Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain

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ABSTRACT

Results from 2004 field observations, integrated with those from prior studies, allow definition of a unique "Pribilof Domain" in the southeastern Bering Sea. This domain results from its geographic location and bathymetry that supply water from the outer shelf and slope that is replete with dissolved and planktonic material. We highlight temporal variability in this domain and place this in the broader context of mechanisms identified as potentially important in regulating the flow of energy and material in this shelf ecosystem.

In the Pribilof Domain, unique circulation features and mixing are responsible for energy and material dynamics. Rectified tidal currents entrain water from the Outer Shelf Domain, thereby transporting nutrients and plankton to the vicinity of the Pribilof Islands. Near the islands, winds and strong tides interact with bathymetric features to mix nutrients into surface waters, resulting in localized regions of high new production well after the cessation of new production in the highly stratified waters of the Middle Shelf Domain. Large, oceanic species of zooplankton are episodically advected into the Pribilof Domain where they provide an important source of prey for predators.

In 1999, a cold year, sea ice was present in the southeastern Bering Sea until late May, summer stratification over the middle shelf was weaker than in 2004, "large" crustacean zooplankton were abundant, and microzooplankton productivity was greater than in 2004. In contrast, 2004 was a warm year in which sea ice retreated in early March, summer stratification was strong, summer primary production was lower than in 1999, and small shelf species dominated the mesozooplankton, the biomass of which was comparable to some of the lowest values in 50 years. In 2004, microzooplankton consumed about half of the primary production in the Middle Shelf Domain.

Evidence is mounting that the eastern Bering Sea is undergoing a major change in the structure and function of its ecosystem. The lack of large zooplankton in Middle Shelf Domain waters in summer, possibly linked to the lack of an early spring, ice-associated phytoplankton bloom, can be expected to affect the distribution, and possibly growth, of planktivorous groundfish, such as walleye pollock (*Theragra chalcogramma*). Bottom temperatures also affect the distribution of fish, with warm temperatures allowing many groundfish species to extend their distributions northward and eastward. We review mechanisms influencing productivity and its fate, and the impacts of a changing ecosystem on apex predators tied to the Pribilof Islands for reproduction.

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1. Introduction

The Pribilof Islands are renowned as an important breeding locale for pinnipeds and seabirds. The rookeries of northern fur seals (*Callorhinus ursinus*) there are the largest in the world despite their depletion from historically high densities, and the seabird colonies are among the largest in the Northern Hemisphere. Roger Tory Peterson, when showing the famous British naturalist Sir Ronald Fisher the natural wonders of North America, went to the Pribilof Islands to explore the immense numbers and diversity of seabirds breeding there (Peterson and Fisher, 1956). The Pribilof Islands and their surrounding waters still support the greatest biomass of pinnipeds and marine birds of any island or island group of comparable size in the North Pacific.

Commercial exploitation and culling destroyed the population of sea otters (*Enhydra lutris*) that lived in Pribilof Islands' waters,

and contributed to severe declines in the abundance of both fur seals and Steller sea lions (*Eumetopias jubatus*) there (Hanna, 1923; Hunt et al., 2002). Fur seal numbers stabilized by the late 1960s, while sea lions were restricted to remnant breeding colonies on Walrus Island, a small, low island to the east of St. Paul Island (Fig. 1). However, starting some time in the late 1970s or early 1980s, sea lion, fur seal and piscivorous seabird numbers declined steeply (Hunt et al., 2002; Towell et al., 2006). The fur seal populations appeared to stabilize from the mid-1980s through the mid-1990s, and then resumed their decline; sea lions numbers probably continued to decline, though their status is not monitored. The numbers of piscivorous seabirds attending the colonies on St. Paul Island continue to decline, whereas on St. George Island, numbers have stabilized or increased since the mid-late-1980s (Byrd et al., 2008a).

The research reported in this special issue, and summarized in this paper, was initiated to investigate what differentiates the waters of the Pribilof Islands from other parts of the southeastern Bering Sea shelf and supports the large populations of pinnipeds and seabirds breeding on the islands. The initial research, conceived in 2002, was designed to compare the waters of the Pribilof region with those considered typical of the southeastern Bering Sea Middle Shelf Domain (Coachman, 1986; Stabeno et al., 1999a). We sought to contrast post-bloom conditions in summer around the Pribilof Islands with conditions in the Middle Shelf Domain at site M2, where a biophysical mooring has been maintained since 1995 by the National Oceanographic and Atmospheric Administration's (NOAA) Pacific Marine Environmental Laboratory (Fig. 2) (Stabeno et al., 2007). We hypothesized that, around the Pribilof Islands, nutrient- and zooplankton-rich water from the Outer Shelf Domain and slope (Bering Slope Current) would be advected to the island region, and would support post-spring-bloom new production. The advected water also would contain large, oceanic species of zooplankton that are the prey of locally breeding planktivorous auklets, as well as of local populations of juvenile walleye pollock (*Theragra chalcogramma*) and other small fish (Hunt et al., 1996b; Schabetsberger et al., 2000, 2003; Springer et al., 2007).
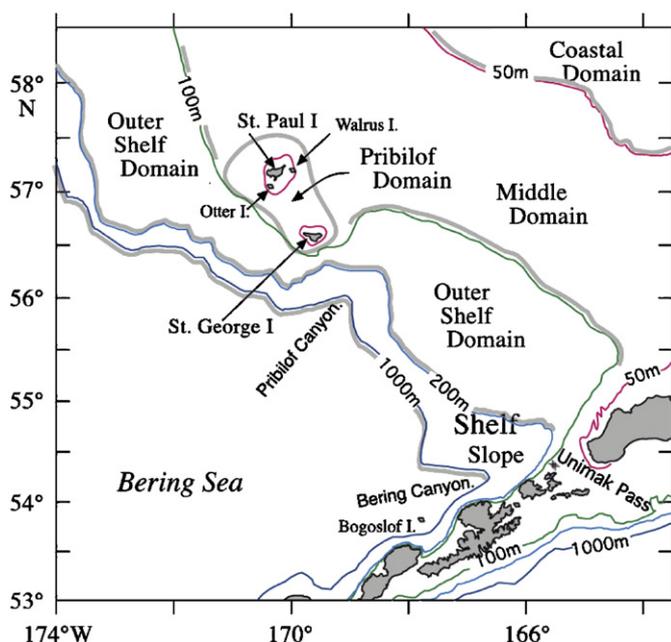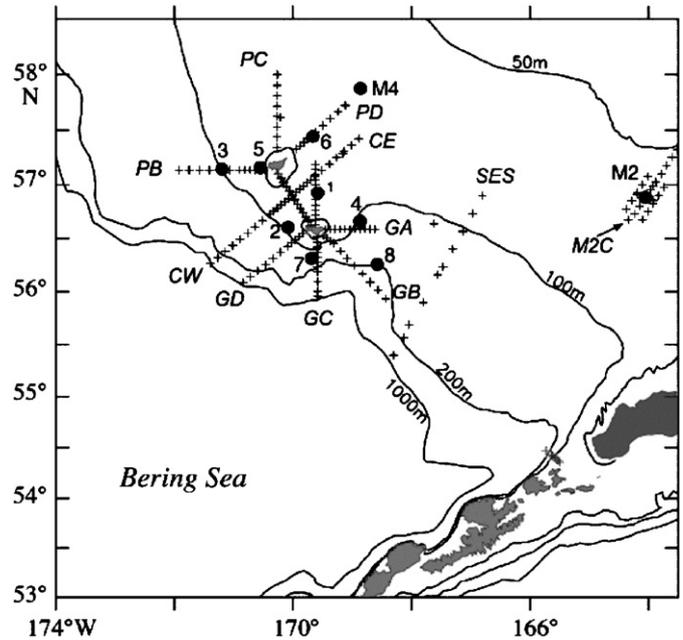

Fig. 2. Map of the study area showing transects and oceanographic stations in the vicinity of the Pribilof Islands and mooring M2. CTD stations on the shelf and around the Pribilof Islands are shown by (+). Labels indicate transect lines and large filled circles indicate position of additional moorings specific to this study. After Sullivan et al. (2008), with permission.

Between the mid-1970s and late 1980s research in the eastern Bering Sea focused on resource assessment. Results from such studies greatly enhanced our knowledge of the ecosystem from atmospheric and oceanic physics through the characteristics of upper trophic level species and their population dynamics (e.g., Hood and Calder, 1981; McRoy et al., 1986). The physical environment was partitioned into four domains (Oceanic, Outer Shelf, Middle Shelf and Coastal or Inner Shelf) with identifiable hydrographic (Kinder and Schumacher, 1981a) and current features (Kinder and Schumacher, 1981b; Schumacher and Kinder, 1983) that are separated by transition zones or fronts (Schumacher et al., 1983). Numerous connections have been identified between the domains and the attendant biological features and processes (e.g., Kinder et al., 1983; Hunt et al., 2002). With some refinement in details (e.g., Stabeno et al., 2001), this system of domains forms the basic pattern or schematic of the southeastern Bering Sea shelf. As such, it has formed the underpinning of numerous papers in the scientific literature (e.g., Walsh and McRoy, 1986; Hunt et al., 2002) and programmatic scientific plans (e.g., BEST, 2004; NRC, 2004; NPRB, 2005). Although Ciannelli et al. (2004) used energy flow to identify the region of ocean needed to support the "Pribilof ecosystem" and there was an indication that physical and biological conditions around the Pribilof Islands were different than those over the rest of the shelf (Stabeno et al., 1999b), this region was not identified as a unique domain until this special issue. Knowledge of this uniqueness could have altered the direction of research conducted during the 1990s by the NOAA Coastal Ocean Program (Macklin and Hunt, 2004).

In assembling the papers in this special issue, we also sought to examine the temporal scales of variation affecting the numbers and diversity of top predators that exploit the waters of the Pribilof Archipelago. The striking differences between conditions in 2004 and previous years became evident only as the 2004 field work progressed and post-cruise analyses were conducted. Therefore, to augment the picture of how the Pribilof region,

Fig. 1. Southeastern Bering Sea study area. After Sullivan et al. (2008), with permission. Eastern Bering Sea shelf hydrographic domains, Coastal, Middle, Outer Shelf, Pribilof, and Shelf Slope are indicated.

and the middle shelf region in general, differed in 2004 as compared to earlier years, a number of investigators in addition to the original group that initiated the 2004 R/V *Alpha Helix* study (K. Coyle, K. Fredrickson, G. Hunt, J. Jahncke, C. Mordy, J. Napp, A. Pinchuk, R. Sambrotto, P. Stabeno, S. Strom, S. Zeeman) were invited to submit papers to the special issue. These papers by Benowitz-Fredericks et al. (2008), Byrd et al. (2008a, b), Call et al. (2008), Kokubun et al. (2008), Loher (2008), Mizobata et al. (2008), Sinclair et al. (2008), Sydeman et al. (2008) and Takahashi et al. (2008) provide a spatial and temporal context in which to place the limited set of data that could be obtained on a single 25-day cruise, as well as important insights into the mechanisms that control productivity and energy transfer near the Pribilof Islands and over the Middle Shelf Domain.

In this overview paper, we first describe the circulation and hydrography of the Pribilof Domain, and then contrast the ecology of the Pribilof Domain and the Middle Shelf Domain as we found them in the summer of 2004. We then provide an examination of temporal variability, primarily in the Pribilof Domain and, where possible, between the cold summer in 1999 and the much warmer summer of 2004. Finally, we explore mechanisms that may have been responsible for ecosystem responses to climate forcing in the southeastern Bering Sea. We neglect the possible role of disease in the changes documented, as well as the role of fisheries takes, which are on the order of 1.5 to 2.0 million metric tons of groundfish annually over the southeastern Bering Sea shelf (Ianelli et al., 2006). The potential for fisheries to impact the southeastern Bering Sea marine environment by competition with top predators for prey has been the subject of study since the 1970s (e.g., Favorite et al., 1977). And, although the amount of pollock on the shelf since the early 1980s has been as great or greater than in the 1960s and early 1970s (Ianelli et al., 2006), concern remains that fishing activity may be impacting pinniped populations in the southeastern Bering Sea (Alverson, 1991; Ferrero and Fritz, 1994; Hennen, 2006). This is an important question and deserves a careful analysis of the distribution and abundance of commercially exploited fish stocks as well as the amount and distribution of fisheries takes over the past decades, a task too great for this review.

2. Mesoscale spatial patterns: the Pribilof Domain

2.1. Circulation and hydrography

The Pribilof Archipelago consists of two large islands, St. George and St. Paul, both of which support Aleut communities, and three small islands, Otter, Walrus and Sea Lion Rock, which are not inhabited (Fig. 1). The islands are located on the eastern Bering Sea shelf at approximately 56.5°N between the 70-m and 100-m isobaths, which is the outer portion of the Middle Shelf Domain (Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 2001). However, because the Pribilofs are located close to the 100-m isobath where Pribilof Canyon intersects the slope and because the Outer Shelf Domain is particularly narrow there (Fig. 1), the archipelago is often bathed in Outer Shelf Domain and shelf-slope waters, as well as with water of the Middle Shelf Domain (Stabeno et al., 1999b, 2008; Sullivan et al., 2008).

Along the 100-m isobath southeast of the Pribilof Islands there is a northwestward flow that plays an important role in transferring nutrients and plankton along the shelf to the Pribilof region (~5 cm s^{-1}; Stabeno et al., 1999b). As the shelf narrows south of St. George Island, the flow is confined and accelerates to as much as 40 cm s^{-1} (Fig. 3). The origin of the flow along the 100-m isobath is a combination of inflow at Unimak Pass, flow
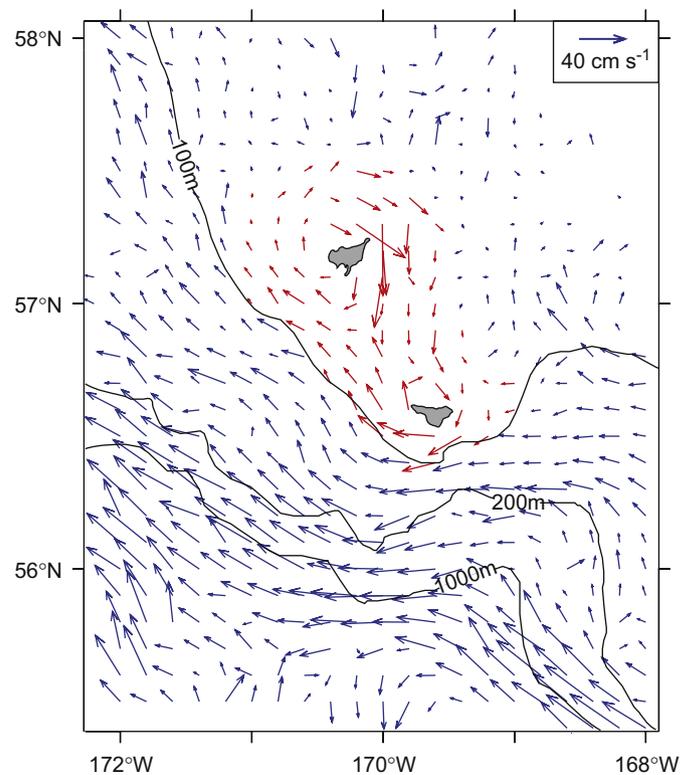

Fig. 3. Composite of drifter tracks showing the region around the Pribilof Islands where rectified tidal currents result in a region of recirculation (red arrows) that differentiates the Pribilof Domain from the surrounding Middle Shelf Domain. Flow at ~40 m as determined from Lagrangian measurements. Mean current velocities interpolated to 0.1° latitude × 0.2° longitude. A minimum of four independent estimates of velocity was required to determine velocities in each grid cell. From Stabeno et al. (2008), with permission.

onto the shelf at Bering Canyon, and pulses of on-shelf flow elsewhere along the slope (Schumacher and Stabeno, 1994; Stabeno and van Meurs, 1999; Stabeno et al., 1999b; Mizobata et al., 2008). These on-shelf flows introduce nutrient-rich basin and Bering Slope Current water onto the shelf. Subsequently, this current flows northward along the west side of the Pribilof Islands. As it passes St. Paul Island, the current bifurcates, with a portion continuing northward along the 100-m isobath and some turning eastward and circulating around the islands (Kowalik and Stabeno, 1999; Stabeno et al., 1999b). Coarse-scale maps of zooplankton community structure from the Russian literature show intrusion of oceanic species onto the shelf north of the Pribilof Islands (Cooney, 1981; Coyle et al., 1996). The strength of on-shelf flow appears to vary by pathway and on seasonal or longer time scales. Which of these patterns of flow predominates is not yet known, but data from a series of moorings and satellite-tracked drifters indicate that on-shelf flows are common (P.J. Stabeno, unpublished data).

