COMPARISON OF COLONIAL BREEDING SEABIRDS IN THE EASTERN BERING SEA AND GULF OF ALASKA

SHAWN W. STEPHENSEN & DAVID B. IRONS

U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road
Anchorage, Alaska 99503-6199, USA
(shawn_stephensen@fws.gov)

Received 23 April 2003, accepted 22 September 2003

SUMMARY

STEPHENSEN, S.W. & IRONS, D.B. 2003. A comparison of colonial breeding seabirds in the eastern Bering Sea and Gulf of Alaska. *Marine Ornithology* 31: 167-173.

We examined populations of colonial breeding seabirds in Alaska. We compared data on populations from the eastern Bering Sea (EBS) and the Gulf of Alaska (GOA) using U.S. Fish and Wildlife Service (USFWS) data from the Beringian Seabird Colony Database. The EBS and GOA are vast areas that support large diverse populations of breeding seabirds. Seabird distribution in Alaska is highly clumped: 12 of the 1714 colonies support 50% of all breeding birds, with most of these large colonies located in the EBS. The EBS has nearly three times as many seabirds as the GOA. The large numbers of seabirds in the EBS are due in part because the EBS is larger than the GOA and to the millions of planktivorous auklets that breed in the EBS but are virtually absent from the GOA. In the Bering Sea, Least *Aethia pusilla* and Crested *Aethia cristatella* Auklet colonies appear to be restricted to volcanic islands near highly productive upwelling areas in the central and western Aleutian Islands, the shelf-break in the central Bering Sea and the Anadyr Stream in the northern Bering Sea. They are conspicuously absent from the volcanic eastern Aleutian Islands east of Samalga Pass that are surrounded by warmer, fresher, water from the Alaska Coastal Current compared to the cooler, saltier oceanic water in the western and central Aleutians. The piscivorous species are more evenly distributed between the two regions. The most abundant piscivore, the Common Murre *Uria aalge*, is evenly split between the two regions. The EBS is more productive than the GOA, but both areas support similar biomass/km^2 of breeding seabirds. This pattern may in part be due to greater predation by foxes in the Bering Sea. Foxes still remain on some Aleutian Islands from introductions years ago and are indigenous on the northern Bering Sea Islands and the eastern Aleutian Islands. Relatively few islands in the GOA support foxes.

Keywords: distribution, oceanography, Bering Sea, auklets, *Aethia*, murres, *Uria* , piscivores, planktivores

INTRODUCTION

Present day seabird distributions are a product of many factors including: evolution, dispersal, predator-free nesting habitat, food resources, competition, and human influences (Ashmole 1963, Lack 1966, Udvardy 1974, Birkhead & Furness 1985). Seabirds generally live on predator-free islands with abundant food resources nearby. Their populations are often thought to be limited by food (Ashmole 1963, Lack 1966, Furness & Monaghan 1987, Springer 1991, Hunt *et al*. 1993). In Alaska, seabirds have been greatly affected by introduced predators (Bailey 1993), fisheries interactions (Degange *et al*. 1993), oils spills (Piatt *et al*. 1990), and climate change (Agler *et al*. 1999, Anderson & Piatt 1999). Nevertheless, Alaska still has some of the largest and most diverse seabird colonies in the North Hemisphere (Lensink 1984).

Alaska's breeding seabird population is estimated to be about 29 million birds composed of 35 species (USFWS 2004). Ninety-five percent of the colonial nesting seabirds in Alaska inhabit the large, diverse marine environments of the eastern Bering Sea (EBS) and Gulf of Alaska (GOA) (USFWS 2004). The seabird communities in the EBS and the GOA, however, are quite different from each other, being dominated by different species of birds (USFWS 2004). The objective of this study was to describe and compare some of the patterns of the seabird communities breeding in the rich areas of the EBS and the GOA, and to explore some of the potential factors that may contribute to differences in species composition and overall bird numbers between the two regions.

STUDY AREA

The study area is located in Alaska and is divided into 2 regions: the eastern Bering Sea (EBS) and the Gulf of Alaska (GOA) (Fig. 1). The EBS consists of coastal lands, islands, and waters between Alaska and Russia, including the Aleutian Islands, west side of the Alaska Peninsula, and the western Alaska coastline to the Seward Peninsula in the Bering Strait. The GOA includes southeast Alaska,

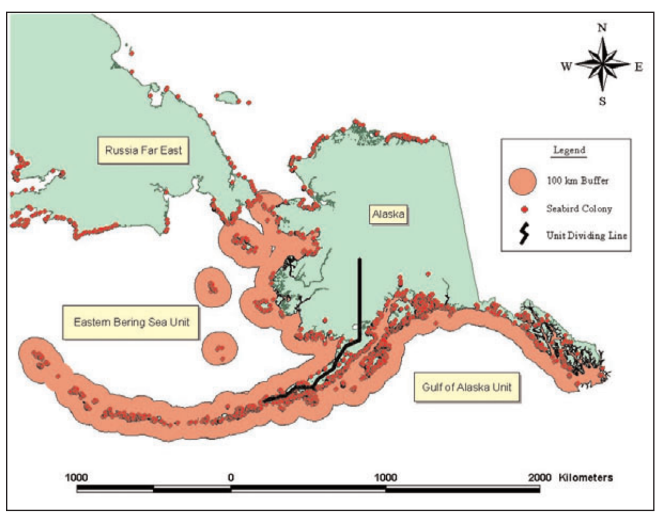

Fig. 1. Alaska seabird colony map with the eastern Bering Sea Unit and Gulf of Alaska Unit study areas identified (USFWS 2004).

