ADVECTION, PELAGIC FOOD WEBS AND THE BIOGEOGRAPHY OF SEABIRDS IN BERINGIA

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SUMMARY

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Despite its great distance from productive shelf-edge habitat, the inner shelf area of the Bering Sea, from St. Lawrence Island to the Bering Strait, supports a surprisingly large number (>5 million) of seabirds during summer, mostly small plantivorous auklets (65%) and large piscivorous murres (19%) and kittiwakes (5%). This paradox of seabird biogeography is explained by the Anadyr "Green Belt" - a current that advects nutrients and plankton over 1200 km from the outer Bering Sea shelf-edge to the central Chukchi Sea. Turbulent upwelling of this nutrient-rich water at Anadyr and Bering straits further enhances high levels of primary production (360 gC $m^{-2}y^{-1}$) and helps sustain the enormous biomass of zooplankton entrained in the Anadyr Current. Primary production in adjacent waters of the Chukchi Sea (420 gC $m^{-2}y^{-1}$) exceeds that observed below Bering Strait, and zooplankton are equally abundant. Auklets account for 49% of total food consumption below Bering Strait (411 mt d^{-1}), whereas piscivores dominate (88% of 179 mt d^{-1}) in the Chukchi Sea. Of 2 million seabirds in the Chukchi region, auklets (6%) are supplanted by planktivorous phalaropes (25%), and piscivorous murres (38%) and kittiwakes (15%). Average carbon flux to seabirds (0.65 mgC $m^{-2}d^{-1}$) over the whole region is more typical of upwelling than shelf ecosystems. The pelagic distribution of seabirds in the region appears to be a function of advection, productivity and water column stability. Planktivores flourish in areas with high zooplankton concentrations on the edge of productive upwelling and frontal zones along the "Green Belt", whereas piscivores avoid turbulent, mixed waters and forage in stable, stratified waters along the coast and in the central Chukchi Sea.

Keywords: Bering Sea, Chukchi Sea, seabird, auklet, murre, zooplankton, production, Green Belt, planktivore, piscivore, food web, carbon flux, Alaska, North Pacific

INTRODUCTION

The continental shelf of the northern Bering Sea and Chukchi Sea- encompassing Bering Strait- constitutes the largest shelf sea and one of the most productive biological regimes in the world (Coachman & Shigaev 1992). Northward flow of nutrient-rich oceanic water in the Anadyr Current, which originates far to the south, in the basin of the Bering Sea, promotes extremely high primary productivity and transports great numbers of oceanic zooplankton across the western and central portion of the region (Springer *et al*. 1989, Springer & McRoy 1992). The northward advection of nutrients and biomass, or "Green Belt" (Springer *et al*. 1996), in turn sustains a huge biomass of benthic invertebrates (Grebmeier *et al*. 1988), marine mammals (Frost & Lowry 1981) and seabirds (Springer *et al*. 1987) in the region. This rich oceanic environment contrasts with the relatively impoverished coastal zone of the eastern shelf, which owes its' character to the nutrient-poor water advected north in the Alaska Coastal Current (Coachman *et al*. 1975). Food web productivity and species diversity are both low by comparison to the oceanic regime (Springer *et al*. 1987, 1989, Grebmeier *et al*. 1988, Springer & McRoy 1992).

The feeding ecology of seabirds and their pelagic distribution in relation to local oceanographic features of this region have been reasonably well described (Bedard 1969, Springer *et al*. 1984,

Springer & Roseneau 1985, Piatt *et al*. 1990a, 1991, 1992; Harrison 1990, Hunt & Harrison 1990, Hunt *et al*. 1990, Haney 1991, Schauer 1991, Elphick & Hunt 1993, Russell *et al*. 1999). In the first overview of seabird ecology for the region, Springer *et al*. (1987) showed that two distinct environmental settings in the northern Bering-Chukchi ecosystem lead to characteristic pathways of energy flow through pelagic food webs to avian consumers. The diversity and abundance of nesting seabirds are much higher in the western region dominated by oceanic water, than in the eastern region dominated by coastal water. For example, some of the largest colonies in the world of primarily planktivorous Least Auklets *Aethia pusilla*, Crested Auklets *A. cristatella*, and Parakeet Auklets *A. psittacula* and primarily piscivorous Common Murres *Uria aalge* and Thick-billed Murres *Uria lomvia* are found on St. Lawrence Island and the Diomede islands. In contrast, only Parakeet Auklets nest in the coastal zone of the northeastern Bering Sea, and in small numbers, there are very few Thick-billed murres, and abundances of other species also are low (Sowls *et al* 1978).

In this paper, we examine how oceanography and biology influence the pelagic distribution and ecology of seabirds throughout Beringia. We examine seabird diversity and abundance at sea using data collected on seabirds during the 1970s and 1980s by the U.S. Fish and Wildlife Service (USFWS) as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP). We analyze the distribution of planktivorous and piscivorous

seabird species that occur in the region during summer, measure the carbon flow through seabird communities on a sub-regional basis, and consider the observed patterns of seabird distribution at sea with respect to published information on oceanography, primary and secondary productivity, and pelagic fish communities. This overview of pelagic seabird ecology in the northern Bering and Chukchi seas represents a relatively rare attempt to integrate seabird biogeography with respect to topography, oceanography, and productivity over basin-wide spatial scales in Alaska (e.g., Schneider *et al*. 1986).

METHODS

Surveys for seabirds were conducted on ships of opportunity between 1976 and 1984 using protocols developed by the USFWS (Gould & Forsell 1989). Seabirds were censused in a 300 m-wide strip on the left or right of the ship's center line and over a 10-min time interval (a transect). Numbers of all birds swimming on the water were recorded by species. Instantaneous counts of flying birds were made three times during a 10-min transect, which combined with counts of sitting birds, provided the total numbers of birds per transect with which to calculate densities (numbers/km^2). Areas were determined from strip width, time traveled and ship speed. Ancillary data on bird behavior, weather and sea conditions, ship position, etc., were collected for each transect. For details on methods and sources of data, see Gould & Forsell (1989) or go online to the North Pacific Pelagic Seabird Database (NPPSD) at http://www.absc.usgs.gov/research/NPPSD/ where all the data used in this analysis are compiled.

Analyses and mapping of bird distributions and abundance were accomplished with a GIS system designed for working with marine bird and mammal data (Computer Aided Mapping and Resource Inventory System (CAMRIS, copyright 1987, 1988 by R. Glenn Ford Consulting Inc., Portland OR, www.camris.com). For mapping, and for estimating bird abundance, transect data were binned into selected latitude-longitude blocks and the average density (birds km^{-2}) for each species was calculated from strip transects (length times width) falling within the block. Density polygons were generated as contoured isopleths of density, and missing blocks were extrapolated from the densities of adjacent blocks. Missing blocks were not filled if they were more than 1 block away from a block containing data. Bird abundance was estimated (mean density times area) for 30° latitude-longitude blocks. Maps of distribution are presented as density contour isopleths generated from a grid of 15° latitude-longitude blocks and scaled geometrically.

USFWS transects conducted in June through September were used to calculate summer densities of species and to map their distributions. For purposes of examining biogeography, data were grouped over all years. In areas with sufficient transects to examine inter-annual variability, patterns of distribution for common species were similar among years. About 3160 km^2 of area were surveyed on a total of 2630 strip transects. The region was divided into three sub-regions for analysis: St. Lawrence Island- lower Chirikov Basin (SLI-CB), an area of 99 470 km^2 bounded by 62° 30' N, 64° 30' N, 164° 00' W, and 174° 00' W; the Bering Strait (BER-STR), an area of 55 437 km^2 bounded by 64° 30' N, 67° 00' N, 164° 00' W, and 171° 00' W; and the central/eastern Chukchi Sea (CHUKCHI), an area of 61 753 km^2 bounded by 67° 00' N, 69° 30' N, 164° 00' W, and 170° 30' W. Survey effort was widely distributed throughout the sub-regions, except for areas west of the International Convention Line separating U.S. and Russian waters, where few or no surveys were conducted. To estimate regional bird populations, data were first binned into 165 30' x 30' latitude-longitude blocks, so that 95%, 94%, and 100% of blocks were sampled in sub-regions SLI-CB, BER-STR, and CHUKCHI, respectively. Abundance in each sub-region was then calculated by summing the totals in each 30° block (mean number of birds times block area) over the marine area sampled in each sub-region.

TABLE 1
Body mass and field metabolic rate (FMR) of seabird species or genera found in the northern Bering Sea and Chukchi Sea.

