Sea birds as proxies of marine habitats and food webs in the western Aleutian Arc

ALAN M. SPRINGER,[1] JOHN F. PIATT[2] AND GUS VAN VLIET[3]

[1] *Corresponding author. Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775, U.S.A.*
[2] *National Biological Service, Alaska Science Center, 1011 E. Tudor Road, Anchorage, AK 99503, U.S.A.*
[3] *PO Box 210442, Auke Bay, AK 99821, U.S.A.*

ABSTRACT

We propose that ocean conditions of the Near Islands in the western Aleutian Arc mimic those of the shallow continental shelf of the eastern Bering Sea to the extent that the marine community, including assemblages of forage fishes and their avian predators, has distinctly coastal characteristics. In contrast, marine avifauna and their prey at neighbouring Buldir Island are distinctly oceanic. For example, at the Near Islands, the ratio of thick-billed to common murres, *Uria lomvia* and *U. aalge*, is low and black-legged kittiwakes, *Rissa tridactyla*, but not red-legged kittiwakes, *R. brevirostris*, nest there. Diets of murres and kittiwakes are dominated by sand lance, *Ammodytes hexapterus*, an abundant coastal species. At Buldir Island, thick-billed murres greatly outnumber common murres, red-legged kittiwakes and black-legged kittiwakes are both abundant, and diets of the birds consist primarily of oceanic squid and lanternfish (Myctophidae). This mesoscale difference in food webs is apparently a consequence of the local physiography. A broad escarpment on the Near physiographic block creates a comparatively expansive, shallow, shelf-like habitat around the Near Islands, where a pelagic community typical of coastal regions flourishes. Buldir Island is the only emergent feature of the Buldir physiographic block, with little shallow water surrounding it and, apparently, little opportunity for other than oceanic species to exist. Patterns in the distribution of fishes, and thus of sea birds, throughout the Aleutian Islands might be largely explained by the presence or absence of shelf-like habitat and the relationship between physical environments and food webs. In the larger context of fisheries oceanography, this model for the Aleutian Islands improves our ability to interpret physical and biological heterogeneity in the ocean and its relationship to regional community dynamics and trends in the abundance and productivity of individual species at higher trophic levels.

Key words: sea bird, food web, forage fish, Bering Sea, Aleutian Islands, marine ecology

INTRODUCTION

The abundance of four species of primarily piscivorous sea birds, common and thick-billed murres (*Uria aalge* and *U. lomvia*, respectively) and red-legged and black-legged kittiwakes (*Rissa brevirostris* and *R. tridactyla*, respectively) on Buldir Island and the Near Islands in the western Aleutian Islands increased rapidly in the decade from the mid 1970s to the mid 1980s (Byrd and Douglas, 1989). The exceptional growth of those populations suggested that birds nesting there likely were not limited by food during that time, and contrasted with a simultaneous decline of similar magnitude in numbers of the same species on the Pribilof Islands in the southeastern Bering Sea (Byrd, 1989; Dragoo *et al.*, 1989). On the Pribilofs, walleye pollock (*Theragra chalcogramma*) generally supports most of the piscivorous sea birds, as well as fur seals (*Callorhinus ursinus*) which indicates that it is a particularly abundant forage species (Lucas, 1899; Hunt *et al.*, 1981a; Johnson, 1985; Sinclair *et al.*, 1994; Decker *et al.*, 1995).

Studies on the Pribilofs in the late 1980s concluded that nesting sea birds were food stressed, which might have caused low productivity, high mortality (particularly of juveniles) and the observed population decline (Springer, 1994). The decline in abundance of sea birds was indeed matched by generally poor productivity during those years (Dragoo *et al.*, 1989), as well as by a decline in pup production of fur seals on the Pribilofs and by a widespread, continuing decline in numbers of Steller sea lions (*Eumetopias jubatus*) in the Aleutian Islands, Bering Sea, and Gulf of Alaska (Merrick *et al.*, 1987; York and Kozloff, 1987; Trites and Larkin, 1989). Together, these changes raised concerns over the status of forage fish stocks, including the commercially important pollock stock, and the relationship of climate

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change and commercial fishing to ecosystem change and the stability of marine bird and mammal populations (Swartzman and Hofman, 1991; Alverson, 1992; Springer, 1992; Wooster, 1994).

In an attempt to help explain the situation in general, and the divergent trends in sea bird populations between the western Aleutian Islands and the Pribilof Islands in particular, we undertook a study of sea bird feeding ecology in the western Aleutians in the summers of 1988–89. An understanding of trophic dependencies of murres and kittiwakes there was lacking, and was needed to interpret the population changes and, apparently, ecosystem changes that were occurring in the Bering Sea.

METHODS

The Aleutian Islands are the peaks of a submerged mountain range, the Aleutian Ridge, formed by the collision of the Pacific plate with the Bering Sea plate (Gard, 1977). The eastern third of the ridge forms the Alaska Peninsula that rises from the shallow continental shelf of the western Gulf of Alaska and south-eastern Bering Sea. In deep water to the west of this shelf, only the highest peaks of the range emerge. Depending on local physiography, the peaks are surrounded by escarpments of greater or lesser extent forming a chain of islands encircled by differing amounts of shallow water. Some of the larger islands and island groups have rather broad escarpments with water depths less than 200 m. Small islands that are isolated or lie a distance off the centre of the ridge have narrow escarpments and little shallow water surrounding them.

The Near Islands include Attu, Agattu, Shemya, and Nizki-Alaid islands (Fig. 1). They all lie within a radius of approximately 50 km on the Near physiographic block toward the western end of the Aleutian Arc (Gard, 1977). Buldir Island lies about 150 km east of the Near Islands and is the only emergent feature of the Buldir block. Waters less than 200 m deep are extensive around the Near Islands, but are nearly absent around Buldir Island (Fig. 2).

Figure 1. Location of the study area in the North Pacific Ocean. Bathymetry in metres.

