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Carbon Flux to Seabirds in Waters with Different Mixing Regimes in the Southeastern Bering Sea

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Abstract

The southeastern Bering Sea is characterized by three mixing regimes, separated by fronts associated with the 50, 100, and 200 m isobaths. Phytoplankton to zooplankton transfer-rates are high in waters over the outer shelf and slope (seaward of the 100 m front) relative to transfer in waters over the middle shelf (between the 50 and 100 m fronts). To see whether this difference is reflected at a higher trophic level, we computed carbon flux to the 11 commonest seabird species. Bird-density data (for the period 1975 through 1979) were combined with daily caloric requirement, which is an allometric function of body size in this endothermic group. Minimum transfer to seabirds over a 153 d period (April–August) was 30 mg C m⁻² for the middle shelf and 48 mg C m⁻² for outer shelf and slope waters. Trophic transfer to subsurface-feeding birds (shearwaters, murres and auklets) differed little between regions. In contrast, trophic transfer to surface-feeding birds (fulmars, petrels, and kittiwakes) in the outer shelf and slope waters was 3 times greater than in the waters of the middle shelf. Thus, for seabirds as a whole, pathways of energy transfer differed more between regions than did total carbon flux.

Introduction

The southeastern Bering Sea is a relatively wide continental shelf with low cross-shelf advection (Coachman and Charnell, 1979). Because advective flow is small, shelf waters become divided into four distinct mixing regimes separated by three fronts (Kinder and Schumacher, 1981). An inner front (Schumacher *et al.*, 1979) separates homogeneous coastal waters (less than 50 m depth) from stratified waters over the middle shelf (50 to 100 m depths). A middle front (Coachman and Charnell, 1979) separates a two-layer system on the middle shelf from a three-layer system on the outer shelf (100 to 200 m depths). The outer, or shelf-break front (Kinder and Coachman, 1978), separates shelf waters from saltier oceanic waters.

Primary productivity is on the order of $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the middle and outer shelf (McRoy and Goering, 1976). But while the outer shelf region is dominated by a pelagic food web, the middle shelf region is dominated by a benthic food web (Iverson *et al.*, 1979). The difference results from low carbon flux to zooplanktonic grazers on the middle shelf, compared to high flux to grazers on the outer shelf (Cooney and Coyle, in press). The greater transfer to pelagic food webs in the outer shelf waters led us to predict a concomitant pattern of greater transfer to an apex predator, seabirds.

For endotherms such as seabirds, food requirements and metabolism are proportional to weight raised to a power of 0.75 (Lasiewski and Dawson, 1967; Kendeigh, 1970). As a result of this allometry, a given biomass of large-bodied consumers requires a smaller daily ration than an equal biomass of small-bodied consumers. Thus, abundance and weight data must be combined with an allometric scaling in order to test whether carbon flux to birds differs between middle and outer shelf mixing regimes.

