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Prey consumption and energy transfer by marine birds in the Gulf of Alaska

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Abstract

We investigated prey consumption by marine birds and their contribution to cross-shelf fluxes in the northern Gulf of Alaska. We utilized data from the North Pacific Pelagic Seabird Database for modeling energy demand and prey consumption. We found that prey consumption by marine birds was much greater over the continental shelf than it was over the basin. Over the shelf, subsurface-foraging marine birds dominated food consumption, whereas over the basin, surface-foraging birds took the most prey biomass. Daily consumption by marine birds during the non-breeding season ("winter") from September through April was greater than daily consumption during the breeding season, between May and August. Over the shelf, shearwaters, murres and, in winter, sea ducks, were the most important consumers. Over the basin, northern fulmars, gulls and kittiwakes predominated in winter and storm-petrels dominated in May to August. Our results suggest that marine birds contribute little to cross-shelf fluxes of energy or matter, but they do remove energy from the marine system through consumption, respiration and migration.

1. Introduction

There is a long-standing interest in the relative importance of continental shelf versus deep oceanic waters for supporting higher trophic-level organisms such as groundfish, seabirds and marine mammals. In general, shelf waters are more productive and support higher densities of these top predators than basin waters (Cooney, 1986; DeGange and Sanger, 1986; Sambrotto and Lorenzen, 1986). However, the connections and energy transfer between these habitats warrant further investigation on many trophic levels. To investigate these questions in the northern Gulf of Alaska, we calculated avian energy demand and prey consumption using estimated densities of marine birds in shelf and basin waters.

More than 65 species of marine birds have been identified in the northern Gulf of Alaska, although only about 20 of these are found in either shelf or

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basin waters in densities greater than 1 km^{-2} (Appendix A). Several estimates of the numbers of seabirds using the Gulf of Alaska and their prey demands are available. DeGange and Sanger (1986) estimated that prey consumption of marine birds (excluding waterfowl, loons, grebes and shorebirds) in the Gulf of Alaska was ~18 kg km^{-2} d^{-1} over continental shelf waters and ~2.4 kg km^{-2} d^{-1} over basin waters. More recently, Hunt et al. (2000) estimated that during the summer months of June, July and August, marine bird prey consumption in the Gulf of Alaska was between 0.74 and 1.72 MT km^{-2} over the 92-day period or 8.0–18.9 kg km^{-2} d^{-1}. Neither of these studies included the sea ducks, loons or grebes, and neither examined the impacts of winter migrants on the shelf and basin habitats.

Many of the species of marine birds that occupy the Gulf of Alaska are seasonal migrants, and even for those species that are year-round residents, there can be considerable flux in and out of the Gulf or redistributions within the region (G. Hunt, personal observations). For example, in this study, 14 of the 19 most abundant species are seasonal migrants, and a number of these are sea ducks whose contribution to marine bird prey consumption in the Gulf has previously been neglected (Appendix A). It is therefore useful, as part of a fresh examination of the marine ecosystem of the Gulf of Alaska, to re-examine the role of marine birds and compare winter and summer use of the shelf and basin habitats.

2. Methods

We determined the density of seabirds, by species and species groups (Appendix A) by extracting counts from the North Pacific Pelagic Seabird Database (NPPSD), which is maintained by the US Geological Survey, Alaska Science Center (http://www.absc.usgs.gov/research/NPPSD/index.htm) within a 350 km by 660 km box bisected by the shelf break (300 m) in the northern Gulf of Alaska (Table 1, Fig. 1). The shelf and basin regions of this box were further divided into a pair of northeastern-sectors and a pair of southwestern sectors in recognition of spatial variability in the along-shelf dimension.

Table 1
Distribution of survey effort by regions and season

Season	Region	On-shelf	Off-shelf
(May–Aug.)	N. East	241	133
	S. West	1915	43
(Sept.–Apr.)	N. East	458	172
	S. West	3899	118

Units are individual transect segments.

For most marine bird species, shipboard surveys were used directly to calculate the mean density of birds km^{-2}. Surveys were conducted with one observer who scanned a 300 m-wide transect from the bow to 90° of the side of the ship with the best visibility. The majority of transect segments were 10–15 min long. In our analyses, all transects, regardless of length were treated as equivalent. Within each of the four sectors in each of the two seasons, we totalled the number of birds observed in a transect segment and divided by the area surveyed in that segment to obtain the mean density of birds km^{-2}. Although survey effort varied greatly by sector, the use of seabird densities provided us a de facto standardization of our measures and allowed comparisons among sectors.

Two species of albatrosses, three species of shearwaters and northern fulmars in the Gulf of Alaska are ship-attracted or clumped in their distributions (see also Hyrenbach, 2001), for which a simple summing of the estimates based on the shipboard counts resulted in totals that differed greatly from known world populations of these species based on colony counts alone (Hunt et al., 2000). Hunt et al. assumed that the ratios of the densities of each of these species across the PICES regions represented the proportion of the North Pacific population of each species in each region. Therefore, to obtain the number of individuals of a species in each region (e.g., the Gulf of Alaska), they multiplied the percentages of each species seen in a region by the estimated population for the entire PICES region (Hunt et al., 2000). This procedure was modified further for sooty/short-

