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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 extracted data from the North Pacific Pelagic Seabird Database (NPPSD), and from these data we then modeled 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, sub-surface 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, whereas over the basin northern fulmars, gulls and kittiwakes predominated in "winter". Our results suggest that marine birds contribute little to cross-shelf fluxes of energy or matter, but that they do remove energy from the marine system through consumption, respiration and migration.

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. However, it is of interest to investigate the flux of material between these habitats and to understand better the connections between them. To investigate these questions in the northern Gulf of Alaska, we estimated densities of marine birds in shelf and basin waters and from these calculated avian energy demand and prey consumption.

More than 65 species of marine birds have been identified in the northern Gulf of Alaska, though only about 17 of these are found in either shelf or basin waters in densities greater than 1 km^{-2} (Appendix 1). 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 to 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. For example, 14 of the 17 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 heretofore been neglected (Appendix 1). It is therefore timely, 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.

METHODS

We determined the density of seabirds, by species and species groups (Appendix 1) by extracting counts from the North Pacific Pelagic Seabird Database (NPPSD), which is maintained by the U.S. 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 (Fig. 1).

For most marine bird species, shipboard surveys were used directly to calculate birds km^{-2}. However, Hunt et al. (2000) identified two species of albatrosses, three species of shearwaters and northern fulmars, which are ship-attracted or clumped in their distributions, 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. Hunt et al. assumed that the ratios of the densities of each of these species across the PICES subregions represented the proportion of the North Pacific population of each species in each subregion. Therefore, to obtain the number of individuals of a species in each subregion (e.g., the Gulf of Alaska), they multiplied the percentages of each species seen in a subregion by the estimated population for the entire PICES region (Hunt et al., 2000). This procedure was modified further for sooty/short-tailed shearwaters 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 to estimate the ratio of one species to the other in each area and then using that ratio 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 (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^{-1} 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 the grouped taxa.

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. 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 Birt-Friesen et al. (1989) that predicts energy requirements as a function of body mass:

$$\text{Log } Y = 3.24 + 0.727 \log M$$

where Y = daily energy requirements is in kJ, and M = mass in kg (Birt-Friesen *et al.,* 1989). 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).

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 2). 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, as well as with its condition when ingested (Hunt et al., 2000). We have used updated values from the literature to provide best estimates of prey energy density: miscellaneous invertebrates, 3 kJ g^{-1}; mollusks, 2 kJ g^{-1}; gelatinous zooplankton, 0.6 kJ g^{-1}; crustacean zooplankton, 2.6 kJ g^{-1}; cephalopods, 5.5 kJ g^{-1}; fish, 5.7 kJ g^{-1}; birds and mammals, 7 kJ g^{-1}; carrion, offal and discards, 6 kJ g^{-1} (Davis et al., 1998).

RESULTS

Our search of the North Pacific Pelagic Database yielded a sample of 6996 bird counts obtained between 1975 and 1984. Of these, 2,150 counts were obtained over continental shelf waters and 182 counts over the basin during May through August, the northern breeding season (Figure 1). During the non-breeding season of September through April, 4,334 counts were obtained over the shelf and 330 over the basin (Figure 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 1134 for February and a low of 131 for January. Coverage of basin waters was sparse. The monthly mean was 43 bird counts, with a high of 88 for September and a low of 1 for December. Coverage in January (6 counts) and August (6 counts) was also minimal.

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 both the May-August period (32 times higher) and between September and April (33x) (Figure 2, Table 1). The densities of surface-foraging birds were much lower than those of subsurface-foragers, and there was little difference in the densities of surface-foraging birds on and off the shelf in either the May-August period (8x) or the September-April period (1x). Although outside of the scope of this paper, there was also a striking pattern in the on-shelf distribution of marine birds. Particularly in the May-August period, the densities of birds and counts with high numbers of birds were greater southwest of Cook Inlet than to the northeast (Figure 2).

Seasonal patterns in the density of marine birds were surprisingly uniform (Table 1) given that many of the species that frequent the Gulf of Alaska are migratory. On the shelf, there were slightly higher densities of marine birds in September-April (91.7 km^{-2}, using the adjusted data) as compared to May-August (81.2 km^{-2}), as was also the case over the basin (September-April, 10.3 km^{-2} vs. May-August, 7.5 km^{-2}). 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, whereas between September and April shearwaters for the most part had migrated to the Southern Hemisphere and had been replaced by wintering murres and sea ducks (Figure 3). Among surface-foraging species, there was an influx of gulls and fulmars, particularly over basin waters during the months of September to April (Figure 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 2). Within the sub-surface foragers, sea ducks and murres have a greater per individual biomass than the shearwaters (Appendix 1), and thus on the shelf between September and April, the sea ducks and murres had greater energy demands km^{-2} than shearwaters (Table 3). For surface-foragers over the basin, the amount of energy required daily between September and April was almost 5 times greater than between May and August because of the influx of gulls and kittiwakes into the region (Table 4).