Materials and Methods

Bird densities were estimated from 981 transects (10 min each) made in the southeastern Bering Sea from 1975 through 1979. The following numerically dominant species were studied: northern fulmar (*Fulmarus glacialis*), fork-tailed storm petrel (*Oceanodroma furcata*), sooty shearwater (*Puffinus griseus*), slender-billed shearwater (*P. tenuirostris*), black-legged kittiwake (*Rissa tridactyla*), red-legged kittiwake (*R. brevirostris*), thick-billed murre (*Uria lomvia*), least auklet (*Aethia pusilla*), crested auklet (*A. cristatella*), parakeet auklet (*Cyclorrhynchus psittacula*), and tufted puffin (*Lunda cirrhata*). The two species of *Puffinus* are difficult to distinguish in the field, and thus data were
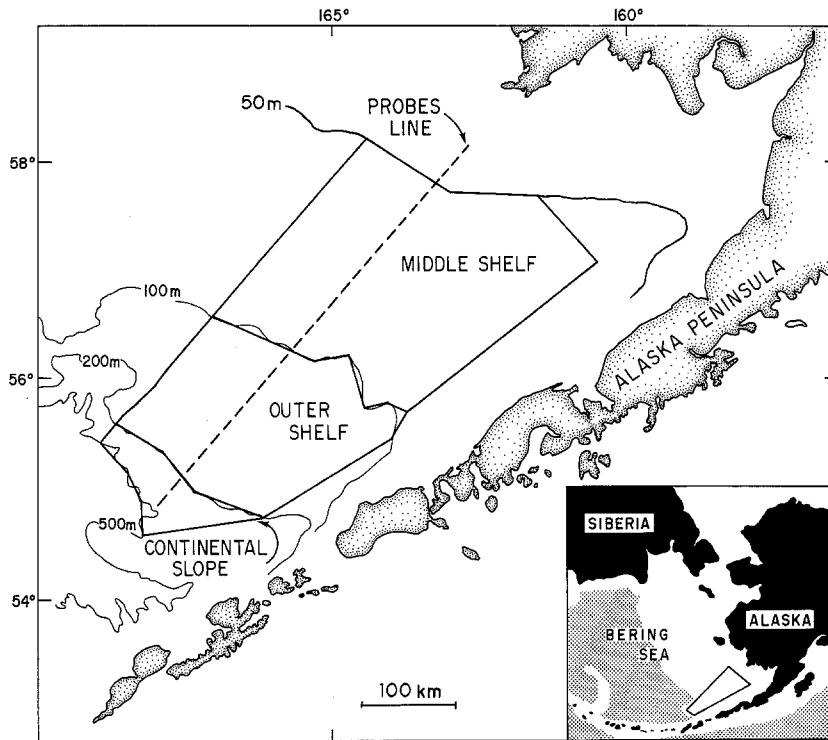
Fig. 1. Polygons for computing bird densities over the middle shelf, outer shelf, and continental slope in southeastern Bering Sea

lumped for analysis. Data for large auklets (*A. cristatella* and *C. psittacula*) were lumped for similar reasons. Major prey of these species include squid, large copepods (*Neocalanus* spp.), hyperiid amphipods, euphausids, and fish, most notably myctophids and a gadid, *Theragra chalcogramma* (Hunt et al., 1981a).

Counts during 1978 and 1979 were made during PROBES cruises (Processes and Resources of the Bering Sea Ecosystem). Counts were made in a 90° sector extending 300 m abeam from the ship while steaming at known speeds. Details on count procedure have been reported elsewhere (Hunt et al., 1980, 1981c). Possible bias by attraction of birds to ships was checked by observing birds from a helicopter in 1977. For ship-attracted species, a correction factor was computed from ship and helicopter counts, paired by location.

Regions for analysis were delimited by bathymetry, with each region centering around the PROBES transect (Fig. 1). Occupancy of each region by each species was defined as the average density for each month, multiplied by the number of days in the month, then summing these products over a period of maximum bird activity (April through August). The precision of this measure was taken as the average within-month variance, weighted by sample size. That is, the standard deviation was computed from the within-month sum of squares, rather than the total sum of squares.

Weights were obtained from birds collected in the southeastern Bering Sea. For non-breeding birds, daily food requirements were assumed to be 2.5 times the standard metabolic rate on the basis of work by MacMillen and Carpenter (1977) and by Weathers and Nagy (1980). Standard metabolic rates (SMR) were obtained from the equation for non-passerine birds (Lasiewski and Dawson, 1967):

$$SMR = 78.3 \ M^{0.723},$$

where $SMR = kcal \ d^{-1}$ and $M = kg$. The modified equation to account for diurnal activity (Aschoff and Pohl, 1970) was not used because seabirds were active at night. The following literature values were used to convert energy requirements to grams of carbon: 0.7 kcal assimilated $kcal^{-1}$ ingested (Kendeigh et al., 1977); 5 kcal g^{-1} dry wt of fish (Nishiyama, 1977); and 0.4 g C g^{-1} dry wt of fish, squid and arthropods (Curl, 1962). A few estimates of daily food consumption by seabirds were available in the literature. These were compared to daily food (fish) requirements by using a conversion of 0.27 g dry wt g^{-1} wet wt (Wiens and Scott, 1975).

Behavioral observations suggested that density estimates for fulmar might be high due to attraction of birds to ships, including research vessels. The mean density for ship counts was 3.4 times that for helicopter counts. The difference was almost significant for a two-tailed test (paired $t = 1.31$, $p = 0.07$). Since the variances involved were large and the sample size was small, it was prudent to compute the difference in means that could be detected with this sample size. The statistical test was sensitive enough to detect a 5-fold difference between ship and helicopter counts. To avoid Type II statistical error, we concluded that fulmar density estimated from ship counts fell within the range of 1 to 5 times the density estimated from helicopters. We reduced estimates of fulmar usage by a factor of 3.4 for the study areas.