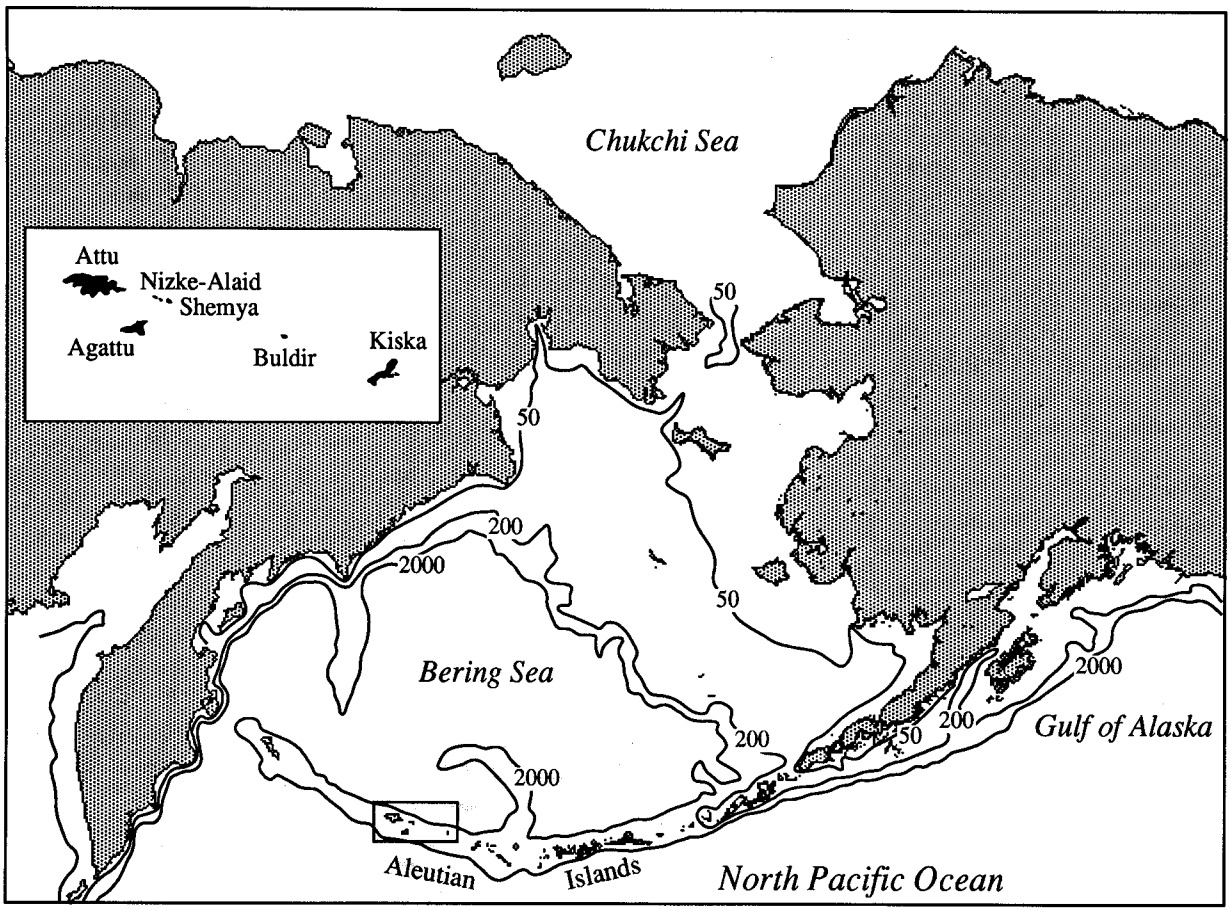
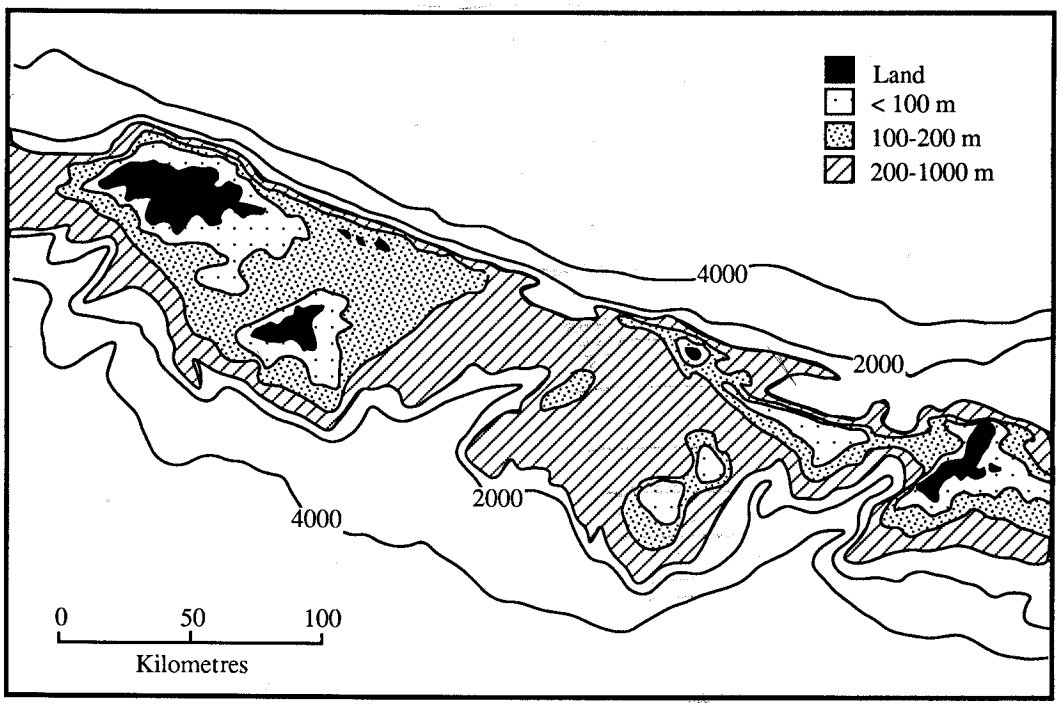


Figure 2. Bathymetry of the Near and Buldir physiographic blocks of the western Aleutian Ridge.



We sampled sea birds at both locations in the summers of 1988 and 1989 as part of a programme of coordinated studies of sea birds and their trophic relationships in the western Aleutians. Most birds were collected near shore as they returned to the colonies from feeding, although some were taken at sea during pelagic transects run to determine foraging distributions (J. Piatt *et al.*, unpubl. data). Collections were made at various times of day between early morning and late evening. In addition, regurgitated meals from black-legged and red-legged kittiwake chicks were collected at Buldir Island.