Monthly prey consumption by marine birds was greater on the continental shelf than over the basin and, on a seasonal basis, in the non-breeding season than in the breeding season (Table 5). Between May and August, marine bird prey consumption on the shelf was 35.3 kg m^{-2} d^{-1}, and over the basin, 1.9 kg m^{-2} d^{-1}. For the period between September and April, daily prey consumption by marine birds over the shelf was 55 kg m^{-2} d^{-1} and over the basin, 4.3 kg m^{-2} d^{-1}. Over both the shelf and the basin, 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. On the shelf, the major increase in prey demand came from the sub-surface 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 (Figure 5). Over the basin, the major component of marine bird diets was fish, followed by crustaceans and cephalopods. The mean daily consumption of seabirds on the shelf in May-August included 22.7 kg km^{-2} d^{-1} crustaceans, most of which were euphausiids consumed by shearwaters, and 9.1 kg km^{-2} d^{-1} of fish, of which most were forage fish such as capelin (*Mallotus villosus*). In September- April, on-shelf consumption of crustaceans (18.9 kg km^{-2} d^{-1}) was almost the same as the consumption of epi-benthic mollusks by sea ducks (18.6 kg km^{-2} d^{-1}) and more than the consumption of fish (13.4 kg km^{-2} d^{-1}). Over the basin in winter, marine birds consumed an estimated 1.4 kg km^{-2} d^{-1} of fish and 1.3 kg km^{-2} d^{-1} of crustaceans, most of which would have been components of the neuston. The composition of prey taken by marine birds over the basin was more diverse than that over the shelf, with consumption more evenly divided among the prey categories.

DISCUSSION

Bearing in mind the caveats and sources of error discussed below, several major 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 Figures 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 to August) whereas we estimated 35 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 (1.9 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 that over the basin (Cooney, 1986; Sambrotto and Lorenzen, 1986).

A second major finding was that prey consumption rates were greater in “winter” than in “summer”, both on and off the shelf. 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 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 notably 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).

Sub-surface foraging marine birds predominate on shelf, whereas surface foraging birds predominate over the basin. It is no surprise that epi-benthically foraging sea ducks are confined to shallow waters where they can reach the bottom. It is less clear that other sub-surface foraging species should be found predominately over the shelf and not over the basin. However, there is a growing literature that indicates that for successful sub-surface foraging, high prey densities may be necessary, whereas light-bodied surface foragers with low wing loading may succeed in areas with lower productivity (e.g. Ainley, 1977; Balance 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, perhaps 10 or 20%, 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 over the basin during the breeding season (May – August) are very low, and the species foraging over the basin that are likely to be provisioning young (storm-petrels, northern fulmar) occur at very low densities. Thus, it is it would appear that marine birds must contribute little to cross-shelf flux of energy or material.

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, 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. In the Gulf of Alaska study area, there were a small number of reports of exceptionally high numbers of birds in flocks. It is likely that some unknowable portion of these were over-estimated. Such over-estimates would bias upwards our estimates of prey consumption.

The distribution of counts within the study area will also bias upward our estimates of birds foraging over the continental shelf. The majority of counts were made in the vicinity of Kodiak Island, in the 1970s the base from which many of the ships were deployed. This region is also an area where high numbers of big flocks were seen, especially when compared to shelf areas to the northeast of Cook Inlet. Averaging the counts across the shelf area in our study area will overweight the high numbers near Kodiak Island. A examination of marine bird densities along the shelf with narrowly set sub-samples would allow exploration of northeast-southwest differences in the density of marine birds along the shelf, but such an analysis was beyond the scope of the present study.

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 very 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 requirement of individual birds are likely far more accurate that the estimates of their abundance.

Thus for the present study, the likelihood is that we have overestimated the amount of prey consumed by marine birds over the continental shelf; estimates for basin waters are likely less biased and are about as good as can be achieved. Since both DeGange and Sanger (1986) and Hunt et al. (2000) relied on the same data set, their estimates were likely similarly biased.

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Appendix 1. Body mass (kg), individual energy requirements (kJ d^{-1}) and unadjusted density of marine birds (birds km^{-2}) in the Gulf of Alaska.

Common Name	Scientific Name	Body Mass	Energy Required	Density On-Shelf (May-Aug)	Density On-Shelf (Sept-Apr)	Density Off-Shelf (May-Aug)	Density Off-Shelf (Sept-Apr)
Red-necked Grebe	*Podiceps grisegena*	1.023	1766.8		0.27		
Horned Grebe	*Podiceps auritus*	0.453	977.2		0.16		
Unidentified Grebe		0.738	1393.4		0.02		
Laysan Albatross	*Phoebastria immutabilis*	3.042	3901.7	0.00	0.00	0.15	0.05
Black-footed Albatross	*Phoebastria nigripes*	3.148	4000.1	0.01	0.00	1.13	0.11
Unidentified Albatross		3.095	3951.0	0.64	0.18	0.13	0.20
Northern Fulmar	*Fulmarus glacialis*	0.544	1116.3	0.68	0.30	2.54	6.36
Mottled Petrel	*Pterodroma inexpectata*	0.316	752.1		0.00	0.11	
Cory's Shearwater	*Calonectris diomedea*	0.535	1102.8				0.01
Buller's Shearwater	*Puffinus bulleri*	0.380	860.0	0.00		0.01	
Short-tailed Shearwater	*Puffinus tenuirostris*	0.543	1114.8	16.75	4.57	0.25	0.06
Sooty Shearwater	*Puffinus griseus*	0.787	1460.1	18.75	4.90	0.62	0.78
Unidentified Shearwater		0.563	1143.9	51.37	8.81	2.24	4.43
Leach's Storm-Petrel	*Oceanodroma leucorhea*	0.040	166.8	0.00		0.07	0.00
Fork-tailed Storm-Petrel	*Oceanodroma furcata*	0.055	211.8	0.70	0.20	3.16	0.66
Unidentified Storm-petrel		0.048	189.8	0.00	0.00	0.02	0.13
Double-crested Cormorant	*Phalacrocorax auritus*	1.674	2527.4	0.01	0.01		
Red-faced Cormorant	*Phalacrocorax urile*	2.157	3038.8	0.02	0.01		
Pelagic Cormorant	*Phalacrocorax pelagicus*	1.868	2737.1	0.07	0.07		
Unidentified Cormorant		1.900	2770.8	0.25	3.53	0.00	0.22