Results

The common seabird species found in the Bering sea showed considerable phenological variation (Table 1), which was related to differences in flight capacities. The alcids, with small wings and short foraging ranges (Hunt *et al.*, 1980, 1981 b, c), decreased in numbers in June (Table 1) as the birds withdrew to the breeding colonies. This pattern was seen in 4 common alcids in the study area – *Uria lomvia, Aethia pusilla, A. cristatella*, and *Cyclorrhynchus psittacula*.

The remaining species belong to the Procellariidae (tube-noses) and Laridae (gulls), families with well developed capacities for gliding and soaring. These species, with long foraging ranges, increased in density during the summer (Table 1). Two of the procellariids (*Puffinus griseus* and *P. tenuirostris*) are non-breeding species moving into the Bering Sea after breeding in Australia and New Zealand. The two other procellariids (*Fulmarus glacialis* and *Oceanodroma furcata*) and the two larids (*Rissa tridactyla* and *R. brevirostris*) move onto the shelf to breed during the summer.

Standing stock of seabirds was computed from weights shown in Table 2. Differences in standing stock of seabirds among shelf and slope regions depended on month (Fig. 2). Biomass rose sharply during the summer in the outer shelf and slope regions, while rising less sharply in the middle shelf region (Fig. 2). The sharper rise on the outer shelf was due to a seasonal influx of surface-feeding species (*Fulmarus glacialis, Oceanodroma furcata, Rissa tridactyla*, and *R. brevirostris*) after May (cf. Table 1). This influx of surface-foraging species is related to the well-developed pelagic food web on the outer shelf (Hunt and Schneider, in preparation). The pattern for subsurface foraging species was more complex. Alcids (*Uria lomvia, Aethia pusilla, A. cristatella*, and *Cyclorrhynchus psittacula*) left the middle and outer shelf regions in May (Table 1), to be replaced by shearwaters (*Puffinus griseus* and *P. tenuirostris*). The observed pattern of change in standing stock between shelf regions was due to a seasonal influx of surface-feeding species, combined with seasonal replacements of subsurface-foraging species. The middle shelf supported about half the seabird biomass found on the outer and slope regions. The average monthly biomass for the middle shelf was 11.6 kg km^{-2}, compared to 21.2 and 22.5 kg km^{-2} for the outer and slope regions, respectively (Fig. 2).

Food requirements of seabirds are not directly proportional to biomass differences because of the allometric relation between body weight and food requirements (Table 2). When the allometric factor is taken into account, food requirements were about equal for outer shelf and slope waters (Fig. 3). Food requirements were 37% lower on the middle shelf than the outer shelf (Fig. 3). This difference was due primarily to the lack of surface-feeding species on the middle shelf.

The food requirement of subsurface-foraging species was about equal in the middle and outer shelf regions, and only slightly reduced over the continental slope (Fig. 3).
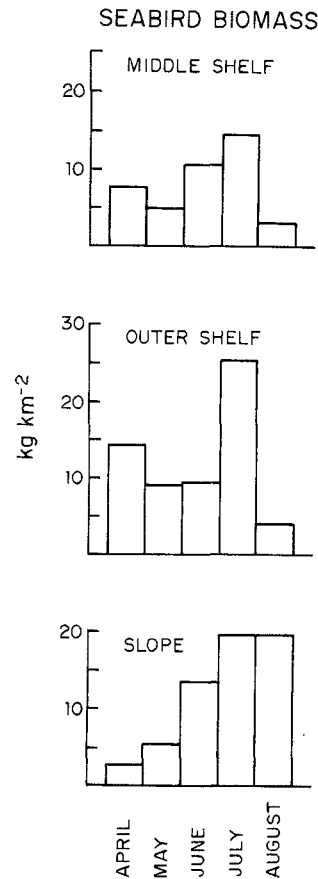
SEABIRD BIOMASS