Prince William Sound, Cook Inlet, Kodiak Archipelago, the east side of the Alaska Peninsula, and associated islands and waters.

METHODS

We examined populations of colonial breeding seabirds in the EBS and GOA. We then related the seabird parameters to colony site attributes and indices of ocean productivity. We used data from the Beringian Seabird Colony Database (Stephensen 2001, USFWS 2004), a computerized and expanded version of the Catalog of Alaskan Seabird Colonies (Sowls *et al*. 1978). The database stores current and historical data on breeding population sizes, species composition, and location of seabird colonies in Alaska and the Russian Far East. Population data in the database were obtained by counting or estimating breeding bird numbers using standardized techniques (USFWS 1999). These data have been collected over many years, by different observers, and using differing survey methods; thus inhibiting long-term comparisons due to the variable data quality (Stephensen & Mendenhall 1998). For this paper, we used the most representative estimates for each colony in the database (USFWS 1994). In most cases the most representative estimate is the most recent. However, sometimes an earlier census was deemed more reliable (e.g., if the colony was recently subject to disturbance or the recent census was conducted under poor conditions). We believe that the general patterns reported here are accurate, but remind readers that the actual numbers of breeding birds should be interpreted with caution. We used the following parameters in our analysis: number of colonies, colony size, seabird biomass, and foraging guilds. We calculated seabird biomass using published mean body mass data (Hunt *et al*. 2000) multiplied by species-specific population sizes (USFWS 2004). We excluded six species with populations below 100 individuals in our study area.

Thirty-one seabird species were grouped into 2 foraging guilds, piscivores and planktivores, using the dietary data compiled in Gaston and Hipfner (2000), Hatch (2002), and Hunt *et al*. (2000). Birds that eat squid were combined with the piscivores, and omnivores (species with broad diets) were placed into whichever prey category (fish-squid or plankton) was the dominant diet constituent. We calculated the total population and biomass for each guild in each area separately. Unidentified murres were classified as Common Murres *Uria aalge* or Thick-billed Murres *U. lomvia* based on the proportions of identified birds in each region.

To assess the degree of clumping of seabirds we ranked colonies by size and calculated how many colonies were needed to support half of a bird's total population. These colonies were deemed especially important for the species. We did this for all colonies, including mixed-species colonies, and for each species separately. Finally, we assessed the importance of each colony by adding up the number of species, for which that colony was deemed important (i.e., one of the colonies that were needed to support half of the breeding population).

We obtained data from the Alaska Volcano Observatory, U.S. Geological Survey (USGS) and compared land mass age and surface substrate (Beikman 1994, Miller *et al*. 1998) of nesting areas.

To compare the relative area available for foraging in the EBS and the GOA, we used a 100 km buffer around all colonies as an index of foraging range. If foraging area of two colonies overlapped, the overlap area was only counted once. Although many seabirds forage closer to the colony and many forage at greater distances, by using a single radius, we were able to compare the relative foraging area for the two regions. The seabird foraging habitat (100 km buffer) areas were calculated by selecting poly-lines of a geographic layer in ArcView GIS version 3.2 and performing a summary statistic function.

To investigate relative oceanic productivity of each area, we compared estimates of carbon produced per year (Springer *et al*. 1989, Springer & McRoy 1993), chlorophyll concentrations and summer plankton biomass (Sugimoto & Tadokoro 1997). Lacking data on forage fish, we also reviewed the 2003 fish stock abundance assessment and the 2002 groundfish catch data from the National Marine Fisheries Service (NMFS weekly production and observer reports).

RESULTS

About 29 million seabirds nest in 1 714 mixed species colonies in Alaska. The distribution of seabirds among these colonies is highly skewed. A few colonies have over a million birds while hundreds of colonies have fewer than 1 000 birds (USFWS 2004). Fifty percent of Alaska's seabirds breed in 12 massive, mixed-species colonies, the remainder are spread throughout other 1 702 colonies. Ten of the 12 largest colonies are in the EBS and two are in the GOA (Fig. 2).

Fifty percent of the populations of all Alaskan breeding species can be found within 148 colony sites. These colonies are split more evenly between the GOA and the EBS than the 12 largest colonies (Fig. 2). Forty of these 148 sites are important (i.e., one of the colonies needed to support 50% of a species breeding population) colonies for more than one species (Fig. 3).