Greater Scaup	*Aythya marila*	0.945	1667.1		0.18		
Lesser Scaup	*Aythya affinis*	0.820	1504.3		0.03		
Unidentified Scaup		0.882	1586.5	0.00	0.68		
King Eider	*Somateria spectabilis*	1.618	2465.1		1.07		
Steller's Eider	*Polysticta stelleri*	0.808	1487.6		0.14		
Unidentified Eider		1.497	2330.4		0.23		
Harlequin Duck	*Histrionicus histrionicus*	0.623	1231.2	0.01	1.81		
Unidentified Duck		1.156	1930.9	0.01	0.20	0.00	0.01
Surf Scoter	*Melanitta perspicillata*	0.950	1674.2	0.00	0.56		
Black Scoter	*Melanitta nigra*	0.850	1544.1		4.81		
White-winged Scoter	*Melanitta fusca*	1.757	2617.9	0.28	3.73		0.00
Unidentified Scoter		1.156	1930.9		9.17		0.03
Common Goldeneye	*Bucephala clangula*	0.900	1609.7	0.00	0.04		
Barrow's Goldeneye	*Bucephala islandica*	0.910	1622.6		1.04		
Unidentified Goldeneye		0.905	1616.2	0.00	0.13		
Bufflehead	*Bucephala albeola*	0.404	898.4		0.11		
Common Merganser	*Mergus merganser*	1.471	2300.1		0.07		
Red-breasted Merganser	*Mergus serrator*	1.022	1764.9	0.00	0.17		
Unidentified Merganser		1.246	2039.1		0.05		
Red Phalarope	*Phalaropus fulicaria*	0.056	212.9	0.06	0.00	0.01	0.20
Red-necked Phalarope	*Phalaropus lobatus*	0.034	148.1	0.69	0.19	0.06	0.00
Unidentified Phalarope		0.045	181.6	0.21	0.01	0.05	0.04
Long-tailed Jaeger	*Stercorarius longicaudus*	0.297	718.1	0.02	0.00	0.06	0.01
Parasitic Jaeger	*Stercorarius parasiticus*	0.465	995.2	0.09	0.00	0.04	0.01
Pomarine Jaeger	*Stercorarius pomarinus*	0.694	1332.5	0.21	0.01	0.10	0.02
Unidentified Jaeger		0.485	1026.9	0.04	0.00	0.01	0.02

Mew Gull	*Larus canus*	0.404	898.4	0.06	1.95		0.03
Herring Gull	*Larus argentatus*	1.135	1905.4	0.02	0.04	0.06	0.14
Glaucous Gull	*Larus hyperboreus*	1.413	2233.8	0.00	0.01		0.03
Glaucous-winged Gull	*Larus glaucescens*	1.010	1750.4	1.34	2.22	0.11	2.74
Sabine's Gull	*Xema sabini*	0.191	521.6	0.02	0.00	0.00	
Unidentified Gull		0.819	1503.1	1.56	0.67	0.02	0.55
Black-legged Kittiwake	*Rissa tridactyla*	0.407	904.0	5.45	3.83	0.53	1.86
Red-legged Kittiwake	*Rissa brevirostris*	0.391	878.0	0.00	0.00	0.07	0.00
Unidentified Kittiwake		0.399	891.1	0.50	0.12		
Arctic Tern	*Sterna paradisaea*	0.110	349.2	0.23	0.03	0.14	0.17
Aleutian Tern	*Sterna aleutica*	0.120	372.0	0.05		0.01	
Unidentified Tern		0.115	360.7	0.17	0.00	0.00	0.01
Common Murre	*Uria aalge*	0.993	1728.3	1.45	13.97		0.08
Thick-billed Murre	*Uria lomvia*	0.964	1692.1	0.02	0.03		0.07
Unidentified Murre		0.978	1710.2	1.38	9.95	0.01	0.73
Pigeon Guillemot	*Cepphus columba*	0.487	1030.0	0.47	1.51		
Ancient Murrelet	*Synthliboramphus antiquus*	0.206	551.0	0.23	0.04	0.02	0.01
Kittlitz's Murrelet	*Brachyramphus brevirostris*	0.224	585.6	0.03	0.03		
Marbled Murrelet	*Brachyramphus marmoratus*	0.222	581.8	0.34	2.21		0.03
Unidentified Murrelet	*Brachyramphus spp.*	0.223	583.7	0.63	0.78		0.03
Cassin's Auklet	*Ptychoramphus aleuticus*	0.188	515.6	0.32	0.01	0.03	0.02
Parakeet Auklet	*Cyclorrhynchus psittacula*	0.258	649.0	0.18	0.00	0.37	0.01
Crested Auklet	*Aethia cristatella*	0.264	659.9	0.01	8.93		
Rhinoceros Auklet	*Cerorhinca monocerata*	0.520	1080.3	0.01	0.00	0.03	

Tufted Puffin	*Fratercula cirrhata*	0.779	1449.3	6.12	0.63	0.61	0.42
Horned Puffin	*Fratercula corniculata*	0.619	1226.2	0.50	0.10	0.02	0.02
Unidentified large Alcidae		0.775	1443.7		0.02		0.12
Red-throated Loon	*Gavia stellata*	1.551	2391.0	0.00	0.00		
Arctic Loon	*Gavia arctica*	3.355	4189.7	0.00	0.01	0.05	0.01
Common Loon	*Gavia immer*	4.134	4876.4	0.00	0.03		
Yellow-billed Loon	*Gavia adamsii*	5.500	6001.3		0.01		
Unidentified Loon		3.635	4441.1	0.00	0.35	0.00	

Appendix 2. Diets of marine birds as used in this paper. Diet estimates were in many cases modified for season or location. Modified diets rounded to the nearest 5%. Original sources should be consulted for actual diet data.