Fig. 2. Seabird biomass in southeastern Bering Sea, averaged 1975–1979 data
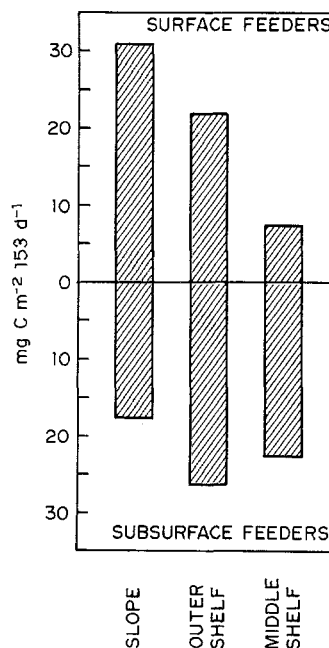

Fig. 3. Carbon flux to seabirds, for period April through August (averaged data for 1975–1979). Surface feeders were: *Fulmarus glacialis, Oceanodroma furcata, Rissa tridactyla, R. brevirostris.* Subsurface feeders were: *Puffinus griseus, P. tenuirostris, Uria lomvia, Aethia pusilla, A. cristatella, Cyclorrhynchus psittacula, Lunda cirrhata*

Table 1. Monthly bird densities (birds km^{-2}) in middle shelf (M), outer shelf (O), and slope (S) waters of southeastern Bering Sea, based on counts made from 1975 through 1979. Occupancy is in bird-days km^{-2} ± (m) (s^2 DF^{-1}), where m is average days mo^{-1} (30.6), s^2 is the within-group (month) variance, and DF is the associated degrees of freedom (sample size minus 1)

Species and region	Density during:					Occupancy
	April	May	June	July	August	
Procellariids						
Fulmarus glacialis[a]						
M	0.37	0.99	3.53	3.27	3.27[b]	349± 5
O	1.27	2.91	4.69	15.95	2.8	851±36
S	0.97	3.24	11.99	8.29[d]		1 004±30
Oceanodroma furcata						
M	0.023	0.351	2.02	4.03	0[c]	197± 9
O	0.012	2.08	6.15	22.97	0.0	961±39
S	0.31	6.63	13.38	0.06[d]		620±65
Puffinus griseus and *P. tenuirostris*						
M	0.01	3.70	8.86	15.70	0[c]	897±26
O	0.0	3.32	3.00	12.98	0.62	615±46
S	0.0	0.0	0.99	9.12[d]		595±21
Larids						
Rissa tridactyla						
M	1.04	0.48	1.30	0.0	0.0[b]	85± 4
O	1.08	2.27	1.35	1.87	3.00	294± 5
S	0.73	1.04	2.90	2.71[d]		255± 8
Rissa brevirostris						
M	0.04	0.02	0.16	0.13	0.13[b]	14± 1
O	0.02	0.74	0.49	1.87	0.53	113± 3
S	0.0	1.53	2.20	10.79[d]		782±21
Alcids						
Uria lomvia						
M	6.20	1.30	0.75	0.26	0.26[b]	265±16
O	12.49	2.83	2.03	0.53	0.13	544±21
S	1.46	1.40	1.65	1.28[d]		216±10
Aethia pusilla						
M	0.84	0.05	0.03	0.0	0.0[b]	28± 3
O	0.46	0.20	0.06	0.0	0.0	22± 2
S	0.14	0.12	0.15	0[d]		12± 2
Aethia cristatella and *Cyclorrhynchus psittacula*						
M	0.26	0.06	0.0	0.0	0.0[b]	10± 1
O	0.22	0.01	0.0	0.8	0.0	9± 1
S	0.0	0.0	0.0	0.47[d]		29± 8
Lunda cirrhata						
M	0.06	0.05	0.45	1.06	0[c]	50± 1
O	0.08	0.16	0.95	2.81	0.0	123± 2
S	0.07	0.54	0.65	1.08[d]		1± 3
Sample sizes						
M	177	78	132	8	0	
O	169	90	180	52	6	
S	24	24	32	9		

[a] All values reduced by a factor of 3.4 to account for ship attraction
[b] Assigned same value as July, based on phenology in outer domain
[c] Assigned value of zero, based on phenology in outer domain
[d] Averaged over 2 mo period

Table 2. Weights and food requirements of common seabird species in southeastern Bering Sea. Average weights for each species are to nearest 5 g, with sample sizes in parentheses. Food requirements = 2.5 × standard metabolic rate (see "Materials and Methods")