Common Name	Code	Scientific Name (g) (kJ/d) type*	Mass	FMR	Food
Northern Fulmar	NOFU	*Fulmarus glacialus*	620	991	O
Short-tailed Shearwater	STSH	*Puffinus tenuirostris*	610	980	O
Pelagic Cormorant	PECO	*Phalacrocorax pelagicus*	1800	1972	F
Red Phalarope	REPH	*Phalaropus fulicaria*	55	207	P
Jaeger (spp.)	UNJA	*Stercorarius* spp.	490	851	F
Herring Gull	HEGU	*Larus argentatus*	1130	1460	F
Glaucous Gull	GLGU	*Larus hyperboreus*	1410	1684	F
Black-legged Kittiwake	BLKI	*Rissa tridactyla*	420	770	F
Arctic Tern	ARTE	*Sterna paradisaea*	120	343	F
Pigeon Guillemot	PIGU	*Cepphus columba*	530	895	F
Tufted Puffin	TUPU	*Fratercula cirrhata*	800	1168	O
Horned Puffin	HOPU	*Fratercula corniculata*	540	906	F
Kittlitz's Murrelet	KIMU	*Brachyramphus brevirostris*	240	537	F
Murre (spp.)	UNMU	*Uria* spp.	980	1331	F
Parakeet Auklet	PAAU	*Aethia psittacula*	290	606	P
Least Auklet	LEAU	*Aethia pusilla*	90	285	P
Crested Auklet	CRAU	*Aethia cristatella*	300	620	P

* Food type - predominant food (by volume) taken by species during the breeding season: O= omnivorous (fish and plankton); F= fish; P= plankton.

Alaskan seabird colony data were obtained from USFWS archives (provided by A. Sowls, Alaska Maritime National Wildlife Refuge, Homer, Alaska), which included updated colony estimates from Sowls *et al.* (1978). Order of magnitude estimates of Siberian seabird colony populations were provided by N. Konyukhov and L. Bogoslovskaya (Institute of Evolutionary Ecology and Morphology of Animals, Moscow). Estimates of seabird populations on Big Diomede Island (V. Zubakin, A. Kondratiev, and J. Piatt, unpubl. data) and Little Diomede Island (A. Fowler and S. Hatch, unpubl. data) were obtained during joint U.S.-Russian studies in 1991.

An allometric equation was used to estimate daily individual energy requirements for each seabird species (Table 1), based on the measured field metabolic rates (FMR) of seabirds in cold ocean environments (Birt-Friesen *et al.* 1989): $\log_{10}$ FMR = 3.13 ± 0.646 * $\log_{10}$ [mass (in kg)]. Body masses vary over time and geographically, as well as between sexes in dimorphic species. Body masses (±5 g) during the breeding season were obtained from USFWS data archives and from published sources (Dunning 1984, Piatt *et al.* 1990a, 1991). Unweighted mean weights of sexes were calculated for sexually dimorphic species. For generic groups not distinguished or grouped in the at-sea data set (2 murres, 3 jaegers), unweighted means of species' weights were used for calculations. From FMR's, average daily energy intake was calculated (Schneider *et al.* 1986) for each species as: E intake (in kJ m^{-2} d^{-1}) = 1.33*FMR*(birds per unit area); where 1.33 is the ratio of energy ingested to energy assimilated. Numbers of birds estimated from ship-based surveys rather than colony surveys were used in these calculations. Conversion factors of 20.9 kJ g^{-1} dry and 0.4 gC g^{-1} dry were used to convert energy transfer to mass transfer (Schneider *et al.* 1986). Conversion factors of 0.20, 0.27, and 0.24 g(dry)/g(wet) were used to estimate wet weight consumption of food biomass by planktivores, piscivores, and omnivorous species (Table 1), respectively (Wiens & Scott 1975). We did not calculate the additional food requirements of chicks at colonies owing to a lack of local production and diet data for many species. In most cases these would be small relative to needs of adult and non-breeding members of populations thoughout the breeding season.

The image of sea surface temperature (SST) was developed using data from advanced very high-resolution radiometer (AVHRR) sensors aboard NOAA Polar Orbiting Satellites. For this report, we selected the best single "cloud-free image" available in the month of July during 1991, when we were concurrently doing surveys for auklets in Bering Strait (Piatt *et al.* 1992). Raw AVHRR data was calibrated and georeferenced at the Alaska Science Center.

## BACKGROUND: OCEANOGRAPHY

Water masses
Based on extensive sampling of water masses in the northern Bering and Chukchi seas over many years from the 1950s to 1980s and numerous measures of current flow, the oceanography of the region during summer is well known. Three distinct water masses (Fig. 1), each with different origins, move northward through the Bering Strait (Fleming & Heggarty 1966, Coachman *et al.* 1975, Coachman 1993, Stabeno *et al.* 1999). Anadyr Water, a "river" of cold, high-salinity (ca. 32.8-33.0 ppt), nutrient-laden oceanic water that originates along the slope of the Bering Sea continental shelf, flows northward through Anadyr Strait and western Bering Strait, and finally into the central Chukchi Sea where it blends with

Bering Shelf Water (Figs. 2 & 3). As much as 72% of the water transported through Bering Strait during summer may come through Anadyr Strait (Overland & Roach 1987). Alaska Coastal Water originates in the Gulf of Alaska. This low salinity (ca. <32.0 ppt), seasonally warm water hugs the Alaskan coast and retains its character as it transits the Bering and Chukchi seas (Figs. 2 & 3). It is influenced by freshwater runoff from major rivers (e.g., Yukon), particularly in summer. Bering Shelf Water is the resident water mass of the central shelf region south of St. Lawrence Island. Intermediate in character (ca. 32.0-32.8 ppt) between Anadyr and Alaska Coastal waters, Bering Shelf Water is advected northward around both sides of St. Lawrence Island, and then flows through Bering Strait where it eventually blends with Anadyr Water and Alaska Coastal Water (Figs. 2 &3).

Currents
Current flow through Bering Strait is almost always in a northerly direction, particularly in summer. Residence times of Anadyr Water in the Chirikov Basin range from 10-20 d in July, in contrast to 20-50 d in late August-September (Coachman & Shigaev 1992). Currents flow faster at points of topographic constriction (Anadyr, Shpanberg, and Bering straits) and around major headlands; and slower in the meanders, eddies, and gyres that form downstream from those points (Fig. 2). In the absence of significant wind stress, currents are fastest in the Bering Strait (Overland & Roach 1987), particularly in the compressed Alaska Coastal Current where flow rates range from 50-150 cm sec^{-1}.

The Anadyr Current is a topographic boundary current. In the Gulf of Anadyr, it is steered in a clockwise direction along the 50 m isobath (Fig. 1) and transit time to Anadyr Strait is about one month. Most Anadyr Water enters Anadyr Strait, but some continues east around the south side of St. Lawrence Island where it mixes with Bering Shelf Water. More recent evidence suggests that nutrient-rich slope water may enter Anadyr Strait from the
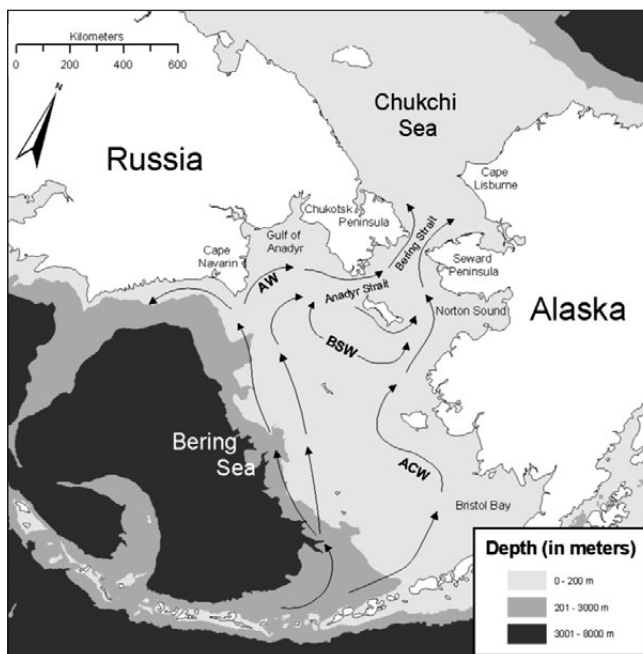
Fig. 1. The Bering and Chukchi seas, with circulation patterns and origins of the principal water masses flowing north through Bering Strait. See text for sources. AW - Anadyr Water; BSW - Bering Shelf Water; ACW - Alaska Coastal Water.

outer Bering Sea Shelf, after having been advected onto the shelf at lower latitudes (Stabeno *et al*. 1999). Whatever its' origin, "Anadyr" water flows through the canyon in the Chirikov Basin leading north to the Bering Strait. After emerging from Bering Strait, the deep "core" of Anadyr Water is diverted to the west along the 50 m isobath (Figs. 1 & 2). Upper water layers continue to move northward where they converge with westward flowing Bering Shelf/Anadyr waters (Coachman *et al*. 1975). Alaska Coastal Water follows 20-30 m isobaths throughout its transit of the Bering Sea and into the Chukchi Sea where it veers sharply to the east towards Kotzebue Sound before continuing northward along the coast, around Pt. Hope, and into the Beaufort Sea. Bering Shelf Water is advected northward around both ends of St. Lawrence Island and may be disrupted by westward expansion of the Alaska Coastal Current or by eastward expansion of the Anadyr Current. Northward flow continues through the Chirikov Basin, and clearly identifiable Bering Shelf Water is sandwiched between Alaska Coastal and Anadyr waters as they transit Bering Strait.