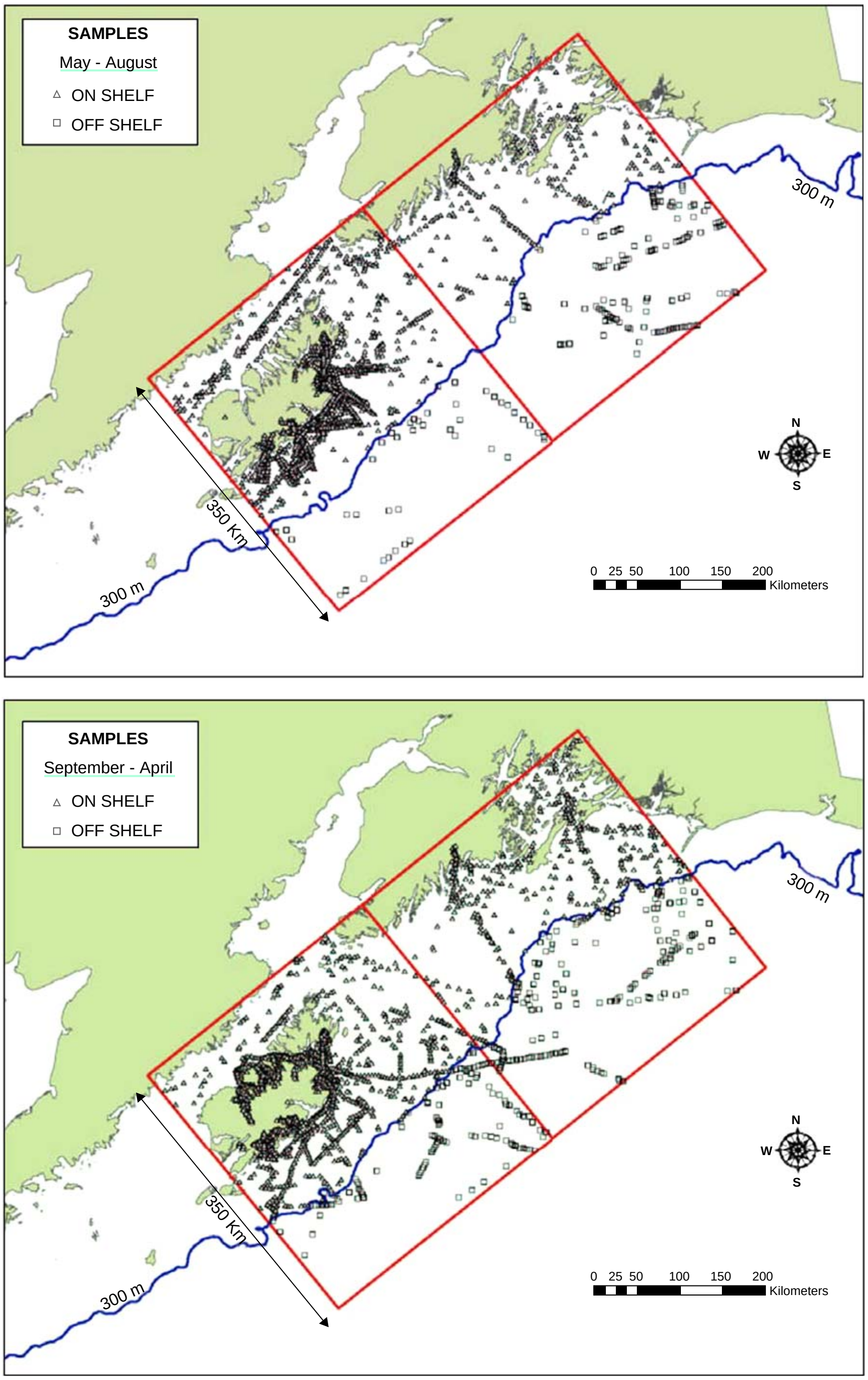

Fig. 1. Distribution of survey effort within the survey regions. Top: survey effort between May and August, the breeding season of most Alaska marine birds; bottom: survey effort between September and April, the non-breeding season for marine birds in Alaska. Kodiak Island is the large land mass on the southwestern portion of the shelf.

tailed shearwaters (*Puffinus griseus* and *Puffinus tenuirostris*, respectively) because most of the data for these two difficult-to-differentiate species were in terms of "dark shearwaters". The densities for dark shearwaters in each PICES region were partitioned into sooty and short-tailed shearwaters by using data from the literature (see Hunt et al., 2000) to estimate the ratio of one species to the other in each PICES region. That ratio was then used to separate the estimates of shearwater densities into the numbers of each species. For the above calculations, they assumed the following North Pacific populations: Laysan albatross (*Phoebastria immutabillis*) (2,500,000), black-footed albatross (*Phoebastria nigripes*) (200,000), northern fulmar (*Fulmarus glacialis*) (4,600,000), sooty shearwater (30,000,000), short-tailed shearwater (30,000,000), and Buller's shearwater (*Puffinus bulleri*) (2,500,000). For the present paper, we present estimates of the density of the above species in the Gulf based both on the "raw" data from shipboard counts, and by using the modification factors for these species in the Gulf of Alaska as determined by Hunt et al. (2000): Laysan albatross, 0.72; black-footed albatross, 0.06; northern fulmar, 0.18; sooty shearwater, 0.61; short-tailed shearwater, 2.73; Buller's shearwater, 1.67.

Marine bird biomass distribution in the Gulf of Alaska was determined by multiplying the mean density of birds km^{-2} for a season by the biomass of the species as given in Dunning (1993). Where separate values for each sex were given, we used the mean value to represent the species. Similarly, in taxa such as "gulls" or "dark shearwaters", we calculated an average value for the mass of the species in the group. Although difference in mass between the species will inevitably lead to errors, we could not create a weighted mean as we could not reconstruct the relative abundance of the species composing taxa that had been grouped by the observers in the original observations.

Marine birds require high rates of energy intake because they are endothermic and active. Because heat loss is a function of the ratio of body surface are to mass, the metabolic demands of a small bird are proportionally greater than those of a large bird. Thus, metabolic rates scale to body mass to a power of between 0.6 and 0.8 (Furness, 1984; Furness and Tasker, 1996). Therefore, when estimating the energy requirements of a community of birds, it is necessary to determine the energy requirements of each species individually and then sum across species (Furness, 1984).

To determine energy demand by marine birds in the Gulf of Alaska, we estimated daily energy requirements of individual birds by using the allometric equation of that predict energy requirements as a function of body mass (Table 2). Because different taxa vary in their daily activity levels and thus energy requirements, we used equations developed for the taxa found in our study. Although there are several alternative methods of calculating energy requirements (Furness and Tasker, 1996), we chose this one to facilitate comparison with the results of Hunt et al. (2000). To estimate energy that must be consumed to meet these requirements, one has to account for the ability of marine birds to assimilate the energy that they ingest. This ability varies with nutritional state, food type, and the amount of lipid in the food, with energy assimilation from lipid-rich foods being more efficient (Furness and Tasker, 1996). However, since values for assimilation efficiency were lacking for most of the prey and predator species in this study, we assumed an assimilation efficiency of 0.75, as did Furness and Tasker (1996) and Hunt et al. (2000).

Table 2
Allometric equations used to calculate mass-specific energy demands of seabirds, where m = mass in grams

Taxon	Equation	R^2	N	S.E. intercept	S.E. exponent	Reference
Podicipediformes and Anseriformes	$10.50\ m^{0.681}$	0.938	95	—	—	Nagy et al. (1999)
Procellariiformes	$22.06\ m^{0.594}$	0.921	14	1.350	0.047	Ellis and Gabrielsen (2001)
Pelecaniformes	$3.90\ m^{0.871}$	0.953	4	4.209	0.196	Ellis and Gabrielsen (2001)
Charadriiformes	$11.49\ m^{0.718}$	0.814	12	1.716	0.095	Ellis and Gabrielsen (2001)

To determine the biomass of prey consumed by marine birds in the Gulf of Alaska, we apportioned the energy requirements of each species across prey types in its diet and then summed use of prey types across bird species. To estimate prey consumption, we needed, in addition to the individual daily energy requirements, the proportion of prey types in the diet and the energy density of those prey items. Diet composition of marine birds in the Gulf of Alaska was obtained from a variety of sources and reflected not only the most recent information from the literature, but our judgment as to the appropriate estimates to use for birds in the Gulf of Alaska (Appendix B). There are no comprehensive sources of information on the energy density of seabird prey from the Gulf of Alaska. The energy content varies with the age of the prey, the season, and even the region (Van Pelt et al., 1997; Robards et al., 1999; Iverson et al., 2002), as well as with its condition when ingested (Hunt et al., 2000). We have used updated values from the literature to provide the following estimates of prey energy density: miscellaneous invertebrates, $3\,\mathrm{kJ\,g^{-1}}$; mollusks, $2\,\mathrm{kJ\,g^{-1}}$; gelatinous zooplankton, $0.6\,\mathrm{kJ\,g^{-1}}$; crustacean zooplankton, $2.6\,\mathrm{kJ\,g^{-1}}$; cephalopods, $5.5\,\mathrm{kJ\,g^{-1}}$; fish, $5.7\,\mathrm{kJ\,g^{-1}}$; birds and mammals, $7\,\mathrm{kJ\,g^{-1}}$; carrion, offal and discards, $6\,\mathrm{kJ\,g^{-1}}$ (Davis et al., 1998).