Diet samples were preserved in 70% ethanol and enumerated using preserved reference material and standard taxonomic keys. The biomass of individual prey was approximated using relationships between otolith length and fish length and weight, size categories of squid based on beak size in intact specimens (small, 2 g; medium, 7 g; and large, 30 g), fresh volumes of individual zooplankton, and fresh weights of other invertebrates (e.g. Bedard, 1969; Springer *et al.*, 1984, 1986). A standard weight of 5 g was assigned to unidentified fishes unless the fresh weight of the unidentified material in the stomach exceeded 5 g, in which case the actual weight was used.

It was not possible to correct for the differential digestion and passage rates of hard parts from various prey types in estimating their importance in diets. For example, squid beaks are known to persist in stomachs of sea birds for longer periods than otoliths and other hard parts of fishes (Furness *et al.*, 1984; van Heezik and Seddon, 1989). Isotopic studies also indicate that the importance of squid in relation to fishes is overestimated for species that consume squid (Hobson *et al.*, 1994). However, comparisons of diets that we make should not be affected by this problem, because passage rates of prey remains likely do not differ greatly between conspecifics.

RESULTS

There were no conspicuous differences in diets of any species between years, although in most cases the sample sizes were too small to allow meaningful comparisons. The frequency of occurrence and number of prey in adult diets pooled by species and location are shown in Table 1. The estimated contributions of each prey species or taxon to the total prey biomass for each species of sea bird and for kittiwake chicks are shown in Figs 3–11.

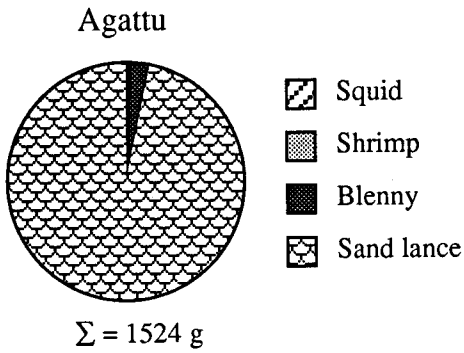
Red-faced cormorants (*Phalacrocorax urile*) were collected only at Agattu, where over 95% of their diet was sand lance (*Ammodytes hexapterus*). Minor amounts of

Table 1. Frequency of occurrence and (number) of prey in diets of sea birds in the western Aleutian Islands.

	RFCO[a]	BLKI			RLKI	COMU			TB MU		PIGU	HO PU		TUPU		
	Agattu	Buldir	Agattu	Attu	Buldir	Buldir	Agattu	Attu	Buldir	Agattu	Agattu	Buldir	Agattu	Buldir	Agattu	Attu
Number examined	10	103	30	17	11	24	46	15	65	11	2	7	2	26	31	3
Number empty	0	14	13	0	5	6	11	0	7	1	0	1	1	7	9	0
Polychaeta		1 (2)	1 (1)	7 (52)			2 (2)	1 (1)	1 (1)				1		10 (76)	2 (25)
Squid	1 (1)	17 (90)		2 (21)	3 (5)	4 (16)	4 (5)		43 (209)	1 (1)		6 (29)	1 (1)	19 (108)	15 (49)	
Copepoda		4 (115)														
Neocalanus cristatus		7 (424)														
Neocalanus plumchrus		7 (5549)														
Gammaridea		7 (12)	1 (2)													
Lysianassidae		2 (6)	1 (2)		1 (1)											
Parathemisto pacifica		19 (1306)			1 (18)											
Thysanoessa inermis		2 (179)				1 (600)			2 (270)							
Thysanoessa spinifera		1 (38)														
Thysanoessa raschii		12 (4960)							3 (932)							
Thysanoessa spp.		19 (3798)	1 (62)			2 (27)			6 (330)						1 (P)	
Crab											2 (2)					
Shrimp	3 (15)				1 (1)											
Unidentified crustaceans		3 (P)				1 (P)			1 (P)							
Northern lanternfish, *Stenobrachius leucopsarus*		23 (67)	2 (1)	6 (6)	2 (5)		1 (1)	2 (2)	2 (4)							
Walleye pollock, *Theragra chalcogramma*						5 (39)	1 (2)	1 (3)	6 (43)	1 (1)						
Cod–Gadidae							2 (11)					1 (1)				
Kelp greenling, *Hexagrammos decagrammus*									1 (2)							
Sculpin–Cottidae		1 (3)					1 (1)		1 (6)							
Northern ronquil, *Ronquilus jordani*									1 (2)							
Searchers, *Bathymaster signatus*									1 (1)							
Blenny, *Lumpenus* spp.	2 (4)															
Sand lance, *Ammodytes hexapterus*	7 (83)	16 (22)	11 (25)	6 (15)		7 (25)	30 (177)	11 (48)	2 (2)	6 (15)		1 (8)			6 (21)	3 (12)
Unidentified fish		9 (57)	2 (2)	1 (1)	2 (4)	3 (5)	1 (1)	2 (2)	13 (20)	3 (3)	1 (1)				1 (1)	1 (1)

[a]RFCO, red-faced cormorant; BLKI, black-legged kittiwake; RLKI, red-legged kittiwake; COMU, common murre; TBMU, thick-billed murre; PIGU, pigeon guillemot; HOPU, horned puffin; TUPU, tufted puffin.

Figure 3. Relative biomass of prey in diets of red-faced cormorants at Agattu Island.



squid (primarily Gonatidae), shrimp (*Pandalus* spp.), and blenny (*Lumpenus* spp.) also were consumed (Fig. 3).

Diets of black-legged kittiwakes were more diverse at Buldir than at either Agattu or Attu (Table 1, Fig. 4). At Buldir, birds that fed at night or very early in the morning took primarily lanternfish (mainly *Stenobrachius leucopsarus*) and squid, while those that fed during the afternoon took mainly euphausiids (*Thysanoessa* spp.), hyperiid amphipods (*Parathemisto* spp.) and copepods (*Neocalanus* spp.) (Fig. 5). With the possible exception of polychaetes (*Nereis* spp.) at Attu, invertebrates were not important at the Near Islands, where black-legged kittiwakes fed mainly on sand lance and lanternfish. Diets of chicks were similar to adult diets (Fig. 6).

Red-legged kittiwakes do not nest on the Near Islands. On Buldir their diets consisted of about half squid and half lanternfish (Fig. 4). Chicks were fed on a diet similar to that of the adults (Fig. 6). In general, diets of red-legged kittiwakes were much less diversified than diets of black-legged kittiwakes at Buldir Island.

Diets of common murres at all three sites were dominated by sand lance, particularly at Agattu and Attu where other prey were hardly represented (Fig. 7). Squid, in addition to sand lance, were important to common murres at Buldir.

