coast (Sverdrup, 1929; Wiseman and Rouse, 1980; Royer, 1982; Schumacher et al., 1982: Stabeno et al., 1995; Weingartner et al., 2005a). Near the northern reaches of Barrow Canyon, ACW and other Pacific-origin waters are redirected eastward as part of a Beaufort Sea shelf break jet (Pickart, 2004; Spall et al., 2008; Nikolopoulos et al., 2009).

To maintain mass balance with the northward flux of water through Bering Strait, outer Bering Sea shelf waters must be replaced, although the precise locations and mechanisms for this are not well known (Aagaard et al., 2006). Continuity of water-mass properties southwest of Bering Strait suggests that much of the on-shelf flux occurs along the shelf break just south of the Gulf of Anadyr (Coachman et al., 1975). Flowing through the western portion of Bering Strait, AW is relatively salty, rich in nutrients, highly productive, and carries with it immense numbers of crustacean zooplankton (Walsh et al., 1989; Springer et al., 1996).

BSW occupies a density range between that of ACW and AW and is made up of a mixture of ACW and water from along the Bering slope. Because of the small mean flows over the middle Bering Shelf, BSW likely has a longer shelf residence time than ACW and AW (Muench et al., 1988). North of Saint Lawrence Island, dense AW intrudes below BSW, resulting in a highly productive and stable water column (Walsh et al., 1989; Hunt and Harrison, 1990; Springer et al., 1996). Pelagic primary production is important here, and a portion of it descends to the bottom, supporting amphipods and the gray whales that feed on them (Highsmith et al., 2006; Coyle et al., 2007). Another portion is advected northward to the Chukchi Sea, where gray and bowhead whales forage on the benthos and crustacean zooplankton (Walsh et al., 1989; Piatt and Springer, 2003; Bluhm et al., 2007). Intense mixing caused by shears in the swift flows through the straits blends AW and BSW (Coachman et al., 1975), introduces dissolved nutrients to the euphotic zone, and helps support additional production.

AW and ACW create a physical continuity for Pacific water from the outer shelf and coastal regions of the eastern Bering Sea to the Chukchi Sea. In contrast, there is a thermal discontinuity between near-bottom waters of the southeastern middle Bering Sea shelf and the middle shelf farther north (Stabeno et al., 2010; Figure 3). The volume of near-bottom water with temperatures less than 2°C is commonly called the "cold pool" (Figure 3), and it persists from winter until the water column is homogenized in the fall by wind mixing and cooling. It is re-established in early winter as the water column again cools to near-freezing temperatures. The cold pool varies annually in meridional extent (Takenouti and Ohtani, 1974; see also Figure 4). Of particular importance to our study is that during the recent warm years of 2001–2005, the middle shelf temperature measured at a mooring southwest of Saint Lawrence Island was similar to measurements made in the subsequent cold years of 2007–2010 (Stabeno et al., provisionally accepted), evidence that the cold pool persists irrespective of the annual average shelf temperature.

Downstream of the Bering Sea, the shallow Chukchi shelf primarily contains waters of Pacific origin, although some small contributions likely result from eastward flows originating in the East Siberian Sea (Weingartner et al., 1999). The Chukchi's northward mean flow field is bathymetrically steered and opposes the prevailing winds; however, the instantaneous flow field responds strongly to the synoptic wind field both in summer open-water conditions and in winter months with complete pack ice cover (Weingartner et al., 2005b). Fronts often occur near Barrow Canyon, where bowhead whales and seabirds gather to forage on euphausiids in late summer and fall (Berline et al., 2008; Ashjian et al., 2010; Moore et al., 2010; Quakenbush et al., 2010).