Owing to mixing in the Bering Strait, Bering Shelf Water may become indistinguishable from Anadyr Water in the Chukchi Sea.
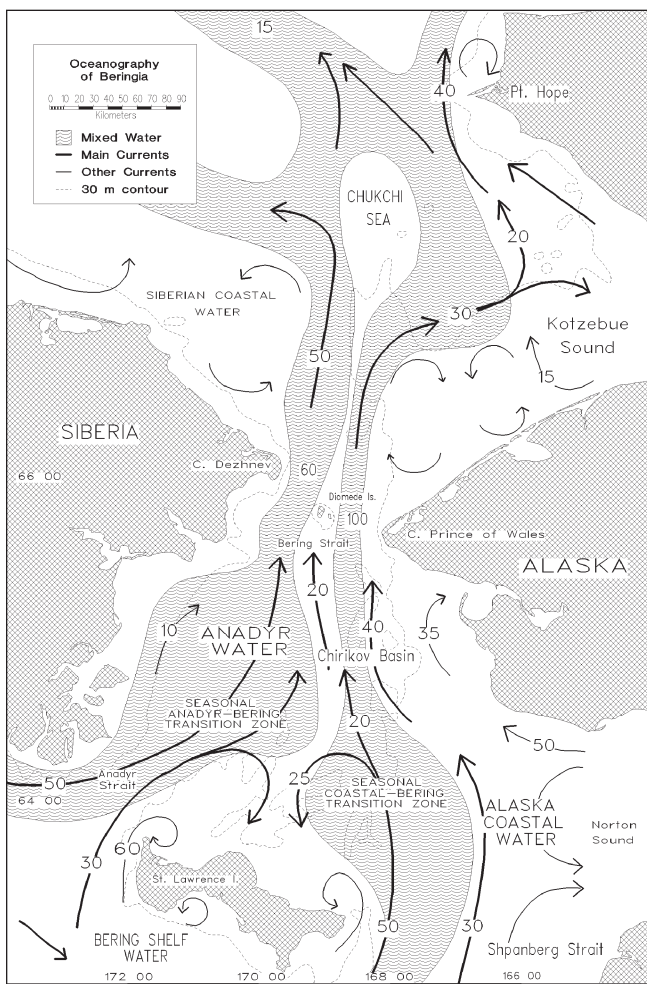
Termed Shelf/Anadyr water, there is a divergence of this flow from the deep Anadyr core above the Bering Strait (Fig. 2). Shelf/Anadyr water loops to the east as it winds around the 30 m contour toward Kotzebue Sound, before turning northwest off Pt. Hope (Coachman & Shigaev 1992). A pool of Shelf/Anadyr water (typically 32.2-32.6 ppt) forms between the flows of Shelf/Anadyr water and the Anadyr core, and is noted as a center for extremely high primary production (see below). The exact location of the pool appears to vary considerably over time (Springer & McRoy 1992).

Eddies and gyres are very common in the Bering Strait (Coachman *et al*. 1975) and in other regions of Alaska where strong currents flow past islands and mainland promontories (Schumacher & Kendall 1991). Persistent barotropic (pressure-driven) eddies form downstream from major headlands and islands (St. Lawrence Island, Cape Prince of Wales, Pt. Hope, etc.).

Transitional waters
Anadyr, Bering Shelf, and Alaska Coastal waters are arranged sequentially from west to east in Bering Strait (Fig. 2). There is little lateral mixing or diffusion in the system. Transition zones between water masses are often less than 10 km in width in areas of strong current flow (Coachman & Shigaev 1992). However, the width and location of these boundaries may vary considerably over summer as winds, tides, and freshwater runoff influence current regimes, water mass volume, and vertical stratification (Fig. 2). An eastward bulge of Anadyr Water and a westward bulge of Alaska Coastal Water are persistent features in Chirikov Basin.
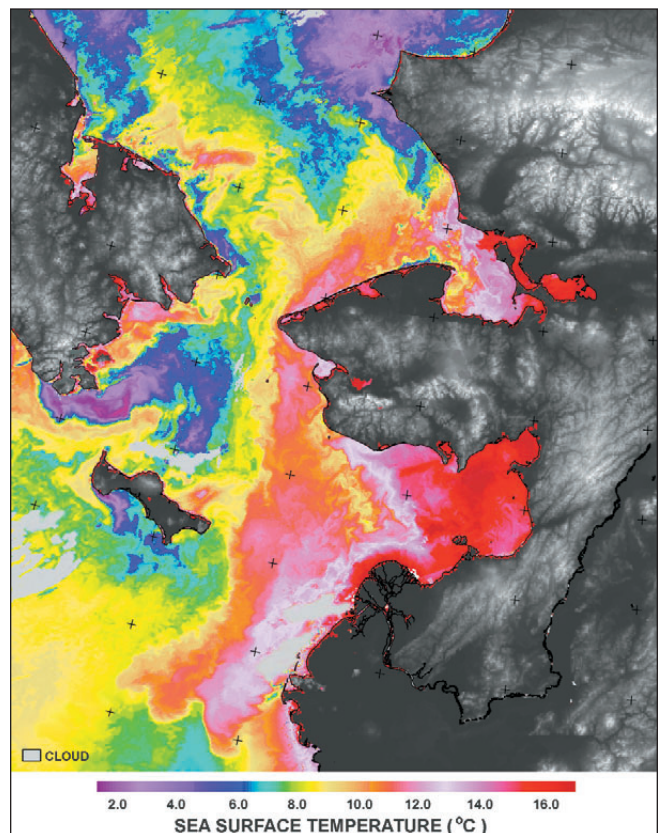

Fig. 2. Detailed oceanography of Beringia. "Mixed Water" shading shows the seasonal range in location of un-stratified water in the turbulent Anadyr current and in the transition zone between Bering Shelf and Alaska Coastal waters (drawing modified from Coachman *et al*. 1975, Grebmeier and McRoy 1989). Numbers = current speed in cm sec^{-1}.

Fig. 3. Sea surface temperatures in the northern Bering and Chukchi seas, July 6, 1991. The image was developed using data from Advanced Very High-Resolution Radiometer (AVHRR) satellite sensors (courtesy of David Douglas, USGS).

Transitional water between coastal and shelf waters is well-defined as a zone of mixed water fronting two stratified water masses on each side (e.g., see Harrison & Hunt 1990). The transition zone between Bering Shelf and Anadyr waters is harder to define because Anadyr Water is already mixed by upwelling turbulence. Any attempt to illustrate mixed water zones in Beringia (e.g., Fig. 2) must therefore allow for the seasonal movements of transition zones between currents, and seasonal changes in size and strength of currents. In contrast, an instantaneous AVHRR snap-shot of sea surface temperatures (Fig. 3) reveals only some of the known features, i.e., a sharp transition between Coastal and Bering Shelf waters, and an eastward bulge of cold, Anadyr water above St. Lawrence Island.

Stratification and mixing

In all waters, summer warming of the sea surface leads to vertical stratification and stability of the water column. Pycnoclines range from 10-20 m in depth in most areas. Stratification is greatly enhanced by freshwater runoff, which reduces the salinity of the surface layer and dramatically increases structural stability of the water column. In addition, vertical heat flux to deep water is inversely related to vertical salinity gradients, so that freshwater runoff promotes further warming of surface layers, thermal stratification, and water column stability (Coachman *et al*. 1975). Thus, Alaska Coastal Water is typically an order of magnitude more stable than Bering Shelf Water, and AVHRR imagery reveals little upwelling of cooler water in the Alaska Coastal Current until it enters the northern Chukchi (Fig. 3). Fresh water from rivers and melting ice along the Siberian coast also tends to warm and stratify a narrow band of Anadyr Water along that shore. Layering and eddies are very common in waters entering Bering Strait, but are destroyed by downstream turbulence in and just north of the strait (Coachman *et al*. 1975, Coachman & Shigaev 1992).

Mixing of the water column occurs at current boundary fronts, because of topographically induced upwelling. Winds can mix surface waters in any water mass, and this occurs regularly in summer with passing storms. Owing to the difference in densities between water masses, strong fronts form at the borders of Alaskan Coastal, Bering Shelf, and Anadyr waters. Frontal zones between water masses may contain completely mixed and unstratified water, with upwelling or downwelling at the boundaries. Topographically induced upwelling is a major source of mixing in the Bering Strait region. The Anadyr Current speeds up as it constricts in Anadyr Strait, and a tremendous amount of kinetic energy is converted to turbulent energy as water enters the shallow Chirikov Basin (Fig. 1). The result is a large plume of cold, well-mixed water downstream of the strait (Fig. 2), readily apparent in most AVHRR images of the region (Fig. 3). Any layering or stratification that develops in Chirikov Basin is broken down again as water passes through Bering Strait, and another plume of mixed water forms downstream. Minimum stratification is always observed directly downstream from Anadyr and Bering straits (Coachman & Shigaev 1992). Upwelling also occurs close to shore around St. Lawrence and Diomede islands (Springer & Roseneau 1985, Piatt *et al*. 1992).