3. Results

Our search of the North Pacific Pelagic Database yielded a sample of 6979 bird counts obtained between 1975 and 1984. Of these, 2156 counts were obtained over continental shelf waters and 176 counts over the basin during May through August, the northern breeding season (Table 1, Fig. 1). During the non-breeding season of September through April, 4357 counts were obtained over the shelf and 290 over the basin (Table 1, Fig. 1). Counts from shelf waters were about evenly divided between the 1970s and the 1980s; counts from the basin were almost exclusively from pre-1980. Counts were concentrated on the shelf in the vicinity of Kodiak Island because this was a port from which many ships left to conduct surveys throughout the Gulf, and because of intensive surveys by the Kodiak National Wildlife Refuge. On-shelf surveys were fairly evenly spread throughout the year, with a monthly mean of 540 counts and a high of 1138 for February and a low of 131 for January. Coverage of basin waters was sparse. The monthly mean was 38 bird counts, with a high of 85 for September and a low of 1 for December. Coverage in January (6 counts) and August (5 counts) was also minimal.

Based on adjusted data, the densities of subsurface-foraging marine birds were an order of magnitude higher over the continental shelf waters of the Gulf of Alaska than over the basin in the May–August period and between September and April in the southwestern portion of the study area (Table 3, Fig. 2). In both the northeast sector and the southwest sector, the differences between on-shelf and off-shelf densities were greater for subsurface-foraging birds (e.g., May–Aug., 13.7 ×, 15.1 ×, respectively) than for surface-foraging seabirds (May–Aug., 2.5 ×, 1.7 ×, respectively) (Table 2). In both seasons, surface-foraging seabirds were less abundant on the shelf than subsurface-foraging seabirds. Over the basin, surface-foraging seabirds had similar or greater densities than subsurface-foragers. There was also a striking pattern in the on-shelf distribution of marine birds. Particularly in the September–April period, the densities of subsurface-foraging seabirds and counts with high numbers of birds were greater over the southwestern shelf than to the northeast (Table 3, Fig. 2). A similar northeast–southwest pattern was not evident for subsurface-foraging seabirds over the basin. In May–August over the shelf, surface-foraging seabirds showed a weak northeast–southwest pattern, with more birds to the northeast, while in winter there were moderately higher densities of seabirds to the southwest. In both seasons over the basin, there was no evidence of a strong northeast–southwest pattern in the densities of surface-foraging seabirds.

Seasonal patterns in the density of marine birds were surprisingly uniform (Table 3) given that many of the species that frequent the Gulf of Alaska are migratory. Although on the northeastern sector of the shelf there were higher densities of marine birds in May–August (77.4

Table 3
Mean densities of marine birds (birds km^{-2}) in the Gulf of Alaska

Feeding	Season	Region	Raw data				Adjusted data		
			On-shelf	± SE	Off-shelf	± SE	On-shelf	Off-shelf	Ratio On/off shelf
Diving	(May–Aug.)	N. East	99.2	23.8	27.8	12.6	54.8	4.0	13.7
		S. West	128.4	17.1	37.5	26.6	110.0	7.3	15.1
Diving	(Sept.–Apr.)	N. East	35.1	23.3	7.7	1.8	22.0	5.4	4.1
		S. West	126.0	8.2	6.1	2.0	109.5	3.1	35.3
Surface	(May–Aug.)	N. East	29.3	4.9	13.3	1.9	22.6	8.9	2.5
		S. West	17.4	1.5	17.2	3.8	15.2	9.2	1.7
Surface	(Sept.–Apr.)	N. East	17.0	5.7	14.4	1.5	10.1	10.7	0.9
		S. West	20.2	2.6	24.7	4.3	18.8	11.4	1.7

Raw data are taken directly from the NPPSD database. The adjusted data have been modified by application of the correction factors used in Hunt et al. (2000) to account for ship attraction and clumped distributions of selected species.

birds km^{-2}) as compared to September–April (32.1 birds km^{-2}, using the adjusted data), over the southwestern portion of the shelf, densities of birds were similar between seasons (May–August, 125.2 birds km^{-2} vs. September–April, 128.3 km^{-2}) as was also the case over the basin (northeast: May–August, 12.9 birds km^{-2}, September–April, 16.1 birds km^{-2}; southwest: May–August, 16.5 birds km^{-2}; September–April, 14.5 birds km^{-2}) (Table 3). Of the sub-surface foraging species, sooty and short-tailed shearwaters constituted the majority of marine birds both on and off the shelf in May–August (Fig. 3), whereas between September and April shearwaters for the most part had migrated to the Southern Hemisphere and had been replaced by wintering murres, other alcids, and sea ducks (Fig. 3C). Among surface-foraging species, storm-petrels declined over the shelf in winter and there was an influx of albatrosses, gulls and fulmars, particularly over basin waters during the months of September to April (Fig. 4).

Patterns in the distribution of avian biomass within the study area were, as expected, similar to the patterns for distribution, although the impact of species body mass accentuated some of the seasonal differences (Table 4). Within the subsurface-foragers, shearwaters and puffins dominated in May–August (Appendix A), and sea ducks and murres dominated the demand for energy in September–April (Table 5). For surface-foragers over the basin, the amount of energy required daily between September and April was greater than between May and August, primarily because of the influx of gulls (Table 6, Fig. 4).

Monthly prey consumption by marine birds was greater on the continental shelf than over the basin (Table 7). On a seasonal basis, in the northeastern sectors, monthly prey consumption was greater in May–August (762.9 kg km^{-2} d^{-1}) than in September–April (493.5 kg km^{-2} d^{-1}) (Table 7). In contrast, monthly prey consumption was greater in September–April in the southwestern sectors (2050.0 kg km^{-2} d^{-1}) than in May–August (1618 kg km^{-2} d^{-1}) (Table 7). Over the southwestern shelf, the influx of winter migrants more than offset the decrease in consumption due to the departure of shearwaters and other migrants that moved out of the Gulf of Alaska. This pattern also was seen over the northeastern basin. On the shelf, the major increase in prey demand came from the subsurface-foragers, whereas over the basin, the increase came from an influx of surface-foragers.

Over the continental shelf, the major component of marine bird diets was crustaceans, followed by fish and epi-benthic mollusks (Fig. 5A,C). Over the basin, the major component of marine bird diets was fish followed by crustaceans and cephalopods (Fig. 5B,D). Seabird consumption of prey on the shelf in May–August was