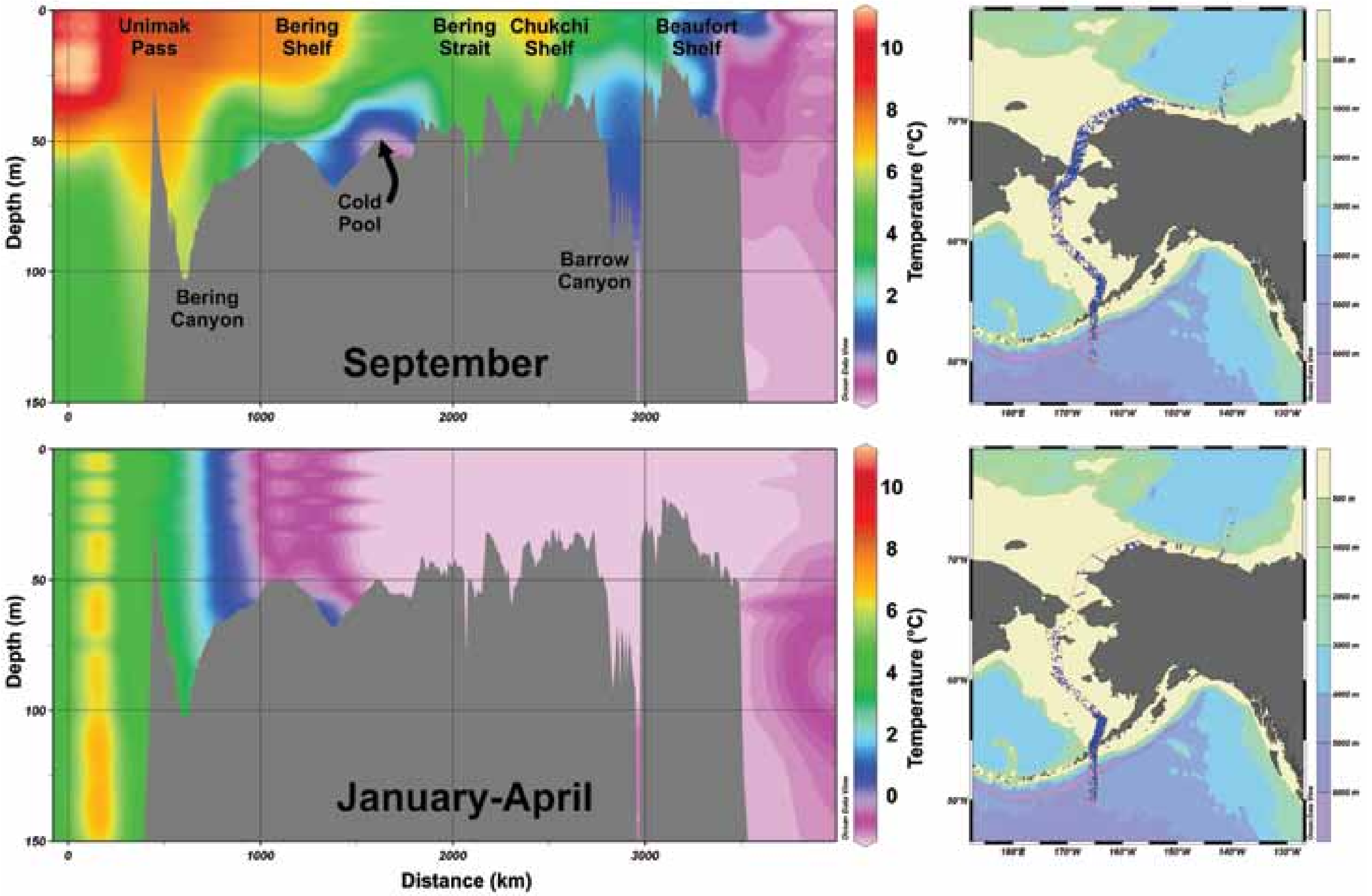

Figure 3. Cross section of temperatures between the North Pacific and the Beaufort Sea in mid-winter (January–April) and at the end of summer (September). Distances are relative to the southern end of the transect. Data are from the World Ocean Database 2009 (Boyer et al., 2009) collection of hydrographic profiles.

In contrast to the Chukchi Sea, the Beaufort Sea has no direct communication to subarctic waters and is strongly influenced by winds, shelf break upwelling, and river inputs (Carmack and Wassmann, 2006; Dunton et al., 2006). The Alaskan Beaufort shelf receives westerly contributions of Pacific origin water advected across the Chukchi shelf (Mountain et al., 1976; Aagaard, 1984; Pickart, 2004; Spall et al., 2008) and easterly contributions from the Canadian Beaufort (Carmack et al., 1989; Macdonald et al., 1989; Macdonald and Carmack, 1991). An atmospheric high-pressure system forces anticyclonic motion of the near-surface (< 50 m)

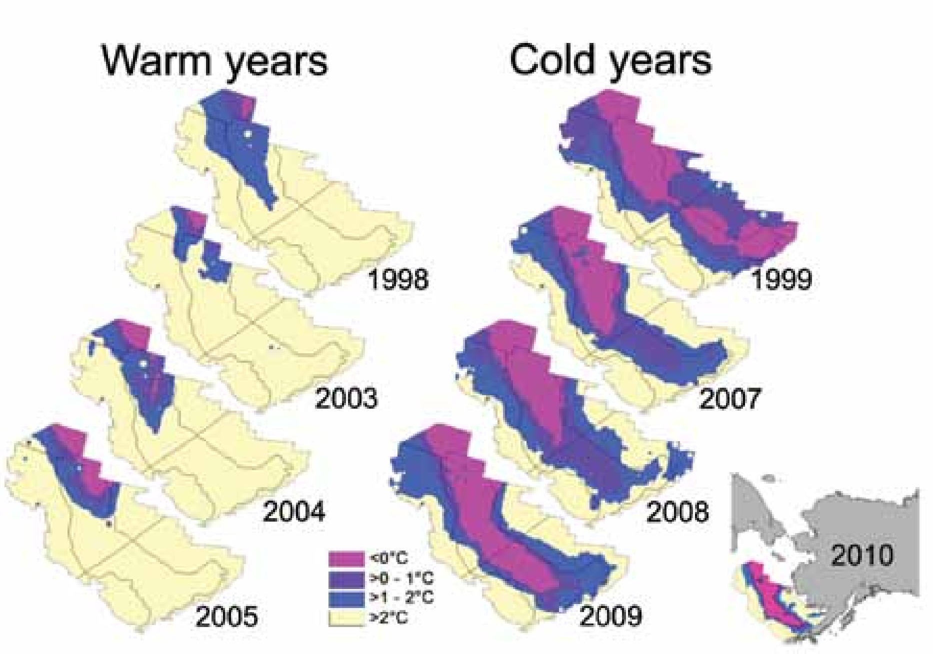

Figure 4. Variation in the extent of the cold pool during recent warm and cold year summers as measured by a bottom temperature probe deployed on the NOAA summer bottom trawl surveys. The 50- and 100-m isobaths are shown. The straight lines mark boundaries of survey strata.

basin waters (Coachman and Aagaard, 1974), resulting in westward flow along the shelf break (Figure 1). Shelf currents are strongly wind-driven except under landfast ice, which covers the inner shelf between October and June (Weingartner et al., 2009). Flux of shelf water to the Arctic Ocean deep basin via canyon outflow, eddy transport, and other mechanisms likely is biologically important (Mathis et al., 2007) and also helps maintain the upper Arctic halocline, which insulates sea ice from warm subsurface Atlantic water (Aagaard et al., 1981). Upwelling events in canyons and along the shelf break can periodically introduce the underlying (> 200 m depth) Atlantic water to the outer Chukchi and Beaufort shelves.

In years of reduced ice extent or early retreat, the spring bloom occurs in open water over the southern Bering Sea shelf, and substantial primary production is captured by a pelagic food web (Hunt et al., 2002, 2010). With sea ice retreat in April and May, much of the spring primary production of the central and northern Bering Sea is associated with ice algae and with an ice-edge bloom (McRoy and Goering, 1974; Alexander and Niebauer, 1981; Grebmeier and McRoy, 1989; Lovvorn et al., 2005; Jin et al., 2007). This early spring production largely sinks to the bottom and helps support a rich benthic fauna dominated by invertebrates and small epibenthic fishes (Barber et al. 1997; Cui et al., 2009; Norcross et al., 2010). Seasonal ice and strong coupling between pelagic and benthic production are characteristic of shallow, ice-dominated systems (Grebmeier et al., 2006b). Ice retreat in the Chukchi Sea begins in May or early June with melting driven by solar radiation and the advection of relatively warm waters from the Bering Sea (Figure 2). In contrast, ice retreat in the Beaufort Sea occurs between June and August and is driven by both solar radiation and by lateral advection of heat from both the Chukchi shelf (flow from the west) and the Mackenzie River outflow (flow from the east) (Weingartner et al., 2009). Ice-associated primary production plays an important (Gradinger, 2009) but still not fully appreciated role in total Arctic production (Mundy et al., 2009).