The EBS supports almost three times as many seabirds as the GOA. The total breeding population of all seabird species in the EBS is approximately 20.3 million birds while the GOA has only 7.2 million (Table 1). Planktivorous seabirds are nearly five times as

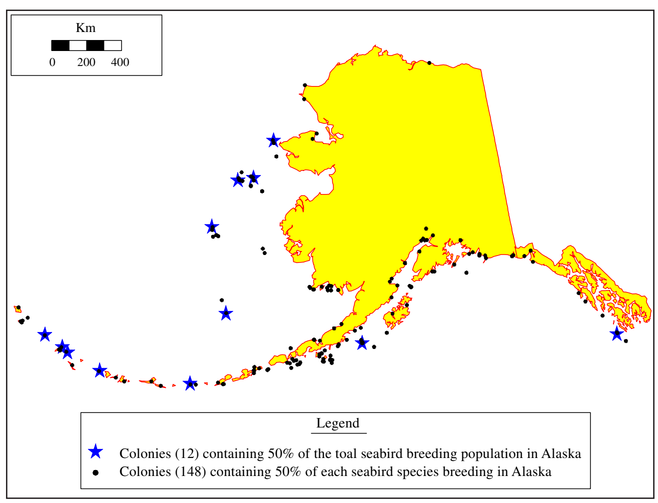

Fig. 2. Locations of the twelve seabird colonies containing half of the total breeding seabird population in Alaska and locations of 148 seabird colonies containing half of each seabird species breeding in Alaska (USFWS 2004).

abundant in the EBS as in the GOA, but piscivorous seabirds are only 1.6 times more numerous in the EBS (Table 1). Four planktivores, Crested Auklet *Aethia cristatella*, Least Auklet *Aethia pusilla*, Fork-tailed Storm-Petrel *Oceanodroma furcata*, and Leach's Storm-Petrel *Oceanodroma leucorhoa* and 1 piscivore; Thick-billed Murre account for 98% of the higher populations in the EBS (Fig. 4 & Appendix 2 & 3).

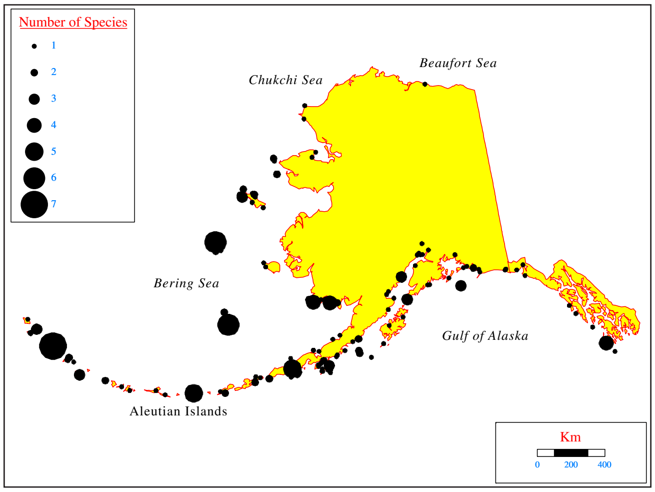

Fig. 3. Locations of 148 seabird colonies containing half of each seabird species breeding in Alaska, size of dot indicates how many species breed at each site (USFWS 2004).

TABLE 1
Comparison of seabird and groundfish parameters of the eastern Bering Sea and Gulf of Alaska (Hunt *et al*. 2000, NMFS 2002a, NMFS 2002b, NMFS 2003a, NMFS 2003b, Sugimoto and Tadokoro 1997, USFWS 2004). Add

Parameter	Eastern Bering Sea	Gulf of Alaska
Total foraging area (km^2)	942,552	549,763*
Total number of seabirds	20,870,286	7,156,926
Number of piscivorous seabirds	7,123,044	4,625,126
Number of planktivorous seabirds	13,747,242	2,531,800
Total seabird biomass (metric tons)	7,343	3,678
Piscivorous seabird biomass (metric tons)	5,773	3,461
Planktivorous seabird biomass (metric tons)	1,571	217
Total number of colonies	472	1,120
Median colony size	463	103
Number of seabird species	25	22
Chlorophyll concentration (mg m^{-3})**	1.88	1.35
Zooplankton biomass (mg m^{-3})**	386	221
2002 groundfish catch (metric tons)	1,760,275***	165,568***
2003 fish stock abundance (metric tons)	19,781,300***	4,005,170***

* Western Gulf of Alaska and SE Alaska foraging area 406,592 and 143,171 respectively.
** calculated mean from 1980-1994 from Sugimoto and Tadokoro 1997.
*** National Marine Fisheries Service (NMFS weekly production and observer reports).

Total seabird biomass in the EBS was 1.85 times higher than in the GOA (Table 1). This ratio is smaller than the ratio of numbers (2.82) because GOA supports a higher proportion of the large-bodied piscivorous murres and puffins, compared with the small-bodied planktivorous auklets and storm-petrels (Appendix 4).

Although more seabirds inhabit the EBS, the GOA supports more seabird colonies (i.e., 1,120 versus 472 respectively) (USFWS 2004). Consequently, seabird colonies are larger in the EBS than in the GOA. The median colony size of the EBS (463 individuals) is over 4 times greater than the GOA (103 individuals) (Table 1). The largest colony in the EBS, Buldir Island, is located in the Aleutian Islands with over 3.5 million birds. The largest colony complex in the GOA is the Semidi Islands with a breeding population of nearly 1.5 million birds (USFWS 2004).