Squid was the primary prey of thick-billed murres at Buldir (Fig. 8). They also took a wide variety of fishes there, including pollock, greenlings (*Hexagrammos decagrammus*), sculpins (Cottidae), ronquils (*Bathymaster signatus* and *Ronquilus jordani*), lanternfish, and sand lance. Squid was relatively unimportant on Agattu, where a small sample of birds instead fed primarily on pollock and sand lance (Fig. 8).

Information on diets of pigeon guillemots (*Cepphus columba*) is inconclusive because the sample size was so small. Unidentified small crabs were present in both

Figure 4. Relative biomass of prey in diets of black-legged kittiwakes (BLKI) at Buldir, Agattu and Attu islands and red-legged kittiwakes (RLKI) at Buldir Island.

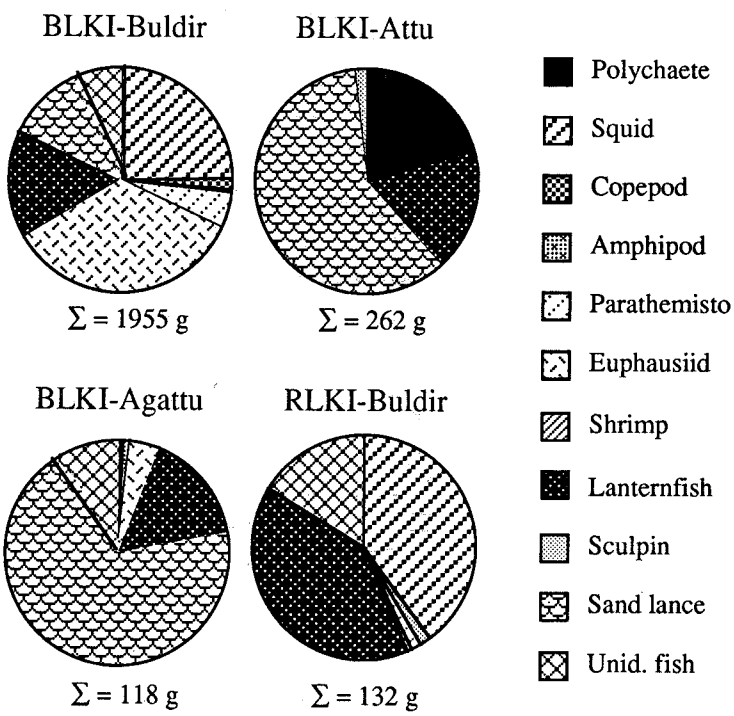
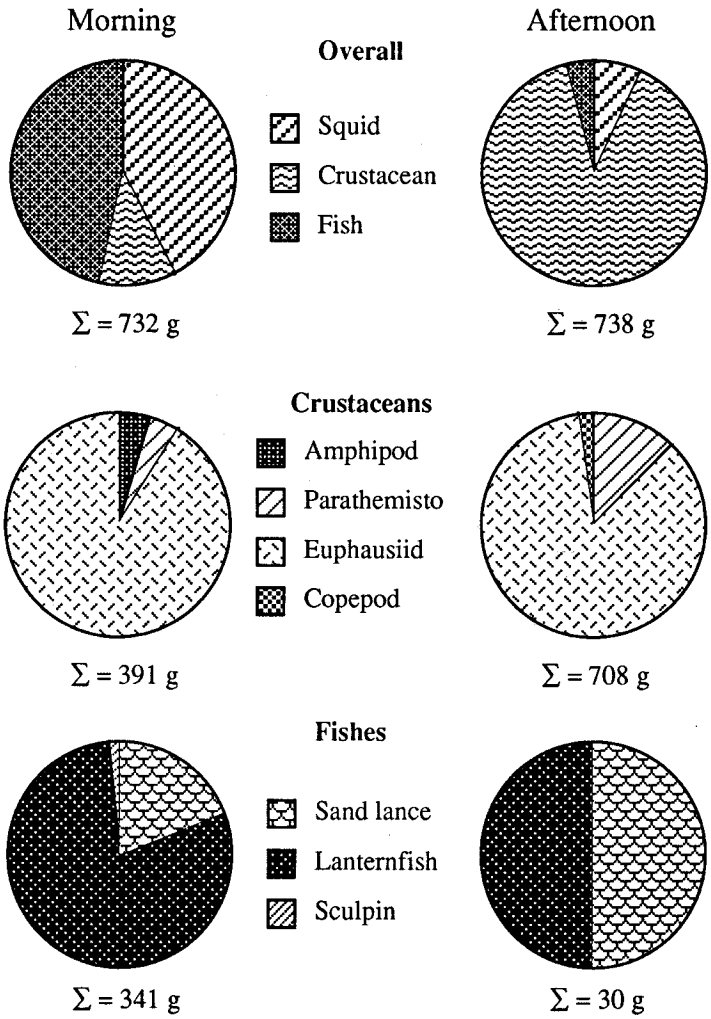


Figure 5. Relative biomass of prey in diets of black-legged kittiwakes at Buldir Island in the morning and afternoon.



birds examined and an unidentified fish was present in one bird (Table 1).

Likewise, the sample size of horned puffins (*Fratercula corniculata*) was small and inconclusive. Squid was the most common prey on both Buldir and Agattu (Fig. 9).

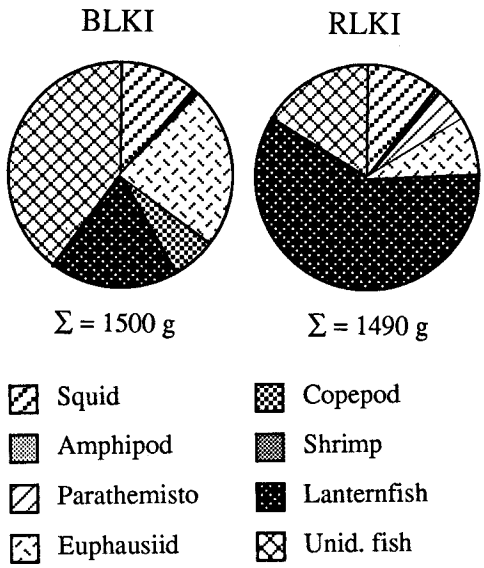
Squid was the only prey found in diets of tufted puffins (*Fratercula cirrhata*) at Buldir and it contributed most of the biomass at Agattu (Fig. 10). Sand lance was most important in the small sample from Attu.