ZOOPLANKTON DISTRIBUTION

A cluster analysis of the small zooplankton taxa (e.g., small copepods such as *Pseudocalanus* sp. and *Oithona* sp., bivalve and barnacle larvae, polychaetes, and small larvacea) grouped the Chukchi and northern Bering Seas in one cluster and the central and southern Bering Seas in another cluster, and separated the Beaufort Sea from both (Figure 5). The Beaufort, Chukchi, and northern Bering Seas were distinguished by higher relative abundances of meroplankton (particularly bivalvia and cirripedia [barnacles]; Figure 6). Conversely, copepods became more important to the south. In contrast to other regions, the Beaufort Sea small zooplankton assemblage was dominated by larvacea. Overall, the highest total abundances for small zooplankton were in the northern Bering and Chukchi Seas (43,000–45,000 individuals m^{-3}), followed by the southern and central Bering Sea (9,000–19,000 individuals m^{-3}) and the Beaufort Sea (3,000 individuals m^{-3}).

As with the small zooplankton taxa, a cluster analysis of the large zooplankton taxa (e.g., large copepods such as *Calanus marshallae*, *C. glacialis*, and *Eucalanus bungii*, euphausiids, amphipods, chaetognaths, and the cnidarian *Aglantha digitale*) grouped the Chukchi and northern Bering Seas in one cluster and the central and southern Bering Seas in another cluster (Figure 5). Copepods were common in all regions, although less dominant in the Beaufort than elsewhere (Figure 7). The dominant copepod species shifted and distinguished the regions with *Calanus glacialis* dominant in the Beaufort Sea, *Eucalanus bungii* dominant in the Chukchi and northern Bering Seas, and *Calanus marshallae* dominant in the central and southern Bering Sea. In addition, euphausiids were common in the northern Bering and Chukchi Seas, *Aglantha digitale* were common in the central Bering Sea, and chaetognaths were common in the Beaufort and southern Bering Seas. Crustacean zooplankton (large copepods, euphausiids, amphipods) made up ~ 90% of the total abundances in the northern Bering and Chukchi Seas compared to 55–60% in the southern and central Bering Sea and 30% in the Beaufort Sea. Similar to the small zooplankton, the highest total abundances for large zooplankton were in the northern Bering and Chukchi Seas (1,400–2,300 individuals m^{-3}), followed by the southern and central Bering Sea (100–300 individuals m^{-3}) and the Beaufort Sea (15 individuals m^{-3}).

The zooplankton clusters potentially were affected by the taxonomic resolution of the Beaufort Sea data because some of the Beaufort Sea identifications were at a coarser taxonomic scale than the other regions. For example, gammarid amphipods often were identified to species in the other regions but were grouped in the Beaufort Sea data. We reran the cluster analyses of the small and large zooplankton data for the other regions (excluding the Beaufort Sea data) at the finest taxonomic scale available and found the same groupings (Chukchi and northern Bering Seas, central and southern Bering Sea). An analysis based on zooplankton biomass instead of abundance may alter these results since large taxa, such as *Neocalanus* spp., may gain importance in relation to smaller, more numerous copepods, such as *C. marshallae*. Lastly, we note that *C. glacialis* and *C. marshallae* are difficult to distinguish, and work is underway to resolve their taxonomy (e.g., Nelson et al., 2009).

FISH DISTRIBUTION

A cluster analysis of the bottom fish taxa separated the Beaufort and Chukchi Seas from the Bering Sea regions (Figure 5). The Bering Sea was distinguished from the Chukchi and Beaufort Seas by the presence of Arctic cod, which was the most abundant bottom fish species north of Bering Strait (Figure 8). A group of subarctic species, including walleye pollock, northern rock sole, and yellowfin sole, were common in the southern and central Bering Sea. In addition, Alaska plaice, a cold-tolerant species with antifreeze in its blood (Knight et al., 1991), was found throughout the Bering Sea and was more abundant in the northern Bering Sea. Planktivorous species were common in all five regions, whereas piscivorous species were common only in the southern and central Bering Sea. The highest total densities for bottom fish were in the southern (261 kg ha^{-1}) and central (115 kg ha^{-1}) Bering Sea, followed by the northern Bering (36 kg ha^{-1}), Beaufort (30 kg ha^{-1}), and Chukchi (4 kg ha^{-1}) Seas (1 ha [hectare] = 10^4 m^2).

Regions clustered differently for surface fish taxa compared to bottom fish taxa (Figure 5 [no surface trawl surveys have been conducted in the Beaufort Sea]). In particular, immature (ocean age 1+) chum salmon and juvenile sockeye salmon and walleye pollock were common species in the southern Bering Sea, which distinguished this region from the other surveyed regions (Figure 9). Pacific herring is unusual in being the most common species in all