The EBS has a total foraging area of 942,552 km^2 and the GOA has a total foraging area of 549,763 km^2 (Table 1) (Fig. 1). Hence, the total density of seabirds in the EBS (21.6 km^{-2}) is less than twice as much as in the GOA (13.0 km^{-2}). The seabird biomass density is similar in the two regions: 7219 g km^{-2} in the EBS and 6689 g km^{-2} in the GOA, (Table 2).

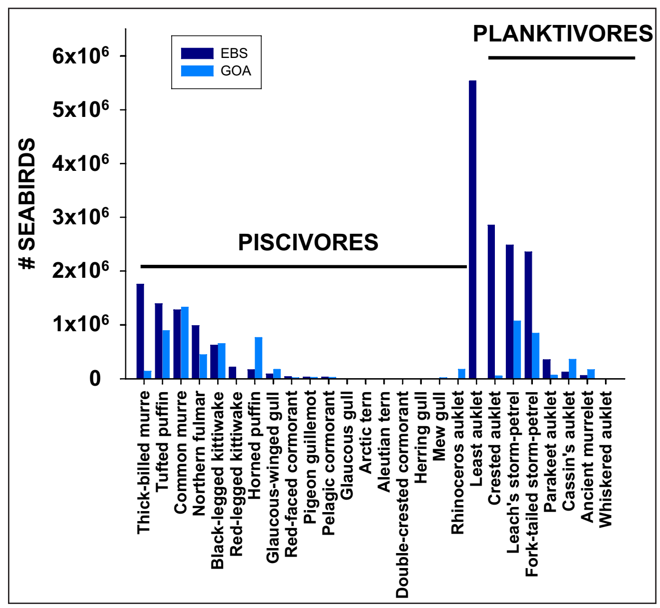

Fig. 4. Population size piscivorous and planktivorous seabird species in the eastern Bering Sea and Gulf of Alaska (USFWS 2003).

TABLE 2
Seabird population and biomass density, per km^2 in the eastern Bering Sea (EBS) and Gulf of Alaska (GOA) for piscivores and planktivores (Hunt *et al*. 2000, USFWS 2004).

	Seabird Population/km^2		Seabird Biomass/km^2	
Guild	EBS	GOA	EBS	GOA
Piscivorous	7.6	8.4	6.124	6.295
Planktivorous	14.6	4.6	1.666	.394
All Species	22.2	13.0	7.790	6.689

DISCUSSION

Ocean productivity appears to be higher in the EBS than in the GOA. The Bering Sea is considered one of the world's most biologically productive environments (Beringia Conservation Program, National Research Council 1996 and World Wildlife Fund 2001). Regions of high primary productivity occur at upwellings at the edge of the continental shelf, Aleutian Islands arc, and along the GOA mainland (Springer *et al*. 1989, Springer & McRoy 1993). Annual primary production in the GOA has been estimated to be as high as 300 gC m^{-2} in Lower Cook Inlet and the Kenai shelf (Sambrotto & Lorenzen 1987). In the EBS, annual primary production has been estimated to be as high as 300 gC m^{-2} along the Aleutian Islands, 365 gC m^{-2} along the continental shelf break, and up to 800 gC m^{-2} in the Anadyr Stream across the Bering-Chukchi shelf in the northern Bering Sea and southern Chukchi Sea (Springer & McRoy 1993). Generally, phytoplankton and zooplankton biomass levels in the Bering Sea are higher than those of the central and eastern sub arctic Pacific (Sugimoto and Tadokoro 1997). From 1980 to 1994, zooplankton biomass was on average 1.7 times higher and chlorophyll concentration 1.4 times higher in the EBS than in GOA (Sugimoto & Tadokoro 1997) (Table 1).

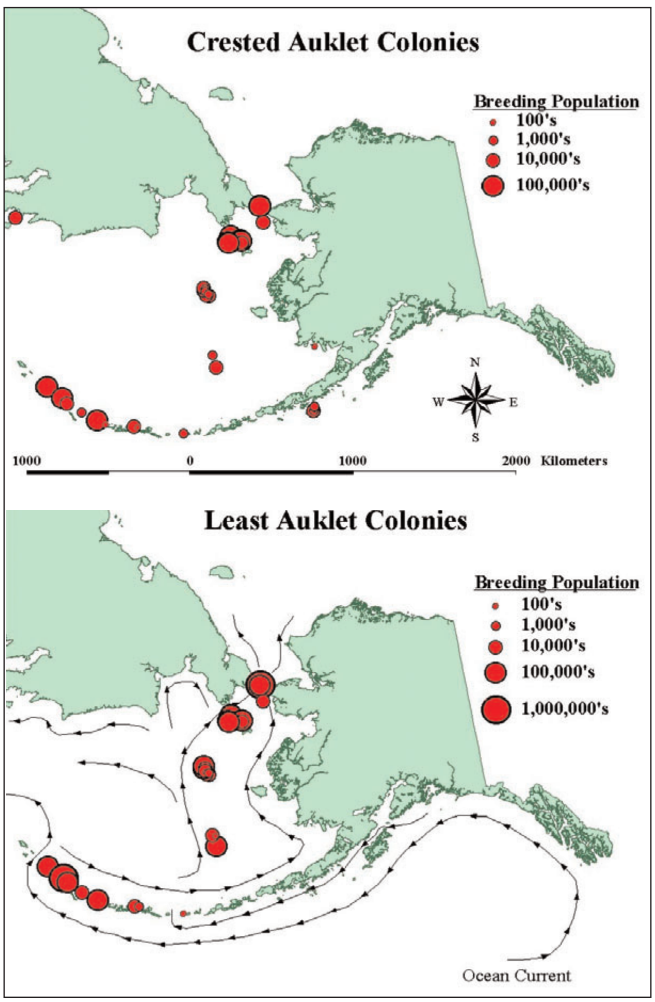

Fig. 5. Location and size of Crested and Least Auklet colonies (with breeding populations >100) and ocean currents in Alaska (Stabeno *et al*. 2003, USFWS 2004).