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 & 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 (1993)
Black-footed Albatross				0.05	0.35	0.60				Whittow (1993)
Unidentified Albatross				0.10	0.55	0.35				
Unidentified Albatross				0.10	0.55	0.35				
Northern Fulmar				0.01	0.96	0.03				Degange & Sanger 1987
Mottled Petrel					0.75	0.25				Prince & Morgan 1987
Buller's Shearwater	0.03			0.05	0.01	0.91				Gould et al. 1998
Short-tailed Shearwater	0.01			0.73	0.02	0.24				Degange & Sanger 1987
Sooty Shearwater				0.01	0.27	0.72				Degange & Sanger 1987
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 & Silva (2001)
Unidentified Storm-petrel				0.50		0.50				
Double-crested Cormorant						1.00				Sanger 1986
Red-faced Cormorant						1.00				Sanger 1986
Pelagic Cormorant						1.00				Degange & Sanger 1987
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 & 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& Savard (1995)
White-winged Scoter			0.50	0.50						Brown & 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 & 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)
Red-necked Phalarope				0.95		0.05				Rubega et al. (2000)
Unidentified Phalarope				0.95		0.05				
Long-tailed Jaeger						0.90	0.10			Best Guess
Parasitic Jaeger						0.90	0.10			Best Guess
Pomarine Jaeger						0.90	0.10			Best Guess
Unidentified Jaeger						0.90	0.10			
Ivory Gull						1.00				Haney & Macdonald (1996)
Mew Gull	0.10			0.20		0.50		0.20		Moskoff & Bevier (2002)
Herring Gull	0.15		0.05	0.05	0.05	0.50		0.20		Pierotti & 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 & Sanger 1987
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 & Sanger 1987
Aleutian Tern	0.01		0.79		0.20				Degange & Sanger 1987
Unidentified Tern			0.90		0.10				
Unidentified Tern			0.90		0.10				
Common Murre			0.11		0.86			0.03	Degange & Sanger 1987
Thick-billed Murre			0.10	0.74	0.16				Degange & Sanger 1987
Unidentified Murre			0.10	0.35	0.55				
Pigeon Guillemot	0.01		0.39		0.60				Degange & Sanger 1987
Ancient Murrelet			0.78		0.21			0.01	Degange & Sanger 1987
Kittlitz's Murrelet			0.24		0.76				Degange & Sanger 1987
Marbled Murrelet			0.16		0.84				Degange & Sanger 1987
Unidentified Brachyramphus			0.20		0.80				
Unidentified Murrelet			0.50		0.50				
Cassin's Auklet			0.94	0.01	0.05				Degange & Sanger 1987
Parakeet Auklet			0.59		0.41				Degange & Sanger 1987
Crested Auklet			1.00						Degange & Sanger 1987
Rhinoceros Auklet				0.01	0.97			0.02	Degange & Sanger 1987
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 Alciadae					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				

Table 1. Densities of marine birds (birds km^{-2}) in the Gulf of Alaska. 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.

	Raw Data		Adjusted Data		
	On-Shelf	Off-Shelf	On-Shelf	Off-Shelf	Ratio On/Off Shelf
Divers (May-Aug.)	99.3	4.3	69.6	2.2	31.6
Divers (Sept.-Apr.)	85.2	7.1	82.4	2.5	33.0
Surface (May-Aug.)	12.8	8.6	11.6	5.3	2.2
Surface (Sept.-Apr.)	9.8	13.4	9.3	7.8	1.2

Table 2. Biomass of marine birds (kg km^{-2}) in the Gulf of Alaska. Raw data are taken directly from the NPPD 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.

	On-Shelf	Off-Shelf	Ratio On/Off Shelf
Divers (May-Aug.)	43.6	1.5	29.1
Divers (Sept.-Apr.)	73.4	2.3	31.9
Surface (May-Aug.)	5.5	1.6	3.4
Surface (Sept.-Apr.)	5.3	5.1	1.0

Table 3. Daily energy demand, based on adjusted densities, of selected species of sub-surface-foraging marine birds over the Gulf of Alaska continental shelf.

Species Group	May-August MJ/ km^{-2} d^{-1}	September-April MJ/ km^{-2} d^{-1}
Shearwaters	67.7	18.3
Murres	4.9	41.2
Sea Ducks	0.8	45.9
Total	73.1	105.4

Table 4. Daily energy demand, based on adjusted densities, of selected species of surface-foraging Marine birds over the Gulf of Alaska basin.

Species Group	May-August MJ/ km^{-2} d^{-1}	September-April MJ/ km^{-2} d^{-1}
Albatrosses	0.7	0.2
Northern Fulmar	0.5	1.3
Gulls & Kittiwakes	0.9	7.6
Total	2.1	9.1

Table 5. Monthly prey consumption by marine birds in the Gulf of Alaska, based on adjusted densities of all species combined.

Species Group	May-August kg km^{-2} mon^{-1}	September-April kg km^{-2} mon^{-1}
Sub-surface Foragers, on Shelf	973	1594
Surface Foragers, on Shelf	105	102
Sub-surface Foragers, Basin	29	35
Surface Foragers, Basin	30	95

Figure Legends

Figure 1. Distribution of survey effort within the survey region. 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.