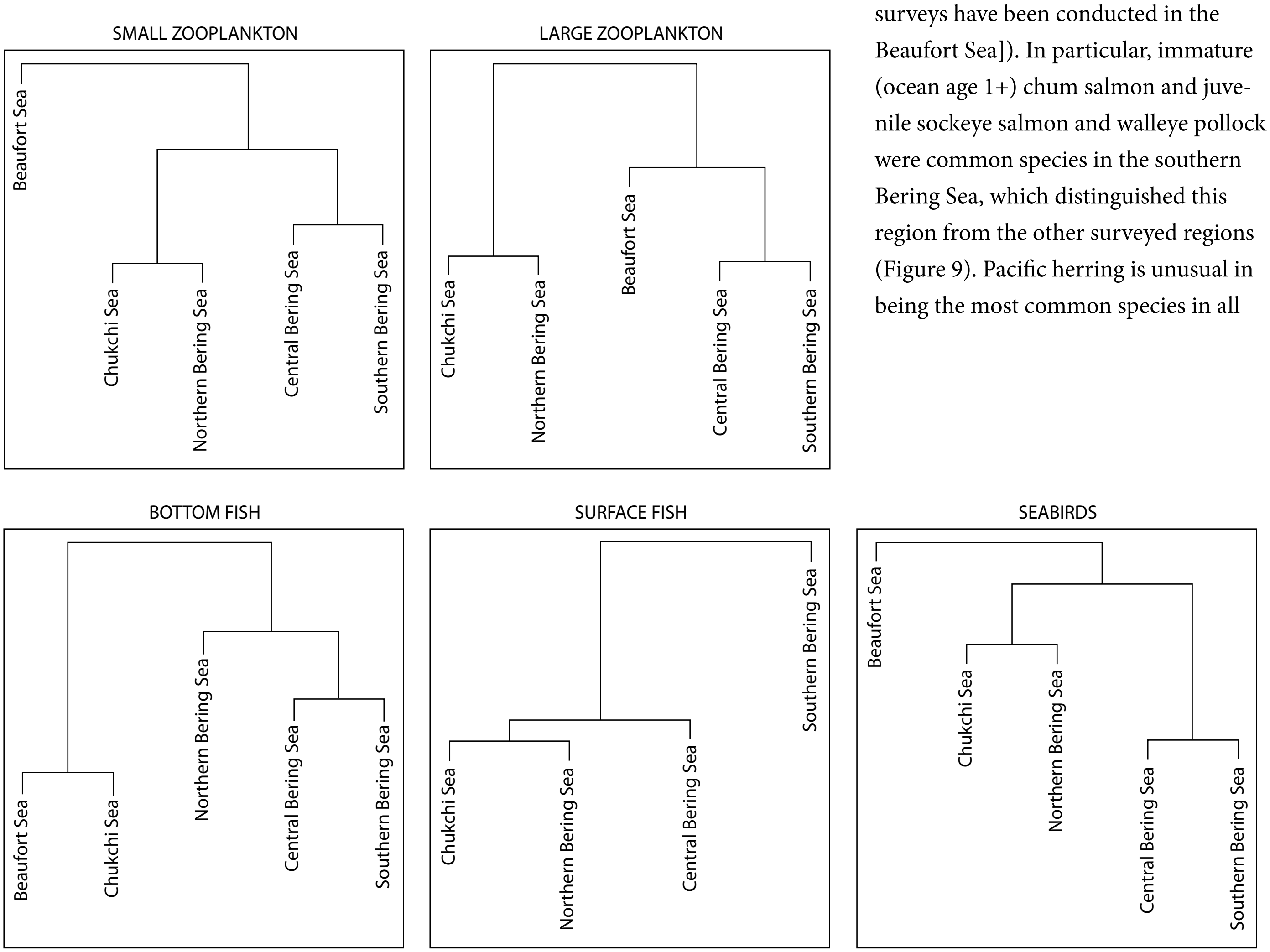

Figure 5. Results of cluster analysis of regions using the relative abundance of commonly found small zooplankton (Figure 6), large zooplankton (Figure 7), bottom fish (Figure 8), surface fish (Figure 9), and seabirds (Figure 10).

surveyed regions. Planktivorous species were common in all surveyed regions, whereas piscivorous species were abundant only in the southern Bering Sea. The highest total densities for surface fish were in the Chukchi Sea (5.1 kg ha^{-1}) followed by the northern (3.5 kg ha^{-1}), central (2.1 kg ha^{-1}), and southern (1.8 kg ha^{-1}) regions of the Bering Sea.

SEABIRD DISTRIBUTION

Like the zooplankton taxa, analysis of the seabird taxa grouped the Chukchi and northern Bering Seas in one cluster, the central and southern Bering Sea in another cluster and separated the Beaufort Sea from both (Figure 5). A strong discontinuity in seabird faunas between the Beaufort Sea and all other regions was driven by the prevalence in the Beaufort of benthic-foraging sea ducks (common eiders, king eiders, and long-tailed ducks) and the Glaucous Gull, a large Arctic bird that scavenges along the shore and at ice edges (Figure 10). Two other species that helped define the Beaufort Sea region as different were the Arctic Tern and the

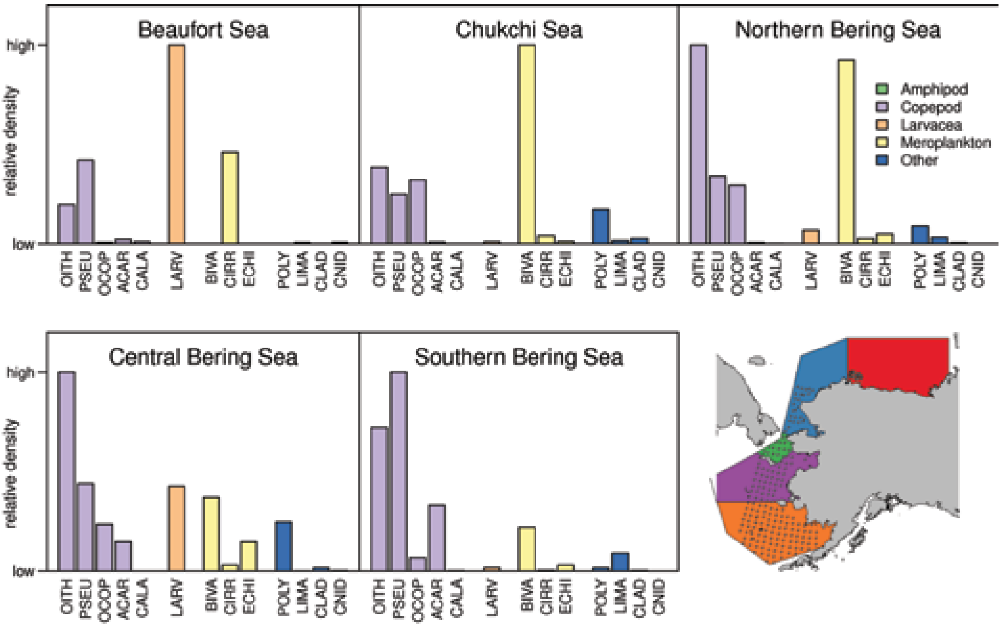

Figure 6. Relative densities (number) of the most common small zooplankton (mean weight < 0.3 mg from 150 µm net) from each region, all grouped by common taxa in the Bering, Chukchi, and Beaufort Seas, August–September 2007 (Bering and Chukchi) and August–September 2008 (Beaufort). Map colors indicate regions: Orange = southern Bering Sea. Purple = central Bering Sea. Green = northern Bering Sea. Blue = Chukchi Sea. Red = Beaufort Sea. Bars are standardized against the most abundant species in each region. Map shows effort, with small dots indicating the location of each sampling station. Species codes are: OITH = *Oithona* sp. PSUE = *Pseudocalanus* sp. OCOP = Other Copepoda. ACAR: *Acartia* sp. CALA = Calanidae (mostly CI, CII). LARV = Larvacea. BIVA = Bivalvia. CIRR = Cirripedia. ECHI = Echinodermata. POLY = Polychaeta. LIMA = Thecosomata and *Limacina* sp. CLAD = Cladocera. CNID = Cnidaria.