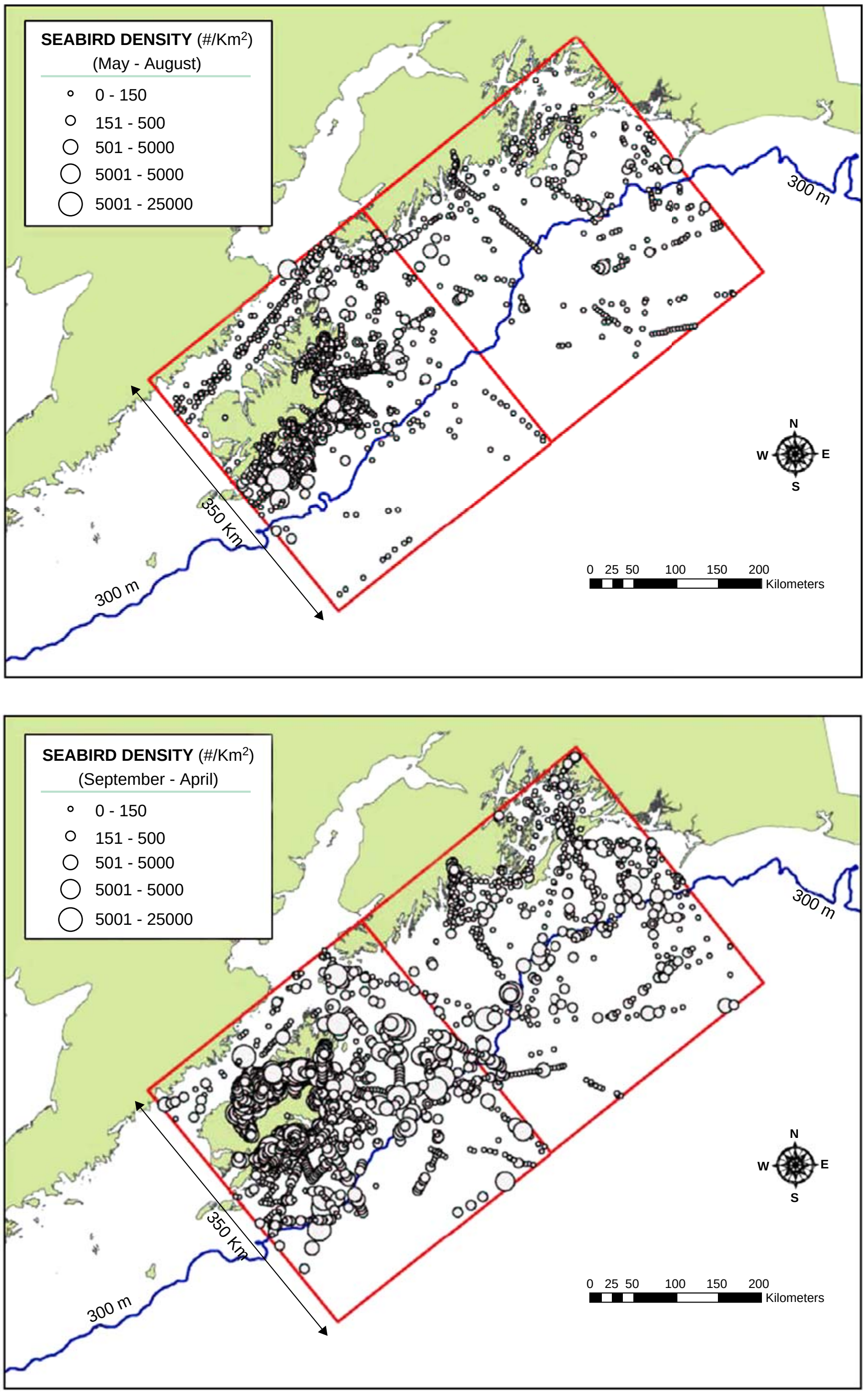

Fig. 2. Distribution and abundance of all species marine birds combined within the study regions. Top: survey results from May through August; bottom: survey results from September through April.

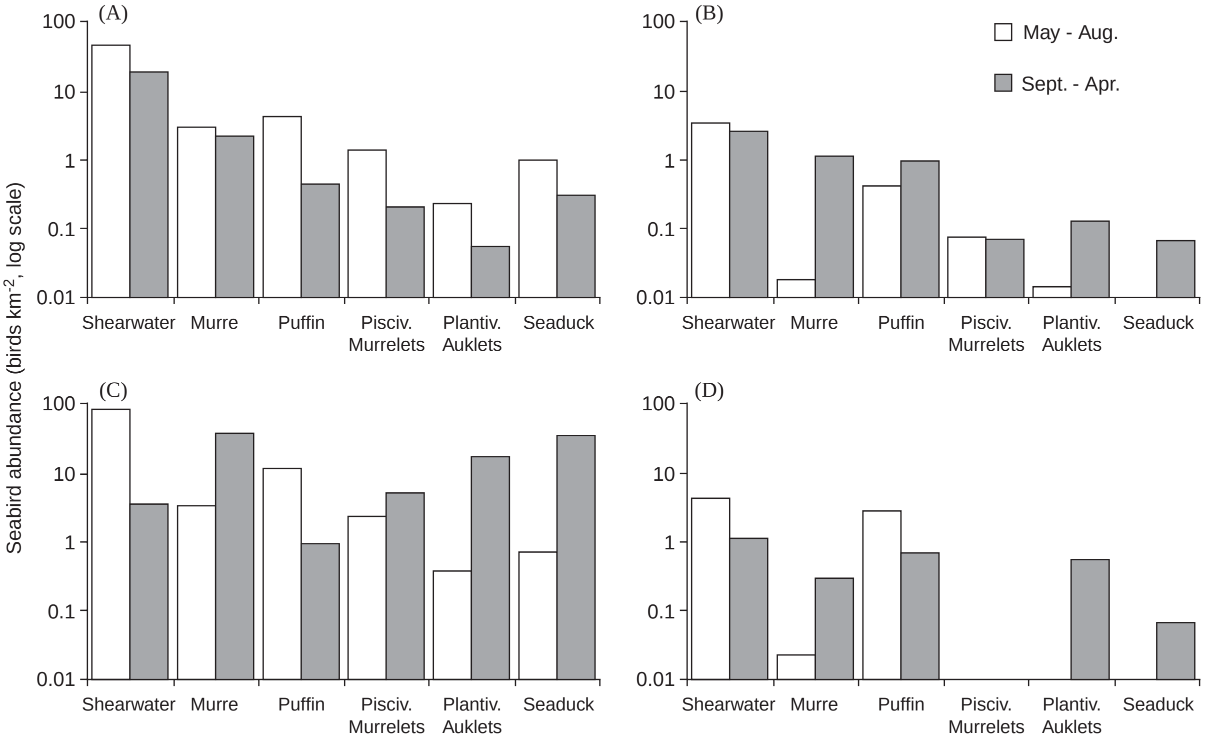

Fig. 3. Abundances of selected species of subsurface-foraging marine birds within the study area. (A) Densities over the northeastern shelf, (B) densities over the northeastern basin, (C) densities over the southwestern shelf, (D) densities over the southwestern basin.

dominated by crustaceans, most of which were euphausiids consumed by shearwaters, and forage fish. In September–April, on-shelf consumption of mollusks by sea ducks was similar in magnitude to the consumption of crustaceans by shearwaters and planktivorous auklets, and fish. The composition of prey taken by marine birds over the basin was more evenly divided among the prey categories than that over the shelf.

4. Discussion

Bearing in mind the caveats and sources of error discussed below, several important patterns emerge from our analyses. First, both in ‘‘summer’’ and in ‘‘winter’’, the consumption of prey by marine birds over continental shelf waters is much greater than that over the basin of the Gulf of Alaska. That is obvious from the raw data presented in Figs. 2 and 3, and will hold through the most careful dissection of the known biases. DeGange and Sanger provided an estimate of 18 kg km^{-2} d^{-1} for marine bird prey consumption over the shelf in ‘‘summer’’ (June–August) whereas we estimated between 22 and 49 kg km^{-2} d^{-1} of prey were consumed over the shelf between May and August. Their estimate of 2 kg km^{-2} d^{-1} for oceanic waters of the Gulf is similar to ours (3.3 kg km^{-2} d^{-1}). These patterns of prey consumption fit well with published information on higher levels of primary production and higher zooplankton standing stocks on the shelf than over the basin (Cooney, 1986; Sambrotto and Lorenzen, 1986).