Figure 2. Distribution and abundance of all species marine birds combined within the study area. Top: Survey results from May through August; Bottom: Survey results from September through April.

Figure 3. Abundances of selected species of sub-surface foraging marine birds within the study area. a. densities over the shelf, May-August; b. densities over the basin, May-August; c. densities over the shelf, September-April.

Figure 4. Abundances of selected species of surface-foraging marine birds within the study area. a. densities over the shelf, May-August; b. densities over the basin, May-August; c. densities over the shelf, September-April.

Figure 5. Prey consumed by marine birds within the study area; top: Consumption by sub-surface foraging marine birds; bottom: Consumption by surface-foraging marine birds.

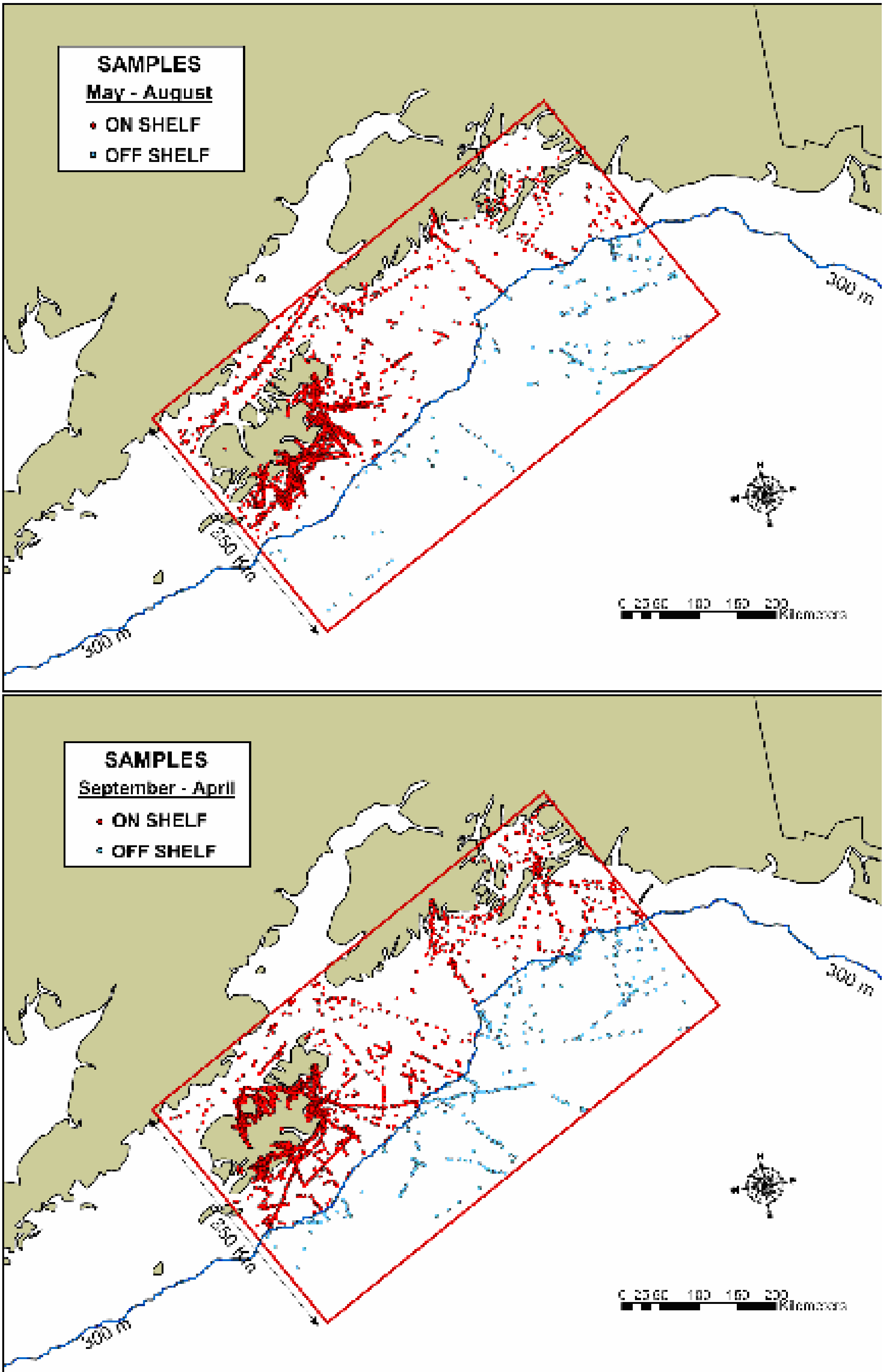
SAMPLES
May - August
ON SHELF
OFF SHELF
300 m
250 Km
300 m
SAMPLES
September - April
ON SHELF
OFF SHELF
300 m
250 Km
300 m