Circulation in the vicinity of the Pribilof Islands is complex, contributing to the development of well-defined boundary zones characteristic of the area (Fig. 3). Near each of the two main islands, there is a clockwise (anti-cyclonic) rotation which is partly tidally induced (Kowalik and Stabeno, 1999; Stabeno et al., 1999b, 2008) and partly baroclinic. Farther from the islands (water depths 50–100 m), the circulation is still clockwise, and currents may circle each island individually, or may circle the two islands together (Stabeno et al., 2008; Sullivan et al., 2008) (Fig. 3). This region, where the recirculation of water around the islands constitutes a physically identifiable "Pribilof Domain," allows for both the advection of water and retention of organisms there

(Stabeno et al., 2008). These flows may be associated with the fronts to the east of the Pribilof Islands described by Flint and Sukhanova (2002) (see also Flint et al., 2002; Sambrotto et al., 2008). Less commonly, the flow along the 100-m isobath southeast of the Pribilof Islands can become weak, and this weak flow may continue northward east of St. George Island, where it eventually decays. Such a pattern occurred in the winter and spring of 2004 (Fig. 4).

Where the water shoals around the islands and over reefs (e.g., a reef between the islands, Fig. 5), tidal mixing coupled with wind mixing is sufficient to break down the strong summer stratification that is a hallmark of the Middle Shelf Domain (Kinder and Schumacher, 1981a; Schumacher and Stabeno, 1998; Overland et al., 1999). Around each island this mixing results in a structure front (Kinder et al., 1983; Coyle and Cooney, 1993). Because St. George Island is closer to the 100-m isobath than St. Paul Island, the frontal structure at St. George Island is more influenced by currents associated with 100-m isobath, which are stronger south of St. George Island. At St. Paul Island, the structure front, analogous to the inner front of the eastern shelf (Kachel et al., 2002), is located at the ~40-m isobath and, as such, limits exchange of water between the Middle Shelf Domain and the coastal region around the island during late spring, summer and early fall (Kowalik, 1999; Kowalik and Stabeno, 1999; Stabeno et al., 1999b, 2008). The more energetic flow in the vicinity of St. George Island results in a weaker structure front, and thus permits greater exchange of materials between the Middle Shelf

Domain and the inshore region during late spring, summer and early fall. In addition, St. George Island is often directly influenced by the presence of eddies in Pribilof Canyon. The structure fronts around the islands have been identified as areas of enhanced foraging opportunities for seabirds (Kinder et al., 1983; Schneider et al., 1990; Decker and Hunt, 1996; Hunt et al., 1996b), but not necessarily for juvenile fish such as age-0 walleye pollock (Brodeur et al., 2002).

3. Spatial comparisons: the Middle Shelf Domain at M2 versus the Pribilof Domain

3.1. Nutrients, chlorophyll, and phytoplankton growth and production

In summer, the Middle and Outer Shelf domains outside the Pribilof Domain are strongly stratified, and the upper mixed layer is depleted of macronutrients (Figs. 5 and 6) except when storms cause deepening of the pycnocline and upward mixing of nutrients from below (Sambrotto et al., 1986, 2008). In contrast, nutrients in the surface waters of the Pribilof Domain, in particular the fronts around the islands and the region between the islands, are replenished by a combination of tidal action and wind mixing (Kinder et al., 1983; Stabeno et al., 2008). The frontal areas support high concentrations of chlorophyll and elevated primary production (Coyle and Cooney, 1993; Hunt et al., 1996a;
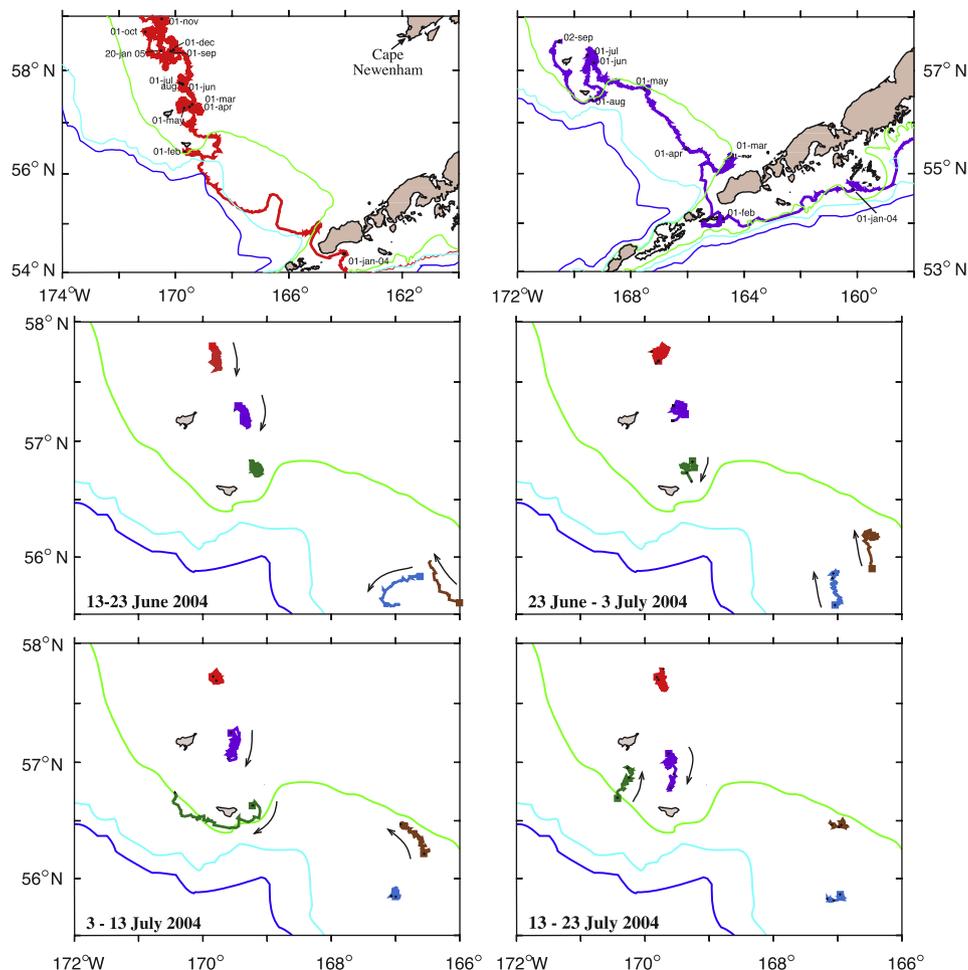

Fig. 4. Upper two panels: Tracks of two drifters released in the Gulf of Alaska that passed to the east of St. George Island. Lower four panels: Tracks of three drifters drogued at 40 m which had moved northward on the east side of St. George Island, and, after stalling in place for 2–3 weeks, began to move south and then westward around the south side of St. George Island. Images courtesy of N. Kachel, NOAA, Pacific Marine Environmental Laboratory.
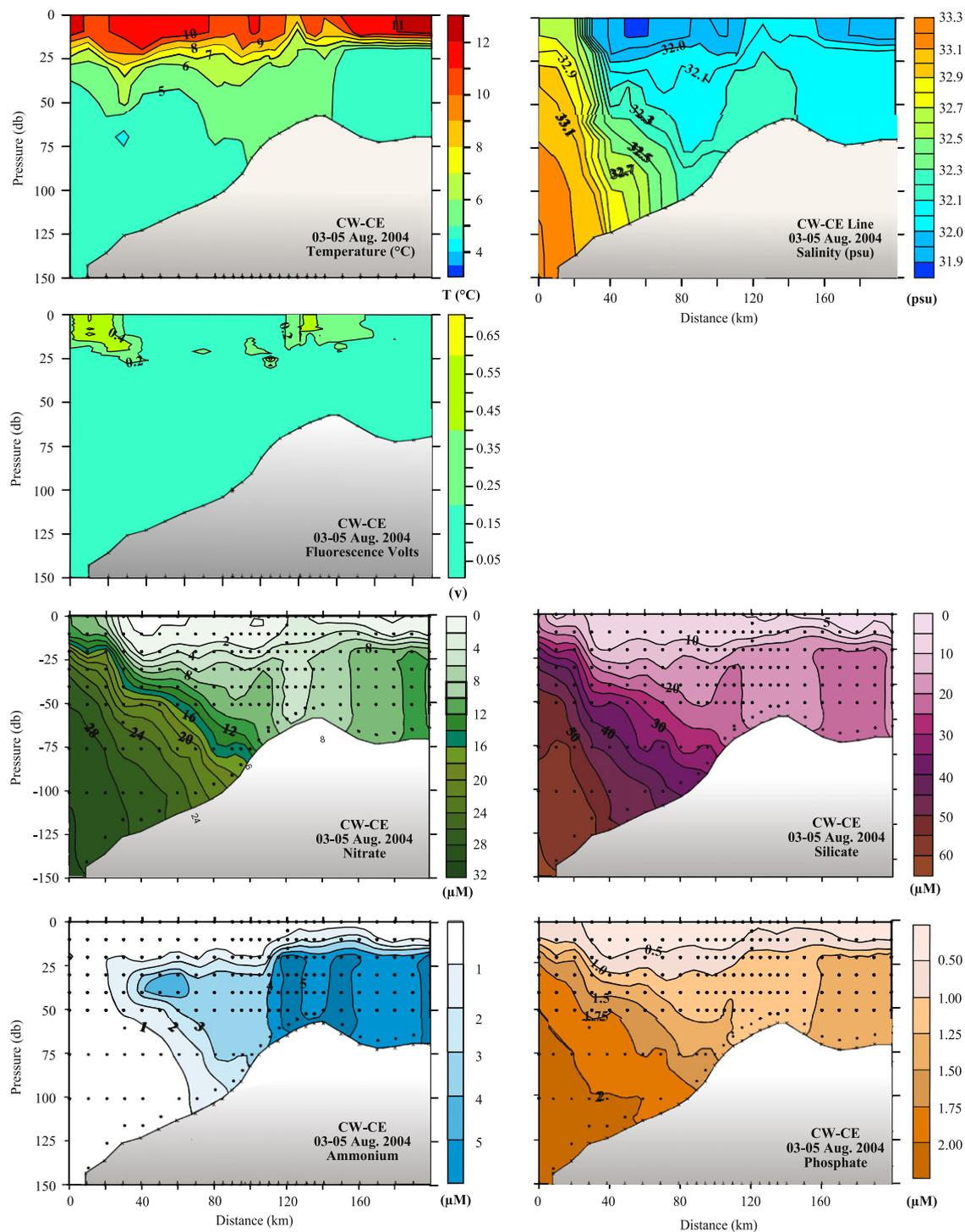
Fig. 5. Cross section from the slope northeastward between the Pribilof Islands on the CW-CE lines (see Fig. 2). Nutrient data courtesy of C. Mordy. Methods as described in Sullivan et al. (2008). The shallow area at about 150 km is a reef above which there was a high concentration of phytoplankton, as seen in Fig. 5. Contours and colors represent gradients of salinity, temperature, chlorophyll (as represented by fluorescent volts), nitrogen, silica, ammonia and phosphates as indicated. Figure courtesy of N. Kachel, NOAA Pacific Marine Environmental Laboratory, Seattle, WA.

Flint and Sukhanova, 2002; Kopylov et al., 2002) (Fig. 7). Between the islands, nutrients in surface waters are replenished by vertical mixing when tidal currents impinge on shallow bathymetry (Fig. 5). As a result of the mixing, near-bottom nutrient concentrations between the islands are lower than in the "source waters" of the Outer Shelf Domain, or in the bottom layer of the well-stratified waters of the Middle Shelf Domain, which are isolated from the upper mixed layer by a strong thermocline (Figs. 5 and 6). Between the islands, nutrients in bottom waters

are replenished with cold, salty waters of the shelf-slope, which are rich in macronutrients (Sullivan et al., 2008) (Fig. 5), and by bottom waters from the Middle Shelf Domain (Stabeno et al., 2008). These waters can be advected into the Pribilof Domain by entrainment in the 100-m isobath flow and the rectified tides surrounding the islands (Fig. 3). There is also evidence of ammonium transport from Middle Shelf Domain waters to the Outer Shelf Domain by the circulation around the islands (Mordy et al., 2008; see also Rho et al., 2005).
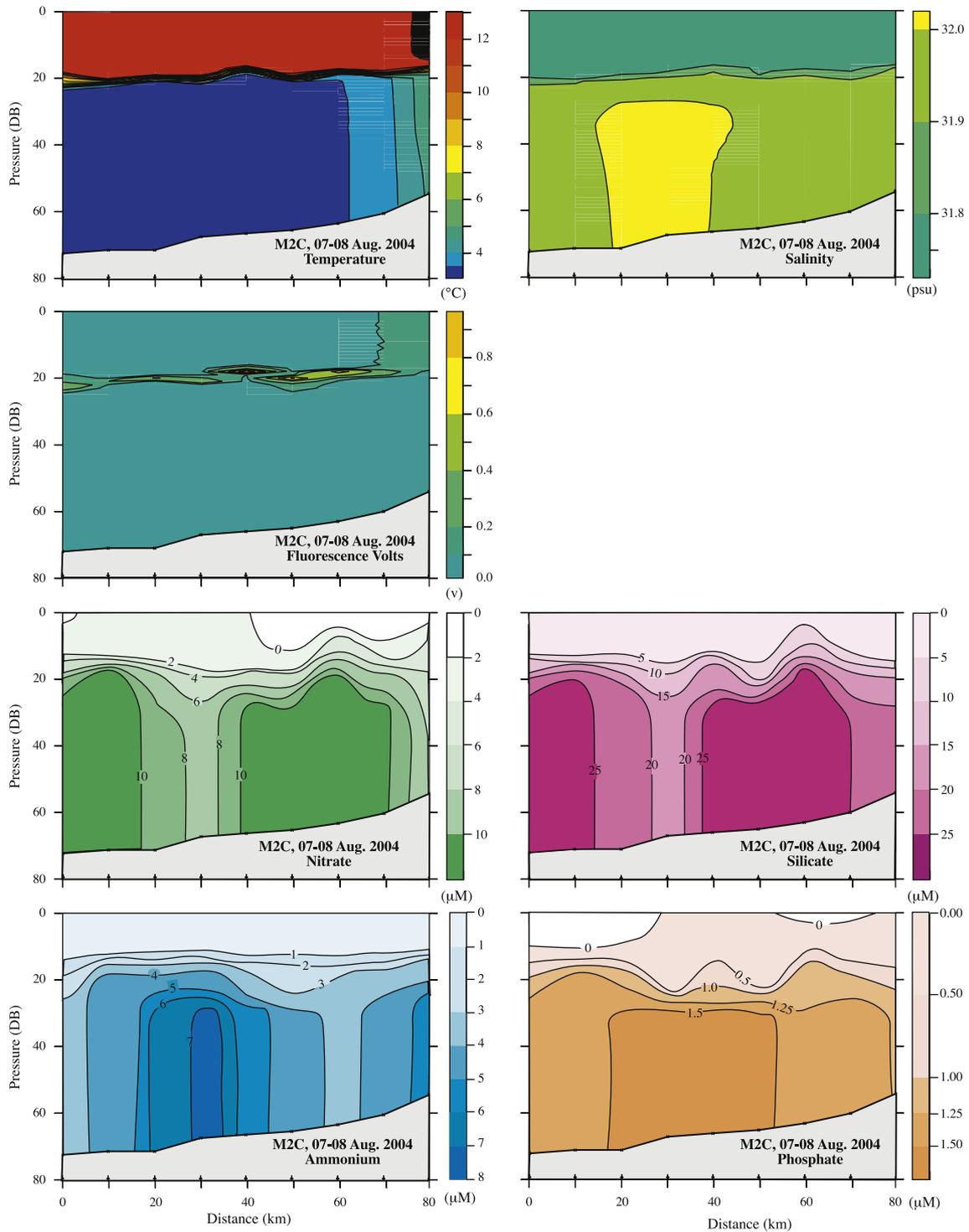
Fig. 6. Hydrographic and nutrient section of the Middle Shelf Domain at mooring site M2 (see Fig. 2). The downward bending of the isotherms at the right side of the temperature plot demarks the location of the Inner Front. Section taken on 7 August 2004. Nutrient data courtesy of C. Mordy. Methods as described in Sullivan et al. (2008). Contours and colors represent gradients of salinity, temperature, chlorophyll (as represented by fluorescence [in volts]), nitrogen, silica, ammonia and phosphates as indicated. Figure courtesy of N. Kachel, NOAA Pacific Marine Environmental Laboratory, Seattle, WA.