Species	Weight (g)	Feeding behavior	Food requirements (kcal d^{-1})
Procellariids			
Fulmarus glacialis (northern fulmar)	650 (8)[a]	Surface	143
Oceanodroma furcata (fork-tailed storm petrel)	65 (6)[a]	Surface	27
Puffinus griseus and *P. tenuirostris* (shearwaters)	710[c]	Subsurface	153
Larids			
Rissa tridactyla (red-legged kittiwake)	455 (164)[b]	Surface	111
Rissa brevirostris (black-legged kittiwake)	390 (49)[b]	Surface	99
Alcids			
Uria lomvia (thick-billed murre)	1 095 (167)[b]	Subsurface	209
Aethia pusilla (least auklet)	90 (120)[b]	Subsurface	34
Aethia cristatella (crested auklet)	289[c]	Subsurface	78
Cyclorrhynchus psittacula (parakeet auklet)	289[c]	Subsurface	78
Lunda cirrhata (tufted puffin)	770 (26)[b]	Subsurface	162

[a] Birds collected at sea in 1980
[b] Birds collected on Pribiloff breeding colonies 1975–1978
[c] Weighted average based on Table 13 of Hunt *et al.* (1980)

Thus, the waters over middle and outer shelf differed more in the pathways of energy transfer than in aggregate energy transfer to seabirds. The reduced carbon flux to zooplankton in waters over the middle shelf was associated with reduced energy transfer to surface-feeding birds. There was no replacement of subsurface-foraging birds by surface-foraging birds in the outer shelf domain. Substantial carbon flux to seabirds occurred over the middle shelf region, despite a considerable transfer of carbon to benthic food webs.

Discussion

The differences we found in food requirements between one region and the next are independent of the formula used to compute food requirements. For seabirds, at least four techniques are available (Table 3). The most frequently used method for seabirds (Wiens and Scott, 1975) gave values that were 20% higher than ours (Table 3). A more recent method, using weight losses in starved seabirds (Jouventin and Mougin, 1981), gave values that were 60% higher than ours. Two other techniques ("daily energy budget" of Kendeigh *et al.,* 1977, with interpolation to 5 °C; and "daily energy expenditure" of King, 1974) also

gave values higher than ours. Such alternative methods, when applied to our data, produced higher values, although the differences among regions remained the same on a proportional basis, giving equal rates for the outer shelf and slope and a 36 to 40% reduction in rate for the middle shelf (Table 3).

Our estimates of aggregate trophic transfer to seabirds must be considered minimum values. The estimates presented here do not include energy transfer to young or eggs, since there was no way to distinguish breeding and non-breeding birds at sea. The estimates were also limited to a period of 153 d during the summer. Food transfer between September and March must amount to some appreciable fraction of the summer consumption by seabirds. Several species (*Fulmarus glacialis, Puffinus griseus, P. tenuirostris*) remain abundant into October. Large gulls (*Larus glaucescens*) were abundant along the outer shelf in October, 1980, and may move offshore in the fall.

The standard conversion factor of 78.3 kcal kg^{-1} d^{-1} (Lasiewski and Dawson, 1967) may be low for high-latitude seabirds, based on the fact that high-latitude species tend to fall above rather than below expected values. For *Uria lomvia* the observed metabolic rate was 159 kcal d^{-1}, (Johnson and West, 1975) compared to the expected value

Table 3. Comparison of available methods for computing food requirements of seabirds on middle shelf (M), outer shelf (O), and slope (S) waters of southeastern Bering Sea. Values are mg C m^{-2} for the 153 d season

Method	Region			Ratio
	Middle	Outer	Slope	M : O : S
2.5 Standard metabolic rate (present study)	30.2	48.1	48.9	1 : 1.6 : 1.6
Starvation (Jouventin and Mougin, 1981)	48.5	83.0	78.5	1 : 1.7 : 1.6
1.4 existence metabolism (Wiens and Scott, 1975)	36.5	58.7	57.6	1 : 1.6 : 1.6
Daily energy expenditure (King, 1974)	49.5	77.3	74.6	1 : 1.6 : 1.5
Daily energy budget (Kendeigh et al., 1977)	39.1	63.1	62.1	1 : 1.6 : 1.6

of 83.6 kcal d^{-1} (Lasiewski and Dawson, 1967). The observed metabolic rate of *Oceanodroma furcata* was 16 kcal d^{-1} (Iversen and Krog, 1972), compared to the expected value of 10.9 kcal d^{-1}.