A second finding was that seabird densities in both summer and winter were much greater over the southwestern shelf around Kodiak Island (summer: 125 birds km^{-2}; winter: 128 birds km^{-2}) than elsewhere in the study area. This region is

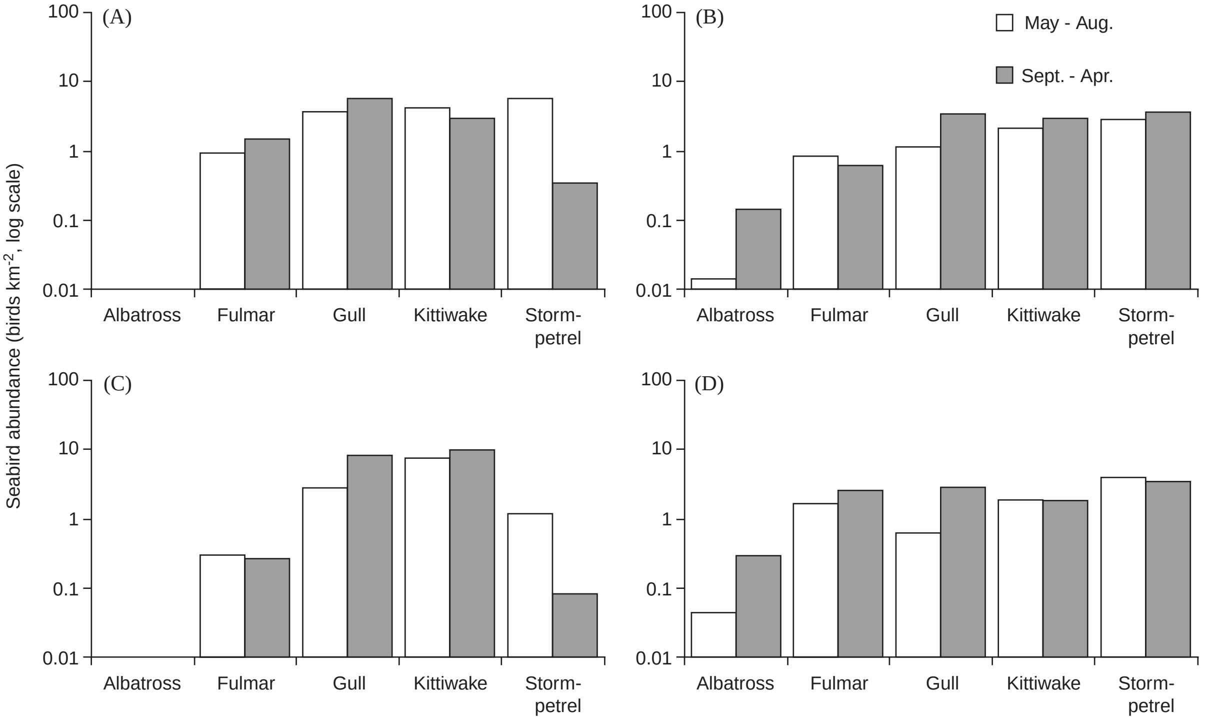

Fig. 4. Abundances of selected species of surface-foraging marine birds within the study area. (A) Densities over the northeastern shelf, May–August, (B) densities over the northeastern basin, May–August, (C) densities over the southwestern shelf, September–April, (D) densities over the southwestern basin, September–April.

Table 4
Biomass of marine birds (kg km^{-2}) in the Gulf of Alaska based on adjusted values for densities (see methods)

Feeding	Season	Region	On-shelf	Off-shelf	Ratio On/off shelf
Diving	(May–Aug.)	N. East	44.1	3.3	13.4
		S. West	68.5	5.7	12.1
Diving	(Sept.–Apr.)	N. East	18.1	4.5	4.0
		S. West	100.9	2.0	50.1
Surface	(May–Aug,)	N. East	6.4	3.1	2.1
		S. West	6.6	3.0	2.2
Surface	(Sept.–Apr.)	N. East	7.0	5.5	1.3
		S. West	10.5	6.1	1.7

also an area where large flocks were commonly seen, especially when compared to shelf areas to the northeast. These observations suggests that this area, with its many submarine canyons and strong currents, is a much richer foraging ground than shelf waters to the northeast, or basin waters. This finding is not the result of the heavy bias toward counts in the vicinity of Kodiak Island, which, in the 1970s, was the base from which many of the ships were deployed. Although analyses accounted for variation in effort, the inshore distribution of the counts around Kodiak Island

Table 5
Daily energy demand ($\mathrm{MJ\,km^{-2}\,d^{-1}}$), based on adjusted densities, of selected species of sub-surface-foraging marine birds over the Gulf of Alaska continental shelf

Species group	Region	May–August ($\mathrm{MJ\,km^{-2}\,d^{-1}}$)	September–April ($\mathrm{MJ\,km^{-2}\,d^{-1}}$)
Shearwater	N. East	51.5	21.2
	S. West	86.0	4.0
Murre	N. East	4.7	3.6
	S. West	5.7	65.3
Seaduck	N. East	1.2	0.4
	S. West	1.3	43.8

Table 6
Daily energy demand ($\mathrm{MJ\,km^{-2}\,d^{-1}}$), based on adjusted densities, of selected species of surface-foraging marine birds over the Gulf of Alaska basin

Species group	Region	May–August ($\mathrm{MJ\,km^{-2}\,d^{-1}}$)	September–April ($\mathrm{MJ\,km^{-2}\,d^{-1}}$)
Albatross	N. East	0.0	0.4
	S. West	0.1	0.8
Fulmar	N. East	0.8	0.6
	S. West	1.5	2.3
Gulls and Kittiwakes	N. East	3.8	7.8
	S. West	2.7	6.3

Table 7
Monthly prey consumption ($\mathrm{kg\,km^{-2}\,month^{-1}}$) by marine birds in the Gulf of Alaska, based on adjusted densities of all species combined

Feeding	Season	Region	On-shelf	Off-shelf
Diving	(May–Aug.)	N. East	525.5	39.8
		S. West	1354.8	83.6
Diving	(Sept.–Apr.)	N. East	207.8	65.4
		S. West	1717.9	36.4
Surface	(May–Aug.)	N. East	137.2	60.4
		S. West	124.2	55.4
Surface	(Sept.–Apr.)	N. East	120.9	99.4
		S. West	192.6	103.0