Figure 1

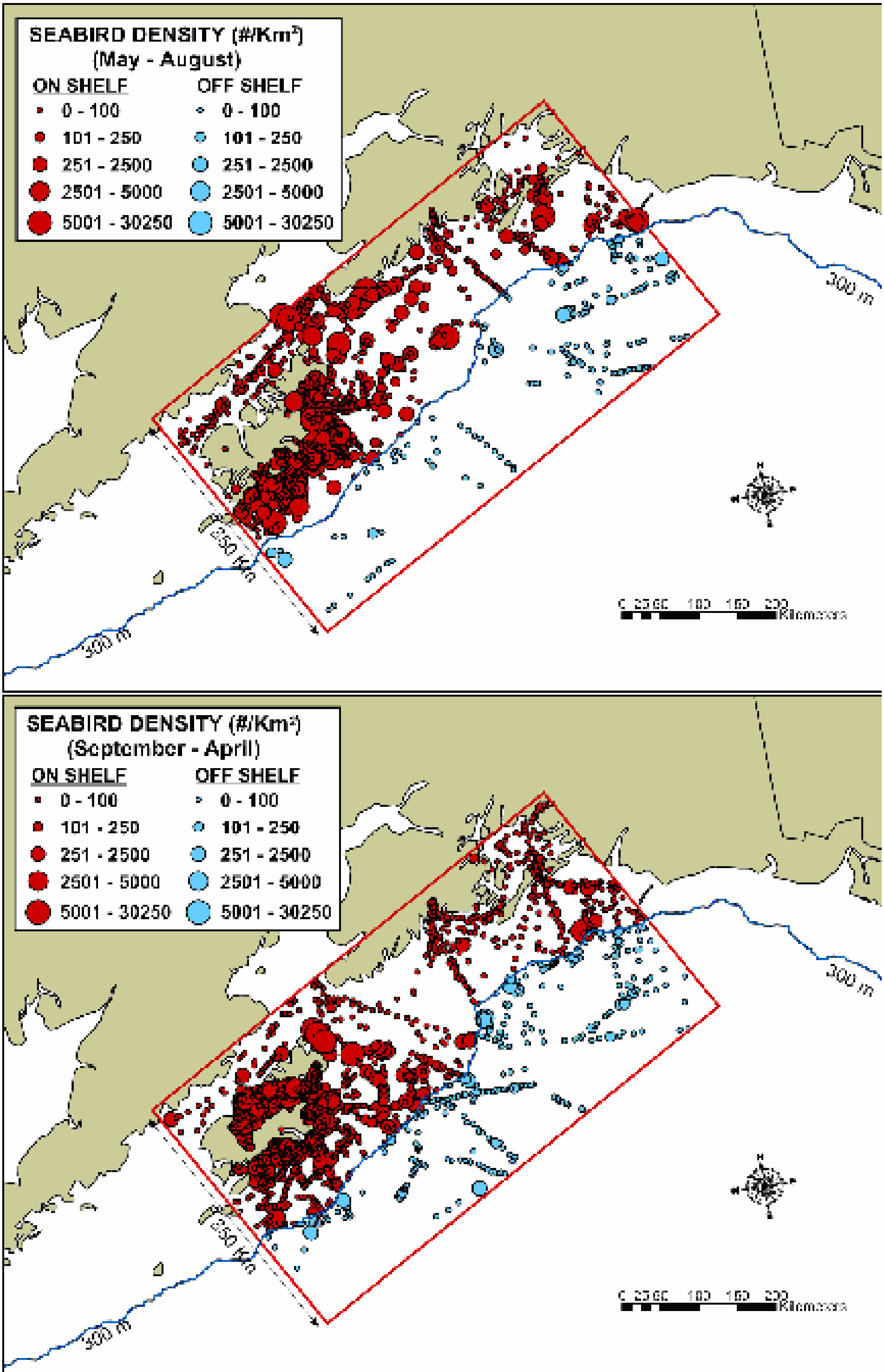
SEABIRD DENSITY (#/Km²)
(May - August)
ON SHELF
OFF SHELF
0 - 100
101 - 250
251 - 2500
2501 - 5000
5001 - 30250
0 - 100
101 - 250
251 - 2500
2501 - 5000
5001 - 30250
300 m
250 Km
300 m
SEABIRD DENSITY (#/Km²)
(September - April)
ON SHELF
OFF SHELF
0 - 100
101 - 250
251 - 2500
2501 - 5000
5001 - 30250
0 - 100
101 - 250
251 - 2500
2501 - 5000
5001 - 30250
300 m
250 Km
300 m