BACKGROUND: BIOLOGICAL PRODUCTION

Nutrients and primary production

Primary production in the northern Bering and Chukchi Sea ecosystem is largely a function of three factors: nutrient concentrations, water column stability and light (Sambrotto *et al*. 1984, Springer *et al* 1996). Advection plays the over-riding role in determining nutrient levels and production along this northern branch of the "Green Belt" (Springer *et al*. 1996). Three major production centers are recognized (Springer & McRoy 1992, Coachman & Shigaev 1992). The first center is in the large gyre of Anadyr Water in the Gulf of Anadyr (Fig. 4), which originates at depth over the slope and outer continental shelf (beginnings of the "Green Belt"), flows up onto the north-western shelf near Cape Navarin, circles the Gulf of Anadyr and continues north through Bering Strait and into the Chukchi Sea. Production is initiated when nutrients from deep waters rise into the euphotic zone as the Anadyr Current shoals off Cape Navarin (Figs. 1 & 4). Downstream of the upwelling, stratification develops in the upper water layers and primary production at the center of the gyre attains 700 g C m^{-2} yr^{-1}. As the Anadyr current transits the northern gulf, lateral mixing reduces stratification, thus diminishing production (Coachman & Shigaev 1992).

Although it is not evident from the synoptic (August, 1988) cruise data presented in Fig. 4, Anadyr Water in Anadyr Strait can have extremely high production levels (800+ mg m^{-2} chlorophyll), although production drops rapidly with distance from the strait (Springer & McRoy 1992). This occurs in a relatively small area where Siberian coastal freshwater runoff creates stratification and stability in the water column in Anadyr Strait (Coachman *et al*. 1975). Thus, the north side of Anadyr Strait, though small in area, is a high production center. In addition, production is often quite high (50-200 mg m^{-2} chlorophyll) close to the west and east coasts of St. Lawrence Island (Springer & McRoy 1992) because in water depths of 20-30 m light penetrates below the nutricline and into fingers of Anadyr Water. Turbulent mixing in Anadyr Strait interrupts the developing bloom but "resets" the system, allowing another center of high production (up to 770 g C m^{-2} y^{-1}) to form downstream in the northern Chirikov Basin (Springer *et al*. 1996). Production is enhanced because freshwater runoff from Siberia layers over denser Anadyr Water and results in thermal stratification along the coast (see Fig. 3), which serves to increase stability of the water column just south of the Bering Strait (Coachman & Shigaev 1992).

Turbulence through the Bering Strait "resets" the system again, and a major production center develops in more stable water downstream in the central Chukchi Sea (Fig. 4), corresponding in area to the "pool" of Shelf/Anadyr water (Fig. 2). Primary production in this center (up to 830 g C m^{-2} y^{-1}) is extremely high and rivals the highest levels observed anywhere else in the World Ocean (Springer & McRoy 1992). This represents the northern terminus of the "Green Belt" (Springer *et al*. 1996). Average production in Anadyr Waters of the Gulf of Anadyr (400 g C m^{-2} y^{-1}), Chirikov Basin (360 g C m^{-2} y^{-1}), and Chukchi Sea (420 g C m^{-2} y^{-1}) far exceeds that of Bering Shelf Water (140 g C m^{-2} y^{-1}) and Alaska Coastal Water (50 g C m^{-2} y^{-1}) as measured in the southeastern Bering Sea. Rather, these high levels of production are typical of upwelling systems (Springer & McRoy 1992) and similar to levels observed in shelf-edge waters in the "Green Belt" of the Bering Sea (e.g., 225-470 g C m^{-2} y^{-1}, Springer *et al*. 1996).

Zooplankton

Zooplankton abundance and distribution in the Bering Strait region are closely related to current and production regimes described above. Patterns of distribution have been established for the entire
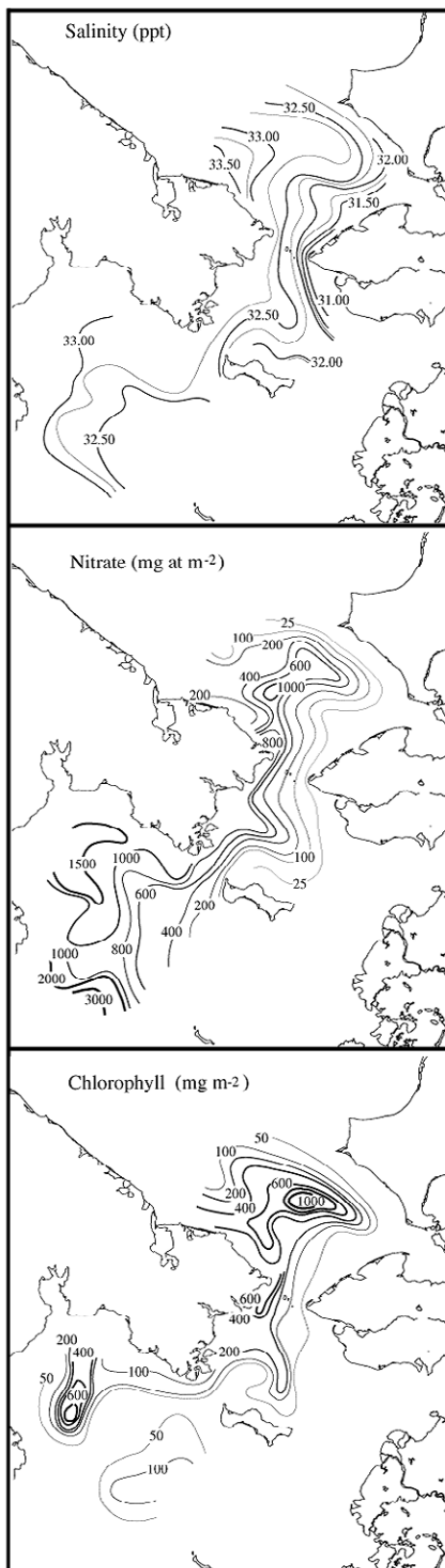
Fig. 4. Areal distribution of bottom salinity (top figure), nitrate (middle) and chlorophyll (bottom) on the Bering-Chukchi shelf (typical example from a cruise on 26 July - 2 September, 1988; from Springer and McRoy 1992). Chlorophyll and nitrate integrated from surface to bottom. Anadyr Water is predominantly above 32.5 ppt.

region by American and Russian investigations conducted over many different months and years, beginning in earnest during the 1950's (Johnson 1956, English 1966, Springer *et al*. 1989, Hunt & Harrison 1990, Piatt *et al*. 1992, Coyle *et al*. 1996 [and references therein]). Among the copepods, the large, oceanic species *Neocalanus cristatus*, *N. plumchru*s, *Eucalanus bungii*, and *Metridia pacifica*, predominate in Anadyr Water (Fig. 5), routinely attaining average densities of 2-4 g_{dry} m^{-2} from spring through late summer. They are replaced in shelf waters mostly by the single large species, *Calanus marshallae*, with typical densities of 0.2-1.2 g_{dry} m^{-2}. Nearshore in Alaska Coastal Water, *C. marshallae* is replaced by a number of small species, particularly *Acartia longiremis*, and *Eurytemora* spp. Biomass densities in coastal water are typically less than 0.5 g_{dry} m^{-2}. Some species are widely distributed in all water types (e.g., *Pseudocalanus* spp., *Oithona similis*), but owing to their smaller sizes, add little to the total standing biomass.

Adult euphausiids are poorly sampled by plankton nets. It is clear from studies of seabird diets (below), however, that in the Chirikov Basin and Bering Strait, euphausiids must be extremely abundant. Perhaps an indicator of adult abundance, euphausiid furcilia (principally *Thysanoessa* spp.) are much more abundant in Anadyr Water (1000s m^{-2}) compared to shelf waters (100s m^{-2}), and are rare in coastal waters (Springer *et al*. 1989). Large pelagic amphipods are also poorly sampled by plankton nets. In the Bering Strait region, *Parathemisto pacifica* is associated with Anadyr Water (Springer *et al*. 1989, Piatt *et al*. 1992).

Patterns of copepod distribution (Fig. 5) reinforce our picture of the oceanographic regime (Fig. 2). Alaska Coastal Water is remarkable for its overall low biomass of zooplankton. *C. marshallae* is a good indicator of Bering Shelf Water, with highest densities found in shelf water northeast of St. Lawrence Island, and east (Fig. 5) of the 32.4 ppt salinity isopleth in the central Chukchi pool (Fig. 2).
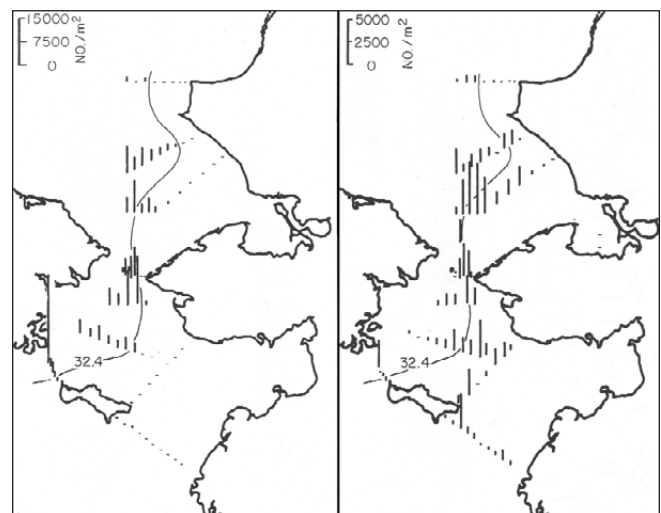
Fig. 5. Areal distribution of oceanic copepods (left panel) and *Calanus marshallae* (right panel) on the Bering-Chukchi shelf (typical example from cruise on 11-26 July, 1986; from Springer *et al*. 1989). Oceanic copepods include combined numbers of *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica*. The line marks the location of the 32.4 ppt salinity isopleth demarcating the interface between Anadyr Water and Bering Shelf Water.