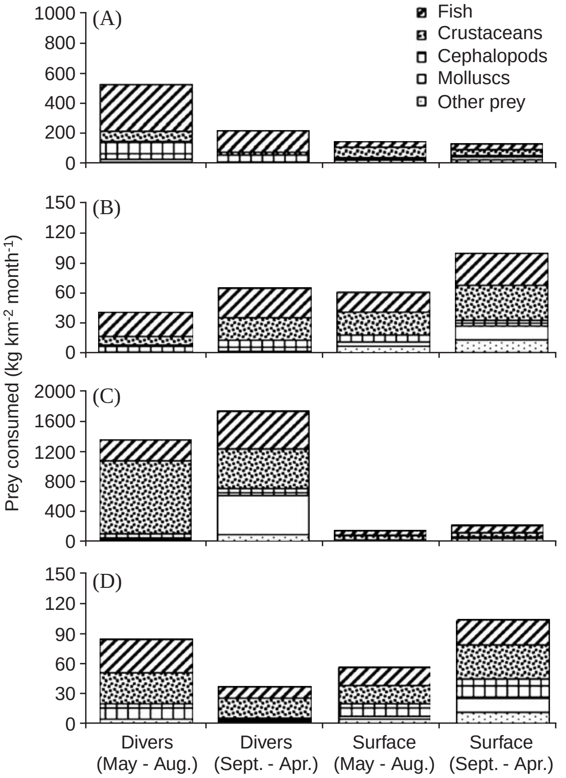

Fig. 5. Prey consumed by marine birds within the study regions. (A) Consumption over the northeastern shelf, May–August, (B) consumption over the northeastern basin, May–August, (C) consumption over the southwestern shelf, September–April, (D) consumption over the southwestern basin, September–April.

will have included sea ducks and other species that prefer inshore waters that would not be included in the more offshore surveys of the northeastern shelf region.

A third finding was that prey consumption rates were greater in “winter” than in “summer”, both on and off the shelf. The pattern of prey consumption varied somewhat from northeast to southwest, with winter populations being most important on the shelf in the southwest and off the shelf in the northeast. This is the first attempt to estimate winter consumption, and the first effort to include the prey demands of sea ducks. The high “winter” demand is driven by sea ducks, murres and auklets on the shelf and by fulmars, gulls and kittiwakes offshore. Our results show that the Gulf of Alaska is an important winter refuge for species that, in summer, nest far to the west or north of the Gulf. Our results also show that much of the prey consumption by marine birds in the Gulf is decoupled in time from the production season. The birds are dependent on organisms that obtain much of their energy earlier in the production season and store it in economically harvestable packets. In that regard, it is noteworthy that marine birds known to be copepod specialists (e.g., Cassin's auklet and least auklet, *Aethia pusilla*) are scarce in the Gulf of Alaska, perhaps because their copepod prey spend much of the year in diapause at great depth (Miller and Clemons, 1988).

Subsurface-foraging marine birds predominate on the shelf, whereas surface-foraging birds predominate over the basin. It is no surprise that epibenthically foraging sea ducks are confined to shallow waters where they can reach the bottom. It is less clear why other subsurface-foraging species, such as shearwaters and murres, should be found predominately over the shelf and not over the basin. However, there is a growing literature that indicates that for successful subsurface foraging, high prey densities may be necessary, whereas light-bodied surface-foragers with low wing loading may succeed in areas with lower productivity (Ainley, 1980; Ballance et al., 1997; Lovvorn et al, 2001).

Most of the carbon consumed by marine birds in the Gulf of Alaska is promptly respired back to the atmosphere (except for that amount recycled in feces). In that sense, it is exported from both the basin and the shelf waters, and does not enter further into local food chains. A small amount of the energy ingested by seabirds is converted into fat, muscle and feathers, and removed from the region during annual migrations. Very little is transferred between the basin and the shelf. The mechanism for cross-shelf transport would be foraging by birds that were provisioning young on colonies located on islands and promontories around the Gulf of Alaska. However, densities of marine birds (both local breeders and migrants) over the basin during the breeding season (May–August) are very low. Thus, it would appear that marine birds must contribute little to cross-shelf flux of energy or particulate carbon.

There are a number of biases and potential errors in the development of the estimates used in this report. These include the reliability of the counts, the relative distribution of effort on the shelf and offshore, the temporal variation in when counts were made in different regions, and the paucity of information on diets of marine birds foraging in the Gulf of Alaska, particularly in winter. The reliability of counts varies among observers and with observation conditions. Birds at the outer margins of the survey strip are likely to be under-reported, whereas those that are attracted to the ship may be over-reported. Exceptionally large flocks are impossible to count and difficult to estimate accurately. When a flock crosses the boundary of the survey track, it is hard to determine which of the birds are within and which are outside the survey track. However, the large number of samples and the large spatial extent of sampled areas should have had a mitigating effect on these sources of variation.

The lack of accurate diet data obtained from marine birds in the Gulf of Alaska is a potential source of error, but it is likely a minor one compared to the issues raised above. Diet data for the most common birds were available from the Gulf of Alaska, or are sufficiently typical for a species throughout its range, that the coarse diet categories use in our analyses are not likely to be misleading. Similarly, estimates of the daily energy requirements of individual birds (Table 2) are likely far more accurate than the estimates of their abundance. In the present study, it is likely that we have about as accurate an estimate of the amount of prey consumed by marine birds over the continental shelf and basin waters as can be achieved with the limited historical data base available.

Our study provides the first evidence that winter consumption of prey by seabirds can be remarkably similar to that in summer, though the types of prey used may differ. This finding suggests that prey consumption of seabirds and their roles in pelagic ecosystems may be severely underestimated if consumption estimates are based solely on values obtained in summer. Our analyses confirm that the predominance of seabirds in the Gulf of Alaska forage over the shelf and that the basin supports only a minor component of the seabird fauna. This pattern is not surprising given that shelf regions are usually more productive than adjacent regions of deep ocean. Among the species foraging over the basin are albatrosses, which export energy to islands to the southwest of the study area (Hyrenbach et al., 2002), and storm-petrels that may export small amounts of energy to the coastal zone where they nest. Hunt et al. (2000)

found that the Gulf of Alaska PICES region had the highest densities of seabirds in any of the PICES regions for which data were available. We now show that within the Gulf of Alaska, the region around Kodiak Island is an exceptionally rich one for seabirds, particularly when compared to the shelf region in the northeast of the study area. The cause of this along-shelf variability remains to be investigated.

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Appendix A

See Table 8 for body mass, energy requirement and abundance of marine birds in the Gulf of Alaska as determined from the North Pacific Pelagic Seabird Database.

Table 8
Body mass (kg) (Dunning, 1993), energy requirement (kJ d^{-1}) (calculated in this study) and abundance (adjusted where appropriate—see methods) of marine birds (birds km^{-2}) in the Gulf of Alaska as determined from the North Pacific Pelagic Seabird Database (http://www.absc.usgs.gov/research/NPPSD/index.htm)