In August 2004, integrated chlorophyll levels in the study area ranged from 13 to 202 mg m^{-2}, with the highest levels found between the islands and along the shelf-slope, and the lowest at M2 (Strom and Fredrickson, 2008) (see Fig. 7 for surface chlorophyll values near the Pribilof Islands). As could be expected, during summer in regions with a sharp interface at the bottom of the surface mixed layer, there was a sub-surface chlorophyll maximum at the pycnocline (Figs. 5 and 6). Large-celled phytoplankton usually dominated regions with high chlorophyll concentrations, whereas smaller-celled species dominated regions with low levels of chlorophyll (Strom and Fredrickson, 2008).

In the upper mixed layer, the unenriched growth rates of phytoplankton community as a whole ranged between 0.00 and 1.00 d^{-1}, with cells in the largest size fraction ($>20\,\mu$m) growing
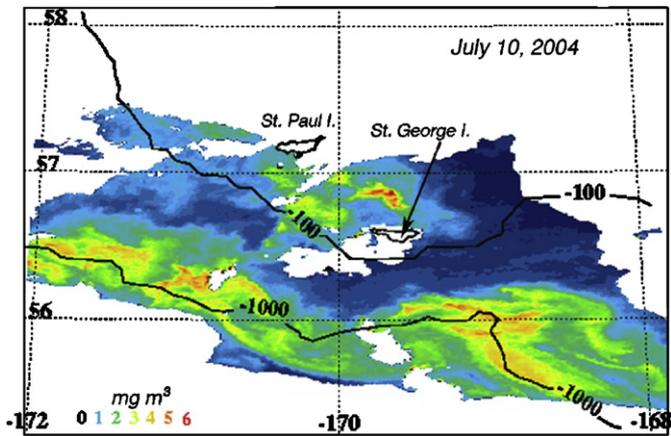
Fig. 7. MODIS image from July 10, 2004, showing chlorophyll concentrations at the shelf edge and over the reef between St. George Island and St. Paul Island, Pribilof Islands. Figure courtesy of S. Salo, NOAA Pacific Marine Environmental Laboratory, Seattle, WA.

faster ($0.44\,d^{-1}$ on average) than smaller cells (5–20 μm, $0.10\,d^{-1}$; <5 μm, $0.24\,d^{-1}$) (Strom and Fredrickson, 2008). At all but two stations where the effects of nutrient amendments on algal growth rates were investigated, there was evidence of nutrient limitation, with ammonium and nitrate amendments having about equal impacts (Strom and Fredrickson, 2008). One of these two stations (GB-9) was to the southeast of St. George Island at the head of the eastern horn of Pribilof Canyon, and the other, GD-5, was southwest of St. George Island at the 100-m isobath and just downstream of the flow out of the western horn of Pribilof Canyon (Strom and Fredrickson, 2008). Because the microzooplankton community (see below) responded to the bloom at these two stations with an increase in both biomass and grazing activity, it is reasonable to infer that mesozooplankton might also find enhanced foraging opportunities in the bloom regions. Enhanced near-surface concentrations of mesozooplankton would be favorable to forage fish and planktivorous seabirds (e.g., Obst et al., 1995; Hunt et al., 1996a; Kokubun et al., 2008).

The above differences in the nutrient field and phytoplankton growth rates resulted in substantial differences between the Pribilof Domain and the rest of the Middle Shelf Domain, not only in total primary production, but also in new production (Fig. 8). As predicted, and observed in previous years, summer production over most of the Middle Shelf Domain was primarily ammonium-based, regenerated production, with new production limited to periods just after storms (Sambrotto et al., 1986, 2008). In the vicinity of M2, the small amount of fluorescence present in August 2004 was confined to the bottom of the pycnocline. In contrast, much higher levels of primary production were recorded in the Pribilof Domain (Fig. 8) (Sambrotto et al., 2008). In the areas of strong mixing, high concentrations of chlorophyll occurred near the surface (Figs. 5 and 7), the same areas where reduced sea-surface temperatures (SST) were identified in a satellite image from 1 August 1977 (see Fig. 1 in Kinder et al., 1983). The chlorophyll patches observed between the islands were similar in concentration to those along the shelf edge, in the "Green Belt" (Springer et al., 1996; Sambrotto et al., 2008). Thus, the proximity to the nutrient-rich Outer Shelf Domain and shelf-slope waters and the presence of strong tidal currents are important for sustaining the patches with high levels of production and standing stocks of phytoplankton that are typical of the Pribilof Domain in summer.

New production showed similar patterns to those of primary production: rates of new production were high along the shelf-
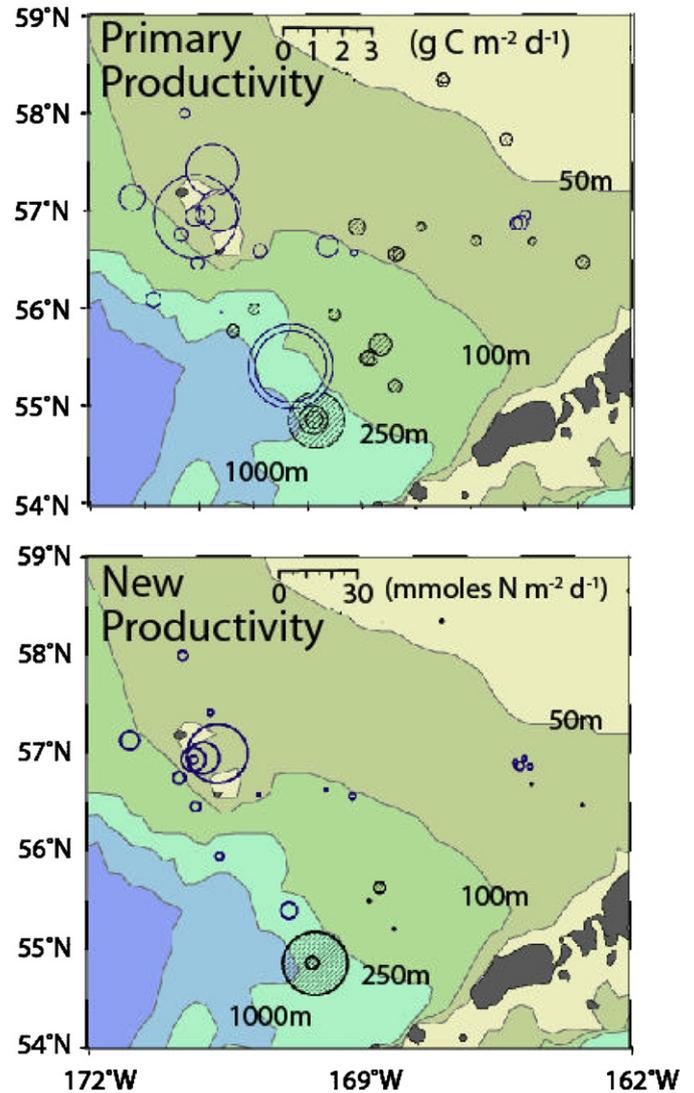

Fig. 8. Measures of primary production over the shelf. Primary production was measured by ^{14}C uptake ($g\,C\,m^{-2}\,d^{-1}$), and new production was measured by ^{15}N uptake ($mmoles\,N\,m^{-2}\,d^{-1}$). Note, open circles are from data gathered in 2004, whereas hatched circles are from data gathered in 1981. Figure modified from Sambrotto et al. (2008), with permission.

break front in the "Green Belt" and in the Pribilof Domain (Fig. 8) (Sambrotto et al., 2008). Rates of new production were low over most of the Outer and Middle Shelf domains, where strong stratification isolated phytoplankton in the euphotic zone from nitrate present at depth. The presence of new production in the vicinity of the Pribilof Islands is potentially important. With the exception of the shelf-break front, new production on the shelf was minimal and presumably declined through the summer as nitrate was lost from the upper water column. This would then result in diminishing food resources for grazers. In contrast, in the Pribilof Domain, there was likely strong, albeit patchy, new production throughout the summer, which would have provided food for grazers and the food webs leading to juvenile fishes and thence to marine birds and pinnipeds.

In summary, the enhanced productivity of the Pribilof Domain relative to the Middle Shelf Domain in summer is due to a combination of advection of nutrient- and plankton-rich Outer Shelf Domain and shelf-slope water and the vertical mixing of the nutrients into surface waters by tidal currents impinging on areas of shallow bathymetry.

3.2. Microzooplankton grazing

In August 2004, microzooplankton biomass was related positively to total chlorophyll concentration, and consequently was greatest (up to 118 μgC l^{-1}) in areas of phytoplankton blooms, such as between the islands, along the slope, and at stations with elevated nutrient concentrations near the head and downstream of Pribilof Canyon (Strom and Fredrickson, 2008). In contrast, in the strongly stratified region of the Middle Shelf Domain in the vicinity of M2, microzooplankton biomass was uniformly low ($<15 \mu$g C l^{-1}). However, microzooplankton grazing rates were overall low across the entire study area, with an average of 0.13 d^{-1}. Only over the slope and at one station (CW-6) on the 100-m isobath were grazing rates >0.2 d^{-1}. The ratio of microzooplankton grazing rates to phytoplankton growth rates, a measure of the fraction of daily primary production consumed by microzooplankton, averaged 0.49 for the entire study.

3.3. Meso- and macrozooplankton: species composition, distribution and abundance

In August 2004, the species composition of the mesozooplankton communities of the southeastern shelf showed a distinct pattern: there was an oceanic community over the outer shelf and shelf edge seaward of the 32.4 psu isohaline; there was a distinct, shelf community in the vicinity of M2; and the region around the Pribilof Islands had a mixture of these two communities (Fig. 9) (Coyle et al., 2008). An unexpected finding in 2004 was that *Calanus marshallae*, historically the dominant large copepod over the Middle Shelf Domain, was virtually absent from plankton tows in the vicinity of M2 and the Pribilof Islands, but was common in Outer Shelf Domain and shelf-slope waters (Fig. 10) (Coyle et al., 2008). The boundaries of these communities, as shown in Fig. 9, do not conform exactly with the boundaries of the Pribilof Domain, as shown in Fig. 1, but rather reflect the results of the advective processes that draw water and associated plankton into the Pribilof Domain from the Outer Shelf and Oceanic domains, thereby creating a mixture of the Middle and Outer Shelf Domain communities.

Euphausiid abundance was greater in the vicinity of the Pribilof Islands than in the Middle Shelf Domain near M2, and greater still in the oceanic region as defined by Pinchuk and Coyle (2008). The shelf species *Thysanoessa raschii* was absent from the oceanic region, present in low numbers near M2 (median abundance—1.4 individuals/1000 m^3) and most abundant near the Pribilofs (61 individuals/1000 m^3) (Pinchuk and Coyle, 2008). *Thysanoessa inermis* was also most abundant around the Pribilof Islands (128 individuals/1000 m^3), with few found at M2. In contrast, *Thysanoessa longipes* and *Thysanoessa spinifera* were most abundant in the oceanic region as defined by Pinchuk and Coyle (2008). In past studies of marine bird foraging around the Pribilof Islands, *T. raschii* was the dominant euphausiid species in the diets of short-tailed shearwaters (*Puffinus tenuirostris*) foraging near St. Paul Island (Hunt et al., 1996a), whereas *T. inermis* was the most commonly identified species in the stomachs of thick-billed murres (*Uria lomvia*) collected while foraging at a reef to the east of St. George Island in the same year (1989) (Coyle et al., 1992). These observations suggest that around the Pribilof Islands there may be some fine-scale partitioning of marine habitats by euphausiids.

3.4. At-sea distributions and foraging behavior of marine birds and northern fur seals

3.4.1. Seabirds

In summer 2004, seabird densities were highest in the Outer Shelf and Oceanic domains (95.9 birds km^{-2}), intermediate in the region between the islands (54.2 birds km^{-2}), and lowest over
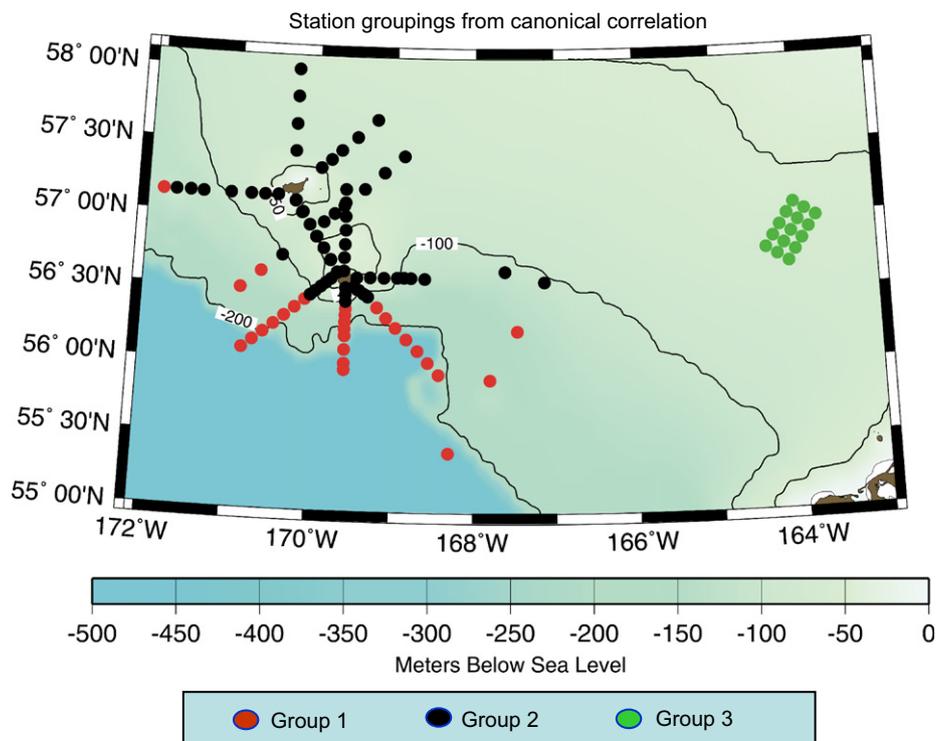

Fig. 9. Distribution of mesozooplankton communities on the eastern Bering Sea shelf in August 2004. Green circles: stations where the neritic community was present; red circles: stations where the oceanic community was present; black circles: stations where there was a mix of oceanic and neritic species. From Coyle et al. (2008), with permission.
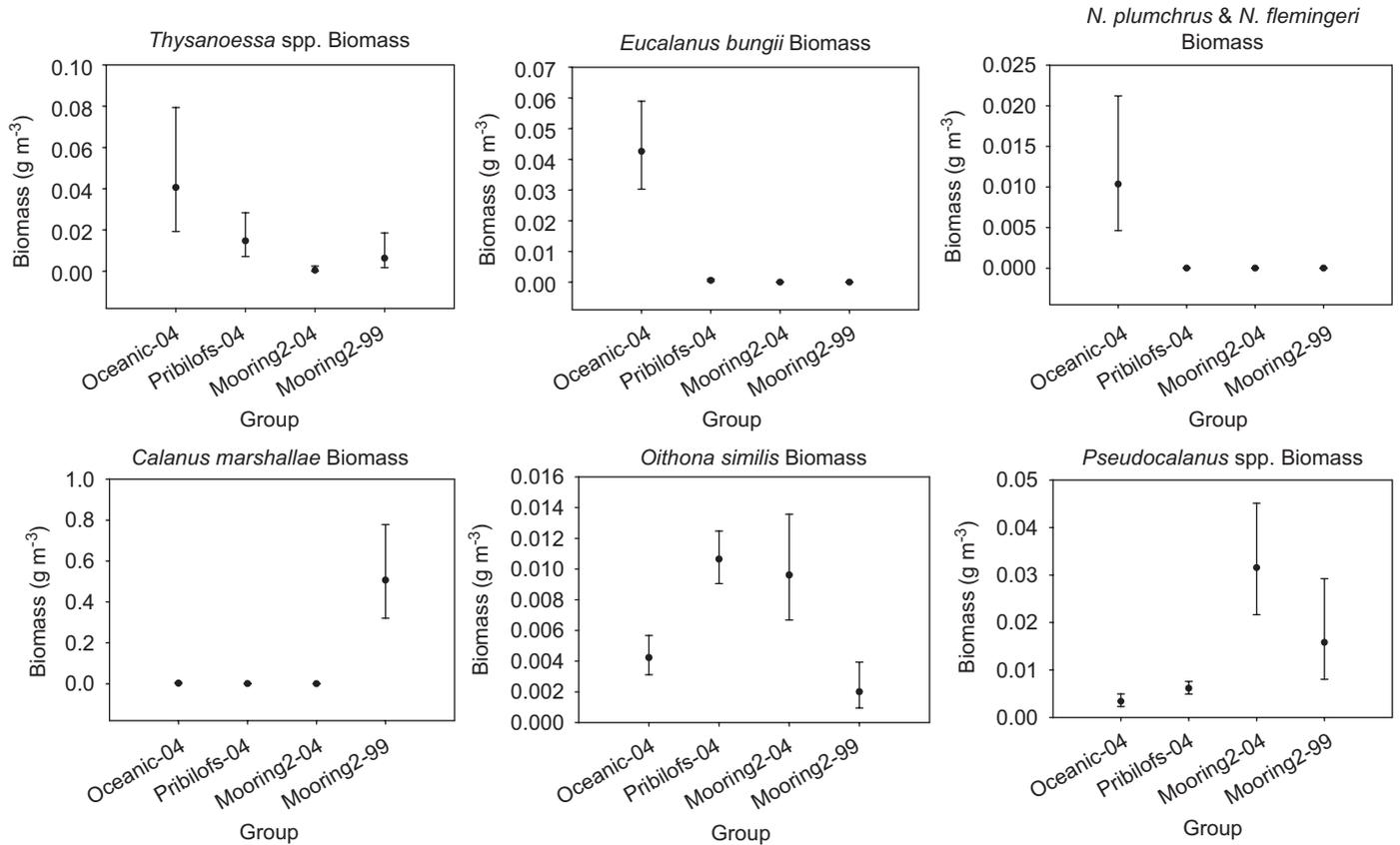
Fig. 10. Abundance of selected zooplankton species and groups in 2004 and 1999. The 1999 data come from MOCNESS tows near mooring site M2 in the southeastern Bering Sea middle shelf. Data from 2004 are from the M2 area (stations marked in green in Fig. 8), the Pribilof Domain (stations marked in black in Fig. 8) and the outer shelf domain and slope waters ("oceanic community", stations marked in red in Fig. 8). For details of the sampling, see Coyle et al. (2008). Graph courtesy of K.O. Coyle, University of Alaska, Fairbanks, AK.