Groundfish are also more abundant in the EBS than in the GOA. The EBS produces nearly 5 times the amount of groundfish as the GOA (19.8 versus 4.0 million metric tons, respectively) (Table 1) (NMFS unpublished). In addition, the groundfish catch in the EBS, 1.8 million metric tons in 2002, is much higher than in the GOA, 166 000 metric tons in 2002 (NMFS unpublished).

We suggest that the higher numbers of seabirds in the EBS compared to the GOA is partly due to the EBS being larger than the GOA and partly due to the presence of millions of small colonial planktivorous auklets that occur in the EBS but not in the GOA. There is evidence that two factors may contribute to the auklets limited distribution; the availability of quality nesting habitat and areas rich in their food resources.

Least Auklets and Crested Auklets, the two most numerous breeding seabird species in Alaska, nest at 45 and 39 colonies, respectively (Fig. 5). All are located on volcanic islands, most of which are in the Bering Sea (Biekman 1994, USFWS 2004). The northern Bering Sea Islands are older volcanic islands and nearly all of the Aleutian Islands are relatively young (< 2 million years old) volcanic rock, largely basalt pyroclastic lava flows and volcaniclastic debris (Biekman 1994). Moreover, volcanic activity continues in the Aleutians: at least 29 volcanic centers had eruptions and 12 additional volcanic centers may have had eruptions since 1760 (Miller *et al*. 1998). The GOA on the other hand is characterized by very little volcanic rock close to the shoreline. Bedrock is approximately 40 to 70 million years old and is mainly sedimentary, including sandstone, shale, and mudstone (C. Neal, pers. comm.). There are only 7 very small Crested and 1 tiny Least Auklet colonies in the GOA, all situated on the few islands of volcanic origin (Biekman 1994, USFWS 2004). However, while the correlation of volcanic islands and nesting auklets fit relatively well, the eastern Aleutians form an exception, having no auklets despite recent volcanic activity. This scarcity of auklets may be due to a lack of suitable colony sites close to upwelling areas (J. Piatt, pers. comm).

The distribution of Crested and Least Auklet colonies among the volcanic islands in the Bering Sea appears to be determined by ocean productivity and prey availability. These dominant species of planktivores flourish in areas with high zooplankton concentrations on the edge of upwelling and frontal zones (Hunt *et al*. 1993, Stabeno *et al*. 2003, USFWS 2004) (Fig. 5). During summer, high concentrations of nutrients and plankton from the Bering Sea shelf edge are advected north over 1200 km to the central Chukchi Sea and provide a conveyor belt of abundant food to huge seabird colonies in the northern Bering Sea (Piatt & Springer 2003). The western and central Aleutians have areas of upwelling and high productivity that provide food for the largest colonies of auklets (Springer *et al*. 1996).

Least and Crested Auklets are absent from the volcanic islands in the eastern Aleutians. The reason for this void may lie in the type of water that surrounds these islands. The Alaska Coastal Current flows west along the GOA down the Alaska Peninsula and into the Bering Sea through eastern passes. Recent studies have shown that this relatively warmer, fresher water flows west as far as Samalga Pass, the end of the contiguous continental shelf, between Umnak Island and the Islands of Four Mountains. The water to the west of Samalga Pass is colder, saltier, oceanic water (C. Ladd unpublished). Samalga Pass is beginning to be recognized as a biogeographic break in the Aleutian Islands, the distributions of benthic species such as the sunflower star *Pycnopodia helianthoides* and bull kelp *Neroecystis luetkeana* which are common in the GOA end there (J. A. Estes, pers. comm.). Steller sea lion *Eumetopias jubatus* diets are similar throughout the western and central Aleutians, but change dramatically at Samalga Pass (Sinclair & Zeppelin 2002). All of the auklet colonies in the Aleutians are west of Samalga Pass. Hunt *et al*. (1990) found that Least Auklets avoided the warmer, fresher Alaska Coastal Current water near King Island to forage in colder, saltier oceanic water. Another recent study showed that Short-tailed Shearwaters *Puffinus tenuirostris* and Northern Fulmars *Fulmarus glacialis* consumed different prey in passes in the eastern and central Aleutians. Birds east of Samalga Pass ate more shelf break euphausiids than those in the central Aleutians which ate more oceanic copepods. Salmaga Pass may be an east-west divide between two distinct marine environments in the Aleutian Islands (J. Jahncke unpublished) and the marine environment east of Salmaga Pass may not have the dense concentrations of oceanic copepods and euphausiids that support huge auklet colonies.