Common name	Scientific name	Body mass	Energy required	May–August				September–April			
				A	B	C	D	A	B	C	D
Red-necked grebe	*Podiceps grisegena*	1.023	1177.4							0.34	
Horned grebe	*Podiceps auritus*	0.453	676.1					0.00		0.21	
Unidentified grebe		0.738	942.6							0.02	
Laysan albatross	*Phoebastria immutabilis*	3.042	2585.8		0.01	0.00	0.02	0.00	0.14	0.01	0.27
Black-footed albatross	*Phoebastria nigripes*	3.148	2639.0	0.01	0.16	0.00	0.48	0.02	0.60	0.01	1.72
Unidentified albatross		3.095	2612.5	2.52	0.17	0.80	0.02	0.43	0.23	0.21	0.16
Northern fulmar	*Fulmarus glacialis*	0.544	930.1	5.09	4.96	1.67	9.24	7.86	3.52	1.48	13.92
Mottled petrel		0.316	673.6		0.13		0.43			0.00	0.01
Buller's shearwater	*Puffinus bulleri*	0.380	751.6					0.00	0.02		
Flesh-footed shearwater	*Puffinus carneipes*	0.568	954.3		0.01	0.00					
Short-tailed shearwater	*Puffinus tenuirostris*	0.543	929.1	0.23	0.12	27.47	0.08	0.08	0.32	0.58	0.30
Sooty shearwater	*Puffinus griseus*	0.787	1158.3	72.10	4.83	23.12	6.86	29.80	2.77	3.58	0.64
Unidentified shearwater		0.563	948.9	16.72	22.11	56.97	27.63	1.57	1.79	16.11	3.28
Leach's storm-petrel	*Oceanodroma leucorhea*	0.040	196.8	0.02	0.08		0.04	0.00	0.02		
Fork-tailed storm-petrel	*Oceanodroma furcata*	0.055	239.2	5.33	2.70	1.22	3.93	0.28	3.52	0.08	2.73
Unidentified storm-petrel		0.048	218.7	0.00	0.05	0.00	0.02	0.06	0.07	0.00	0.89
Double-crested-cormorant	*Phalacrocorax auritus*	1.674	2505.9	0.03		0.01		0.02		0.01	
Red-faced cormorant	*Phalacrocorax urile*	2.157	3125.0	0.00		0.02		0.03		0.02	
Pelagic cormorant	*Phalacrocorax pelagicus*	1.868	2757.0	0.03		0.07		0.04		0.14	
Unidentified cormorant		1.900	2797.6	0.12	0.01	0.26		0.19	0.38	4.85	0.01
Greater scaup	*Aythya marila*	0.945	1115.1			0.00				0.21	
Lesser scaup	*Aythya affinis*	0.820	1012.7							0.03	
Unidentified scaup		0.882	1064.5			0.01		0.00		1.23	
King eider	*Somateria spectabilis*	1.618	1608.5							1.91	
Steller's eider	*Polysticta stelleri*	0.808	1002.2							0.17	
Unidentified eider		1.497	1526.0							0.26	
Harlequin duck	*Histrionicus histrionicus*	0.623	839.5			0.01		0.00		2.56	
Unidentified duck		1.156	1279.6	0.33		0.01		0.17		0.21	0.03

Table 8 (*continued*)

Common name	Scientific name	Body mass	Energy required	May–August				September–April			
				A	B	C	D	A	B	C	D
Surf scoter	*Melanitta perspicillata*	0.950	1119.5	0.02		0.00		0.01		0.74	
Black scoter	*Melanitta nigra*	0.850	1037.8			0.00		0.00		6.93	
White-winged scoter	*Melanitta fusca*	1.757	1701.7	0.02		0.72		0.03	0.01	4.91	
Unidentified scoter		1.156	1279.6	0.59		0.01		0.07	0.06	13.53	0.04
Common goldeneye	*Bucephala clangula*	0.900	1079.0							0.05	
Barrow's goldeneye	*Bucephala islandica*	0.910	1087.2							1.48	
Unidentified goldeneye		0.905	1083.1							0.20	
Bufflehead	*Bucephala albeola*	0.404	624.8							0.13	
Common merganser	*Mergus merganser*	1.471	1507.4					0.00		0.09	
Red-breasted merganser	*Mergus serrator*	1.022	1176.2	0.00		0.00		0.00		0.24	
Unidentified merganser		1.246	1346.6							0.06	
Red phalarope	*Phalaropus fulicaria*	0.056	206.0	0.02	0.43	0.14	0.02	0.00	0.01	0.00	
Red-necked phalarope	*Phalaropus lobatus*	0.034	143.9	7.43	0.06	1.38		0.03		0.02	0.05
Unidentified phalarope		0.045	176.0	0.15	0.09	0.22				0.02	0.08
Long-tailed jaeger	*Stercorarius longicaudus*	0.297	684.3	0.02	0.02	0.02	0.17	0.00	0.01	0.00	
Parasitic jaeger	*Stercorarius parasiticus*	0.465	944.5	0.01	0.02	0.10	0.05	0.01	0.02	0.00	0.02
Pomarine jaeger	*Stercorarius pomarinus*	0.694	1260.1	0.01	0.16	0.35	0.07	0.03	0.05	0.01	0.02
Unidentified jaeger		0.485	974.3	0.02	0.03	0.03	0.03	0.03	0.00	0.00	0.02
Ivory gull	*Pagophila eburnea*	0.616	1156.7							0.00	
Mew gull	*Larus canus*	0.404	853.7	0.04	0.01	0.06		0.33	0.04	3.31	0.02
Herring gull	*Larus argentatus*	1.135	1793.9	0.75	0.22	0.01	0.02	0.34	0.20	0.03	0.12
Glaucous gull	*Larus hyperboreus*	1.413	2099.0		0.02	0.00	0.02	0.01	0.02	0.00	0.01
Glaucous-winged gull	*Larus glaucescens*	1.010	1649.8	2.43	0.79	1.92	0.57	2.97	2.49	3.84	2.49
Slaty-backed gull	*Larus schistisagus*	1.327	2007.0							0.00	
Sabine's gull	*Xema sabini*	0.191	499.0		0.01	0.02		0.01	0.00	0.00	
Unidentified gull		0.819	1419.4	0.33	0.12	0.90		1.82	0.60	1.35	0.19
Black-legged kittiwake	*Rissa tridactyla*	0.407	859.0	3.16	1.94	7.61	1.93	2.30	2.24	9.55	1.74
Red-legged kittiwake	*Rissa brevirostris*	0.391	834.6	0.03					0.00	0.00	
Unidentified kittiwake		0.399	846.9	0.73	0.26	0.34	0.02	0.51	0.58	0.31	0.21
Arctic tern	*Sterna paradisaea*	0.110	335.8	1.08	0.84	0.31	0.08	0.01	0.01	0.00	0.04
Aleutian tern	*Sterna aleutica*	0.120	357.4	0.02		0.06	0.05				
Unidentified tern		0.115	346.7	0.02	0.01	0.19				0.00	
Common murre	*Uria aalge*	0.993	1629.2	0.46	0.00	1.11		0.14	0.02	20.17	0.12
Thick-billed murre	*Uria lomvia*	0.964	1595.5	0.00		0.02			0.12	0.03	
Unidentified murre		0.978	1612.4	2.42	0.02	2.37	0.02	2.07	0.98	20.06	0.20
Pigeon guillemot	*Cepphus columba*	0.487	977.2	0.09		0.71		0.04		1.83	
Ancient murrelet	*Synthliboramphus antiquus*	0.206	526.8	0.28	0.02	0.26		0.03	0.01	0.03	0.01
Kittlitz's murrelet	*Brachyramphus brevirostris*	0.224	559.5	0.01		0.03		0.01		0.03	
Marbled murrelet	*Brachyramphus marmoratus*	0.222	555.9	0.64	0.05	0.40		0.07	0.02	2.61	
Unidentified murrelet	*Brachyramphus spp.*	0.223	557.7	0.30		1.04		0.05	0.05	0.97	
Unidentified murrelet		0.217	547.5			0.01					
Cassin's auklet	*Ptychoramphus aleuticus*	0.188	493.4	0.12		0.26		0.01	0.02	0.10	0.03
Parakeet auklet	*Cyclorrhynchus psittacula*	0.258	619.2	0.02	0.01	0.12		0.04	0.10	0.05	0.56
Crested auklet	*Aethia cristatella*	0.264	629.6	0.08		0.00				17.73	
Rhinoceros auklet	*Cerorhinca monocerata*	0.520	1024.3	0.02		0.01		0.01	0.05	0.00	
Tufted puffin	*Fratercula cirrhata*	0.779	1369.1	3.94	0.41	12.65	2.87	0.40	0.91	0.82	0.67
Horned puffin	*Fratercula corniculata*	0.619	1160.8	0.17	0.02	0.49		0.02	0.02	0.19	0.03
Unidentified large alcidae		0.775	1363.9	0.11	0.05	0.23		0.10	0.03	0.10	0.15
Arctic loon	*Gavia arctica*	3.355	3293.7	0.03	0.10	0.00		0.00		0.01	0.01
Common loon	*Gavia immer*	4.134	3773.2	0.05		0.00		0.02		0.03	
Yellow-billed loon	*Gavia adamsii*	5.500	4543.9			0.00				0.01	