Table 1
Densities of selected species of seabirds in the study area, 2004

Common name	Scientific name	Mass	Outer Domain and Basin		Between Islands		Middle Domain	
		g	Birds km²	kg km²	Birds km²	kg km²	Birds km²	kg km²
Sampling effort (km²)			368		188		167	
Short-tailed shearwater	*Puffinus tenuirostris*	543	17.7	9.6	4.2	2.3	13.9	7.5
Northern fulmar	*Fulmarus glacialis*	544	39.9	2.2	9.3	5.0	2.8	1.5
Fork-tailed storm-petrel	*Oceanodroma furcata*	48	15.4	0.7	0.7	0.0	3.9	0.2
Black-legged kittiwake	*Rissa tridactyla*	407	2.3	0.9	3.7	1.5	3.5	1.4
Red-legged kittiwake	*Rissa brevirostris*	391	1.3	0.5	3.1	1.2	0.1	0.0
Unidentified kittiwake	*Rissa* spp.	400	0.2	0.1	0.0	0.0	0.0	0.0
Common murre	*Uria algae*	993	1.9	0.5	5.4	5.4	1.0	1.0
Thick-billed murre	*Uria lomvia*	964	5.8	5.6	8.7	8.4	1.3	1.3
Unidentified murre	*Uria* spp.	985	9.5	9.3	10.8	10.6	0.3	0.3
Ancient murrelet	*Synthliboramphus antiquum*	206	0.1	0.0	0.0	0.0	0.9	0.2
Least auklet	*Aethia pusilla*	84	0.1	0.0	1.0	0.1	0.5	0.0
Crested auklet	*Aethia cristatella*	264	0.0	0.0	3.0	0.8	0.0	0.0
Parakeet auklet	*Cyclorrhynchus psittacula*	258	0.3	0.1	0.9	0.2	0.1	0.0
Horned puffin	*Fratercula corniculata*	619	0.7	0.4	1.7	1.1	0.0	0.0
Tufted puffin	*Fratercula cirrhata*	779	0.7	0.5	1.7	1.3	0.9	0.7
Total			95.9	30.4	54.2	37.9	29.2	14.1

Outer Domain and Basin—waters deeper than 100 m; Between Islands—CW–CE line from 171.4-degrees west to 169.0-degrees W, and the line north from St. George; Middle Domain—other waters <100 and >50 m depth; see Fig. 2. Body masses from Dunning (1993). (Modified from Table 1 in Hunt, G.L. (Ed.), Unpublished Cruise Report, *Alpha Helix* Cruise 288, July–August 2004, on file at the Pacific Marine Environmental Laboratory, Seattle, WA).

southeastern Middle Shelf Domain waters (29.2 birds km⁻²) (Table 1). Differences in the biomass of seabirds birds supported in the three areas sampled during the cruise were more striking, with the Middle Shelf Domain supporting 14.1 kg km⁻² of birds compared to 37.9 kg km⁻² between the islands and 30.4 kg km⁻² in the areas of the Outer Shelf and Oceanic domains. These results were not unexpected; the area between the islands and much of the Outer Shelf and Oceanic domains surveyed in 2004 are close

to the large seabird colonies on the Pribilof Islands (Byrd et al., 2008a). But, the seabird biomass distributions also track integrated chlorophyll levels and probably large-celled phytoplankton. These colonies would not be present if there were not productive waters to support them (Hunt et al., 1981; Schneider and Hunt, 1984; Springer et al., 1996).

Avian species showed conspicuous differences in their distribution among the three regions (Table 1). Murres (*Uria* spp.) dominated the waters between the islands (24 kg km^{-2}) and Outer Shelf and Oceanic domains (15.4 kg km^{-2}), whereas the short-tailed shearwater was the predominant contributor of avian biomass over the Middle Shelf Domain (7.5 kg km^{-2}), as well as an important contributor of biomass in the Outer Shelf and Oceanic domains (9.6 kg km^{-2}). The northern fulmar (*Fulmarus glacialis*) had its highest biomass between the islands (5.0 kg km^{-2}) and was also an important component of the other two regions. Unexpectedly, the red-legged kittiwake (*Rissa brevirostra*), normally a shelf edge and basin species (Jahncke et al., 2008), had its greatest biomass between the islands (0.5 kg km^{-2}). The black-legged kittiwake (*Rissa tridactyla*) had similar biomass densities over the Middle Shelf Domain and the area between the islands (Table 1). Although most planktivorous auklets had left the region by the time of our cruise, in concurrence with the hypothesis that Pribilof waters should be superior foraging grounds for planktivorous auklets (*Aethia* spp.), densities of auklets were higher in the waters between the islands than in either Outer Shelf and Oceanic Domain waters or Middle Shelf Domain waters.

The importance of large mesozooplankton to seabirds in the waters around the Pribilof Islands was seen in the summer of 2004 when a plankton-rich water mass was replaced by one depauperate in mesozooplankton. This was demonstrated when a number of drifters, drogued at 40 m and deployed in previous months in the Gulf of Alaska and the Bering Sea Outer Shelf Domain, were moving northwestward along the 100-m isobath. In early June, three of these drifters took a northward track to the east of St. George Island (Fig. 4). They remained more or less stationary until about 3 July, then began to move south and eventually to the west around the south side of St. George Island, where they rejoined the northwestward 100-m isobath flow (Fig. 4). The water that had moved northeast of St. George and then south again had apparently been rich in large oceanic copepods (*Neocalanus* spp.), as judged by diet samples retrieved from least auklets (*Aethia pusilla*) nesting on St. George and St. Paul islands (Springer et al., 2007; Benowitz-Fredericks et al., 2008). The inter-island water that exited was replaced by water from the Middle Shelf Domain, as judged by the records from moorings between the islands and drifter records (Stabeno et al., 2008; Sullivan et al., 2008). This highly stratified middle shelf water was essentially devoid of large copepods of the species normally consumed by the auklets (Coyle et al., 2008). Within days of this shift in the waters present between the islands, levels of corticosterone, a hormone related to food stress, increased dramatically in the least auklets (Fig. 11), and nest desertions by adult auklets were reported (A.S. Kitaysky, University of Alaska, Fairbanks, pers. comm.). The auklets that were between the islands when we surveyed there were concentrated in tide rips and frontal areas close to the islands and in the area of mixed water between the islands (Fig. 12). As hypothesized at the outset, least auklets at the Pribilof Islands are dependent on the availability of species of large, lipid-rich copepods. When neither the oceanic *Neocalanus* spp. nor the shelf *C. marshallae* are available, the auklets become food stressed.

The Pribilof Domain contains a number of small-scale features where seabird foraging opportunities are enhanced by interaction of tidal currents with bathymetry. As discussed above, each of the larger islands is surrounded by a structure front, and seabirds concentrate their foraging in its vicinity (Kinder et al., 1983; Schneider et al., 1990; Decker and Hunt, 1996). Kokubun et al. (2008) show that the areas of the structure front south of St. George Island and at the head of Pribilof Canyon, where murres concentrate their foraging, and are also areas where fish aggregate below the thermocline. In some years, the upper mixed layer of waters offshore of the structure front has elevated chlorophyll concentrations (Hunt et al., 1996a), and at least on occasion, euphausiids were concentrated at and offshore of the front where they were fed upon by short-tailed shearwaters (Hunt et al., 1996a). Although euphausiids may not be available to seabirds when at depth (Takahashi et al., 2008), they become available to seabirds when they are trapped at shallow depths (Hunt et al., 1988, 1996a; Coyle et al., 1992).

Murres nesting on St. George Island dive primarily to the depth of the thermocline when foraging in deeper, stratified waters, whereas in shallower, unstratified waters, foraging dives were
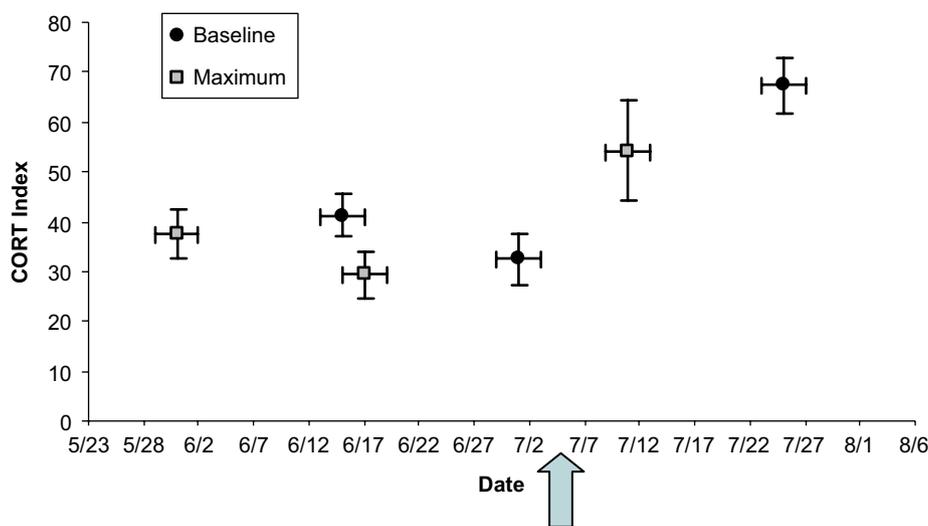

Fig. 11. Index of nutritional stress, based on circulating levels of corticosterone (mean and standard error) in least auklets nesting on St. Paul Island. Baseline corticosterone (Cort) levels are those measured within 3 min of capture, maximum levels of Cort are those measured after holding the bird for an hour. The drifters started moving south on July 3, 2004 (arrow), indicating the intrusion of warm, stratified water from the Middle Domain (see Figs. 3 and 4). Shortly thereafter, indications of nutritional stress began to increase sharply. Diets prior to July 3 were dominated by *Neocalanus* copepods, and those after July 3 by crab megalops. For methods, see Benowitz-Fredericks et al. (2008). Figure courtesy of Z. Morgan Benowitz-Fredericks and A.S. Kitaysky, University of Alaska, Fairbanks.
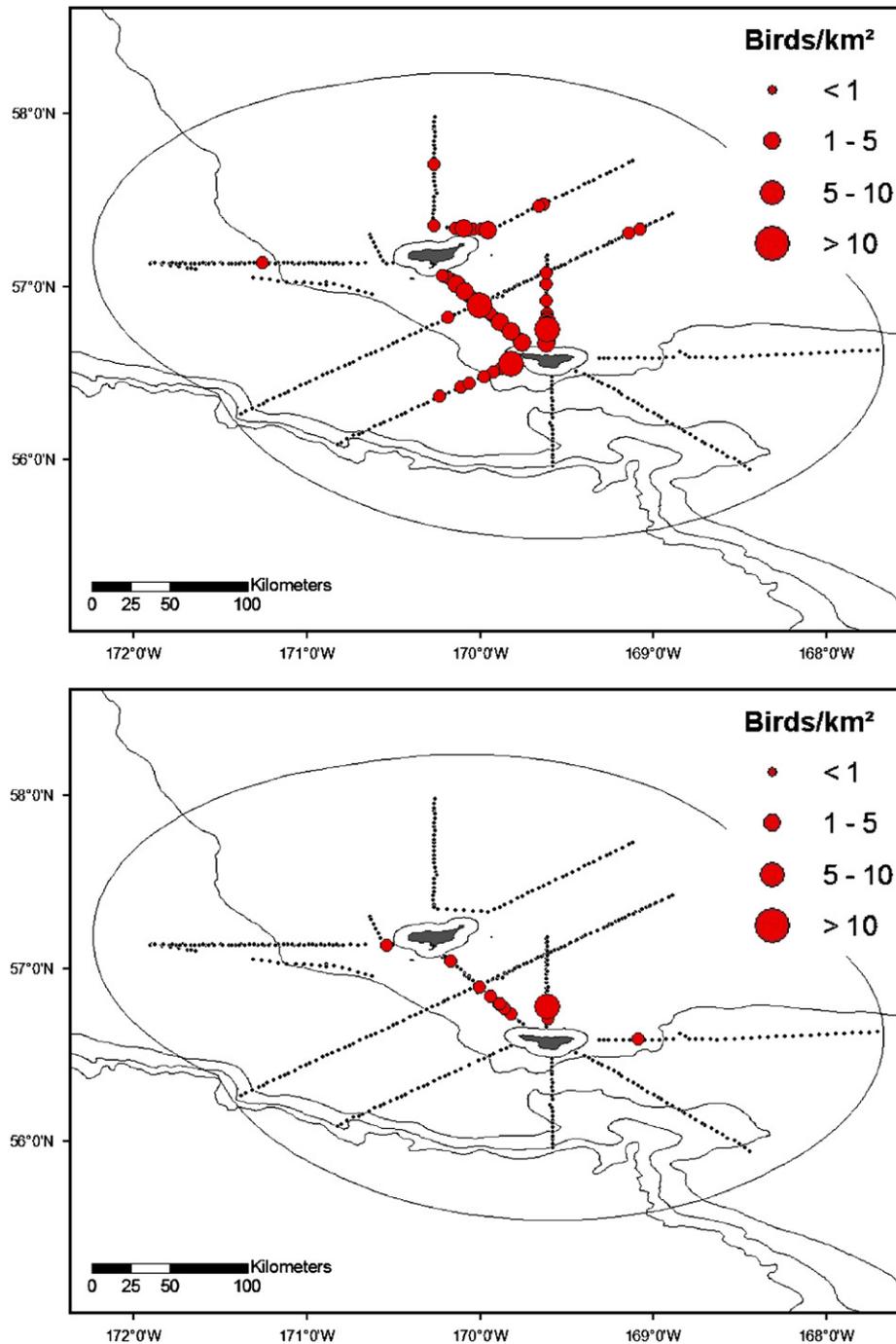
Fig. 12. Distribution of least (top) and crested auklets (bottom) in the vicinity of the Pribilof Islands during the summer of 2004. Figure courtesy of Jaime Jahncke, PRBO Conservation Science, Petaluma, CA.

frequently to the bottom (Takahashi et al., 2008). Previous work by Swartzman et al. (1999), Brodeur et al. (2000) and Swartzman and Hunt (2000) documented daytime concentrations of age-0 walleye pollock at the thermocline north of St. Paul Island, with murres foraging where fish were present in elevated numbers. Kokubun et al. (2008) provide evidence suggesting that inter-annual variation in the breeding success of murres on St. George Island may be influenced by not only the abundance of small fish, but also by their vertical distribution. The vertical distribution of prey, like their horizontal distribution, can play an important role in their availability to seabirds (Hunt et al., 1990; Russell et al., 1999).

In summary, seabirds nesting on the Pribilof Islands depend on predictable concentrations of suitable prey. Preferred prey and foraging areas differ depending on the bird species and the island on which they nest. Particularly large concentrations of seabirds are associated with small-scale features at which high concentrations of prey may be found.