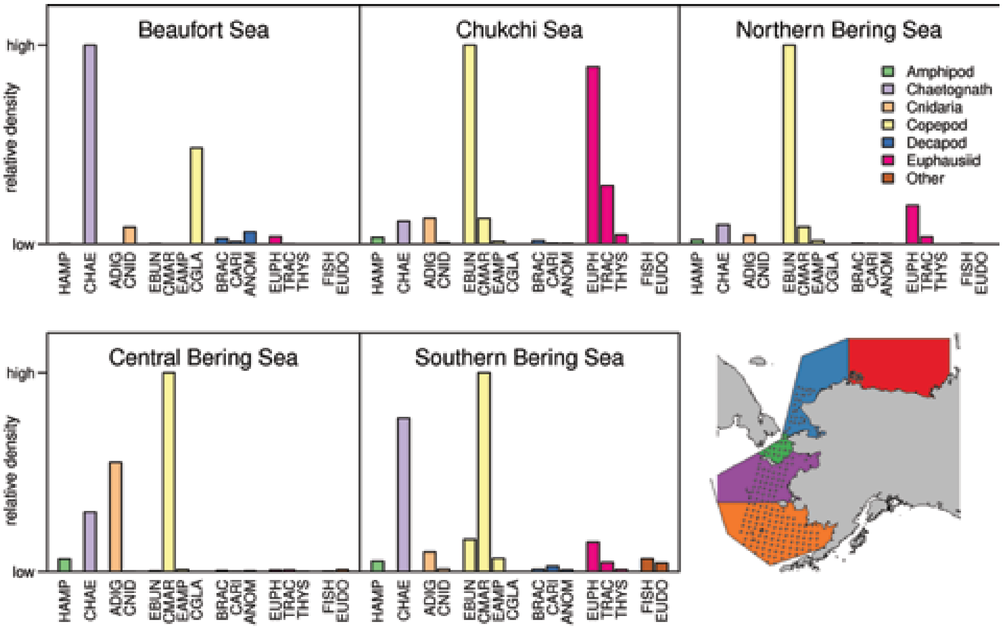

Figure 7. Relative densities (number) of the most common large zooplankton (mean weight ≥ 0.3 mg from 335 and 505 µm nets) from each region, all grouped by common taxa in the Bering, Chukchi, and Beaufort Seas, August–September 2007 (Bering and Chukchi) and August–September 2008 (Beaufort). Bars are standardized against the most abundant species in each region. Map shows effort, with small dots indicating the location of each sampling station. Species codes are: HAMP = hyperid amphipod. CHAE = chaetognath. ADIG = *Aglantha digitale*. CNID = Cnidaria. EBUN = *Eucalanus bungii*. CMAR = *Calanus marshallae*. EAMP = *Epilabidocera amphitrites*. CGLA = *C. glacialis*. BRAC = Brachyura. CARI = Caridea. ANOM = Anomura. EUPH = Euphausiacea. TRAC = *Thyanoessa raschii*. THYS = *Thyanoessa* sp. FISH = fish. EUDO = *Eudorellopsis* sp.

Black Guillemot, both of which have a nearly circumpolar distribution and forage on small pelagic fish, in particular Arctic cod, near the ice edge (personal observation of author Hunt).

The Chukchi and northern Bering Seas formed a cluster dominated by planktivores, in particular, Least and Crested Auklets in the northern Bering and Short-tailed Shearwaters in the Chukchi (Figure 10). The Least Auklets forage primarily on *Neocalanus* spp. copepods at fronts bordering the Anadyr Current, and the Crested Auklets and shearwaters take mainly euphausiids advected into the region in AW and BSW (Piatt and Springer, 2003). In the northern Bering Sea, auklets from King Island, the western end of the north side of St. Lawrence Island, and the Russian coast all forage at fronts and pycnoclines where the copepods are concentrated (Hunt et al., 1990; Elphick and Hunt, 1993). The south side of St. Lawrence Island supports both nesting piscivores and auklets, presumably because of the copepod-rich AW that passes south of