Similarly, oceanic copepods are tightly associated with Anadyr Water below Bering Strait, and are most abundant west of the 32.4 ppt salinity isopleth in the central Chukchi. Spatial segregation of oceanic and shelf copepods in the pool area suggests that Anadyr and Bering Shelf waters retain their identity despite mixing in the Bering Strait. Copepod abundance appears weakly correlated with primary production centers. Highest densities of oceanic copepods were found at production centers on the north side of Anadyr Strait and south of the Diomede islands, but densities in the Chukchi production center were not extraordinary. In contrast, *C. marshallae* densities were highest in the Chukchi center, but otherwise high throughout Chirikov Basin. As most copepods are carried passively by currents, large-scale patterns of distribution may better reflect physical concentration rather than active selection of feeding areas (Sameoto 1982).

Some of the primary production in the Bering-Chukchi system goes toward pelagic secondary production, but most zooplankton biomass is produced in the south and advected northward through the region. Reproduction and growth of most oceanic zooplankton occurs in April-May on the Bering Sea shelf and slope. It takes about 6 weeks for currents to carry this biomass to the northern shelf, producing a peak biomass there in early July. Some species, e.g., *M. pacifica*, reproduce continuously in spring and early summer, resulting in a protracted period of abundance in both regions. Springer *et al*. (1989) estimated that in July 1985, about $35\text{-}41 \times 10^9$ g_{dry} d^{-1} of zooplankton were transported through Anadyr Strait, about 1/3 of which were oceanic copepods (i.e., about 10,000 mt d^{-1} of auklet food). Transport rates were strongly correlated with the volume percent of Anadyr Water in Anadyr Strait. Similarly, about $5.6\text{-}6.4 \times 10^9$ g_{dry} d^{-1} of zooplankton were transported through Shpanberg Strait, about 1/3 of which were *C. marshallae*. Like *M. pacifica*, the breeding season of *C. marshallae* is protracted, and it is likely that in the 3-7 weeks it takes for water to transit from Shpanberg Strait to the central Chukchi, zooplankton biomass increases from local production and growth.

Theoretically, oceanic zooplankton in Anadyr Water can graze 140-250 mg C m^{-2} d^{-1} of (mainly) diatoms, and at their peak abundance, about 560-1000 mg C m^{-2} d^{-1} (Springer *et al*. 1989). This appears insignificant compared to the average daily diatom production of 1-4 g C m^{-2} d^{-1}, with extremes of 10-16 g C m^{-2} d^{-1}. In shelf waters, *C. marshallae* consumes an average of about 30-50 mg C m^{-2} d^{-1}, whereas during peak abundance, all shelf copepods together consume about 420-575 mg C m^{-2} d^{-1}, approaching the total daily primary production over much of the Bering Shelf (Springer *et al*. 1989).

Pelagic fish

Compared to plankton, there has been little directed study of pelagic fishes in the region (Alverson & Wilimovsky 1966, Wolotira *et al*. 1979, Whitemore & Bergstrom 1983, Naumenko 1996, Brodeur *et al*. 1999), although much can be inferred from diet studies of piscivorous marine birds and mammals (Frost & Lowry 1981, Lowry & Frost 1981, Springer *et al*. 1984, 1987; Piatt *et al*. 1991). Alaska Coastal Water contains a greater diversity of pelagic fishes than shelf waters (Mecklenburg *et al*. 2002). Common forage species in coastal water include (in approximate order of abundance): sandlance *Ammodytes hexapterus*, saffron cod *Eleginus gracilis*, Arctic cod *Boreogadus saida*, herring *Clupea harengus*, and capelin *Mallotus villosus*. Many demersal species occur there also, including a variety of sculpins (Cottidae) and flatfishes (Pleuronectidae). Sand lance and saffron cod are more common south of Bering Strait, whereas Arctic cod are more abundant in the Chukchi Sea.

Capelin and sand lance are found in open waters of the Chukchi, but the abundance of Arctic cod exceeds that of all other fish combined by 1-2 orders of magnitude (Alverson & Wilimovsky 1966). Limited studies indicate a similar trend for the Chirikov Basin and Bering Strait (Frost & Lowry 1981, Springer *et al*. 1987). From St. Lawrence Island to the northeastern Chukchi Sea, excluding inner Norton Sound where saffron cod predominate (Springer *et al*. 1987), Arctic cod are the overwhelmingly dominant prey of piscivorous seabirds (Springer *et al*. 1984, 1987). South and southwest of St. Lawrence Island, Arctic cod are replaced by walleye pollock (*Theragra chalcogramma*) and supplemented by capelin (Hunt *et al*. 1981, Springer *et al*. 1986, Brodeur *et al*. 1999). Bathed in Bering Shelf Water, the environment around St. Lawrence Island is similar in many ways to coastal waters (Springer *et al*. 1987). There are shallow banks, eddies and stratified waters which provide habitat for a variety of fishes including sand lance, saffron cod and capelin. The shallow shelf around the Diomede islands provides similar habitat for pelagic fishes in the Bering Strait. There is little or no information on the fish fauna of Anadyr and Siberian Coastal waters, and mesopelagic fishes dominate in the deep Anadyr basin to the south (Sobolevsky *et al*. 1996).

As observed for zooplankton, there are strong associations between some fish species and water masses (e.g., saffron cod and Alaskan Coastal Water, Springer *et al*. 1987), but others are more cosmopolitan (e.g., Arctic cod, Alverson & Wilimovsky 1966). Strong associations may result from a preference for particular water temperatures or salinities (Brodeur *et al*. 1999, Abookire *et al*. 2000, Robards *et al*. 2002), species-specific food requirements, or to substrate requirements (e.g., sand lance require shallow, sandy substrates; Robards *et al*. 1999). In contrast to zooplankton, fish are more abundant in coastal waters than in open shelf waters. In the Chukchi Sea near Pt. Hope, hydroacoustic surveys indicate an order of magnitude difference between pelagic fish densities in Alaska Coastal Water (0.73 g m^{-3}) and adjacent Bering Shelf Water (0.073 g m^{-3}; Piatt *et al*. 1991). Peak densities inshore (up to 249 g m^{-3}) far exceeded peak densities offshore (up to 80 g m^{-3}). Similarly, Alverson & Wilimovsky (1966) caught fewer Arctic cod (mean ±SE, 58 ±12, n=28) during standardized trawls offshore than on trawls conducted inshore (217 ±144, n=7).

Stratification and stability of the water column may play an important part in determining the relative abundance and distribution of fishes in different water masses (Sogard & Olla 1993, Abookire *et al*. 2000). Pelagic fish may also seek out, or be entrained in, eddies and gyres where plankton are concentrated (Schumacher & Kendall 1991). Hydroacoustic surveys conducted in the Chukchi Sea (Piatt *et al*. 1991) revealed that in shallow, stratified Alaska Coastal Water, pelagic fish densities were relatively high (0.3-3.0 fish m^{-3}). Most fish (and fish schools) were distributed near the bottom or in mid-water. In contrast, plankton scattering layers and pelagic fish were highly dispersed in vertically mixed waters of the frontal zone (ca. 20 km wide) between Alaska Coastal Water and Bering Shelf Water. This transition zone was also characterized by strong lateral sea surface temperature and salinity gradients, and fish abundance was negatively correlated with those property gradients (Piatt *et al*.

1991). Similarly, studies around the Pribilof islands revealed that zooplankton and pelagic fish were concentrated near frontal zones–but mostly in the stratified water side of fronts between stratified shelf waters and mixed coastal waters (Coyle and Cooney 1993, Brodeur *et al*. 1997). Fish and plankton were dispersed and relatively scarce in mixed waters away from the edge of the front.

Further offshore in stratified Bering Shelf Water, relatively low densities (<0.1 fish m^{-3}) of pelagic fish were observed at depths of 20-40 m in association with zooplankton below the thermocline but above a cold (<2ºC) deep layer. Water temperature, and the presence of strong thermoclines, can have a marked influence on the distribution and density of pelagic fish schools in the water column (Coyle and Cooney 1993, Sogard & Olla 1993).