DISCUSSION

Despite a broad overlap in the suite of species eaten by sea birds at Buldir and the Near Islands, the proportions of the various prey differed greatly between the two locations. Squid was very important to all birds at Buldir, but only to puffins at the Near Islands. Puffins are squid specialists – adults feed heavily on them elsewhere in the eastern Aleutians and western Gulf of Alaska (Wehle, 1982; Piatt *et al.*, unpubl. data) even though fish are usually fed to chicks (Wehle, 1983; Hatch and Sanger, 1992; J. Piatt *et al.*, unpubl. data). Thick-billed murres are known to feed heavily on squid in the North Pacific during winter (Ogi, 1980).

Lanternfish were the most important of the fishes consumed by both species of kittiwake at Buldir, but were replaced for the most part by sand lance in diets of black-legged kittiwakes at the Near Islands. Thick-billed murres ate mostly squid on Buldir, but sand lance and pollock on the Near Islands. Common murres ate mostly sand lance, which ranked first in their diets even on Buldir, while ranking third, fourth, or lower in diets of the other species there.

Figure 6. Relative biomass of prey in diets of kittiwake chicks at Buldir Island. BLKI, black-legged kittiwake; RLKI, red-legged kittiwake.



Sand lance constituted approximately half or more of prey in diets of most sea birds at the Near Islands. Sand lance were smaller (younger) at the Near Islands than at Buldir, where most fish were large adults. The presence

Figure 7. Relative biomass of prey in diets of common murres at Buldir, Agattu and Attu islands.

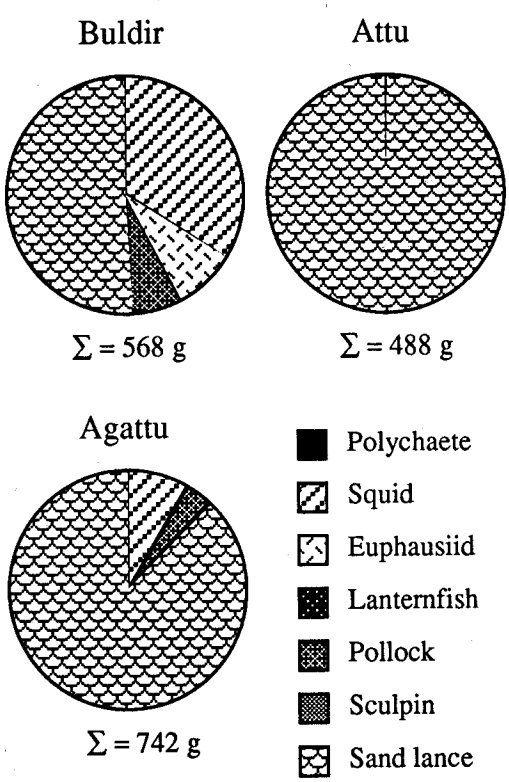
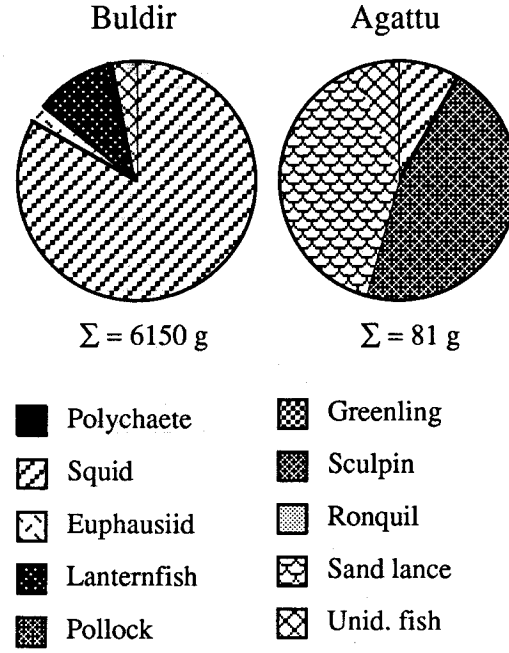


Figure 8. Relative biomass of prey in diets of thick-billed murres at Buldir and Agattu islands.



of abundant younger age classes at the Near Islands implies that (1) sand lance spawn there in much greater numbers than at Buldir, (2) juvenile sand lance congregate there in summer to feed on an abundant community of coastal/shelf zooplankton, as they do elsewhere along mainland coasts (Andriashev, 1954; Springer *et al.*, 1984), or (3) both occur. Juvenile sand lance are found around Buldir, but apparently in small numbers and late in summer when they are fed to puffin chicks (Wehle, 1976; V. Byrd and J. Williams, unpubl.

Figure 9. Relative biomass of prey in diets of horned puffins at Buldir and Agattu islands.

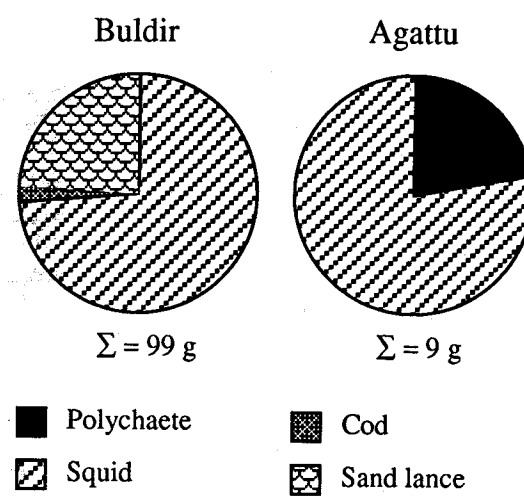
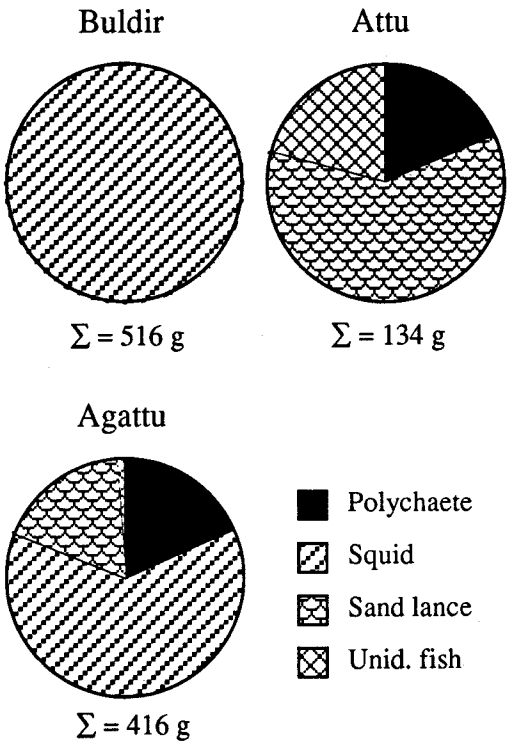


Figure 10. Relative biomass of prey in diets of tufted puffins at Buldir, Agattu and Attu islands.



data). At Buldir there is a limited amount of shallow substrate where sand lance can spawn (Dick and Warner, 1982), and the abundance of zooplankton prey suitable for juvenile sand lance (Rogers *et al.*, 1979; Springer *et al.*, 1987) might also be limited at Buldir compared with the Near Islands.