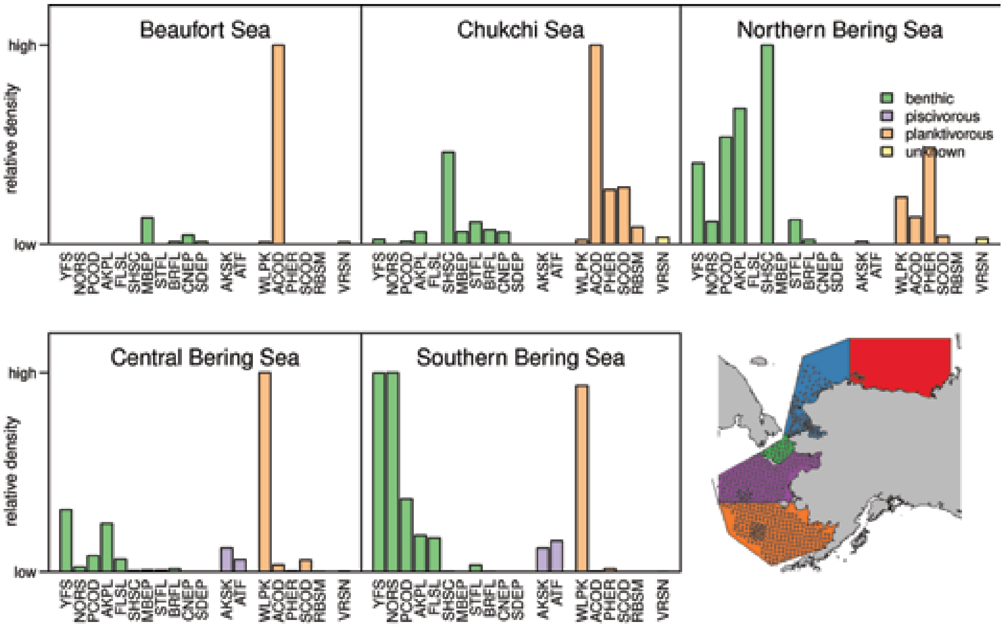

Figure 8. Relative densities (weight) of the most common bottom fish from each region, all grouped by guilds in the Bering, Chukchi, and Beaufort Seas, June–July 2010 (Bering), August–September 1976 (southern Chukchi) and August–September 1991 (northern Chukchi), and August–September 2008 (Beaufort). Bars are standardized against the most abundant species in each region. Map shows effort, with small dots indicating the location of each sampling station. Species codes are: YFS = yellowfin sole. NORS = northern rock sole. PCOD = Pacific cod. AKPL = Alaska plaice. FLSL = flathead sole. SHSC = shorthorn sculpin. MBEP = marbled eelpout. STFL = starry flounder. BRFL = Bering flounder. CNEP = Canadian eelpout. SDEP = saddled eelpout. AKSK = Alaska skate. ATF = arrowtooth flounder. WLPK = walleye pollock. ACOD = Arctic cod. PHER = Pacific herring. SCOD = saffron cod. RBSM = rainbow smelt. VRSN = variegated snailfish.

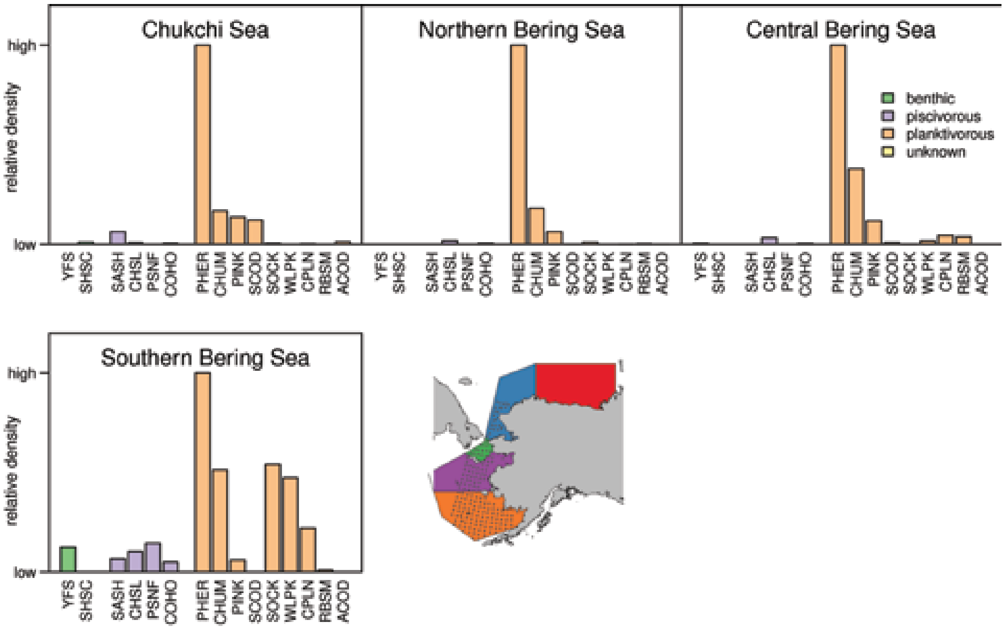

Figure 9. Relative densities (weight) of the most common surface fish from each region, all grouped by guilds in the Bering and Chukchi Seas, August–September 2007. Bars are standardized against the most abundant species in each region. Map shows effort, with small dots indicating the location of each sampling station. Species codes are: YFS = yellowfin sole. SHSC = shorthorn sculpin. SASH = salmon shark. CHSL = chinook salmon. PSNF = Pacific sandfish. COHO = coho salmon. PHER = Pacific herring. CHUM = chum salmon. PINK = pink salmon. SCOD = saffron cod. SOCK = sockeye salmon. WLPK = walleye pollock. CPLN = capelin. RBSM = rainbow smelt. ACOD = Arctic cod.

the island (see Piatt and Springer, 2003).

The central and southern Bering Sea also formed a cluster, with Northern Fulmars and piscivorous kittiwakes and murres as the major components (Figure 10). Planktivorous Fork-tailed Storm Petrels were also an important component. Fulmars not only follow fishing boats for offal but also forage for small squids and zooplankton at the surface (Jahncke et al., 2005; Ladd et al., 2005). There is some evidence of partitioning of the southeastern Bering Sea shelf, with surface foragers more abundant in the outer shelf and slope areas, and subsurface foragers predominating in the middle and inner shelf (Schneider et al., 1986). The highest total densities for seabirds were in the northern Bering Sea (38 birds km^{-2}), followed by the southern and central Bering Sea (32 birds km^{-2} and 18 birds km^{-2}, respectively). Average total densities were slightly lower in the Chukchi Sea (13 birds km^{-2}) and much lower in the Beaufort Sea (3.3 birds km^{-2}).

BIOGEOGRAPHIC PROVINCES

Three distinct biogeographic provinces are apparent during summer from the zooplankton, fish, and seabird analyses. Based on the most common pattern in the cluster analysis, they conform to the Beaufort Sea (Beaufort Sea Province), the northern Bering (Chirikov Basin; Figure 1) and Chukchi Seas (Chirikov-Chukchi Province), and the southern and central Bering Sea (Eastern Bering Shelf Province; Figure 5). This pattern occurs for three of five taxa examined (small and large zooplankton, and seabirds). Even though the bottom and surface fish clustered differently from these three taxa, there were strong similarities in the clustering of regions. For bottom fish, the central and southern Bering Sea group together, and for surface fish, the northern Bering and Chukchi group together. The southern and northern Bering Sea were distinguished for both surface and bottom fish. Others also have identified distinct bottom fish communities for the northern and central Bering Sea regions (north and south of Saint Lawrence Island; Cui et al., 2009).