SEABIRD BIOGEOGRAPHY
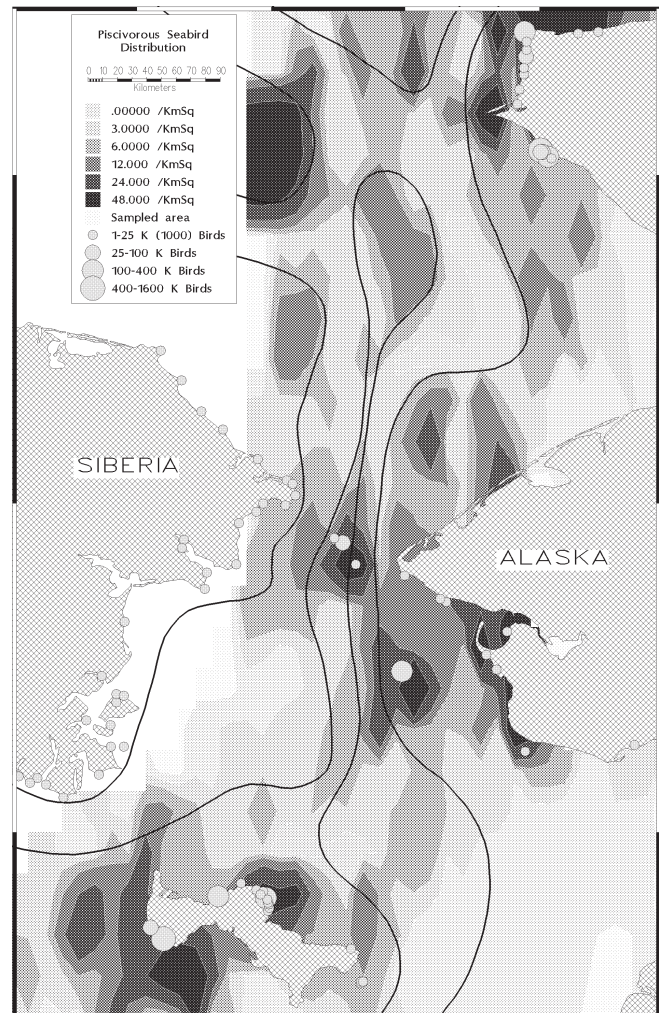
Piscivore distribution
Seabirds that eat primarily fish, including Common and Thick-billed Murres, guillemots *Cepphus* spp., Horned Puffins *Fratercula corniculata*, Black-legged Kittiwakes *Rissa tridactyla*, *Larus* gulls, and cormorants *Phalacrocorax* spp. (Swartz 1966, Springer *et al*. 1984, 1987, Piatt *et al*. 1991), are concentrated in Alaska Coastal Water, and coastally near islands situated in shelf waters (Fig.6). The largest breeding colonies are found on St. Lawrence Island, near Pt. Hope in the northeast Chukchi Sea, and on the Diomede Islands in the Bering Strait. Small colonies dot the entire Siberian and Alaskan coastlines. Because these seabirds forage near colonies (mostly within 70 km) during summer, major at-sea aggregations coincide spatially with colonies. However, a significant fraction (20-40%) of seabird populations in summer may be comprised of sexually immature birds (1-5 y of age), and failed or post-breeding birds that are not constrained to forage just around colonies (Briggs *et al*. 1987).

The occurrence of large concentrations of piscivorous birds at the sea-surface usually indicates that there are prey schools below (Schneider & Piatt 1986, Cairns & Schneider 1990, Piatt 1990, Mehlum *et al*. 1996). Because the grouped data presents a picture of seabird distribution integrated over summer, and over several years, we conclude that piscivorous seabird distribution (Fig. 6) probably reflects moderate to large-scale temporal and spatial patterns of fish distribution. At the largest scale, the distribution of piscivorous seabirds is defined by where birds do not occur, i.e., in areas of mixed water (Fig. 6). Few seabirds are found in the Coastal-Shelf transition zone, or in the stream of Anadyr and Anadyr-Shelf mixed waters. This is consistent with hydro-acoustic surveys that showed a negative correlation between fish aggregations and turbulent, mixed waters (see above). On a smaller scale, birds are most abundant on the shelves around St. Lawrence and Diomede islands, around headlands in the stream of Alaska Coastal Water, and in a number of eddies in the Chukchi Sea (contrast Figs. 2 and 6). This is consistent with observations that fish are more abundant in Alaska Coastal Water (see above) and that fish aggregate in eddies (Schumacher & Stabeno 1994) and near frontal boundaries around islands (Coyle and Cooney 1993). This pattern of distribution was shown by many individual piscivorous seabird species.

Planktivore distribution
Seabirds that feed primarily on zooplankton, comprising mostly auklets *Aethia* spp. and phalaropes *Phalaropus* spp., have a

markedly different distribution from piscivorous seabirds (Fig. 7). Planktivores are for the most part absent from Alaska Coastal Water and coastal-shelf transitional waters. There are few colonies, but they are enormous and positioned strategically in Anadyr and Bering straits to take advantage of the ca. 10 000 mt of zooplankton that are advected daily through the straits (Springer *et al*. 1989). Least and Crested auklets are extremely abundant around the west end of St. Lawrence Island, and also north along the border of the Anadyr Current. Few are found in the downstream plume of Anadyr Water beyond about 100 km from colonies. In Bering Strait, Least Auklets are most abundant to the south in Bering Shelf Water, and Crested Auklets dominate to the west where they straddle the mixed zone of Anadyr-Bering Shelf Water (Piatt *et al*. 1992). The only significant colony of auklets in Alaska Coastal Water is found at King Island (ca. 100 km SSE of Diomedes), but most of these birds over-fly coastal water to forage in Bering Shelf and Anadyr waters to the west (Hunt & Harrison 1990). Planktivores are scarce in the plume downstream of Bering Strait, and most forage within 100 km of the Diomede islands. Large concentrations of planktivores, almost entirely Red Phalaropes *Phalaropus fulicaria*, but also Parakeet Auklets, are found in the central Chukchi Sea. In contrast to piscivores, phalarope
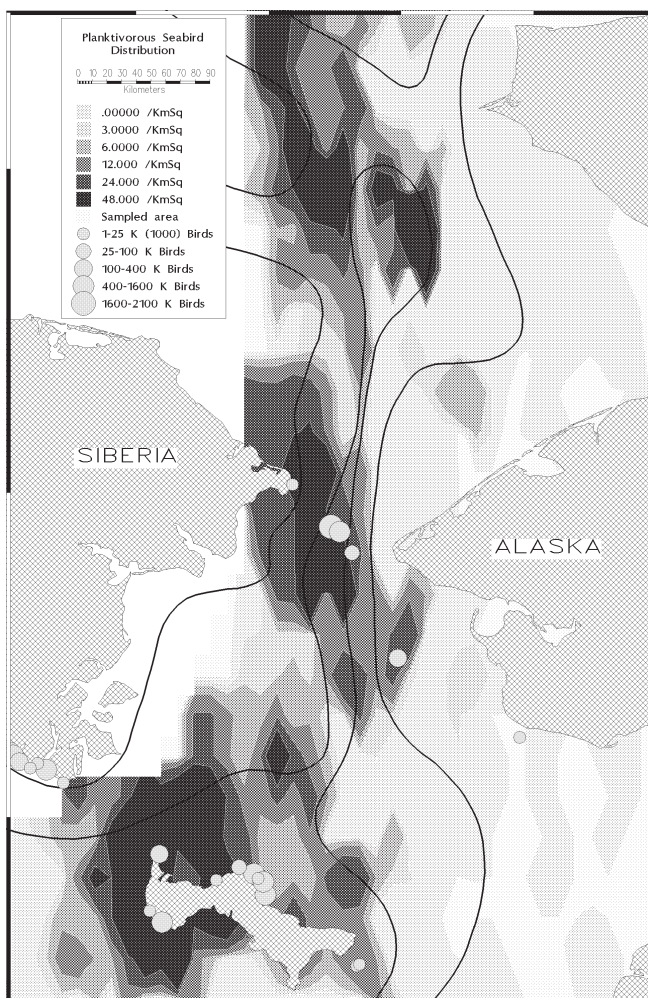

Fig. 6. Areal distribution of piscivorous seabirds on the Bering-Chukchi shelf during summer. "Mixed Water" boundary lines from Fig. 2. See Methods for sources of colony and pelagic distribution data. Note that scales of abundance are the same as in Fig. 7.

aggregations are extended along a southeast to northwest axis, and appear to straddle mixed waters rather than avoid them.