High quality auklet nesting habitat may be available for only relatively few years on islands in the lower latitudes of their range. Planktivorous auklet species nest in crevices within talus slopes with broken, fragmental, blocky rock deposits. As the talus ages, vegetation forms over the rocks and covers the crevice or openings to nest sites, possibly limiting the availability of favorable nest sites (I. Jones, pers. comm). A photograph taken of a historical site of a large auklet colony at Sirius Point, Kiska Island, in the 1940s shows much of the area was unvegetated lava flow. In 2002, biologists visiting Sirius Point found the area to be highly vegetated and devoid of nesting auklets because of inaccessibility to rock crevices (I. L. Jones, pers. comm). Instead, auklets nested nearby in an unvegetated lava flow formed in 1962 (Miller *et al*. 1998). Vegetation growth appears to be more of a factor in limiting nesting auklets in the Aleutian Islands and GOA than on islands in the northern Bering Sea. Most volcanic rock auklet nesting areas on Saint Lawrence and Little Diomede Island are very old (cretaceous and tertiary period), yet there is little vegetative cover, presumably because of the severe climate at that latitude. These observations suggest that substrate age and type may play an important part in determining the locations of Crested and Least Auklet colonies in Alaska.

If productivity is higher in the EBS, why is seabird biomass density similar between the two regions? Springer (1991) suggested that auklet populations may be limited by competition for food with juvenile Pollock. We suggest another possibility: predation. Predators affect seabird distribution and abundance in Alaska. In the Bering Sea, foxes exist naturally on the northern islands, the sea freezes and provides access to the islands during winter. Foxes are also indigenous to the Fox Islands in the eastern Aleutian Islands, they have apparently been there since the Pleistocene, when the islands were connected to the mainland by ice or land bridges (Bailey 1993). In the GOA, foxes are indigenous only to a few large islands. Most islands in the central and western Aleutians and in the GOA were naturally fox free. However, foxes were introduced to more than 450 islands in Alaska from 1750 to the 1930s for fur farming. Islands with large seabird populations were often specifically chosen for introductions so that the foxes would have a ready food source. These foxes decimated burrow- and surface-nesting seabird populations on many of the islands (Bailey 1993). Today, introduced foxes have been eradicated or have naturally died off most islands in the GOA and many islands in the Aleutians (Williams *et al*. 2003). The seabirds are starting to recover, but several populations in the western and central Aleutians are still depressed (Bailey 1993). Interestingly, the two largest mixed species seabird colonies in the Aleutians are on Buldir and Chagulak Islands (USFWS 2004), two islands where foxes were never introduced. The impact of fox predation on seabirds has been greater in the EBS than in the GOA, both because of more islands with indigenous foxes and more successful introductions in the EBS. Predation by foxes, both indigenous and introduced, may be part of the reason that there are not more seabirds in the EBS.

ACKNOWLEDGMENTS

We thank all those that contributed data and reviewed this manuscript. Thanks to all who contributed seabird data to the Beringian Seabird Colony Database. Christina Neal and Robert Gamewell McGimsey from the Alaska Volcano Observatory, USGS contributed geological data and enthusiasm. Jay A. Johnson, USFWS assisted with foraging area data. Alan Springer and John Piatt provided insights on oceanographic information.

REFERENCES

AGLER, B.A., KENDALL, S.J., IRONS, D.B., & KLOSIEWSKI, S.P. 1999. Declines in Marine Bird Populations in Prince William Sound, Alaska Coincident with a Climatic regime Shift. *Waterbirds* 22: 98-103.

ANDERSON, P.J. & PIATT, J. F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189: 117-123.

ASHMOLE, N.P. 1963. The regulation of numbers of tropical oceanic seabirds. *Ibis* 103b: 458-473.

BAILEY, E.P. 1993. Introduction of foxes to Alaskan islands-history, effects on avifauna, and eradication. U.S. Dept. of the Interior, Fish and Wildlife Service Resource Publication 193.

BEIKMAN, H. 1994. Geologic map of Alaska. In: Plafker, G. & Berg, H.C. (Eds.). The Geology of Alaska, Geological Society of America, The Geology of North America, v. G-1, plate 1.

BERINGIA CONSERVATION PROGRAM & WORLD WILDLIFE FUND. 2001. The Bering Sea ecoregion; a call to action in marine conservation. World Wildlife Fund Public Information Report: pp 32.

BIRKHEAD, T.R. & FURNESS, R.W. 1985. The regulation of seabird populations. In: Sibly R.M. & Smith R.H. (Eds.), Behavioral Ecology. Blackwell, Oxford, pp. 145-167.

BROWN, J.H. & LOMOLINO, M.V. 1996. Biogeography. Sinauer Associates. Sunderland, Mass.

DEGANGE, A.R., DAY, R.H., TAKEKAWA, J.E. & MENDENHALL, V.M. 1993. Losses of seabirds in gill nets in the North Pacific. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.). The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Environment Canada. pp. 204-211.

FURNESS, R. & MONAGHAN, P. 1987. Seabird ecology. Chapman and Hall. New York, New York.

GASTON A.J. & HIPFNER, J.M. 2000. Thick-billed Murre (*Uria lomvia*). In: Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 497. The Birds of North America, Inc., Philadelphia, PA.