The Beaufort Sea Province has a narrow shelf and its waters are strongly influenced by winds, shelf break upwelling, and river inputs (Carmack and Wassmann, 2006; Weingartner et al., 2009). It is largely isolated from the input of heat, nutrients, and zooplankton from the Bering Sea (Ashjian et al., 2003, 2010). Arctic zooplankton, some of which have been advected from the deep basin of the Arctic Ocean, are present on the shelf. The Arctic zooplankton fauna, fed upon in summer by bowhead whales, is abundant in large, ice-associated, lipid-rich *Calanus glacialis* (Figure 7). In fall, when euphausiids (advected from the Bering Sea) are near the region of Barrow Canyon, north of Point Barrow, bowhead whales may forage where waters of Bering Sea origin meet Arctic waters (Ashjian et al., 2010; Moore et al., 2010). The shelf is shallow, and benthic-pelagic coupling is strong. Benthic-foraging seabirds are common (Figure 10) and include eider

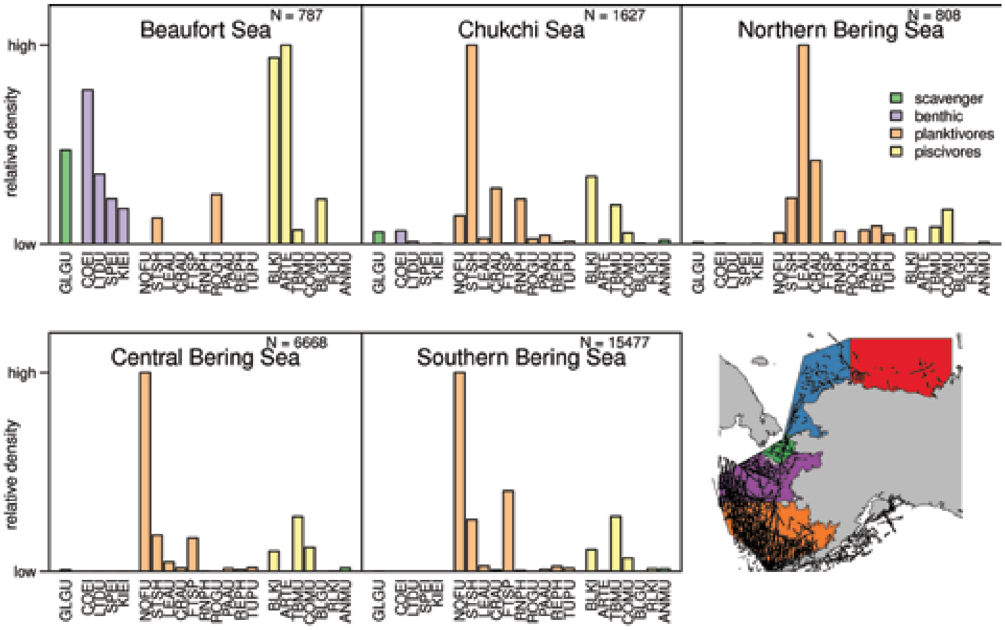

Figure 10. Relative densities (number) of the most common seabirds from each region, all grouped by guilds in the Bering, Chukchi, and Beaufort Seas, June–September 2007–2009. Bars are standardized against the most abundant species in each region. Map shows effort, with small dots indicating the location of each 3-km transect segment. Species codes for seabirds are: GLGU: Glaucous Gull. COEI: Common Eider. LTDU: Long-tailed Duck. SPEI: Spectacled Eider. KIEI: King Eider. NOFU: Northern Fulmar. STSH = Short-tailed Shearwater. LEAU: Least Auklet. CRAU: Crested Auklet. FTSP: Fork-tailed Storm-Petrel. RNPH: Red-necked Phalarope. ROGU: Ross' Gull. PAAU: Parakeet Auklet. REPH: Red Phalarope. TUPU: Tufted Puffin. BLKI: Black-legged Kittiwake. ARTE: Arctic Tern. TBMU: Thick-billed Murre. COMU: Common Murre. BLGU: Black Guillemot. RLKI: Red-legged Kittiwake. ANMU: Ancient Murrelet.

ducks that nest on the tundra and later move to the shallow coastal waters of the Beaufort Sea to forage on benthos while molting and refueling for migration (Suydam, 2000; Phillips et al., 2007). The fish fauna is dominated by Arctic cod (Figure 8; Rand and Logerwell, 2010), which forages both on ice-associated zooplankton and the benthos, and is the essential link in the food web between zooplankton and piscivorous seabirds (e.g., Black Guillemots) and ice-associated seals (e.g., ringed seals).

The Chirikov-Chukchi Province is shallow, has ice-associated plankton blooms, and exhibits strong benthic-pelagic coupling that supports a dense benthic community (Grebmeier et al., 1988; Feder et al., 1994). The biology of the Chirikov-Chukchi Province is strongly impacted by AW, which carries elevated levels of nutrients and zooplankton from the outer shelf and slope of the Bering Sea (Figure 1; Walsh et al., 1989; Piatt and Springer 2003). The high nutrient content and mixing generated as the water converges toward Bering Strait results in hot spots of production in the northern Bering and Chukchi Seas. The advection of zooplankton in the Anadyr Current supports baleen whales that forage for large, lipid-rich copepods (*Neocalanus* spp.) and euphausiids. The Chirikov-Chukchi Province is also the foraging ground for planktivorous seabirds (Figure 10) from St. Lawrence, King, and the Diomede Islands, and for seabird colonies along the Russian mainland north to the Chukchi Sea (Piatt and Springer, 2003). The abundance of large crustacean zooplankton is greater here in late summer than in the central and southern Bering Sea, and many seabirds move northward into the region in late summer to take advantage of this bounty of prey.

Sea ice forms earlier and retreats later in the Chirikov-Chukchi Province than in the Eastern Bering Shelf Province, and as a result, much of the spring primary production is associated with ice algae and an ice-edge bloom. Much of this early spring production sinks to the bottom and supports a rich benthic fauna dominated by small fishes (e.g., shorthorn sculpin, Arctic cod; Figure 8) and benthic prey (e.g., bivalves; Figure 6 [bivalve larvae]).

The Eastern Bering Shelf Province is subarctic and includes both the southern and central Bering regions. Bottom fish like walleye pollock, Pacific cod, and yellowfin sole are abundant here; their densities are several-fold greater than in the Chirikov-Chukchi Province. The boundary between the southern and central Bering regions in waters between 50- and 100-m depth (middle shelf) is marked by the southern edge of the cold pool (Figure 3). South of about 60°N, the cold pool varies annually in extent and intensity. North of this area, the cold pool remains through the summer months and bottom temperatures vary little interannually (Figure 4). The cold pool provides a barrier to the northward movement of bottom fish in the middle shelf. The southern and central Bering shelves are linked by northerly shelf flows (Figure 1). These currents transport heat, phytoplankton, zooplankton, and passively drifting larvae northward. The bottom waters of the outer shelf remain warm (> 2°C) year-round relative to those of the middle shelf at comparable latitudes (< 0°C; Figure 4), and many of the subarctic bottom fish species are abundant over the northern portion of the outer shelf to a latitude of about 63°N, 3° north of the transition in the middle shelf region. For the purposes of this paper, we drew the nominal boundary between the southern and central Bering regions at 60°N, but the functional delineation may in fact bend northward across the outer shelf, generally following the line of minimum ice extent in March (Figure 1).