These patterns of distribution are consistent with the biological oceanography of the region (above), and feeding behavior of planktivores. Crested Auklets feed mostly on euphausiids *Thysanoessa* spp. and on large oceanic copepods (*N. plumchrus* and *N. cristatus*), whereas Least Auklets consume mostly oceanic copepods, and some shelf species (*C. marshallae*; Bedard 1969, Springer & Roseaneau 1985, Hunt & Harrison 1990, Piatt *et al*. 1990a, 1992). Auklets exploit waters rich with these plankton, but they are aggregated in only two main areas of the region–even though much of Anadyr-Bering Shelf waters contain a moderate to high abundance of zooplankton throughout (Fig. 5, Springer *et al*. 1989, Coyle *et al*. 1996). Several factors contribute to this restricted distribution. At the largest scale, auklets are constrained by breeding activities (June-September; Piatt *et al*. 1990a) to forage within a fixed distance of colonies (generally about 50 km; Obst *et al*. 1995, Piatt *et al*. 1992). They also appear to avoid areas with high turbulence and mixed waters (Fig. 7). As with piscivores, however, a substantial proportion (20-40%) of auklets are

Fig. 7. Areal distribution of planktivorous seabirds on the Bering-Chukchi shelf during summer. "Mixed Water" boundary lines from Fig. 2. See Methods for sources of colony and pelagic distribution data. Note that scales of abundance are the same as in Fig. 6.

potentially non-breeders (Jones 1992) and may exploit more distant hotspots, if they are suitable. Auklets prefer to forage in stratified Bering Shelf/Anadyr water where pycnoclines (and zooplankton) rise toward the surface in response to topographic features or at the border of upwelling and fronts (Hunt *et al*. 1990, Hunt & Harrison 1990, Hunt *et al*. 1992, Piatt *et al*. 1992). Auklets may also be found in abundance just on the other (mixed) side of the Anadyr-Shelf frontal zone (Haney 1991) or along the border of upwelled waters on the west coast of St. Lawrence Island (Bedard 1969, Springer & Roseneau 1985, Russell *et al*. 1999).

On a finer scale, Crested and Least auklets are often segregated spatially, presumably because their preferred prey (euphausiids vs. copepods) are found in different habitats (Piatt *et al*. 1992; Hunt *et al*. 1992). Euphausiids are better able to swim against current flow than copepods, and they may be able to maintain school integrity in frontal and upwelled waters. Often found in layers on the bottom during day, euphausiids may be mechanically concentrated and raised from the bottom by subsurface convergence at the border of upwelling fronts (Simard *et al*. 1986, Schneider *et al*. 1990). Parakeet Auklets are generalist plankton feeders and much more dispersed than Least and Crested auklets. They are most abundant in Shelf/Anadyr waters of Bering Strait, but are also widely distributed in areas of Chirikov Basin and the Chukchi Sea that are little used by Least and Crested auklets (Harrison 1990, Schauer 1991).

Phalaropes (mostly Red Phalaropes) replace auklets as the dominant planktivore in the Chukchi Sea. They eat a wide variety of planktonic prey, including amphipods, copepods, mysids and small euphausiids (Divoky 1984, Brown & Gaskin 1988). Away from the coast, where they may forage in the littoral zone, concentrations of Red Phalaropes are almost always associated with convergent fronts where plankton accumulate in surface slicks (Brown & Gaskin 1988). The vast majority of phalaropes in the Chukchi Sea straddle the mixed water zones marking the convergence of Anadyr Water from the south and Shelf/Anadyr/Coastal waters from the east (Fig. 7).

Omnivore distribution

Short-tailed Shearwaters *Puffinus tenuirostris*, Northern Fulmars *Fulmarus glacialis*, and Tufted Puffins *Fratercula cirrhata* are extremely abundant species in the Aleutians and southern Bering Sea, but relatively few venture far beyond the Bering Strait until August (Divoky 1987). A few small colonies of Tufted Puffins are found in the Chukchi Sea. All these large-bodied species eat a wide variety of prey, including euphausiids, shrimp, squid, and fish (Hunt *et al*. 1981, Schneider *et al*. 1986). Distribution patterns reflect foraging behavior as these species are found in all water masses, and along the Coastal/Shelf transition zone (Piatt *et al*. 1991). Main areas of concentration are in Anadyr Strait (fulmar only), Bering Strait, and the central Chukchi Sea. Fulmars appear to favor Anadyr Water (see also Schauer 1991).

Energetics and carbon flux

For most species that breed in the region, population estimates from colony and at-sea censuses are of a similar order of magnitude (Fig. 8). Least and Crested auklet colony estimates exceed at-sea estimates by 2-4 times, but there are many uncertainties in censusing auklets on land (Piatt *et al*. 1990b, Jones 1992). In all regions, some non-breeding or migratory species (shearwaters, fulmars, phalaropes, etc.) are abundant at sea whereas their

colonies are located outside the study area. From a population standpoint, planktivorous auklets are overwhelmingly dominant south of the Bering Strait (Fig. 8). Phalaropes replace auklets as planktivores in the Chukchi Sea, and our estimate is similar to the one million estimated by Divoky (1987) for the region. Murres and Black-legged Kittiwakes are the most abundant piscivorous species in all sub-regions, and are most abundant in the Chukchi Sea. Taking into account the differences in body size among species (Table 1) the relative trophic importance of each species (Fig. 9, upper graph) is quite different from their numerical abundance (Fig. 8). Carbon flux to piscivores rivals that of planktivores south of Bering Strait, and is an order of magnitude greater in the Chukchi Sea. The Bering Strait and the Anadyr Strait (sub-region SLI-CB) support a nearly equal density of auklets. Taking total areas into account, however, it is clear that Anadyr Strait is the nucleus for auklet populations in the region (Fig. 9, lower graph). These estimates do not even account for much (if any) of the huge populations of auklets on the Siberian Coast (Fig. 7), which probably forage in Anadyr Water before it enters Anadyr Strait. Some of the disparity between regional populations may relate to breeding habitat, which is very limited in Bering Strait. Total

seasonal (122 d) food consumption is similar in all three sub-regions (29,000 mt; 21,100 mt; 21,900 mt; in SLI-CB, BER-STR, and CHUKCHI, respectively). Whereas half of all food consumed below Bering Strait goes to planktivores (49% of 411 mt d^{-1}), most goes to piscivores (88% of 179 mt d^{-1}) in the Chukchi Sea.

The trophic importance of piscivores is mostly due to the large numbers of murres. In terms of carbon flux, these large-bodied alcids dominate in all shelf seabird communities from central California to the Chukchi Sea (Wiens & Scott 1975, Briggs & Chu 1987, Schneider *et al.* 1987, this study). In contrast to more southern coastal areas where Common Murres predominate, and to the oceanic Aleutian Islands where Thick-billed Murres predominate, Common and Thick-billed Murres are about equally abundant in the Bering Strait-Chukchi region. As noted by Springer *et al.* (1987), this is a direct consequence of having an abundance of both oceanic and shelf foraging environments in the region. Although Thick-billed Murres rely on pelagic fish in shelf habitats, they are also well-adapted for exploiting a wide variety of oceanic prey including euphausiids, amphipods, and squid. Common Murres feed almost exclusively on pelagic schooling fish during summer. Thus, the large mixed-species murre colonies on St. Lawrence Island, in the Bering Strait, and near Pt. Hope are strategically positioned to make full use of both oceanic, shelf and coastal food webs (Springer *et al.* 1987). As expected, the murres overlap in distribution at sea, but Thick-billed Murres are more common in transitional and Bering Shelf/Anadyr waters, and Common Murres are largely restricted to Alaska Coastal Water (Piatt *et al.* 1991, 1992).

With an extremely productive "Green Belt" flowing north, a massive concentration of planktivores, and proximity of coastal and oceanic environments that support both species of murres, the northern Bering-Chukchi system rivals or exceeds most other shelf and upwelling systems that have been studied in terms of carbon
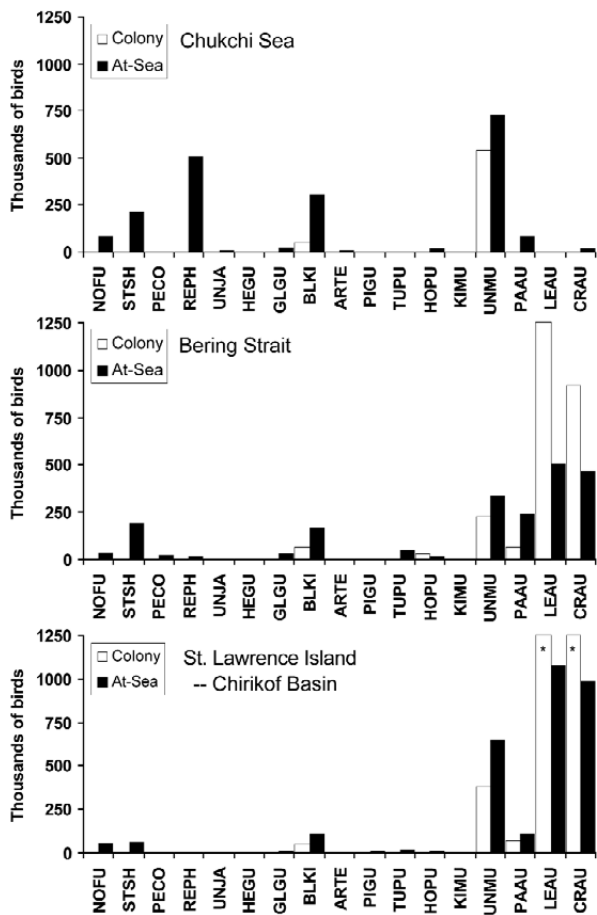
Fig. 8. Total seabird populations in three sub-regions of the Bering-Chukchi shelf. Populations estimated from colony counts (stippled bars) and by extrapolation from at-sea densities (solid black bars). Bars broken by asterisks indicate colony population estimates far in excess of scale (Bering Strait LEAU 2.075 million, Chirikof Basin LEAU 4.125 million, CRAU 3.113 million). Species codes from Table 1. Sub-regions and sources of data described in Methods.
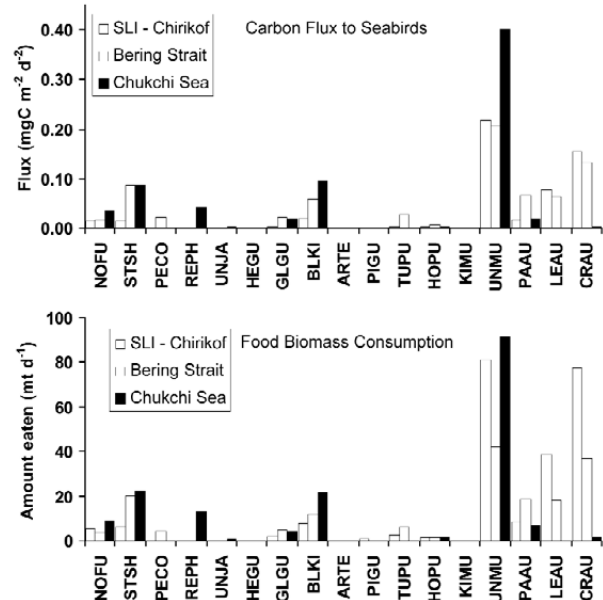
Fig. 9. Carbon flux to seabirds, and estimated biomass consumption of food by seabirds, in three sub-regions of the Bering-Chukchi shelf. Species codes from Table 1. Sub-regions described in Methods.