HATCH, J.J. 2002. Arctic Tern (*Sterna paradisaea*). In: Poole, A. & Gill, F. (Eds.). The Birds of North America, No. 707. The Birds of North America, Inc., Philadelphia, PA.

HUNT, J.L., JR., HARRISON, N.M. & COONEY, R.T. 1990. The influence of hydrographic structure and prey abundance on foraging of least auklets. *Studies in Avian Biology* 14: 7-22.

HUNT, J.L., JR., HARRISON, N.M. & PIATT, J.F. 1993. Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea. . In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.). The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Environment Canada. pp. 18-26.

HUNT, J.L., JR., HIDEHI, O.K. & MCKINNEL, S.M. 2000. Predation by marine birds and mammals in the North Pacific Ocean. PICES Scientific Report No. 14 2000, North Pacific Marine Science Organization.

LACK, D. 1966. Population studies of birds. Oxford University Press, Oxford.

LENSINK, C.J. 1984. The status and conservation of seabirds in Alaska, In: Croxall, J.P., Evans, P.G.H. & Schreiber, R.W. (Eds.). Status and Conservation of the World's Seabirds, Cambridge: International Council for Bird Preservation. pp 13-28.

MILLER, T.P., MCGIMSEY, R.G., RICHTER, D.H., RIEHLE, J.R., NYE, C.J., YOUNT, M.E. & DUMOULIN, J.A. 1998. Catalog of the historically active volcanoes of Alaska. Open File Report 98-582, U.S. Geological Survey, Anchorage, Alaska and Alaska Division of Geological and Geophysical Surveys, Fairbanks, Alaska.

NATIONAL RESEARCH COUNCIL. 1996. The Bering Sea ecosystem: geology, physics, chemistry, and biology of lower trophic levels. National Academy Press, Washington D.C. Chapter 3, pp 28-71.

PIATT, J. F., LENSINK, C. F., BUTLER, W., KENDZIOREK, M. & NYSEWANDER, D. R. 1990. Immediate impact of the 'Exxon Valdez' oil spill on marine birds. *Auk* 107:387-397.

PIATT, J.F. & SPRINGER, A.M. 2003. The paradox of pelagic food webs in the northern Bering Sea—IV: Seabird Biogeography. *Marine Ornithology* 31: 141-154.

SAMBROTTO, R.N. & LORENZEN, C.J. 1986. Phytoplankton and primary production. In: Hood, D.W. & Zimmerman, S.T. (Eds.). The Gulf of Alaska; Physical Environment and Biological Resources. U.S. Departments of Commerce and the Interior, Minerals Management Service Publ. OCS Study MMS 86-0095. pp 249-282.

SINCLAIR, E.H. & ZEPPLIN, T.K. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammology* 83: 973-990.

SOWLS, A.L., HATCH, S.A. & LENSINK, C.J. 1978. Catalog of Alaskan seabird colonies. U.S. Fish and Wildlife Service, Biological Services Project, FWS/OBS-78/78.

SPRINGER, A.M. 1991. Seabird distribution as related to food webs and the environment: examples from the north Pacific Ocean. In: Montevecchi, W.A. & Gaston, A.J. (Eds.). Studies of High Latitude Seabirds 1: Behavioral, Energetic and Oceanographic Aspects of Seabird Feeding Ecology. Canadian Wildlife Service Occasional Paper No 68, Canadian Wildlife Service, Ottawa: pp. 39-48.

SPRINGER, A.M. & MCROY, C.P. 1993. The paradox of pelagic food webs in the northern Bering Sea - III. Patterns of primary production. *Continental Shelf Research* 13: 575-599.

SPRINGER, A.M., MCROY, C.P. & TURCO, K.R. 1989. The paradox of pelagic food webs in the northern Bering Sea - II. Zooplankton communities. *Continental Shelf Research* 9: 359-386.

SPRINGER, A.M., PIATT, J.F. & VAN VLIET, G. 1996. Seabirds as proxies of marine habitats in the western Aleutian arc. *Fisheries Oceanography* 5:45-55.

STABENO, P.J., SCHUMACHER, J.D. & OHTANI, K. 2003. The physical oceanography of the Bering Sea. In: Laughlin, T.R. & Ohtani, K. (Eds.). Dynamics of the Bering Sea: a summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea. North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, pp. 1-28.

STEPHENSEN, S.W. 2001. The Beringian Seabird Colony Catalog Annual Report. Unpublished Report, U.S. Fish and Wildlife Service, Anchorage, Alaska. 26 pp.

STEPHENSEN, S.W. & MENDENHALL, V.M. 1998. Alaska Seabird Recensus Plan. Unpublished Report, U.S. Fish and Wildlife Service, Anchorage, Alaska. 153 pp.

SUGIMOTO, T. & TADOKORO, K. 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fisheries Oceanography* 6: 74-93.

UDVARDY, M.D.F. 1976. Did Santa Rosalia like sea-birds? Proceedings of the 16th International Ornithological Congress, August 1974. Australian Academy of Science Canberra City, A.C.T. 2601, Australia.

U.S. FISH & WILDLIFE SERVICE. 1992. Alaska Seabird Management Plan. Unpublished Report, U.S. Fish and Wildlife Service, Anchorage, Alaska. 102 pp.