CLIMATE CHANGE

The abundant bottom fish of the southern Bering Sea will be blocked from moving north by the cold pool, even as climate warms, for as long as the winter sea ice extent remains unaffected. Over the last 30 years, climate warming has reduced the annual duration of Bering Sea ice cover (Danielson et al., 2011) and in the future may also reduce the spatial extent of seasonal ice cover. With warming in this region, fish population distributions have shifted within the southeastern Bering Sea shelf (Mueter and Litzow, 2008; Spencer, 2008). Subarctic species have been expected to move northward as climate warms, and there is evidence that some species already have done so (Grebmeier et al., 2006a). However, the seasonal ice cover of the northern Bering Sea will continue to form because ocean–to-atmosphere heat fluxes increase when the sun's elevation declines in the fall. Thus, cold bottom waters will remain a barrier to the northward migration of the large bottom fish populations and prolific fisheries now typical of the southeastern Bering Sea shelf (Stabeno et al., provisionally accepted). Most species in the southeastern Bering Sea are cold intolerant, largely avoid cold pool temperatures (< 2°C), and are at or near the northern extent of their ranges (e.g., walleye pollock, yellowfin sole). However, pelagic species, such as salmon, which reside mostly in the upper mixed layer, are not restricted by the cold pool and may move northward in summer.

The Arctic Ocean and the Bering Sea are not closely coupled with respect to seasonal ice cover, and summer and winter climate patterns north and south of Bering Strait can differ and lead to surprising contrasts. For example, Arctic Ocean summer ice cover diminished to a historic low in summer 2007, yet Bering Sea ice cover reached a 30-year high in the winter of 2007–2008, and Alaskans shivered through a cold and wet spring and summer of 2008; Bering Sea winter and spring conditions remained cold for 2007–2010 (Overland et al., provisionally accepted).

In the southern and central Bering Sea, pollock currently dominates fish biomass, and as a subarctic fish, was expected to increase in abundance with climate warming (Hunt et al., 2002). Instead, during a recent warm period (2001–2005), pollock productivity fell dramatically, and only during the following cold period (2006–present) has productivity generally regained previous levels. Recent work by the BEST, BSIERP, and BASIS programs shows that the southern Bering Sea became too warm for pollock and lacked a spring ice-associated bloom for several years in a row (Coyle et al., 2008, 2011; Hunt et al., 2008, 2011). The result was a severe decline in the abundance of the large, lipid-rich copepod *Calanus marshallae* and the shelf euphausiid *Thysanoessa raschii*, both important prey of juvenile and adult pollock (Moss et al., 2009). With reduced availability of large, lipid-rich zooplankton, juvenile pollock were undernourished and also exposed to greater predation pressure from larger fish that, lacking zooplankton prey, switched to eating small juvenile pollock (Coyle et al., 2011; Hunt et al., 2011). When colder conditions returned after 2006, the biomass of the large crustacean zooplankton gradually increased and pollock recruitment improved (Coyle et al., 2011; Hunt et al., 2010, 2011). Thus, counterintuitively, warmer conditions can reduce the abundance of pollock, a species near the northern extent of its range. Statistical analysis of long-term data sets (~ 40 yrs), combined with population modeling and climate scenarios, inform a forecast that indicates that within a few decades, there is a 50:50 chance that pollock abundance will fall 30% from the current average (Mueter et al., 2011).

The waters of the northern Bering and Chukchi Seas will continue to freeze each winter and thus support some species' resilience in the face of changing climate. Spotted seals breed in the Bering Sea and are primarily associated with sea ice during whelping, nursing, mating, and pelage-molting periods, from April through June. Most spotted seals spend the rest of the year making periodic foraging trips from haul-out sites ashore or on sea ice. Although spotted seals were petitioned for listing as threatened under the US Endangered Species Act (ESA) and their abundance is likely to decline gradually for the foreseeable future, a threatened status was found to be unwarranted, primarily because of the expectation that the ice season in the northern Bering Sea will remain long enough that spotted seals can continue giving birth and rearing pups in ice-covered areas (Boveng et al., 2009). While there may be more frequent years in which ice coverage is reduced, the period in which seal reproduction occurs will continue to have substantial ice, particularly in the northern regions of the breeding range (Boveng et al., 2009). In years of low ice, it is likely that seals will adjust at least in part by shifting their breeding locations in response to the position of the ice edge as they have likely done in the past in response to interannual variability.

In contrast, abundances of other ice-associated species are predicted to decline more quickly due to differences in life history and the timing of their ice associations. For example, mammals that depend on sufficient snow cover for lairs in spring (ringed seals; Kelly et al., 2010) or sufficient summer ice as platforms for foraging (polar bears; Department of the Interior, 2008) are predicted to decline, as are various ice-associated prey of marine mammals (Tynan and DeMaster, 1997). Model forecasts indicate that throughout the range of ringed seals, there will be substantial reductions in snow fall during a time of year when snow depth is needed to build subnivean (under snow) lairs (Kelly et al., 2010). Without the protection of the lairs, ringed seals—especially newborn—may be vulnerable to freezing and predation. In the case of the polar bear, the key threat also is loss of sea ice, the species' primary habitat. Polar bears need sea ice as a platform for hunting, for seasonal movements, for travel to terrestrial denning areas, for resting, and for mating. Summer sea ice extent is rapidly diminishing throughout most of the Arctic (Comiso, 2002), and the best available evidence shows that Arctic sea ice will continue to be affected by climate change (ACIA, 2005). In general, the climate models that best simulate Arctic conditions all project significant losses of sea ice over the twenty-first century (Kelly et al., 2010).

Forecasting climate change impacts upon the ecosystem demands a mapping of biogeography and an understanding of the oceanography and biota of each biogeographic province. Results from many research programs are improving our ability to understand past changes and foresee possible future scenarios. As the climate and ecosystems shift, our ability to adapt to changing conditions will depend foremost on our ability to assess and understand the underlying linkages.

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