Evidence from seabirds in captivity also suggests that the values we report are closer to minimum values than to average values. Food consumption by a captive murre (*Uria aalge*), with minimum effort expended for foraging, was 28% of its body wt d^{-1} (Sanford and Harris, 1967). The allometric value, using a conversion of 2.5 times basal rate, is 35% of body wt d^{-1}. A conversion factor of 2.5 times basal rate would appear to be the minimum for active, unrestrained birds. Ebbinge et al. (1975) summarized studies indicating that wild birds require energy at 2 to 4 times basal rates in order to move and feed. For seabirds, Jouventin and Mougin (1981) reported weight losses that amounted, on a caloric basis, to 4 times basal costs, assuming no water losses during their measurements.

The lack of any independently verified estimate of daily food consumption by a bird at sea is the most serious limitation on our estimates of carbon flux at sea. One solution to this problem may lie in examining digestion rates and the proportion of recently fed birds out of a large collection made at sea, a modification of the technique used by Bajkov (1935) for fish, and applied to breeding seabirds by Uspenski (1956) and Belopol'skii (1957).

It is instructive to compare estimates of trophic transfer obtained in this study with those previously calculated for this and other areas. A value of 50 mg C m^{-2} for the 153 d season was taken as the lower limit for carbon flux to birds on the outer shelf. This was converted to grams (wet weight) of food (0.5 g food m^{-2} for the 153 d season) for comparison to other studies. Results of other studies were similarly converted, using literature values listed in the "Materials and Methods" section. Favorite et al. (1977) used a trophic transfer of 2.5 g food m^{-2} yr^{-1} to birds in their model for the entire southeastern Bering Sea; Hunt et al. (1981 a) estimated the rate to be 0.7 to 1.4 g food m^{-2}

yr^{-1} over the same area. These two estimates included shallow coastal waters (50 m or less), which support large aggregations of shearwaters not found in the present study area. For the area around a breeding colony at a similar latitude in the North Sea, Furness (1978) obtained a value of 1.9 g food m^{-2} yr^{-1}. These values are rather similar when compared to values from non-shelf ecosystems. For the eastern north Pacific Ocean, Sanger (1972) obtained a value of 0.09 g food m^{-2} yr^{-1}. For the upwelling system off the Oregon coast (USA), Wiens and Scott (1975) obtained values of 8 g m^{-2} yr^{-1}. For the Peruvian Upwelling, Schaeffer (1970) reported values ranging from 11 to 45 g m^{-2} yr^{-1}, depending on the year.

For the Bering Sea, we compared seabird food requirements to primary production, under the assumption of limited carbon transfer between mixing regimes. Minimum carbon flux to birds during summer, away from breeding colonies, was 0.03% of primary production over the middle shelf, and 0.05% over the outer shelf and slope waters. Annual carbon flux to birds will be higher, since some species remain on the shelf until November, and other species move into the area during the winter. Carbon flux to birds in the vicinity (less than 100 km) of the Pribilof breeding colonies is at least an order a magnitude higher, based on bird densities around these colonies (Hunt et al., 1980).

Comparison with a more familiar marine organism, a commercially important fish, may perhaps provide some sense of scale. The walleye pollock *Theragra chalcogramma* supports a major fishery on the outer shelf of the southeastern Bering Sea. Juvenile pollock (2 to 20 cm) are a major prey item for birds in this area (Hunt et al., 1981 a), while adult pollock (20 to 60 cm) have roughly the same mass as birds (0.06 to 1.5 kg) and take some of the same prey (Smith, 1981). Consumption of pollock by birds has been estimated at 1.5×10^5 metric tons yr^{-1} (Hunt et al., 1981 a). Commercial catch of pollock in the Bering Sea ranged from 1.7×10^5 t yr^{-1} in 1964 to 18.7×10^5 t yr^{-1} in 1972 (Smith, 1981).

Seabirds, because they are ubiquitous and easily measured apex predators, are valuable for examining the transfer efficiency of marine food webs. For regions of similar primary productivity, such as the North Sea and the southeastern Bering Sea (Coachman and Walsh, 1981), one would predict similar standing stocks of seabirds with similar food requirements, unless transfer efficiency were much greater in one ecosystem than the other. Seabirds should prove to be useful in examining mechanisms contributing to high transfer efficiency, as well as in identifying areas with high transfer efficiency.

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