Squid and lanternfish play major roles in the allocation of biomass and transfer of energy to higher trophic levels in the oceanic food web supporting the majority of sea birds at Buldir Island. Because squid and lanternfish are both vertical migrators (Frost and McCrone, 1979), rising at dusk from depth to forage in the rich surface layer, they are more available to sea birds from dusk to dawn than during the day. Notwithstanding the depths to which alcids can dive (Piatt and Nettleship, 1985), it is likely that most feeding by murres and puffins, as well as by surface-feeding kittiwakes at Buldir, occurs during twilight and darker hours.

A striking feature at Buldir was the unusually large consumption of zooplankton by black-legged kittiwakes. Zooplankton were often concentrated near the surface during the day in such densities that birds in flocks of a few hundred would simply sit on the surface and peck them up quickly enough to be full in roughly an hour (J. Piatt *et al.*, unpubl. data). Black-legged kittiwakes feed on euphausiids and other zooplankton elsewhere (Hunt *et al.*, 1981a; Springer *et al.*, 1984), but not to such an extent as at Buldir. Although the consumption of zooplankton by black-legged kittiwakes at Buldir appears to be exceptional, the importance of zooplankton elsewhere in Alaska is likely underestimated because of the rapid digestion of soft-bodied animals (Hobson *et al.*, 1994).

Black-legged kittiwakes are widely distributed in Alaska and prey on numerous species, usually the most abundant one in a given location. Black-legged kittiwakes are primarily daytime foragers throughout most of their range in Alaska, and in addition to sand lance they consume large amounts of Arctic cod, saffron cod, pollock, capelin, and herring (Springer, 1991; Baird, 1994). Crepuscular and nocturnal foraging is probably important at colonies in the Aleutians, particularly those with little shallow water, such as Buldir and at Bogoslof Island in the eastern Aleutians (J. Piatt, unpubl. data), and at other colonies near the edge of the continental shelf, such as the Pribilof Islands and Middleton Island in the Gulf of Alaska (Hunt *et al.*, 1981a; Hatch *et al.*, 1993). Such flexibility might explain the overall success of black-legged kittiwake as a species – it is one of the most abundant and widely distributed sea birds in the Northern Hemisphere.

Red-legged kittiwakes, on the other hand, are very restricted in their diets and in their range (Byrd, 1978; Byrd and Williams, 1993; Hunt *et al.*, 1981a). They usually forage only from dusk to dawn, and have evolved a specialized eye structure to aid vision in low light (Storer, 1987). They nest at only five locations in the Bering Sea, including Buldir Island but not the Near Islands. Appropriate islands apparently are those near oceanic food webs and abundant, nocturnal prey. The real advantage of oceanic sites to red-legged kittiwakes however, might be that the surrounding waters do not support abundant diurnal prey of the kind most sought after by black-legged kittiwakes. This might reduce their appeal to black-legged kittiwakes and, thus, competition between the two species, particularly for nesting space.

Patterns in forage fish distributions associated with regional oceanographic conditions have been cited as explanations for mesoscale differences in ratios of sea bird species nesting on St George I. compared with St Paul I., Pribilof Islands (Hunt *et al.*, 1981a,b), and in Norton Sound compared with St Lawrence I. in the northern Bering Sea (Springer *et al.*, 1987). Likewise, the pelagic distribution of various species of sea birds across the broad eastern shelf of the Bering Sea has been shown to be associated with hydrographic domain structure and the resultant differentiation of food webs (Schneider *et al.*, 1986). On Buldir Island, the ratio of

common murres to thick-billed murres is about 1:9, but on the Near Islands the ratio is about 9:1. The divergent diets of the two species support the hypothesis that the contrasting ratios of murres on the Near Islands compared with Buldir, and varying ratios throughout the Aleutian Islands and elsewhere in their range, are caused by differences in the composition of local pelagic fish communities (Springer, 1991). Common and thick-billed murres nest widely, but not uniformly, throughout the Aleutians (Sowls *et al.*, 1978). The ratio of common murres to thick-billed murres is directly proportional to the area of shallow water surrounding each island colony, presumably because variable physical habitat results in heterogeneous distributions of preferred prey. Although not strictly continental shelf areas, the larger islands and escarpments form mesoscale shelf-like habitats that apparently extend the ranges of typically coastal marine fauna and food webs across the basin of the North Pacific–Bering Sea in much the same way that islands extend the ranges of terrestrial fauna and flora (MacArthur and Wilson, 1967). Coastal communities, therefore, are more or less developed depending on the extent of shallow-water habitat surrounding each island. Elsewhere in Alaska that the two species overlap, common murres characteristically feed on more pelagic fishes, such as sand lance, whereas thick-billed murres feed more on demersal fishes and invertebrates (Hunt *et al.*, 1981a; Springer *et al.*, 1984, 1986, 1987). Differences in diet are parallelled by differences in pelagic distribution as well, with thick-billed murres foraging farther offshore and in a greater variety of marine habitats than common murres (Piatt *et al.*, 1991).

Conversely, extensive shallow water over broad escarpments, like that surrounding the Near Islands, apparently limits the abundance of large-bodied, oceanic zooplankton, such as *Neocalanus* spp., thus excluding many planktivorous sea birds like the least auklet, *Aethia pusilla*. Least auklets do not nest, or nest in very small numbers, in the Near Islands and similar islands in the Aleutians with broad escarpments, whereas they are abundant on Buldir Island and other islands lying off the arc (Sowls *et al.*, 1978) with greater access to zooplankton prey.