3.4.2. Fur seals

It is less clear how enhanced primary production and standing stocks of zooplankton near the Pribilof Islands influence the foraging of piscivorous apex predators, such as northern fur seals, other than through trophic exchange to the juvenile fish and squid that seals consume. Conceivably, concentrations of zooplankton at frontal boundaries would lead to enhanced densities of small

forage fish consumed by seals. Female fur seals from individual rookeries use different foraging grounds on and off the continental shelf (Robson et al., 2004; Call et al., 2008). Female fur seals from rookeries on the northeast end of St. Paul Island focus their foraging over the middle shelf and appear to terminate foraging trips in the vicinity of the inner front (Call et al., 2008). In contrast, female fur seals from rookeries on the south side of St. George Island focus their foraging along the outer shelf and slope. The area between the islands is used primarily by fur seals from the Reef Rookery on the south side of St. Paul Island and by fur seals from the north side of St. George Island (Call et al., 2008). Fur seal diets also show rookery-specific differences in composition (Zeppelin and Ream, 2006). It would be of interest to know if changes in population size, pup survival or weight varied among rookeries in concert with the productivity of the water masses used for foraging.

3.5. Summary of spatial patterns observed in 2004

The large-scale spatial pattern in 2004 was much as hypothesized. The assemblage of drifter trajectories, together with hydrography, provides a physical basis for defining a Pribilof Domain (Fig. 3). The Pribilof Domain, as defined by the drifter tracks, for the most part coincides with the area where the zooplankton community showed a mix of shelf and oceanic species (i.e., the area shoreward of the 32.5 isohaline in 2004), though the Pribilof Domain as defined by the zooplankton community (Coyle et al., 2008) (Fig. 9) is somewhat larger than the domain as defined by the drifter trajectories (Fig. 3). The area of the Pribilof Domain defined by either of these criteria was smaller than that defined by Ciannelli et al. (2004). They identified an area with a 185-km radius, based on balancing energy production and consumption by organisms living on and around the Pribilof Islands, whereas the extent of the Pribilof Domain as defined by the drifters was generally less than half of that. This difference results from the trophic demand of organisms breeding on the Pribilof Islands being greater than the ability of the physical domain as defined by drifter trajectories to support them, despite its enhanced productivity. Fur seals and some seabird species must depend on the production of more distant waters (i.e. allochthanous production).

In the comparison of the Middle Shelf Domain at M2 and the Pribilof Domain, the Pribilof Domain had higher summer primary production and higher standing stocks of zooplankton, which were composed of a mixture of Outer Shelf and Middle Shelf Domain communities, as predicted. The mesozooplankton in the Pribilof Domain and Outer Shelf and Oceanic domains were dominated by large species, whereas over the middle shelf, small species dominated the mesozooplankton. An unexpected finding was the scarcity of *C. marshallae* and *T. raschii* over the Middle Shelf Domain and around the Pribilof Islands, and the increased occurrence of *C. marshallae* in the Outer Shelf Domain. The lack of large copepods and the scarcity of euphausiids in middle shelf waters undoubtedly contributed to the nutritional stress experienced by auklets when outer-shelf-derived water between the islands was replaced by Middle Shelf Domain water in early summer 2004.

The higher productivity, including new production, in the Pribilof Domain was supported by macronutrients, at least some of which were derived from the 100-m isobath flow, and local tidal stirring. However, during summer 2004, areas with high concentrations of chlorophyll in the Pribilof Domain were quite patchy, indicating the importance of small-scale, local features. Microzooplankton were found to consume about 50% of primary production; this additional trophic level was not accounted for in

the model of Ciannelli et al. (2004) and most likely would require an enlargement of their estimate of the Pribilof Domain or an increase in the advective terms necessary to balance consumption in the domain.

4. Temporal comparisons: variation and trends since the 1970s

The research conducted around the Pribilof Islands and at the M2 site prompted an examination of trends in populations of northern fur seals, seabirds and zooplankton and the physical and biophysical mechanisms that might link population changes to climate variability. For these taxa, there are time series that extend for decades (northern fur seals—back to the early 1900s, seabirds—mid-1970s, zooplankton—mid-1950s), whereas for other taxa and processes we relied on comparisons of a single cold year with extensive ice cover (1999) with a warm year in which ice cover was light and retreated early in the season (2004) (e.g., Coyle et al., 2008; Jahncke et al., 2008; Sinclair et al., 2008; Strom and Fredrickson, 2008). First, we examine changes in the populations of seabirds and fur seals breeding at the Pribilof Islands and the numbers of seabirds frequenting the waters surrounding the islands. Then, we examine the potential roles of top-down and bottom-up processes that might have affected them (Section 5).

4.1. Population trends of seabirds and fur seals at the Pribilof Islands

Seabird populations on the Pribilof Islands have shown considerable change since the 1970s (Byrd et al., 2008a) (Fig. 13). On St. Paul Island, piscivorous cliff-nesting species have declined by ∼60% (thick-billed murre) to over 75% (common murre, *Uria aalge*). In contrast, on St. George Island after an initial decline in kittiwakes (particularly red-legged kittiwakes) and murres (particularly thick-billed murres), there was an almost complete recovery to numbers similar to those reported in the 1970s (Hunt and Byrd, 1999; Thomson, 2007; Wright et al., 2007; Byrd et al., 2008a) (Fig. 13). The difference in seabird population trajectories between the islands may reflect differences in seabird access to waters of high summer productivity. Birds nesting on St. Paul Island have a greater distance to fly to reach productive "Green Belt" waters than those nesting on St. George Island (Schneider and Hunt, 1984).

The at-sea abundance of seabirds in the vicinity of the Pribilof Islands changed greatly over the years between 1977 and 2004 because of the presence of non-breeding individuals and migrant species and not necessarily in conjunction with changes in the colonies (Jahncke et al., 2008) (Fig. 14). Between the surveys in 1977 and 1978 and those in 1999 and 2004, the numbers of seabirds within about a 110-km radius of a center between the islands declined. Piscivores, including kittiwakes and murres, had high numbers in 1977 and 1978 and again in 1987 and 1988, followed by a subsequent decrease. In contrast, planktivores, including migrant short-tailed shearwaters and fork-tailed storm-petrels (*Oceanodroma furcata*), whose nesting colonies are distant from the Pribilofs, were 6 times more abundant in the 1980s than in the 1970s, and then declined to low numbers in the 1990s and in 2004.

The surge in the abundance of planktivorous seabirds in the late 1980s coincided with a period when cetaceans were more frequently observed around the Pribilofs than either earlier or more recently (Baretta and Hunt, 1994) (Table 2). In the 1980s (1987–1989), shearwaters and cetaceans were frequently concentrated over shoals of euphausiids, and prey identified from the stomachs of shearwaters collected north and east of St. Paul Island in 1989 were the euphausiid *T. raschii* (Hunt et al., 1996a).
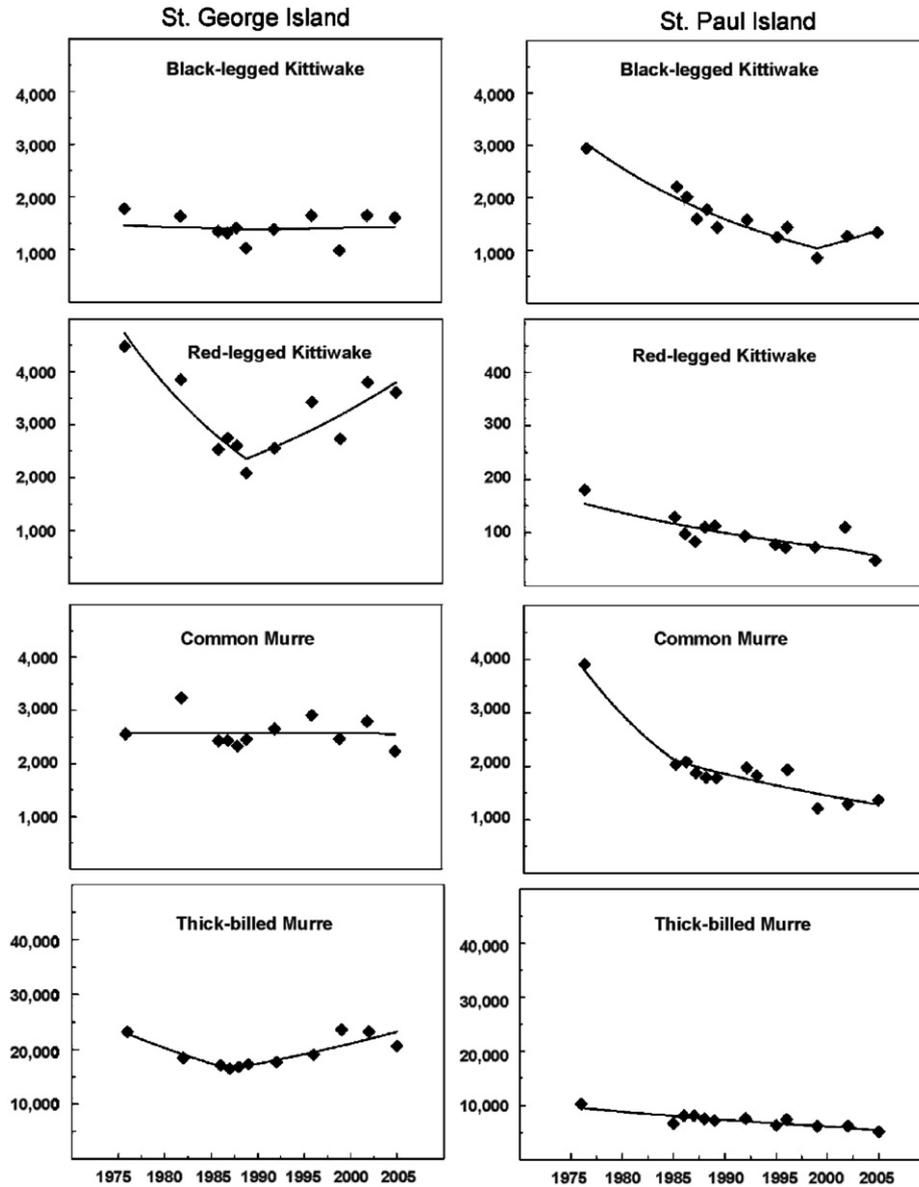
Fig. 13. Changes in numbers of kittiwakes and murres occupying nest sites on St. Paul and St. George islands, Pribilof Islands. Figure from Byrd et al. (2008a), with permission.

Why zooplankton, in particular euphausiids, were more abundant or more accessible or concentrated in the 1987–1989 period is not clear, though Jahncke et al. (2008) point out that the late 1980s was a period in which the number of planktivorous age-1 walleye pollock on the shelf was depressed (Fig. 14). This tentative negative relationship between other planktivores and age-1 pollock might be the result of competition between the pollock and the birds. Alternatively, conditions favorable to the production of abundant large copepods and shelf euphausiids are not necessarily the most favorable for the production of juvenile pollock. In the Sea of Okhotsk, there is a strong, inverse relationship between the productivity of planktivorous and piscivorous seabirds. In cold years when sea-ice cover is extensive, planktivores enjoy greater reproductive success, whereas in warm years piscivores have greater access to juvenile fish (Kitaysky and Golubova, 2000). In the southeastern Bering Sea, recruitment of pollock is enhanced in warm years with early ice retreat (Quinn and Niebauer, 1995; Mueter et al., 2006), whereas recruitment of the large copepod C. marshallae, is stronger in cold years with an

early, ice-associated bloom (Baier and Napp, 2003; Coyle et al., 2008). Interestingly, Benowitz-Fredericks et al. (2008), working on the Pribilof Islands, also found an inverse relationship between the reproductive performance of planktivorous and piscivorous alcids, with the piscivorous species having lower levels of food related stress in warm years with early ice retreat. It will be important to determine whether the scarcity of the shelf euphausiid T. raschii in 2004 was related to the lack of sea ice or the high water temperatures and unusually strong summer stratification of Middle Domain waters then.

Northern fur seals are high-trophic-level predators that consume various species of fish and squid (Antonelis et al., 1997; Zeppelin and Ream, 2006; Sinclair et al., 2008), and which, in turn, are preyed upon by killer whales (Orcinus orca) (Springer et al., 2003) and Steller sea lions (Gentry, 1998). Records of fur seal populations on the Pribilof Islands extend back to the early 1900s, and over this period they have been extensively exploited, as well as being subject to a culling of females in the 1950s that led to a severe decline in the numbers of pups being born on the islands
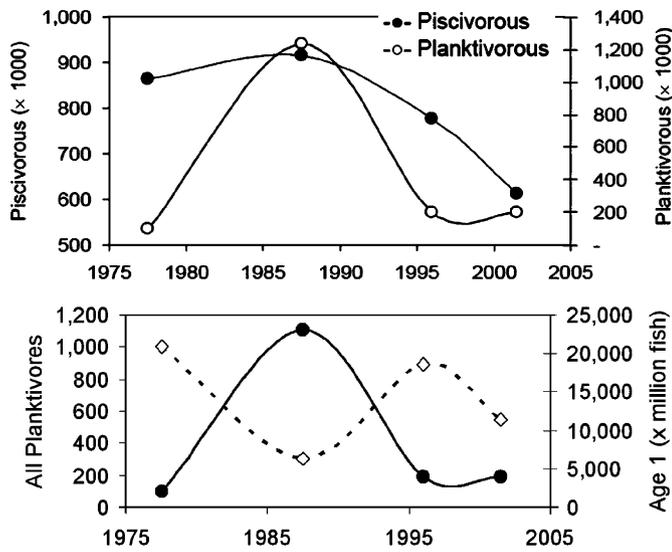
Fig. 14. Top: Changes in the numbers of planktivorous and piscivorous seabirds present in waters out to 100 km from the Pribilof Islands. Bottom: Number of planktivorous seabirds at sea out to 100 km from the Pribilof Islands vs. the abundance of age-1 walleye pollock on the southeastern shelf (Ianelli et al., 2006). Redrawn from Jahncke et al. (2008), with permission.

Table 2
Sightings of baleen whales near the Pribilof Islands made incidentally during seabird surveys in three different time periods

Study years	1975–1978	1987–1988	2004
Km Surveyed	3867	4259	2218
Minke whale *Balaenoptera acutirostris*	4	17	0
Fin whale *Balaenoptera physalus*	0	16	1
Humpback whale *Megaptera novaeangliae*	0	5	0
Unidentified whales	0	27	1
Total sightings	4	65	2
Sightings/100 km	0.08	1.4	0.09

Sightings are of one or more individuals. The methods of observation are provided in Baretta and Hunt (1994). Observations in 2004 were from the same platform (R/V *Alpha Helix*) and with one observer in common (G.L. Hunt) as those made in the 1980s. Data for 1975–1978 and 1987–1988 from Baretta and Hunt (1994); data from 2004, from G.L. Hunt, unpublished.

Fig. 15. Changes in the number of northern fur seal pups born on the Pribilof Islands (mean and standard error). Figure modified from Towell et al. (2006), with permission.

In summary, recent declines in breeding seabirds and fur seals at the Pribilofs commenced at a time in the late 1970s to early 1980s when the marine climate of the Bering Sea was changing and the biomass of adult pollock was increasing (Hunt et al., 2002). Trends in both seabirds and fur seals have differed between St. Paul and St. George islands, with seabird declines more severe and longer lasting on St. Paul Island and fur seal declines more severe on St. George Island. The at-sea abundance of seabirds in the vicinity of the Pribilofs has also varied since the 1970s, with the late 1980s having the highest overall numbers of seabirds present and the late 1990s and 2004 the lowest numbers of birds present. High numbers in the late 1980s were driven in particular by the presence of high numbers of migrant shearwaters and fork-tailed storm petrels that do not breed at the Pribilofs.