Figure 2

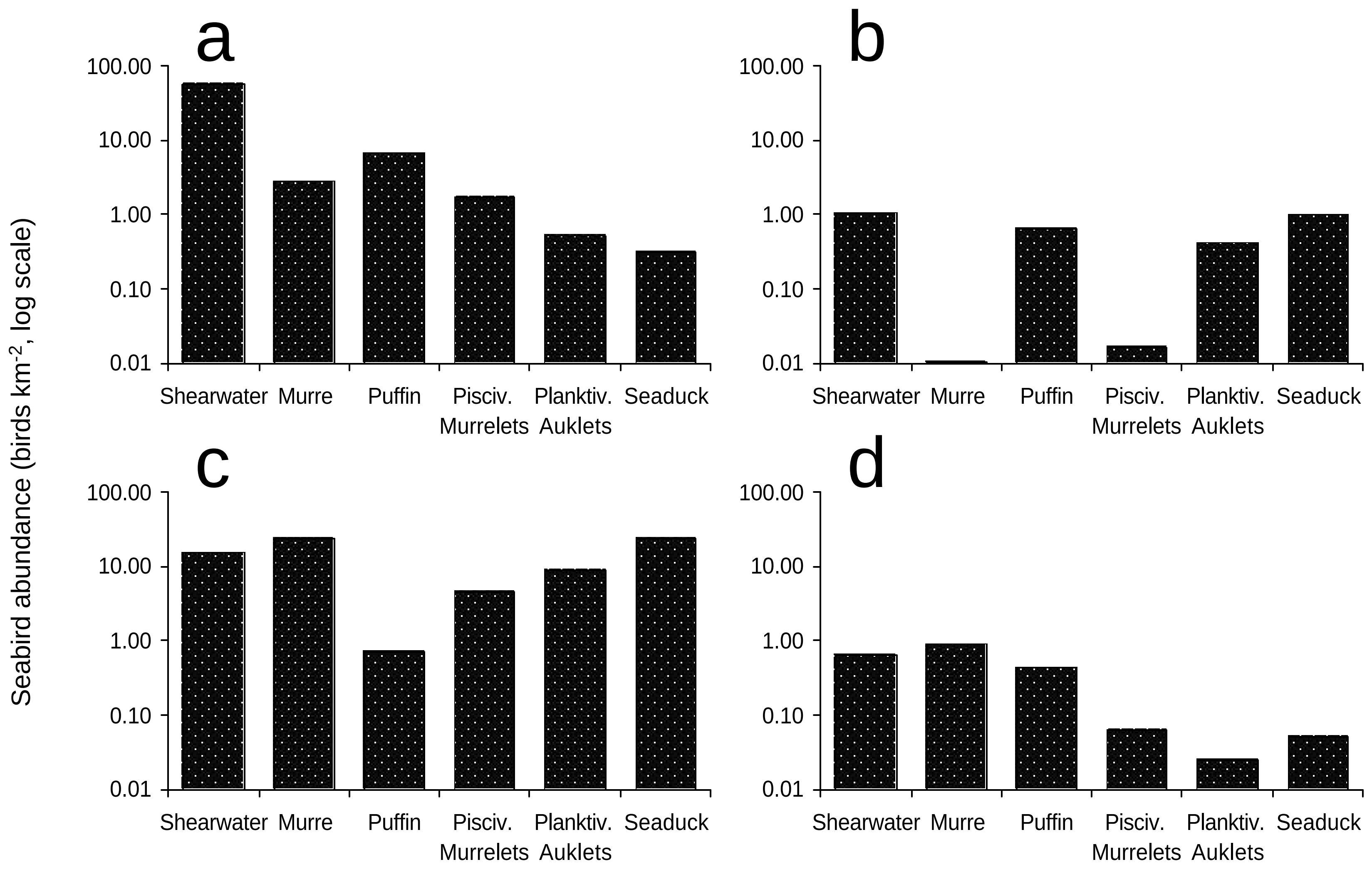
a
b
c
d
Seabird abundance (birds km-2, log scale)
100.00
10.00
1.00
0.10
0.01
Shearwater
Murre
Puffin
Pisciv. Murrelets
Planktiv. Auklets
Seaduck

Figure 3

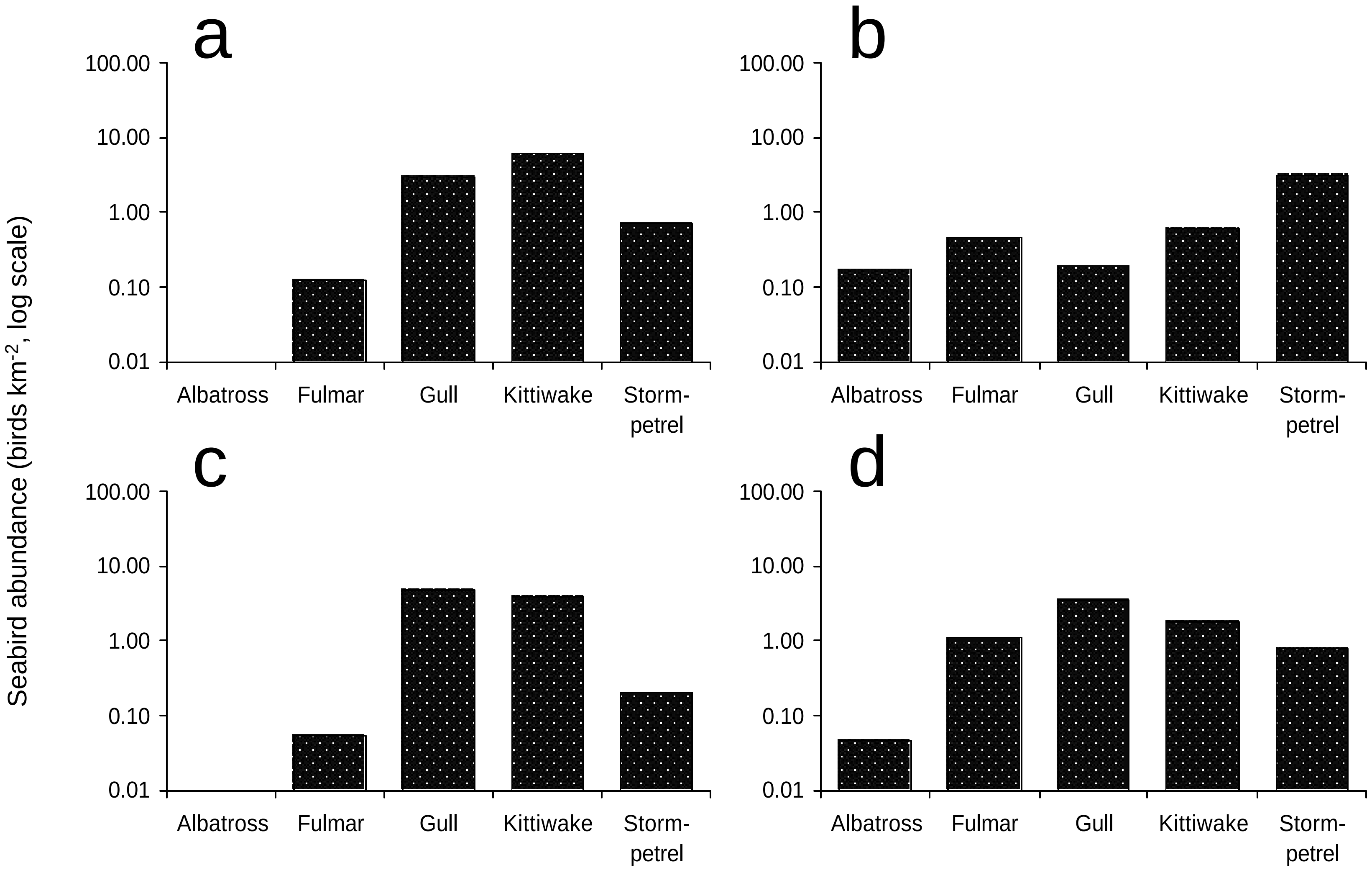
Seabird abundance (birds km-2, log scale)
a
b
c
d
100.00
10.00
1.00
0.10
0.01
Albatross
Fulmar
Gull
Kittiwake
Storm-petrel