CONCLUSIONS

Our observations from the Near Islands and Buldir Island provide the basis for a model of food web differentiation throughout the Aleutian Islands caused by the distribution of shallow, shelf-like habitat. They further support previous conclusions that we can generalize about the importance of various prey species to sea birds, and thus about sea bird distributions, only if we account for regional physical environments and associated marine communities. Although separated by only about 150 km, Buldir Island and the Near Islands are distinct oceanographically. A lack of shallow, shelf-like habitat around Buldir apparently limits coastal/shelf communities, and sea birds there depend on oceanic species for food. At the Near Islands, a broad, shallow escarpment provides an environment suitable for a fauna characteristic of coastal shelves. Thus, the pattern of sea bird distribution in the Aleutian Islands is largely determined by the distribution of physical habitat, e.g. the presence or absence of shallow zones that support particular communities and food webs.

Black-legged kittiwakes on Buldir Island fed both day and night. At night they preyed on lanternfish and squid, but in the day they switched almost entirely to zooplankton, consuming large quantities of euphausiids, hyperiid amphipods and copepods. Intense planktivory has not been previously documented for black-legged kittiwakes.

Because adult black-legged kittiwakes fed day and night, diets of chicks changed between morning and afternoon, e.g. from fish to zooplankton and, among fishes, from lanternfish to sand lance. Such prey-switching must be accounted for when comparing information on diets between dates and locations and when interpreting patterns of growth and survival of kittiwake chicks.

Knowledge of pattern and scale, like that exemplified by fish distributions, sea bird distributions, and sea bird diets in the western Aleutians, and of the mechanisms responsible, is essential to our understanding of what ecosystems are and how they work (Levin, 1992). On a larger scale, differences between sea bird population trends and sea bird prey species in the western Aleutians and in the south-eastern Bering Sea provide clues to ecosystem change. Whereas oceanic (lanternfishes and squid) and coastal (sand lance) forage species were apparently flourishing in the western Aleutians during the mid 1970s to mid 1980s, forage species characteristic of the shelf (pollock and capelin) were apparently not readily available to the birds (Decker *et al.*, 1995; Hunt *et al.*, 1996). Some possible interpretations are: (1) oceanic and coastal species and communities respond to environmental change differently from shelf species and communities; (2) the nature of environmental change was different in the various domains; and (3) food web interactions in the larger domain of the Bering Sea were primarily responsible for fluctuations in abundance of forage species (Springer, 1992).

An obvious next step toward understanding important ocean and food web dynamics and variability in production at higher trophic levels is to ask why conditions in the marine environments of the south-eastern and south-western Bering Sea apparently were so different. The implications of such differences are likely far greater than the observed effect on sea birds, and attempts to reconcile observations like these should be an important part of future research on fisheries oceanography and marine ecosystems.

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REFERENCES

Alverson, D.L. (1992) A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. *Rev. Aquat. Sci.* **6**:203–256.

Andriashev, A.P. (1954) *Fishes of the Northern Seas of the U.S.S.R.* Moscow, Russia: Izdatel'stvo Akad, Nauk SSSR, 617 pp.

Baird, P.H. (1994) Black-legged Kittiwake. In: *The Birds of North America*, No. 92. A. Poole and F. Gill (eds). Philadelphia: Academy of Natural Sciences of Philadelphia, 26 pp.

Bedard, J. (1969) Feeding of the least, crested and parakeet auklets on St. Lawrence Island, Alaska. *Can. J. Zool.* **47**:1025–1050.

Byrd, G.V. (1978) Red-legged Kittiwake colonies in the Aleutian Islands, Alaska. *Condor* **80**:250.

Byrd, G.V. (1989) *Seabirds in the Pribilof Islands, Alaska: trends and monitoring methods.* MSc thesis, Univ. Idaho, Moscow, ID. 95 pp.

Byrd, G.V., and Douglas, H.D. (1989) *The status of ledge-nesting seabirds at monitoring sites in the Aleutian Islands, Alaska in summer 1989.* Homer, AK: U.S. Fish and Wildlife Service. 48 pp.

Byrd, G.V., and Williams, J.C. (1993) Red-legged Kittiwake. In: *The Birds of North America*, No. 60. A. Poole and F. Gill (eds). Philadelphia: Academy of Natural Sciences of Philadelphia, 12 pp.

Decker, M.B., Hunt, G.L., Jr, and Byrd, G.V., Jr (1995) The relationship between sea surface temperature, the abundance of juvenile walleye pollock (*Theragra chalcogramma*), and the reproductive performance and diets of seabirds at the Pribilof Islands, southeastern Bering Sea. *Can. Spec. Publ. Fish. Aquat. Sci.* **121**:425–437.

Dick, M.H., and Warner, I.M. (1982) Pacific sand lance, *Ammodytes hexapterus* Pallas, in the Kodiak island group, Alaska. *Syesis* **15**:43–50.

Dragoo, D.E., Bain, B.K., Sowls, A.L., and Chaundy, R.F. (1989) *The status of cliff nesting seabirds in the Pribilof Islands, Alaska, 1976–1988: a summary.* Homer, AK: U.S. Fish and Wildlife Service. 22 pp.

Frost, B.W., and McCrone, L.E. (1979) Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. *Fish. Bull. U.S.* **76**:751–770.

Furness, B.L., Laugksch, R.C., and Duffy, D.C. (1984) Cephalopod beaks and studies of seabird diets. *Auk* **101**:619–620.

Gard, L.M., Jr (1977) Geologic history. In: *The Environment of Amchitka Island, Alaska.* M.L. Merritt and R.G. Fuller (eds). Springfield, VA: National Technical Information Service, pp. 13–34.

Hatch, S.A., and Sanger, G.A. (1992) Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. *Mar. Ecol. Progr. Ser.* **80**:1–14.

Hatch, S.A., Byrd, G.V., Irons, D.B., and Hunt, G.L., Jr (1993) Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. In: *The Status, Ecology and Conservation of Marine Birds of the North Pacific.* K. Vermeer, K.T. Briggs, K.H. Morgan and D. Siegel-Causey (eds). Ottawa: Can. Wildl. Serv. Spec. Publ., pp. 140–153.

Hobson, K.A., Piatt, J.F., and Pitocchelli, J. (1994) Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* **63**:786–798.