4.2. Trends in seabird reproductive performance at the Pribilof Islands since the 1970s

Since the mid-1970s, there has been considerable interannual variability in reproductive performance of seabirds nesting at the Pribilof Islands. However, with the exception of thick-billed murres on St. Paul Island, which had declining production, most cliff-nesting piscivores on St. Paul and St. George Islands showed no significant trends in productivity over the period 1976–2005 (Byrd et al., 2008b). There was significant co-variation in productivity, both between the two murre species and between the two kittiwake species, as well as co-variation within species between the islands (Byrd et al., 2008b). The productivity of the two kittiwake species has shown positive relationships with increasing sea-ice cover and negative relationships with

(York and Hartley, 1981; NMFS, 2006). Numbers of pups born began to recover in the late 1960s and early 1970s, but since the mid-1970s, the numbers of pups born on St. Paul Island and on St. George Island have declined by about 66% on St. Paul Island and 71% on St. George Island, although more recently, declines have been somewhat steeper on St. Paul Island (Fig. 15) (NMFS, 2006; Towell et al., 2006). The patterns of decline on the two islands differ somewhat, in part due to differences in the base size of the populations on each Island, and also probably due to local factors that have affected populations on the two islands differently. In contrast to the situation at the Pribilof Islands, the fur seal population on Bogoslof Island, 300 km to the southwest of the Pribilofs, although much smaller, has increased from a few tens of pups present in the 1980s to over 12,000 pups in 2005 (NMFS, 2006).
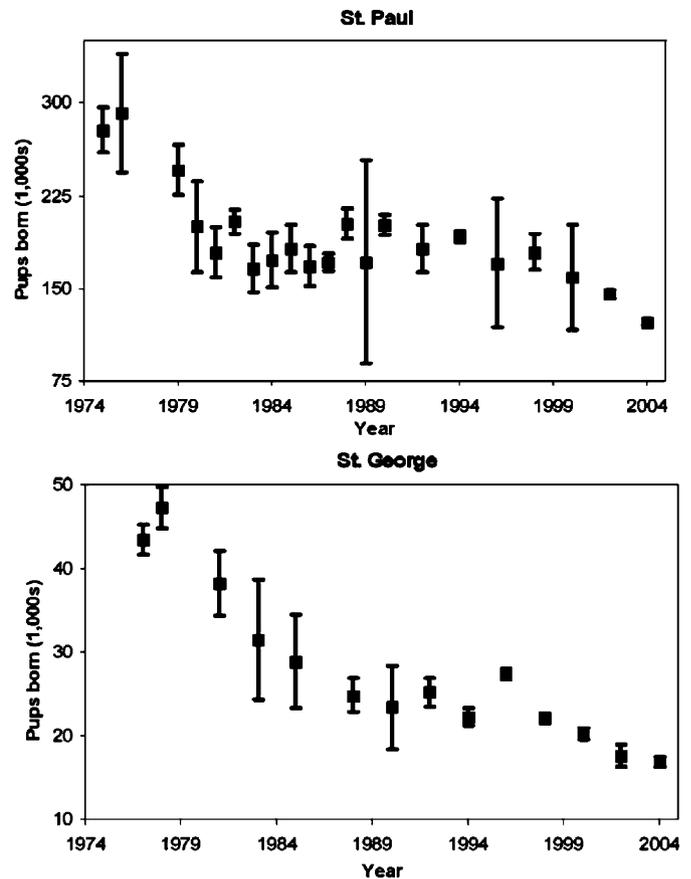
increasing spring and summer sea-surface temperatures (SSTs; Byrd et al., 2008b). Conversely, the productivity of both murre species was unrelated to ice cover or to SST in spring, though there was a negative relationship with summer SSTs.

4.3. Possible causes of "long-term" changes in seabirds and fur seals at the Pribilof Islands

The declines in numbers of seabirds breeding on St. Paul Island and in fur seal numbers on St. Paul Island and St. George Island are likely the result of some combination of top-down control by predators (possibly including disease) and bottom-up limitation from a lack of available prey. When considering bottom-up limitation, at least three different mechanisms may be at work; the amount of southeastern Bering Sea primary production may have changed, thus affecting the amount of energy available for the production of prey organisms, the amount of primary production may have remained "unchanged", but the pathways that the energy took as it passed through the ecosystem may have varied, or fisheries removals may have affected the availability of prey, at least for fur seals. These alternatives are not mutually exclusive. In the following discussion, we evaluate the evidence for two of these alternative mechanisms. We do not attempt to evaluate the potential impact of fisheries removals of pollock on the fur seals, though this remains a possible contributor to their declines and requires evaluation. Competition between seabirds and fisheries for pollock is not an issue, as the birds consume only age-0 and age-1 pollock (Hunt et al., 1996a), age classes not taken in the fishery.

4.3.1. Top-down mechanisms for controlling seabird and fur seal populations

Predation is unlikely to be a factor in controlling the population size of cliff-nesting seabirds, as there are few predators at the Pribilof Islands that pose a serious threat (Byrd et al., 2008a).

Killer whales and Steller sea lions prey on fur seals, but the impact of that predation remains unmeasured. It has been suggested that killer whale predation has been responsible for the fur seal decline (Springer et al., 2003). If killer whales are the principal cause of the decline of fur seals on the Pribilof Islands, it is not clear why they have not had a similar impact on fur seals at nearby Bogoslof Island. Because the fur seals spend much of the year in the North Pacific, it is difficult to rule out the possibility that factors unrelated to events in the Bering Sea have influenced the observed declines. The potential for both direct and indirect impacts of commercial fisheries and other anthropogenic factors also remain unmeasured and should be considered.

4.3.2. Bottom-up mechanisms for controlling seabird and fur seal populations
4.3.2.1. Changes in diets of seabirds and fur seals at the Pribilof Islands. The summer diets of seabirds in the Pribilof region have changed since the 1970s, and those of adult female fur seals at the Pribilof Islands also may have changed compared to diets in the 1960s. Over the period from 1975 to 1987, seabirds nesting at the Pribilof Islands decreased their use of age-1 pollock, capelin (*Mallotus villosus*) and the large amphipod *Themisto libellula*, whereas the use of age-0 pollock, sand lance (*Ammodytes hexapterus*) and squid increased (Decker et al., 1995; Hunt et al., 1996b, c; Sinclair et al., 2008). Results of bottom trawl surveys in the vicinity of the Pribilofs also show declines in the biomass of capelin and age-1 pollock over the same time frame (Hunt et al.,

1996c), suggesting that the diet changes reflect changes in the local availability of these prey.

Age-0 pollock and sand lance are smaller than mature capelin and age-1 pollock, and they have a lower energy density than these larger fish, thus making them poor substitutes for feeding to chicks (Hunt et al., 1996b, c, 2000; Iverson et al., 2002). For example, Baird (1990) found that in a year when black-legged kittiwakes and glaucous-winged gulls (*Larus glaucescens*) nesting near Kodiak Island switched from provisioning their young with primarily capelin to primarily sand lance, their reproductive success was significantly reduced (see also Wanless et al., 2005, 2007).

The greater diversity in the diets of seabirds at St. George Island and their ability to access several different foraging habitats (Oceanic Domain, Shelf-slope, Outer and Middle Shelf domains) may have buffered St. George seabird foraging efforts against the apparent decline in prey availability experienced by birds nesting at St. Paul Island (Schneider and Hunt, 1984; Sinclair et al., 2008). Seabird diets on St. Paul Island have been more dominated by fish (especially pollock) and less dependent on invertebrates than seabirds nesting on St. George Island (Sinclair et al., 2008). Myctophids were more prevalent and diversified the fish component in black-legged kittiwake diets at St. George Island compared to diets at St. Paul Island (Decker et al., 1995).

Unequivocal interpretation of the northern fur seal diet time series is made difficult because of variations in sample collection location and technique (Fritz and Hinckley, 2005; Gudmundson et al., 2006). However, apparent shifts in fur seal diets occurred in concert with those documented in seabird diets and temporal change-points in the consumption of prey were common to both fur seals and seabirds (sometimes negatively correlated) (Sinclair et al., 2008). Changes in the diets of adult female fur seals since the 1960s include the disappearance of capelin by the 1970s and Greenland turbot (*Reinhardtius hippoglossoides*) by the 1980s (Sinclair et al., 2008). These prey species have an affinity for cold water, and they declined in the Pribilof region while, at least in the case of turbot, shifting their distributions northward, as documented in bottom trawl surveys (Hunt et al., 1996c; NPFMC, 2006). Although the apparent increases in the use of sand lance and age-0 pollock beginning in the 1980s is a controversial issue because of a change in diet analysis methodology (Gudmundson et al., 2006), these apparent shifts in fur seal diet parallel those seen in the seabirds at the Pribilofs (Decker et al., 1995; Hunt et al., 1996b, c; Sinclair et al., 2008). Pollock and squid appear to have always been a component of fur seal prey (Fritz and Hinckley, 2005; Sinclair et al., 2008). During the 1970s, gonatid squid and pollock were the only two species that exceeded 10% frequency of occurrence in the diets; since then, pollock have continued to increase in frequency of occurrence, whereas squid may have declined. The combined patterns found in seal and seabird diets over time highlight changes consistent across predators and decades (Sinclair et al., 2008). It is worthy of note that multiplicative factor hypotheses explaining the declines in fur seal, harbor seal (*Phoca vitulina*), Steller sea lion and sea otter all implicate changes in food availability and nutrition as the leading causative factor (DeMaster et al., 2006; Trites et al., 2007a, b; Wade et al., 2007).

The pollock-dominated diets of the declining Pribilof population of fur seals contrasts sharply with the diets of the increasing population of fur seals at Bogoslof Island, where northern smoothtongue (*Leuroglossus schmidti*), and two groups of squids exceed pollock in importance in the fur seal diets (Rolf Ream presentation, posted on the National Marine Mammal Laboratory website at http://nmml.afsc.noaa.gov/AlaskaEcosystems/nfshome/presentations/, 10 August 2007). The emphasis on invertebrate and pelagic prey among Bogoslof Island fur seals is

similar to that observed on St. George Island and is a reflection of the close proximity of the two islands to the Oceanic Domain (Antonelis et al., 1997). It should be noted that negative population trajectories have been somewhat more severe on St. George Island compared to St. Paul Island, despite the enhanced consumption of offshore prey species by fur seals at St. George Island.

In summary, when taken as a whole, the available data support the thesis that there were changes in the diets of seabirds and fur seals at the Pribilof Islands that occurred between the late 1970s and the mid-1980s, a time when sea temperatures were rising and the biomass of adult pollock was increasing rapidly (Hunt et al., 2002). The changes included the loss of some cold-water species (capelin, Greenland turbot) and a shift from lipid-rich forage fish (e.g. capelin, age-1 pollock) to smaller, less lipid-rich prey (sand lance and age-0 pollock), particularly in seabirds. These trends were likely due to changes in the abundance and or distribution of preferred prey.

4.3.2.2. Mechanisms whereby changes in the prey quality or quantity might affect seabird and fur seal populations. A lack of adequate prey availability or the use of poorer quality prey may have affected reproductive success and/or post-reproductive survival of seabirds and possibly fur seals. Evidence shows that when sea-birds experience nutritional stress during the breeding season, they exhibit both impaired reproductive performance (Buck et al., 2007; Kitaysky et al., 2007), and increased post-reproductive mortality away from the colony (Kitaysky et al., 2007). Short-term doubly-labeled water experiments at the Pribilof Islands demonstrate that kittiwake parents work harder to raise their young when food is scarce (Kitaysky et al., 2000). Parent thick-billed murres nesting on St. Paul Island had higher field metabolic rates than those nesting on St. George Island, suggesting that it was harder to obtain prey for young at St. Paul Island. This suggestion was corroborated by evidence from at-sea surveys in 1987 and 1988 that murres foraged farther from St. Paul Island than from St. George Island (Kitaysky et al., 2000). By contrast, in the 1970s, Hunt et al. (1986) found that growth rates of young for both species of kittiwakes and both species of murres were higher in the smaller colonies on St. Paul Island than on St. George Island. They suggested that, at that time, competition for prey might be higher around the large colonies at St. George Island than around St. Paul Island. However, even in the 1970s, Hunt et al. (1986) found that the productivity of seabirds nesting at the Pribilof Island colonies in many cases was lower than that of the same species nesting in smaller colonies elsewhere in the Bering Sea and North Atlantic.

The declines in kittiwake and murre populations, initially at both islands and more recently only at St. Paul Island, have been too steep to be accounted for solely by reduced production of young (Hunt and Byrd, 1999; Byrd et al., 2008b). Thus, emigration and/or mortality away from the colonies are likely to be implicated in the declines. It has been suggested that stress related to the acquisition of sufficient food for provisioning of chicks and for adult needs may have caused elevated levels of corticosteroids (Kitaysky et al., 2006). This could have resulted in post-breeding mortality (Kitaysky et al., 2006, 2007). We lack both time series on stress levels in Pribilof Island kittiwakes and murres and evidence that there has been elevated post-breeding mortality caused by stress.

Although there is no information on the levels of corticosteroids required to cause pathologies in northern fur seals, there is preliminary evidence that there may be differences in corticosteroid levels in fur seals on St. Paul Island and Bogoslof Island. Analysis of corticosteroids from fur seal scats has shown elevated levels of corticosteroids in fur seals at St. Paul as compared to those at Bogoslof Island (Fig. 16) (A.S. Kitaysky, University of
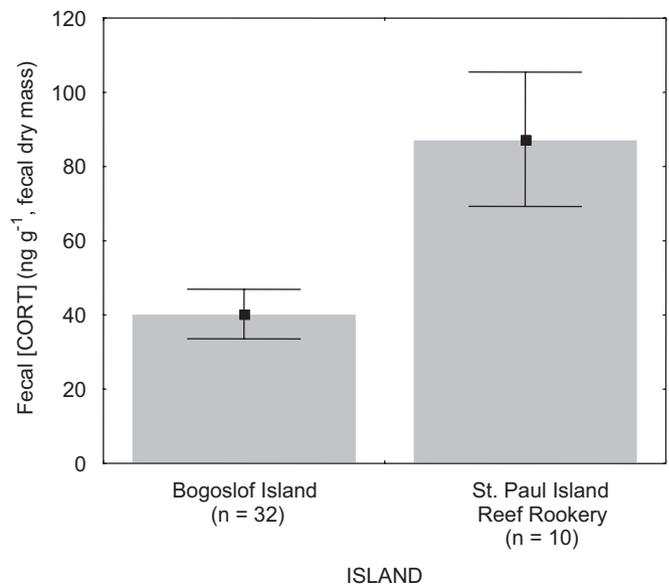

Fig. 16. Corticosterone levels (ng g^{-1}, dry fecal mass) (mean and standard error) in northern fur seal feces collected in the summer of 2000 at rookies on Bogoslof Island, where fur seal populations are increasing, and on St. Paul Island (Reef rookery), Pribilof Islands, where fur seal numbers are declining. Elevated levels of corticosterone are associated with stress, in particular, nutritional stress. Figure courtesy of Z.M. Benowitz-Fredericks and A.S. Kitaysky, Institute of Arctic Biology, University of Alaska, Fairbanks, based on unpublished data. For methods see Kitaysky et al. (2003).

Alaska, Fairbanks, unpubl. data), suggesting that fur seals on the Pribilofs may be more stressed than those on Bogoslof Island. It is possible that differences in the availability of prey have been responsible, at least in part, for the differences in stress levels for animals on the two rookeries sampled. Inadequate prey resources for fur seals during and prior to the breeding season may lead to longer foraging trips resulting in long adult absences from the pup. It is reasonable to infer that stress associated with poor foraging conditions could lead to reproductive failure or decreased post-reproductive survival of either mothers or pups. Data from a variety of taxa indicate that elevated levels of food stress (DeLong and Antonelis, 1991; Vlietstra et al., 2003) and stress hormones can compromise reproductive function and/or survival (Romero and Wikelski, 2001; Wingfield and Kitaysky, 2002; Blas et al., 2007; Kitaysky et al., 2007). Thus, if female fur seals are stressed during the reproductive season, they may experience elevated levels of corticosteroids that can depress post-breeding survival or their ability to implant or carry a fetus to term (Bradley, 1987; Romero et al., 1998; Arck, 2001; Boonstra et al., 2001; Arnould et al., 2003). It is noteworthy that stress associated with decreases in the natural availability of prey could have the same effects as reduction in prey abundance by fisheries. Thus, present data are insufficient to determine the relative contributions to the control of the fur seal populations on the Pribilof Islands of prey limitation by either natural or fisheries takes, or the assessment of the relative importance of natural or anthropogenic predation.

4.4. Summary of temporal patterns in fur seals and marine birds

The broad picture, then, is of a decline since the mid 1970s in fur seal numbers on both St. Paul and St. George Islands and in kittiwake and murre populations on St. Paul Island. For fur seals, declines have been most severe on St. George Island. In contrast, after a decline in numbers from the mid-1970s to the late-1980s, kittiwakes and murre populations on St. George Island rebuilt by

2005 to approximately the levels present in the mid-1970s. Data are lacking on the population dynamics of planktivorous auklets nesting on the islands over this period. However, in the waters around the islands, planktivorous seabirds and baleen whales were abundant in the late-1980s and less abundant during surveys in the 1970s, 1990s and 2004. Between the 1970s and 1980s, diets of fur seals and seabirds nesting on the Pribilof Islands changed, including the loss of some cold-water species (e.g., Greenland turbot, capelin, *Themisto libellula*) and a shift to younger age classes of pollock. For seabirds, changes in population size and reproductive performance are likely the result of changes in the abundance or quality of prey available within foraging range of the nesting colonies. It is unlikely that the seabird population changes are the result of predation. For fur seals the picture is less clear. They, too, appear to have experienced a change in the quality and quantity of prey available, possibly including the effects of fisheries takes, but the possibility of top-down control by predators cannot be ruled out as an additional factor (DeMaster et al., 2006; Trites et al., 2007b; Wade et al., 2007). For seabirds, the lack of food has been most severe for populations nesting on St. Paul Island. These birds forage more over the Middle Shelf Domain than those nesting on St. George Island. Interestingly, there is a positive relationship between sockeye salmon returns in Bristol Bay and Pribilof seabird reproductive success in the year when the returning salmon run went to sea (Sydeman et al., 2008). There is also a strong negative correlation between the biomass of age-3+ pollock on the shelf and kittiwake reproductive success at the Pribilofs (Hunt and Stabeno, 2002), which is similar to the negative effects of increased herring (*Clupea harengus*) populations on the reproduction of black-legged kittiwakes in the Barents Sea (Barrett, 2007). These observations suggest a strong bottom-up coupling between these top predators and their prey (see also Springer (1992) for a

discussion of the possible role of pollock as competitors for seabird and fur seal prey).