A—northeastern shelf, B—northeastern basin, C—southwestern shelf, D—southwestern basin.

Appendix B

Diets of marine birds as used in this paper is provided in Table 9.

Table 9
Diets (% biomass) of marine birds as used in this paper

Common name	Miscellaneous invertebrates (3 kJ/g)	Gelatinous (0.6 kJ/g)	Mollusks (2 kJ/g)	Crustaceans (2.6 kJ/g)	Cephalopods (5.5 kJ/g)	Fish (5.7 kJ/g)	Birds & mammals (7 kJ/g)	Carrion & offal (6 kJ/g)	Unknown prey (3 kJ/g)	References
Red-necked grebe				0.25		0.75				Stout and Neuchterlein (1999)
Horned grebe				0.35		0.65				Stedman (2000)
Unidentified grebe				0.30		0.70				
Laysan albatross		0.05		0.10	0.75	0.10				Whittow (1993a,b)
Black-footed albatross				0.05	0.35	0.60				Whittow (1993a,b)
Unidentified albatross				0.10	0.55	0.35				
Northern fulmar				0.01	0.96	0.03				Degange and Sanger (1986)
Mottled petrel					0.75	0.25				Prince and Morgan (1987)
Buller's shearwater	0.03			0.05	0.01	0.91				Gould et al. (1998)
Flesh-footed shearwater				0.50		0.50				Assumed values
Short-tailed shearwater	0.01			0.73	0.02	0.24				Degange and Sanger (1986)
Sooty shearwater				0.01	0.27	0.72				Degange and Sanger (1986)
Unidentified shearwater				0.35	0.15	0.50				
Leach's storm-petrel		0.05		0.30		0.65				Huntington et al. (1996)
Fork-tailed storm-petrel				0.65		0.35				Boersma and Silva (2001)
Unidentified storm-petrel				0.50		0.50				
Double-crested-cormorant						1.00				Sanger (1983)
Red-faced cormorant						1.00				Sanger (1983)
Pelagic cormorant						1.00				Degange and Sanger (1986)
Unidentified cormorant						1.00				
Greater scaup			0.50	0.10					0.40	Kessel et al. (2002)
Lesser scaup				1.00						Austin et al. (1998)
Unidentified scaup			0.50	0.50						
King eider	0.25	0.05	0.50	0.20						Suydam (2000)
Steller's eider	0.10		0.25	0.60		0.05				Fredrickson (2001)
Unidentified eider	0.20		0.40	0.40						
Harlequin duck	0.10		0.65	0.10		0.15				Robertson and Goudie (1999)
Unidentified duck	0.10		0.54	0.36						
Surf scoter	0.10		0.80	0.05		0.05				Savard et al. (1998)
Black scoter	0.10		0.70	0.20						Bordage and Savard (1995)
White-winged scoter			0.50	0.50						Brown and Fredrickson (1997)
Unidentified scoter	0.10		0.65	0.25						
Common goldeneye			0.50	0.50						Eadie et al. (1995)
Barrow's goldeneye			0.75	0.25						Eadie et al. (2000)
Unidentified goldeneye			0.60	0.40						
Bufflehead			0.30	0.40		0.05			0.25	Gauthier (1993)

Common merganser					0.95			0.05	Mallory and Metz (1999)
Red-breasted merganser					1.00				Titman (1999)
Unidentified merganser					1.00				
Red phalarope			0.95		0.05				Tracy et al. (2002)
Red-necked phalarope			0.95		0.05				Rubega et al. (2000)
Unidentified phalarope			0.95		0.05				
Long-tailed jaeger					0.90	0.10			Assumed values
Parasitic jaeger					0.90	0.10			Assumed values
Pomarine jaeger					0.90	0.10			Assumed values
Unidentified jaeger					0.90	0.10			
Ivory gull					1.00				Haney and Macdonald (1995)
Mew gull	0.10		0.20		0.50		0.20		Moskoff and Bevier (2002)
Herring gull	0.15	0.05	0.05	0.05	0.50		0.20		Pierotti and Good (1994)
Glaucous gull	0.15				0.60	0.25			Gilchrist (2001)
Glaucous-winged gull		0.15	0.30		0.30	0.05	0.20		Verbeek (1993)
Sabine’s gull			0.35		0.65				Day et al. (2001)
Unidentified gull	0.10		0.20		0.60		0.10		
Black-legged kittiwake	0.02		0.11		0.82			0.05	Degange and Sanger (1986)
Red-legged kittiwake				0.02	0.96			0.02	Hunt et al. (1981)
Unidentified kittiwake			0.05		0.90			0.05	
Arctic tern			0.96		0.03			0.01	Degange and Sanger (1986)
Aleutian tern	0.01		0.79		0.20				Degange and Sanger (1986)
Unidentified tern			0.90		0.10				
Common murre			0.11		0.86			0.03	Degange and Sanger (1986)
Thick-billed-murre			0.10	0.74	0.16				Degange and Sanger(1986)
Unidentified murre			0.10	0.35	0.55				
Pigeon guillemot	0.01		0.39		0.60				Degange and Sanger (1986)
Ancient murrelet			0.78		0.21			0.01	Degange and Sanger (1986)
Kittlitz’s murrelet			0.24		0.76				Degange and Sanger (1986)
Marbled murrelet			0.16		0.84				Degange and Sanger (1986)
Unidentified Brachyramphus			0.20		0.80				
Unidentified murrelet			0.50		0.50				
Cassin’s auklet			0.94	0.01	0.05				Degange and Sanger (1986)
Parakeet auklet			0.59		0.41				Degange and Sanger (1986)
Crested auklet			1.00						Degange and Sanger (1986)
Rhinoceros auklet				0.01	0.97			0.02	Degange and Sanger (1986)
Tufted puffin	0.07		0.45	0.22	0.26				Piatt and Kitaysky (2002a)
Horned puffin			0.01	0.19	0.80				Piatt and Kitaysky (2002b)
Unidentified alcidae					1.00				
Arctic loon					1.00				Russell (2002)
Common loon					1.00				McIntyre and Barr (1997)
Yellow-billed loon					1.00				North (1994)
Unidentified loon					1.00				

Diet estimates were in many cases modified for season or location. Modified diets rounded to the nearest 5%. ( )-Values of energy density used in this study for each food category. Original sources should be consulted for actual diet data.

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