Figure 4

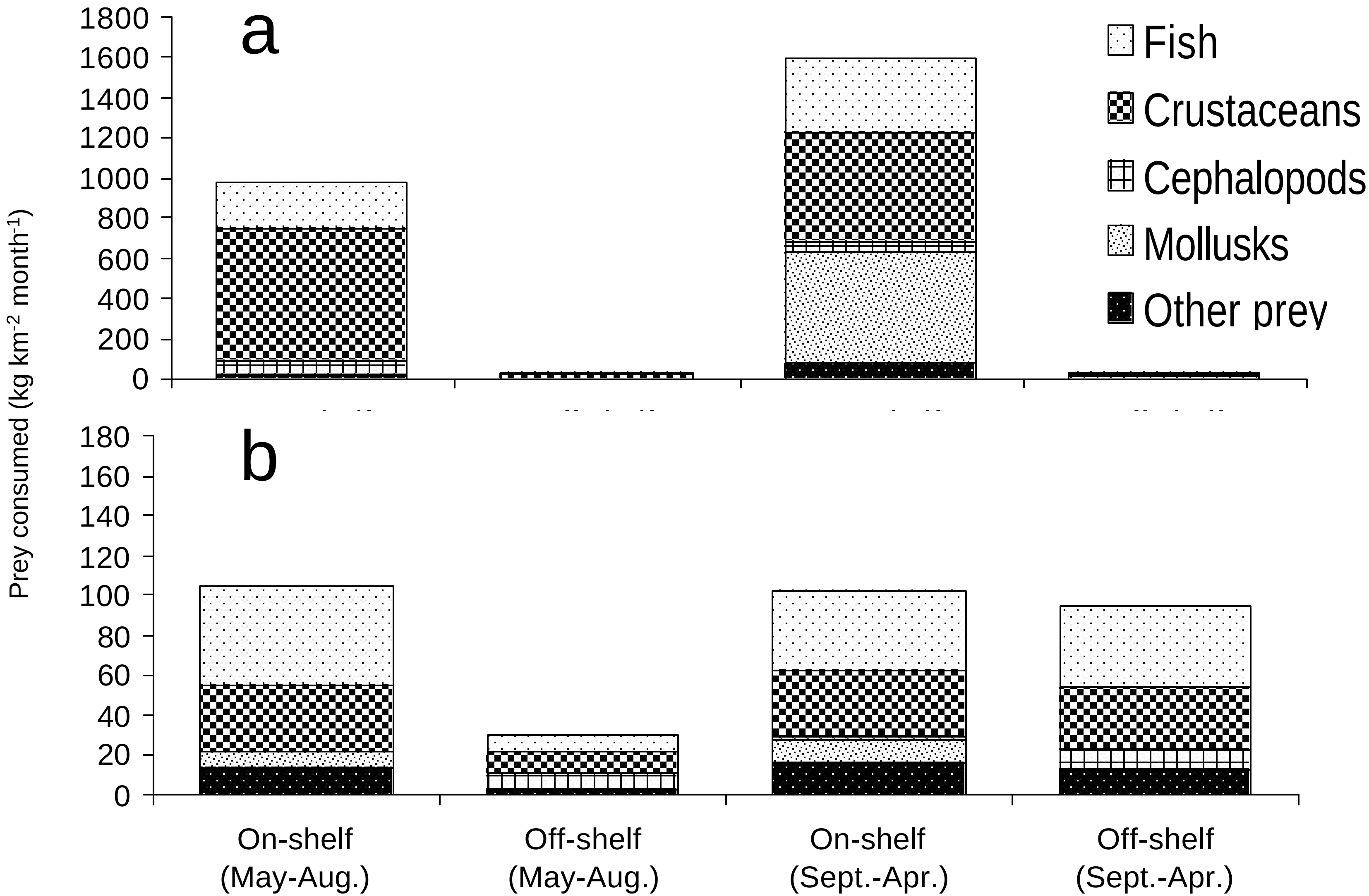
a
b
1800
1600
1400
1200
1000
800
600
400
200
0
180
160
140
120
100
80
60
40
20
0
Prey consumed (kg km-2 month-1)
Fish
Crustaceans
Cephalopods
Mollusks
Other prey
On-shelf (May-Aug.)
Off-shelf (May-Aug.)
On-shelf (Sept.-Apr.)
Off-shelf (Sept.-Apr.)

Figure 5