Hunt, G.L., Jr, Burgesson, B., and Sanger, G.A. (1981a) Feeding ecology of seabirds of the eastern Bering Sea. In: *The Eastern Bering Sea Shelf: Oceanography and Resources*, Vol. 2. D.W. Hood and J.A. Calder (eds). Juneau, AK: NOAA, pp. 629–648.

Hunt, G.L., Jr, Eppley, Z., and Drury, W.D. (1981b) Breeding distribution and reproductive biology of seabirds in the eastern Bering Sea. In: *The Eastern Bering Sea Shelf: Oceanography and Resources*, Vol. 2. D.W. Hood and J.A. Calder (eds). Juneau, AK: NOAA, pp. 649–687.

Hunt, G.L., Jr, Kitaysky, A.S., Decker, M.B., Dragoo, D.E., and Springer, A.M. (1996) Changes in the distribution and size of juvenile walleye pollock as indicated by seabird diets at the Pribilof Islands and by bottom trawl surveys in the eastern Bering Sea. In: *Ecology of juvenile pollock.* R.D. Brodeur, P.A. Livingston, T.R. Laughlin and A.B. Hollowed (eds). Washington, DC: NOAA *Tech. Rep.* (in press).

Johnson, S.R. (1985) Population estimation, productivity, and food habits of nesting seabirds at Cape Peirce and the Pribilof Islands, 1984. Anchorage, AK: MMS/NOAA *Final Rep.* 309 pp.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* **73**:1943–1967.

Lucas, F.A. (1899) The food of the northern fur seals. In: *The Fur Seals and Fur-seal Islands of the North Pacific Ocean*, Vol. 3. D.S. Jordan *et al.* (eds). Washington, DC: Government Printing Office, pp. 59–68.

MacArthur, R.H., and Wilson, E.O. (1967) *The Theory of Island Biogeography.* Princeton: Princeton University Press. 203 pp.

Merrick, R.L., Loughlin, T.R., and Calkins, D.G. (1987) Decline

in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956–86. *Fish. Bull. U.S.* **85**:351–365.

Ogi, H. (1980) The pelagic feeding ecology of thick-billed murres in the North Pacific, March–June. *Bull. Fac. Fish. Hokkaido Univ.* **31**:50–72.

Piatt, J.F., and Nettleship, D.N. (1985) Diving depths of four alcids. *Auk* **102**:293–297.

Piatt, J.F., Wells, J.L., MacCharles, A., and Fadely, B.S. (1991) The distribution of seabirds and fish in relation to ocean currents in the southeastern Chukchi Sea. *Can. Wildl. Serv. Occ. Pap.* **68**:21–31.

Rogers, D.E., Rabin, D.J., Rogers, B.J., Garrison, K., and Wangerin, M. (1979) Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island – including ichthyoplankton, meroplankton (shellfish), zooplankton and fish. BLM/NOAA OCSEAP *Final Rep.* **4**:529–662.

Schneider, D.C., Hunt, G.L., Jr, and Harrison, N.M. (1986) Mass and energy transfer to seabirds in the southeastern Bering Sea. *Cont. Shelf Res.* **5**:241–257.

Sinclair, E., Loughlin, T., and Pearcy, W. (1994) Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. *Fish. Bull. U.S.* **92**:144–156.

Sowls, A.L., Hatch, S.A., and Lensink, C.J. (1978) *Catalog of Alaskan Seabird Colonies*. Biological Services Program. Anchorage, AK: U.S. Fish and Wildlife Service. 32 pp.

Springer, A.M. (1991) Seabird relationships to food webs and the environment: examples from the North Pacific Ocean. In: *Studies of High-latitude Seabirds. 1. Behavioral, Energetic, and Oceanographic Aspects of Seabird Feeding Ecology*. W.A. Montevecchi and A.J. Gaston (eds). Ottawa: Can. Wildl. Serv., pp. 39–48.

Springer, A.M. (1992) A review: walleye pollock in the North Pacific – how much difference do they really make? *Fish. Oceanogr.* **1**:80–96.

Springer, A.M. (1994) Report of the seabird working group. In: *Is it Food?* Fairbanks: Sea Grant, University of Alaska Fairbanks, pp. 14–29.

Springer, A.M., Roseneau, D.G., Murphy, E.C., and Springer, M.I. (1984) Environmental controls of marine food webs: food habits of seabirds in the eastern Chukchi Sea. *Can. J. Fish. Aquat. Sci.* **41**:1202–1215.

Springer, A.M., Roseneau, D.G., Lloyd, D.S., McRoy, C.P., and Murphy, E.C. (1986) Seabird responses to fluctuating prey abundance in the eastern Bering Sea. *Mar. Ecol. Progr. Ser.* **32**:1–12.

Springer, A.M., Murphy, E.C., Roseneau, D.G., McRoy, C.P., and Cooper, B.A. (1987) The paradox of pelagic food webs in the northern Bering Sea – I. Seabird food habits. *Cont. Shelf Res.* **7**:895–911.

Storer, R.W. (1987) The possible significance of large eyes in the Red-legged Kittiwake. *Condor* **89**:192–194.

Swartzman, G.L., and Hofman, R.J. (1991) *Uncertainties and Research Needs Regarding the Bering Sea and Antarctic Marine Ecosystems*. Washington, DC: Marine Mammal Comm. Rep. PB91-201731. 44 pp.

Trites, A.W., and Larkin, P.A. (1989) The decline and fall of the Pribilof fur seal (*Callorhinus ursinus*): a simulation study. *Can. J. Fish. Aquat. Sci.* **46**:1437–1445.

van Heezik, Y., and Seddon, P. (1989) Stomach sampling in the Yellow-eyed Penguin: erosion of otoliths and squid beaks. *J. Field Ornithol.* **60**:451–458.

Wehle, D.H.S. (1976) *Summer foods and feeding ecology of Tufted and Horned Puffins on Buldir Island, Alaska – 1975*. MSc thesis, University of Alaska Fairbanks, 83 pp.

Wehle, D.H.S. (1982) Food of adult and subadult tufted and horned puffins. *Murrelet* **63**:51–58.

Wehle, D.H.S. (1983) The food, feeding, and development of young tufted and horned puffins in Alaska. *Condor* **85**:427–442.

Wooster, W.S. (1994) Is it food? An overview. In: *Is it Food?* Fairbanks: Sea Grant, University of Alaska Fairbanks, pp. 1–3.

York, A.E., and Kozloff, P. (1987) On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980–86. *Fish. Bull. U.S.* **85**:367–375.