4.5. Declines in mesozooplankton over the Middle Shelf Domain in summer

4.5.1. Temporal and spatial patterns of zooplankton biomass

Data on long-term changes in the biomass of net-caught zooplankton in the Bering Sea is available from the T/S *Oshoro Maru* surveys that commenced in the 1950s (Hunt et al., 2002; Napp et al., 2002). Here we extend this time series to 2005. Though interannually variable, summer biomass of net-caught zooplankton has declined since the late 1990s in all four regions sampled (Fig. 17). While the composite wet weight biomass in 2005 is higher than in the previous 4 or 5 years, it is low relative to historical values for most years. The beginning of the most recent decline varied by domain [Basin (= Oceanic)—1998; Outer Shelf—1997, Middle Shelf 1999; Coastal Water (= Inner Shelf)—1998]. Inspection of the entire time series suggests that in several of the domains the declines may have begun much earlier (Basin—1970; Middle Shelf—1991). Zooplankton biomass in summer 2004 was comparable to some of the lowest values observed in this 50-year time series, e.g., in the late 1950s and early 1960s (Fig. 17) when Pacific ocean perch (*Sebastes alutus*) were at the peak of their abundance in the Bering Sea (Boldt et al., 2007).

Examination of time series for individual species of zooplankton shows that trajectories differed among species and regions. Summer *C. marshallae* standing stocks declined after 1999 in both the Outer and Middle Shelf domains (Fig. 18). The data also show that *C. marshallae* can be as abundant in the Outer Shelf Domain as they are in the Middle Shelf Domain. Recent trajectories of
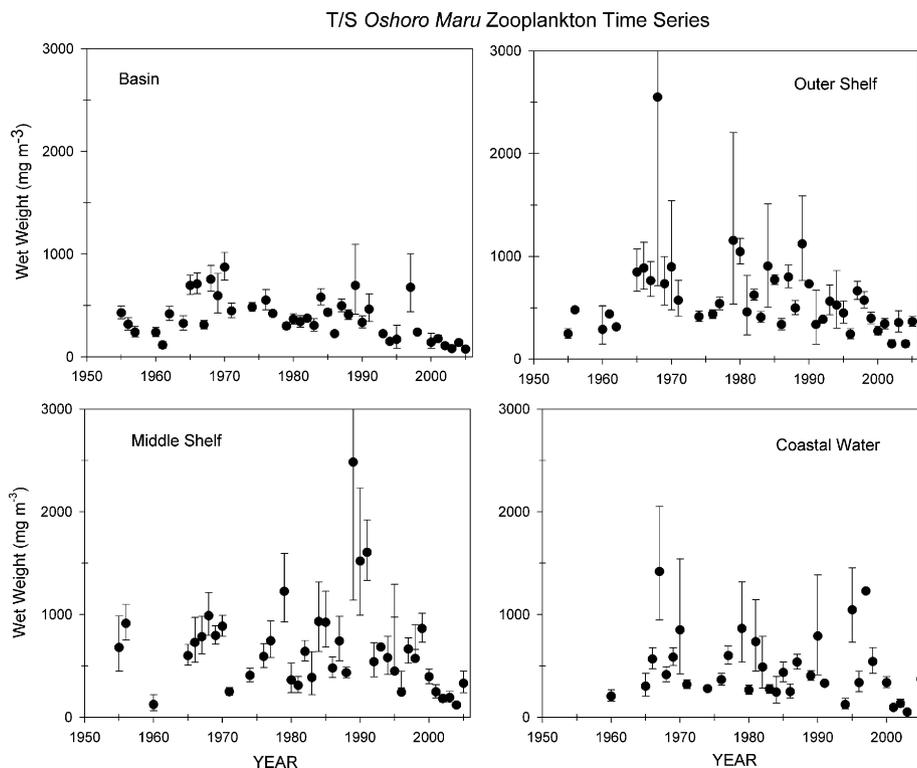

Fig. 17. Time series of wet weight biomass of zooplankton (means and standard errors), by domain, from the T/S *Oshoro Maru* zooplankton surveys, 1950s–2005 (means and standard errors). For methods, see Sugimoto and Tadokoro (1997). Data from 1977 to 1994 from Sugimoto and Tadokoro (1998). Figure modified from Hunt et al. (2002), with permission. Recent data courtesy of Dr. N. Shiga, A. Yamaguchi, and J. Napp, unpublished.
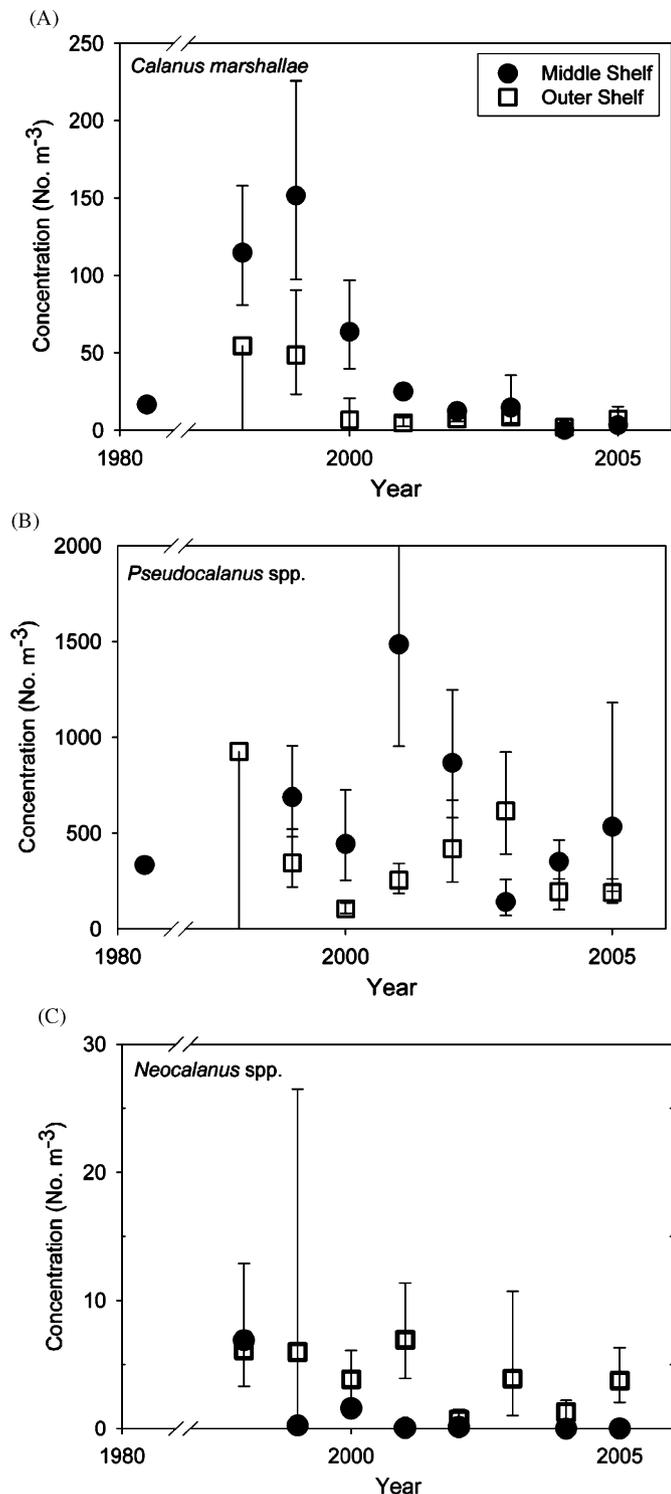
Fig. 18. Time series of selected zooplankton species sampled during summer from the T/S *Oshoro Maru* by NOAA—Alaska Fisheries Science Center in collaboration with scientists from Hokkaido University. (A) Mean (±standard error) density of *Calanus marshallae* over the Outer and Middle Shelves. The 1981 late summer mean concentration for the Middle Shelf domain was obtained from Smith and Vidal (1986), (B) Same as A, but for *Pseudocalanus* spp., (C) Same as A, but for *Neocalanus plumchrus* and *N. flemingerii* combined. J. Napp, unpublished data.

summer *Pseudocalanus* spp. densities differ from those of *C. marshallae* in that densities over both the Middle and Outer Shelf domains have been quite variable, with a recent decline in the Middle Shelf Domain after 2001 and on the Outer Shelf

Domain after 2003 (Fig. 18). Average summer densities of the oceanic *Neocalanus* spp. were low over the middle and outer shelves (Fig. 18) as expected due to its reliance on an "over-wintering" life history strategy in the basin and a seasonally earlier beginning of the diapause phase than *C. marshallae*. Due to the low summer densities and large standard errors, no trends in density of *Neocalanus* spp. could be detected during the study period.

4.5.2. Changes in southeastern Bering Sea zooplankton inferred from seabird diets

Planktivorous seabird diet data provide another way to examine changes in the distribution and relative abundance of zooplankton. In the eastern Bering Sea, four seabird species dominate avian consumption of zooplankton: the trans-equatorial migrant short-tailed shearwater, and three species that breed on Bering Sea islands, the least auklet (discussed in Section 3.4.1), the crested auklet (*A. cristatella*) and the thick-billed murre (*U. lomvia*; Hunt et al., 2000). In the southeastern Bering Sea, short-tailed shearwaters are the most abundant planktivorous seabird, and early records (from the 1970s) of their diets from north and west of the Pribilof Islands suggested that the arctic amphipod *T. libellula* was a major component of their diets (Ogi et al., 1980). Shearwaters captured in Bristol Bay at that time, however, fed almost exclusively on the euphausiid *Thysanoessa raschii*, which was also the primary prey of shearwaters from the Pribilof Islands in the late 1980s (Hunt et al., 1996a). Short-tailed shearwater summer diets in the Bristol Bay region shifted from mostly zooplankton in 1997 to predominately fish in 1998 and 1999 (Hunt et al., 2002). In the latter 2 years, euphausiids were less prevalent in the diets than crab zoea (1998) or copepods (1999). Many shearwaters in the Bering Sea starved in late summer 1997, suggesting that although euphausiids were the most important dietary item that August, they must have been in short supply or difficult to obtain (Baduini et al., 2001a, b).

In the 1970s, between 6% and 13%, by volume, of adult thick-billed murre diets at the Pribilof Islands consisted of the amphipod *T. libellula*. By the late 1980s, these amphipods were no longer being eaten by thick-billed murres at the Pribilof Islands (Decker et al., 1995), and they were also absent in plankton samples (Sugisaki et al., 1998; K.O. Coyle, University of Alaska, Fairbanks, pers. comm.). These observations suggest that the regional decline of this arctic prey species is the result of a range contraction resulting from the reduction in area covered by sea ice in the winter and spring and the warming of the southeastern Bering Sea.

Springer et al. (2007) show that *C. marshallae* was an important component of least auklet diets at St. Paul Island in July of 1997, 2000, 2001 and early July of 2005, but was largely absent from their diets there in 1996, 1998, 2002, 2004 and 2006. Some of this variability likely reflects differences in advective regimes around the islands and the transport of *C. marshallae* to the island waters. However, the absence of *C. marshallae* in years with early ice retreat and the lack of an ice-associated early bloom (2002, 2003, 2004) also may have reflected poor recruitment of *C. marshallae* over the Middle Shelf Domain in those years, as would be expected from the work of Baier and Napp (2003). Interestingly, 2005 was also a year of early ice retreat, but the auklet diets reflected an abundance of *C. marshallae* near St. Paul Island that year, though not in 2006 when there was an early bloom.

In summary, evidence from zooplankton biomass indices and seabird diets suggests significant declines in meso- and macro-zooplankton biomass and changes in species composition over the southeastern Bering Sea shelf, and a decline in an arctic species of amphipod.

5. Mechanisms that might explain the interannual temporal patterns

The climate of the Bering Sea is influenced by forcing from mid-latitude atmospheric patterns and by those from the Arctic (Overland et al., 1999, 2002). Although considerable attention has been paid to decadal-scale climate variability in the North Pacific Ocean (e.g., Hare and Mantua, 2000), the southeastern Bering Sea is most sensitive to climate signals at seasonal and annual scales as opposed to those at longer time scales (e.g., decadal-scale "regime shifts") (Bond and Overland, 2005). Thus, it is instructive to examine mechanisms that may have affected the interannual variability in prey availability to upper trophic level predators including direct responses to changes in temperature, changes in bottom-up processes including primary production, and changes in top-down forcing. We exploit the striking differences in ice cover and summer hydrography in 1999 and 2004 to examine differences in lower trophic level responses to physical conditions. Finally, we relate the patterns observed to recent ideas about the relative importance of top-down and bottom-up forcing of this ecosystem.

5.1. Effects of changes in sea-ice extent, duration and timing of retreat

The extent, quality, duration and timing of seasonal sea-ice cover over the southeastern Bering sea shelf is strongly affected by regional climate forcing, especially the timing and strength of northerly wind events that advect the ice southward from the northern shelf (Hunt et al., 2002). This seasonal sea-ice cover affects the timing, and possibly the duration, magnitude and fate of the spring bloom, as well as spring and summer water temperatures below the seasonal thermocline in the Middle Shelf Domain. The near-bottom temperatures, in turn, affect the degree of water-column stratification and the suitability of demersal habitats for fish intolerant of low water temperatures.

5.1.1. Effects of timing of the spring bloom on zooplankton

The timing of sea-ice retreat in spring, coupled with the cessation of winter storms, appears to have an important effect on the timing of the spring bloom (Stabeno et al., 1999a, 2001; Hunt et al., 2002; Stabeno and Hunt, 2002). An early ice retreat prior to the cessation of strong wind mixing results in a delayed spring bloom that can occur as late as mid-May or even June, after solar heating has sufficiently stratified the water column such that phytoplankton receive adequate light. This "late" bloom occurs in "warm" water ($3–5\,^{\circ}C$). Since water-column stability is initially weak, there is the potential for repeated mixing events and a prolonged bloom in the late spring. Alternatively, if the ice remains sufficiently late in the spring, a drop in storm activity may allow the shallow ($<3\,m$) layer of water freshened by ice melt to stabilize the water column sufficiently to allow an ice-associated bloom to commence (Alexander and Niebauer, 1981; Niebauer et al., 1990, 1995; Hunt et al., 2002). Ice-associated blooms occur over the southern shelf when sea-ice cover is present after late March in "cold" water (-1.7° to $2\,^{\circ}C$).

The timing of the spring bloom may be critical for the production of zooplankton species that play a vital role in repackaging primary production into particles of a size exploitable by large planktivorous fish, cetaceans and seabirds. For example, the spring dynamics of C. marshallae, the only "large" copepod of the Middle Shelf Domain, are related to the availability of an early bloom and thus indirectly to the timing of sea-ice retreat (Baier and Napp, 2003). The estimated time of appearance of C1 copepodites occurred earlier in years when sea ice extended farther to the south and the spring phytoplankton bloom was earlier. The concentration of Calanus copepodites in May was also higher in years when the ice extended farther south (Baier and Napp, 2003). More recent data show low C. marshallae biomass values in summer during warm years relative to the cold or cool years of 1999 and 2000, and not much different than an earlier summer value in the warm year of 1981 (Fig. 18) (Smith and Vidal. 1986). The recent absence of C. marshallae in the southeastern Bering Sea Middle Shelf Domain (Figs. 10 and 18; Coyle et al., 2008) may be directly linked to the lack of seasonal sea ice and absence of an early, ice-associated bloom in the region.

5.1.2. Effects of water-column temperatures on zooplankton

The decrease in sea-ice cover in 2000–2005 resulted in increased water temperatures in the Middle Shelf Domain of the southeastern Bering Sea (Stabeno and Overland, 2001; Schumacher et al., 2003; Overland and Stabeno, 2004); average summer water-column temperature over the Middle Shelf Domain was approximately $3\,^{\circ}C$ warmer in 2004 and 2005 than in 1995 (Stabeno et al., 2007) and $4–5\,^{\circ}C$ warmer in summer 2004 than summer 1999 (Coyle et al., 2008; Strom and Fredrickson, 2008). Increased temperatures can affect zooplankton populations in many ways: decreased generation times, smaller size at stage, and increased number of generations per year. Species near their upper thermal limit may be unable to survive, and there can be shifts in community structure towards smaller zooplankton species. This shift may, in part, reflect a shift toward smaller species of phytoplankton as sea temperatures rise (Hare et al., 2007). For taxa such as Pseudocalanus spp. that reproduce multiple times during the year, decreased development time might allow an additional generation, while for taxa that normally have a single generation in the southeastern Bering Sea (e.g., C. marshallae, Neocalanus spp., Thysanoessa spp.), faster development may mean an earlier retreat from the surface layer (and an earlier entry into diapause for Neocalanus and Calanus).