flux to seabird populations (Table 2). With a high proportion of small-bodied auklets, the standing biomass of seabirds is lower than in most other regions, but this is compensated for by the higher mass-specific metabolic rates of small species.

SUMMARY DISCUSSION

Advection and pelagic food webs

The continental shelf of the northern Bering Sea and southern Chukchi Sea has long been recognized as a region of unusually high marine production – from primary producers (McRoy *et al*. 1972) to seabirds (Fay & Cade 1959, Bedard 1969). The biological richness was paradoxical given the shallow waters of the region and great distance from nutrient sources at the Bering Sea shelf edge. Extensive oceanographic and biological research has resolved this paradox: Advection of oceanic water and biomass from the Bering Sea basin (ca. 800-1200 km away) is primarily responsible for biological richness on the Bering-Chukchi shelf (Sambrotto *et al*. 1984, Springer & Roseneau 1985, Coachman & Shigaev 1992). Extremely high rates of carbon flux to seabirds are clearly a result of this advective regime (Springer *et al*. 1987; this study). Furthermore, advection of oceanic zooplankton accounts for the presence of huge *Aethia* auklet colonies far from upwelling areas typically exploited by these species in the Aleutians and along the Bering Sea shelf edge.

Whereas the advection of nutrients and biomass so far inshore on a continental shelf may be unusual, the process of biomass advection and downstream development on shelf systems is not. For example, a large fraction of pollock larvae produced in Shelikof Strait is advected 300-500 km southwest by prevailing currents along the Alaska Peninsula (Kim & Kendall 1989). Tufted Puffins situated near the beginning of this "conveyor belt" of food eat few of the small pollock larvae, and rely heavily on larger resident pelagic fish like sand lance and capelin (Hatch & Sanger 1992). The proportion and size of juvenile pollock in puffin diets increases dramatically towards the end of the Alaska Peninsula, where juvenile pollock dominate the pelagic fish community. In another advective regime,

nutrient enrichment of surface waters through physical mixing in Hudson Strait results in gradual downstream development of plankton, fish (*Gadus morhua*) and seabird biomass in the Labrador Current (Sutcliffe *et al*. 1983). Seabird and fish densities peak off northeast Newfoundland, about 1200 km south of the site of turbulent mixing. Advection also may be an important mechanism for sustaining large seabird colonies situated in the central Canadian Arctic (Cairns & Schneider 1990).

Biogeography of seabirds

At the largest scale (100s-1000s km), the seabird community in the Bering Strait region is physically and biologically structured in a north-south direction by advection of nutrients and biomass from the south and by turbulent mixing at set points along the way. At intermediate scales (10s-100s km) in an east-west direction, seabird distribution is well-defined by water masses, frontal zones and water column stability (Figs. 1-3). In turn, these properties are influenced locally by bottom topography (including islands and headlands), tides, freshwater runoff, surface layering, and wind. Eddies that are created and driven by current flow (barotropic) and density differences (baroclinic) also appear to be common and important structural features in the region (Coachman *et al*. 1975).

In contrast to the strong physical and biological gradients that run from east to west across the Bering Strait region, north-south gradients are generally weaker. For example, all three currents flow south to north, creating similar habitats across the region, and zooplankton species composition, abundance and distribution are similar with respect to those water masses both below and above the Bering Strait (Fig. 5). The same cannot be said, however, for seabirds: planktivores are relatively insignificant consumers above the Bering Strait whereas carbon flux to piscivores nearly doubles in the Chukchi Sea. This appears to result from both physical processes and time required for downstream development of food-webs. We speculate that fish, and therefore piscivores, are less abundant in the central Bering Strait region because upwelling turbulence and rapid currents downstream from Anadyr and Bering straits disrupt zooplankton aggregations and reduce foraging

TABLE 2
Primary production and carbon transfer to seabirds in the Bering Sea and other regions*.

Oceanic Region	Area (km^2)	Primary production (gC/m^2/y)	Avian biomass (kg/km^2)	Carbon transfer (mgC/m^2/d)
N. Bering-Chukchi	217000	324	15.5	0.65
SLI-Chirikov	99000	360	12.5	0.55
Bering Strait	55000	360	17.1	0.73
Chukchi	62000	420	18.8	0.73
S.E. Bering Shelf	133000	–	18.6	0.49
Inner shelf	39000	75	16.3	0.41
Middle shelf	45000	166	21.2	0.41
Outer shelf	34000	162	36.1	0.68
Slope	14000	225	29.8	0.56
California	163000	130-300	8-20	0.20-0.40
Oregon	22000	300	–	0.86
George's Bank	52000	265-455	–	0.47

* Primary productivity data taken from Springer and McRoy 1993, Springer *et al*. 1996 and following sources. Data on seabird biomass and carbon flux from Wiens and Scott 1975, Schneider *et al*. 1986, 1987, and Briggs and Chu 1987. Southeast Bering Sea biomass and flux calculated from 1980 data in Schneider *et al*. 1986, 1987.

efficiency of fish. In mixed waters adjacent to fronts, zooplankton layers are disrupted by turbulent mixing (Sameoto 1982) and pelagic fish probably avoid well-mixed waters for this reason (Piatt *et al*. 1991). This might seem to contradict a well-established notion that fish and zooplankton are concentrated in frontal areas–but they actually tend to concentrate on the border of the fronts themselves, and most often in stratified waters on the stable side of the front (Coyle and Cooney 1993, Brodeur *et al*. 1997). Well-mixed waters away from frontal boundaries do not provide good foraging habitat for pelagic fish.

Perhaps as importantly, transit time for water between Anadyr and Bering straits is too short (10-20 d in summer) for much growth or development of pelagic fish biomass (Sutcliffe *et al*. 1983) before the system is "reset" again at Bering Strait (Coachman & Shigaev 1992). In the Chukchi Sea, however, currents slow considerably, stratification and eddies develop downstream, and pelagic fish can probably use more fully the plankton biomass advected to them. In contrast, auklets thrive where zooplankton are concentrated on the edge of the turbulent upwelling systems in Anadyr and Bering straits, but no comparable upwelling exists in the Chukchi Sea. Auklets can dive 10-25 m below the surface to capture their prey and they tend to seek out dense plankton layers brought into near-surface waters by upwelling or raised pycnoclines (Hunt *et al*. 1990, 1992). Auklets are replaced by surface-feeding phalaropes in the central Chukchi, which forage on zooplankton concentrated at the surface by convergent fronts (Brown & Gaskin 1988).

Little is known about the overall distribution of fish in the Bering Strait region, but we can assume that the presence of piscivores is a reliable indicator of fish concentrations at many spatial scales (Piatt 1990, Piatt *et al*. 1992, Hunt *et al*. 1990, 1992, Mehlum *et al*. 1996). Piscivores require moderate to high density schools of fish for successful foraging (Piatt 1990), and so their patterns of distribution should also reflect physical mechanisms for concentrating prey of fishes. Some deep-diving (>50 m) piscivores (murres, cormorants) can exploit all of the water column on the Beringian shelf, whereas others (kittiwakes, gulls) must rely on physical or biological mechanisms (e.g., fronts, diel migration) to bring fish to the surface. In any case, the abundance of piscivores in stratified coastal waters and offshore eddies, and their conspicuous absence from mixed and turbulent waters, suggests that these physical factors play a dominant role in structuring piscivorous seabird communities in Beringia.

ACKNOWLEDGEMENTS

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