U.S. FISH & WILDLIFE SERVICE. 1994. Seabird Colony Catalog: manual for interpretation of colony data for data entry. U.S. Fish and Wildlife Service Manual, Migratory Bird Management. Anchorage, Alaska. 33 pp.

U.S. FISH &WILDLIFE SERVICE. 1999. Beringian Seabird Colony Catalog manual for censusing seabird colonies. U.S. Fish and Wildlife Service Report, Migratory Bird Management. Anchorage, Alaska. 27 pp.

U.S. FISH &WILDLIFE SERVICE. 2004. Beringian Seabird Colony Catalog--computer database and Colony Status Record archives. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska 99503.

WILLIAMS, J.C., BYRD, G.V. & KONYUKHOV, N.B. 2003. Whiskered Auklets *Aehtia pygmaea*, foxes, humans and how to right a wrong. *Marine Ornithology* 31: 175-180.

Appendix 1

Seabird species, breeding population and number of colonies in the Eastern Bering Sea (EBS) and Gulf of Alaska (GOA), and number of colonies that contain 50% of the total species population (USFWS 2004). Foraging guilds according to Gaston and Hipfner (2000), Hatch (2002), Hunt et al. (2000). Biomass from Hunt et al. (2000), USFWS (2003)

Species	Foraging guild	Number of colonies		Population		Colonies with 50% of species population	Body Mass (kg)*	Biomass (kg)	
		EBS	GOA	EBS	GOA			EBS	GOA
Northern Fulmar *Fulmarus glacialis*	Pisc.	22	16	983,983	440,217	2	0.544	535,287	239,478
Fork-tailed Storm Petrel *Oceanodroma furcata*	Plank.	56	56	2,354,806	840,530	2	0.0553	130,221	46,481
Leach's Storm Petrel *Oceanodroma leucorhoa*	Plank.	51	43	2,483,392	1,067,952	2	0.0398	98,839	42,504
Double-crested Cormorant *Phalacrocrax auritus*	Pisc.	34	72	2,668	3,400	7	1.674	4,466	5,692
Pelagic Cormorant *Phalacrocorax pelagicus*	Pisc.	173	214	24,184	19,257	15	1.868	45,176	35,972
Red-faced Cormorant *Phalacrocorax urile*	Pisc.	91	122	33,616	13,877	10	2.157	72,510	29,933
Mew Gull *Larus canus*	Pisc.	3	65	234	14,135	4	0.4035	94	5,703
Herring Gull *Larus argentatus*	Pisc.	22	13	861	706	4	1.135	977	801
Glaucous-winged Gull *Larus glaucescens*	Pisc.	223	592	85,199	167,036	42	1.01	86,051	168,706
Glaucous gull *Larus hyperboreus*	Pisc.	63	0	5,680	0	7	1.4125	8,023	0
Black-legged Kittiwake *Rissa tridactyla*	Pisc.	100	249	619,081	648,858	16	0.407	251,966	264,085
Red-legged Kittiwake *Rissa brevirostris*	Pisc.	7	0	208,851	0	1	0.391	81,661	0
Arctic Tern *Sterna paradisaea*	Pisc.	33	114	2,840	7,599	14	0.11	312	836
Aleutian Tern *Sterna aleutica*	Pisc.	34	22	2,770	6,793	3	0.12	332	815
Common murre *Uria aalge*	Pisc.	140	90	1,505,849	1,326,793	7	0.9925	1,494,555	1,316,842
Thick-billed Murre *Uria lomvia*	Pisc.	121	53	2,071,438	134,171	1	0.964	1,996,866	129,341
Pigeon Guillemot *Cepphus columba*	Pisc.	237	643	25,867	23,090	39	0.487	12,597	11,245
Ancient Murrelet *Synthliboramphus antiquus*	Plank.	43	47	54,363	164,403	3	0.206	11,199	33,867
Cassin's Auklet *Ptychoramphus aleuticus*	Plank.	22	30	118,090	354,853	3	0.188	22,201	66,712
Least Auklet *Aethia pusilla*	Plank.	35	2	5,528,743	20	5	0.084	464,414	2
Parakeet Auklet *Cyclorhynchus psittacula*	Plank.	88	107	349,181	57,992	3	0.258	90,089	14,962
Whiskered Auklet *Aethia pygmaea*	Plank.	44	0	6,712	0	2	0.121	812	0
Crested Auklet *Aethia cristatella*	Plank.	36	7	2,851,955	46,050	4	0.264	752,916	12,157
Rhinoceros Auklet *Cerorhinca monocerata*	Pisc.	1	18	30	170,065	1	0.52	16	88,434
Tufted Puffin *Fratercula cirrhata*	Pisc.	248	445	1,389,380	888,864	15	0.779	1,082,327	692,425
Horned Puffin *Fratercula corniculata*	Pisc.	217	391	160,513	760,265	4	0.619	99,358	470,604
TOTALS	Pisc.			7,123,044	4,625,126			5,772,574	3,460,912
	Plank.			13,747,242	2,531,800			1,570,691	216,686
	All Species			**20,870,286**	**7,156,926**			**7,343,265**	**3,677,598**