Earlier retreat of large species of zooplankton, such as C. marshallae, Neocalanus spp. and Thysanoessa spp., from the surface layers may create a mismatch between the food needs of predators and the availability of prey (Coyle and Pinchuk, 2002; Springer et al., 2007), particularly for juvenile pollock that need to accumulate large nutritional reserves to survive the winter (Sogard and Olla, 2000; Buchheister et al., 2006). Large crustacean zooplankton are also important for adult pollock that are facultative planktivores (about 70% of their diets are crustacean zooplankton, e.g. NPFMC, 2006), for planktivorous seabirds (e.g., least auklets, see Section 3.4.1) that require abundant large copepods in late July and early August (Springer et al., 2007; Benowitz-Fredricks et al., 2008), and for the endangered, summer-foraging North Pacific right whale (Eubalaena japonica) (Tynan, 2004; Tynan et al., 2001).

5.2. Have there been changes in summer production?

The frequency of direct measurements of primary production in the Bering Sea is not sufficient to create a time series. Schell (2000) and Hirons et al. (2001), however, have hypothesized, based on results from the analysis of stable isotopes of carbon ($\delta^{13}C$) in the tissues of marine mammals, that there has been a significant decrease in primary production rates in the eastern Bering Sea. Others questioned this interpretation (Tortell et al., 2000; Gervais and Riebesell, 2001; Smith et al., 2002), and suggested alternate mechanisms for a change in carbon isotope ratios that would not involve a change in the overall rate of primary production. More recently, Newsome et al. (2007) investigated $\delta^{13}C$ in the teeth of juvenile male fur seals at the

Pribilof Islands and found a ~1.1% decline in $\delta^{13}C$ values between 1948 and 2000. They concluded that this decline was best interpreted as being driven by anthropogenically forced changes in upper ocean carbon reservoirs and *not* (italics theirs) by a decline in primary productivity in the eastern Bering Sea or western Gulf of Alaska. They, however, did detect short-term, low-amplitude oscillations in both $\delta^{13}C$ and $\delta^{14}N$ of about 20–25 years that were roughly in phase through time, suggesting the possibility of oscillating, decadal-scale changes in the marine environment. Indirect estimation of total production, and even new production, using depletion of water-column nitrate over the production season is not feasible because of the variable but potentially heavy dependence on regenerated production and the remineralization of ammonium in bottom sediments (Rho and Whitledge, 2007).

Changes in post-bloom production that would affect the temporal availability of zooplankton prey in summer have received less attention. Storms, described as the operative mechanism promoting new production over the shelf during the summer (Sambrotto et al., 1986), are currently much less frequent and less intense (Stabeno and Overland, 2001). Coyle et al. (2008) determined that the stratification of the Middle Shelf Domain in the summer of 2004 was 2.5 times stronger than in 1999. Nutrient enrichment experiments in the summers of 1999 and 2004 showed that phytoplankton growth rates were severely nutrient limited in 2004, but not in 1999 (see Figs. 10A and B in Strom and Fredrickson, 2008). Thus, the combined effects of decreased mixing and stronger stratification would be to decrease the amount of annual new production. The combination also would decrease the fraction of total new annual production that occurs outside of the spring and fall blooms and away from the frontal regions that maintain elevated production throughout the summer (Sambrotto et al., 2008). The reduction of summer production would also be expected to reduce food availability for hebivorous zooplankton and thus their biomass in the upper water column.

Microzooplankton are an important and sometimes dominant prey of mesozooplankton (Stoecker and Capuzzo, 1990; Fessenden and Cowles, 1994; Liu et al., 2005), and microzooplankton can consume over 50% of marine primary production, even in productive shelf ecosystems (Strom et al., 2001; Calbet and Landry, 2004; Strom and Fredrickson, 2008). The reduced primary production of 2004 resulted in a >50% reduction of microzooplankton grazing rates when compared to 1999, despite comparable biomasses of microzooplankton in both years (Strom and Fredrickson, 2008). Although it is not known why the grazing rates were reduced, the reduction likely resulted in reduced microzooplankton growth in 2004 relative to 1999. Microzooplankton provide an efficient pathway of energy flow to mesozooplankton, especially when small cells dominate the phytoplankton community (Gifford, 1993; Fessenden and Cowles, 1994; Liu et al., 2002, 2005); a reduction in their growth would be expected to reduce trophic transfer to mesozooplankton. Unfortunately we know little about the diets of dominant Bering Sea mesozooplankton species. The questions of how climate impacts primary production and how microzooplankton affect mesozooplankton in the eastern Bering Sea remain open.

6. Ecosystem implications of climate-forced changes

The temporal and spatial scales of physical attributes of the ocean are intimately related (Stommel, 1963), as are the life spans of organisms and the spatial extent of their lifetime movements (Steele, 1976; Haury et al., 1978; Hunt and Schneider, 1987; Moore, 2005). The potential match or mismatch of temporal scales of physical processes and biological requirements is a critical issue that is exacerbated when climatic changes cause organisms to be out of phase with their environment (Durant et al., 2007). Perhaps underestimated is the importance of event-scale phenomena such as major storms (Moore, 2005). Storms are predicted to increase in the Bering Sea (Salathe, 2006), and they will likely affect timing of ice retreat and the spring and summer stratification of the water column (Sambrotto et al., 1986, 2008; Stabeno et al., 2001; Hunt et al., 2002). Storms also may affect trophic transfer through enhancement or disruption of feeding by plankton and larval fish (Rosthchild and Osborn, 1988; MacKenzie et al., 1994; Mackenzie and Kiørboe, 2000; Peters and Marrasé, 2000). When storms disrupt avian foraging for longer than some critical time limit, starvation may result (e.g., Braun and Hunt, 1983).

The predominate temporal scale of variability in the eastern Bering Sea climate is at periods from seasons to years (Overland et al., 2002; Bond and Overland, 2005). However, the temporal scale of responses of organisms varies from behavioral responses at the scale of seconds to minutes or hours, up to life history responses that may extend over decades in the case of long-lived species. One can then expect that population responses are likely to lag changes in behavior and productivity, particularly for long-lived species that stay away from island rookeries until the delayed age of reproductive maturity. It is also possible that prolonged periods with very weak recruitment may lead to future recruitment failures for lack of a sufficient spawning biomass. These lags in population responses complicate the task of identifying the critical relationships between components of the ecosystem.

6.1. Effects of water temperature on fish distributions over the shelf

Changes in water temperatures have the potential to alter the distribution of fish and their top-down effects on the ecosystem. Recently, Mueter and Litzow (2008) have shown that changes in the size of the cold pool, a large cold ($<2\,^{\circ}C$) body of near-bottom water on the middle shelf resulting from the melting of sea ice, have affected a number of demersal fish species. There was a community-wide northward shift (mean $34\pm56\,km$ SD) and the average catch per unit effort (CPUE) increased in the north relative to the south. In 1982, the CPUE south of $59\,^{\circ}N$ exceeded the catch north of that parallel by 73%, whereas in 2006, the difference was reduced to 26%. Mueter and Litzow (2008) found that sub-arctic taxa near the northern limits of their range have moved northward to areas formerly occupied by the cold pool. However, these shifts are not always recognizable at a local scale; to date, there are no clear impacts on the distribution of halibut around the Pribilof Islands that can be tied to climate variability, though the data available to test this hypothesis are few (Loher, 2008). The results of the analyses of Mueter and Litzow (2008), as well as evidence from seabird and fur seal diets at the Pribilof Islands presented earlier (summarized in Section 4.4), also show that arctic species have declined in the southeastern Bering Sea, suggesting an on-going shift from an arctic to a sub-arctic community. These shifts include crab species that no longer are showing strong recruitment in what were the former centers of their distributions or that have moved north with the warming bottom temperatures (e.g., Orensanz et al., 2004; Loher and Armstrong, 2005). Grebmeier et al. (2006) point out that, as demersal groundfish shift northward, one can expect significant changes in the species composition and biomass of benthic communities that previously had been protected from groundfish exploitation by the presence of the cold pool. Changes in the availability of benthic prey in the northeastern Bering Sea to migratory species, such as grey whales (*Eschrichtius robustus*) already have been observed (Coyle et al., 2007).

Mueter and Litzow (2008) also show that there has been a shoaling in the depth distribution of demersal fishes, indicating that fish were not only shifting northward, but also farther onto the shelf. In the mid-1990s, it was realized the distribution of young pollock may be impacted by near-bottom temperatures over the middle shelf of the southeastern Bering Sea (Ohtani and Azumaya, 1995; Wyllie-Echeverria, 1995). They found that age-1 pollock shifted their distributions from the middle shelf to the outer shelf when there was an extensive cold pool. They hypothesized that, when the distributions of age-1 pollock overlapped that of adults, there was a greater likelihood of cannibalism, the source of 40–76% of age-0 and age-1 mortality in the southeastern Bering Sea (Dwyer et al., 1987; Bailey, 1989; Livingston and Lang, 1996; Wyllie-Echeverria and Wooster, 1998). Mueter et al. (2006) investigated the relationship between the extent of the cold pool and the exposure of age-1 pollock to cannibalism. They found that there was no significant relationship between juvenile mortality from cannibalism and cold pool size because there was little correlation between cold pool size and spatial overlap between juveniles and adult pollock. However, there was a strong relationship between cannibalism and the overlap of adult and juvenile pollock on the shelf (Mueter et al., 2006). Increased cannibalism could affect the availability of age-1 pollock to fur seals and seabirds, either by consumption, or by causing the juvenile fish to change their vertical distribution, thereby becoming unavailable to seabird predators (Springer, 1992; Sogard and Olla, 1993; Decker et al., 1995; Hunt et al., 1996b, c).

6.2. Changes in the trophic organization of Bering shelf ecosystems

6.2.1. Changes in the destination of biological energy

A basic assumption of the Oscillating Control Hypothesis (OCH) (Hunt et al., 2002; Hunt and Stabeno, 2002) is that, in warm years, zooplankton production would be higher than in cold years and that more energy would go into the pelagic system, whereas in cold years, zooplankton production would be lower, and energy would flow predominately to the benthos (Walsh and McRoy, 1986). The favoring of energy flow to pelagic copepods in warm years appears true for small shelf species of copepods, such as *Pseudocalanus* spp. and *Acartia* spp., but not for the larger *C. marshallae*, which requires an early, possibly ice-associated bloom (Baier and Napp, 2003). Additionally, in cold years there may be a temporal mismatch between spring-spawned larval fish and their zooplankton prey (Napp et al., 2000).

Age-1 pollock survival shows an abrupt decline when ice cover over the central and southeastern shelf remains above 20% in early May (Mueter et al., 2006). Thus, when late ice retreat favors energy flux to the benthos, fish in the pelagic realm are also disadvantaged. New analyses suggest that the premise that the benthic and pelagic systems are out of phase in their acquisition of energy may be correct (Mueter et al., 2006, 2007). They report that stock-recruit residuals of gadids (mostly pollock and Pacific cod, *Gadus macrocephalus*) were out of phase with those of shelf flatfishes (Pleuronectidae). Thus, climate may be driving a match or mismatch between trophic levels that results in a shift in the fate of particulate material and energy between the pelagic and benthic systems (Hunt et al., 2002; Durant et al., 2007).

6.2.2. Changes in trophic levels with warming

The recent period of warm temperatures and little sea-ice cover has resulted in a shift in the size composition of the crustacean zooplankton, with small species replacing larger species (Section 4.5 above). The small species of shelf copepods are important prey for age-0 pollock less than about 60 mm;

however, after the pollock reach a length of 60 mm, larger prey such as euphausiids, crab megalopae, fish larvae, and chaetognaths become a larger fraction of the total weight of prey found in pollock stomachs (Schabetsberger et al., 2000, 2003). In 2004, the predominant prey for age-0 pollock were small copepods (Coyle et al., 2008). It is not yet known whether the absence of *C. marshallae* in warm years results in poor growth and reduced early survival of pollock. However, because adult pollock are facultative planktivores and shift to piscivory when preferred large zooplankton are unavailable (Cooney et al., 2001), a lack of large crustacean zooplankton on the shelf would be expected to result in a shift in pollock diets toward increased cannibalism when the adult and juvenile distributions overlap. These shifts in diet are likely to take place over shorter time scales than those envisaged in the original formulation of the OCH (Hunt et al., 2002). Recent work in Japan suggests that control of pollock recruitment may vary between top-down and bottom-up over fairly short time scales (Shida et al., 2007). Mueter and Litzow (2008) report that the mean trophic level of survey catches over the southern and central shelf has increased, suggesting the possibility that top-down control of the ecosystem may be increasing. The negative correlation between kittiwake reproduction at the Pribilof Islands and the biomass of adult pollock on the shelf may also indicate top-down control of intermediate trophic levels on the shelf (Springer, 1992; Hunt and Stabeno, 2002, see also Barrett, 2007). This relationship may be the result of competition for shared prey (small fish), changes in the behavior of juvenile pollock in the presence of predators (Sogard and Olla, 1993), or some other factor that has varied in concert with pollock biomass. Similarly, invertebrate predation also may increase during warm periods. Baier and Terazaki (2005) observed that in their "warm" year, planktivorous chaetognaths, a "gelatinous" zooplankton, had their highest densities (but were smaller). These results support the possibility of a major community reorganization as one result of climate change (Conners et al., 2002; Hunt et al., 2002; Grebmeier et al., 2006; Litzow and Ciannelli, 2007).

7. Summary and conclusions

It is clear from the findings in this special issue that the waters of the Pribilof islands constitute a unique domain; the flow of material and energy there differs from that in the Middle Shelf Domain. Its responses to climate change will likely also differ. Our new results allow a characterization of the Pribilof Domain that can serve as a foundation for scientific endeavors and deliberations in management and policy communities. Elevated nutrient supply, summer post-bloom primary production, and advection of large zooplankton differentiate the Pribilof Domain from the rest of the Middle Shelf Domain. These differences help to sustain populations of fish in the region, and marine mammals and seabirds breeding on the Pribilof Islands. These differences are supported by a combination of on-shelf flow and subsequent distribution of shelf-slope water across the shelf and local vertical mixing by winds and tidal currents. A combination of baroclinic structure and interaction of tides with bathymetry result in circulation around the islands. In addition, there are localized "hot spots" where the interaction of tidal currents and bathymetry result in mixing of nutrients from below the pycnocline into surface waters.

We have also documented both long- and short-term variability in ecosystem components from zooplankton to fish, seabirds and marine mammals. Perhaps most importantly, we have documented a recent marked decline in the large copepod, *C. marshallae* and the shelf euphausiid, *T. raschii*, in Middle Shelf Domain waters. We also have seen a decline in the abundance of

the large arctic amphipod, *Themisto libellula*. These changes mark a shift in the recent warm years from a fauna dominated by large cold-water species of zooplankton to one in which small, warm-water species dominate. This shift is likely to negatively impact marine birds and cetaceans dependent upon these large zooplankton and on the small fish that use these plankton for prey. This loss of the mid-section of the food web also will impact the species of commercial fish that depend on copepods and euphausiids in the southern Middle Shelf Domain.

In response to changes in water temperature or the availability of prey, fish species may shift their distributions farther north, where waters still have seasonal ice cover (Mueter and Litzow, 2008), or they may concentrate in the outer regions of the shelf that appear to be less influenced by warming and the loss of sea ice. In the absence of sea ice, physical mechanisms at the shelf edge still exist to supply nutrients to surface waters. It is not yet clear what the effects will be on the seabird and fur seal populations on the Pribilof Islands, or on the Aleut people who live there and depend on the bounty of the sea for their livelihood. However, if prey resources for the breeding populations of fur seals and seabirds decline, we can expect further declines in their populations, and or the establishment of new colonies/rookeries on other islands in more favorable locations. New research must focus on the mechanisms whereby sea ice and storm events determine the timing and magnitude of ecologically important events, and the roles of sea temperatures and the strength of summer stratification. We need to learn how these aspects of the marine environment influence the transfer of energy to top predators including seabirds, marine mammals, and commercially important fish and shellfish. These top predators have provided an early indication of major on-going changes taking place in the marine ecosystem of the eastern Bering Sea.

Acknowledgments

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