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Journal

Continental Shelf Research, 5(1-2)

ISSN

0278-4343

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Publication Date

1986

DOI

10.1016/0278-4343(86)90017-8

Peer reviewed

Mass and energy transfer to seabirds in the southeastern Bering Sea

DAVID C. SCHNEIDER,*† GEORGE L. HUNT, JR.* and NANCY M. HARRISON*

Abstract—It has been hypothesized that differentiation in food web structure occurs across the Bering Sea continental shelf as a result of seasonal differentiation of water masses. We tested this idea using an apex predator, pelagic birds. Seasonal abundance of birds in central Bristol Bay was estimated from counts made while underway between hydrographic stations. Prey and body mass were determined from birds collected at sea. Daily intake was estimated as an allometric function of body mass. Annual occupancy was estimated as the integral of a normal curve fit to seasonal data. Estimated carbon flux to seabirds in the middle domain was 0.12 gC m^{-2} y^{-1} in 1980, 0.18 gC m^{-2} y^{-1} in 1981. Carbon flux to seabirds in the adjacent waters of the outer shelf domain was 1.8 times higher than in the middle domain in 1980, 1.6 times higher in 1981. Carbon flux to seabirds in the inner domain was 1.2 times higher than in the middle domain in 1980, and 3.3 times higher in 1981. Carbon flux to seabirds in the outer domain was due primarily to non-diving species, principally northern fulmars (*Fulmarus glacialis*) during the summer and autumn, and *Larus* gulls in the autumn and winter. Flux to seabirds in the inner domain was due to diving birds, principally murres (*Uria* sp.) in the spring and shearwaters (*Puffinus* sp.) during the summer. The euphausiid *Thysanoessa raschii* was the primary food source of shearwaters in shallow waters of the inner shelf domain. A more diverse set of prey, including squid, jellyfish, hyperiids, and fish, was taken by shearwaters and fulmars in the deeper waters of the outer and middle shelf domains. This result suggests that prey diversity is higher in seasonally stratified waters of outer Bristol Bay than in mixed waters of inner Bristol Bay. Greater energy flux to diving species in shallow water, and greater energy flux to non-divers in deep water may be a function of topographic control of prey patchiness.

INTRODUCTION

MULTIDISCIPLINARY studies of marine ecosystems have emphasized lower trophic levels and relatively small organisms, in part because of the technical difficulties of measuring the abundance and food requirements of most large marine predators. For a number of reasons birds are a convenient group for testing hypotheses concerning the role of apex predators in pelagic ecosystems. First, bird abundance can be quantified readily using underway censuses. Second, energy intake can be modeled at the species rather than the individual level, because growth is determinate. Third, adult mortality is on the order of 10% y^{-1} (LACK, 1954, 1966), and thus seasonal change in density can be modeled as a single process of population movement (PRESTON, 1966), rather than as the joint outcome of movement, birth and death. Finally, a considerable amount of information on the behavior, energetics, and demography of marine birds already exists. By taking advantage of these circumstances, we have used

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seabirds to test hypotheses about pathways of mass and energy transfer in the southeastern Bering Sea in conjunction with PROBES. The hypothesis that we address here is that in the southeastern Bering Sea, mass and energy transfer to seabirds is a function of the differentiated water masses that form over this relatively wide continental shelf.

Prior to 1978 our knowledge of seabird biomass and food intake in the Bering Sea was limited to colony studies. Energy flux to the largest breeding colony in the southeastern Bering Sea, at the Pribilof Islands, was estimated at 6.5×10^{10} kcal during the 3-month breeding season (WIENS *et al.*, 1978). The most important prey brought to chicks by parents was walleye pollock (*Theragra chalcogramma*), especially fish from the previous year class (HUNT *et al.*, 1981a). This suggested that seabirds might be a major consumer of pollock during mid-summer and might serve as a biological tracer of juvenile pollock populations. Studies prior to 1978 indicated that seabirds might forage in substantial numbers over the Bering Sea shelf. For example, SHUNTOV (1972) estimated densities of 20 birds km^{-2} over the eastern Bering Sea shelf in May to June, and densities of 18 birds km^{-2} in July to August, and WAHL (1978) reported a density of 15 birds km^{-2} in the vicinity of the Pribilof Islands in June to July 1975. IRVING *et al.* (1970) reported feeding activity at the ice edge in March 1968.

Censuses conducted on PROBES cruises during spring and summer of 1978 and 1979 established that known consumers of pollock at the Pribilof Islands, including thick-billed murres (*Uria lomvia*), black-legged kittiwakes (*Rissa tridactyla*) and red-legged kittiwakes (*R. brevirostris*) were not the most frequently encountered seabird species in central Bristol Bay away from island or mainland colonies. Instead, the most frequently encountered species were dark-phase northern fulmar (*Fulmarus glacialis*), fork-tailed storm petrels (*Oceanodroma furcata*) and dark-bellied shearwaters, either sooty shearwaters (*Puffinus griseus*) or slender-billed shearwaters (*P. tenuirostris*). Slender-billed shearwaters were known to consume euphausiids on their breeding grounds in Australia (SERVENTY *et al.*, 1971), but little was known about the diets of shearwaters, fulmars, and petrels in the Bering Sea (HUNT *et al.*, 1981a).

The presence of a large number of non-breeding shearwaters, and the distance to the nearest breeding colonies of storm petrels and dark-phase fulmars (HUNT *et al.*, 1981c), suggested that the distribution of birds in central Bristol Bay was not a function of distance to land and hence that birds might be used to investigate the cross-shelf differentiation in food web structure hypothesized during the latter stages of PROBES. Specifically, we hypothesized that failure of pelagic copepods to capture the spring bloom over the middle shelf (IVERSON *et al.*, 1979; COONEY, 1981) would result in reduced carbon flux to seabirds there, relative to the outer shelf domain. Using 1975 to 1979 data, we found that the total flux to seabirds was reduced in the middle domain relative to the outer domain, and that this was due primarily to a reduction in flux to surface foraging species (SCHNEIDER and HUNT, 1982). These early data were too limited to determine (1) annual carbon flux to seabirds; (2) carbon flux inshore of the inner front; (3) localization of activity within domains; or (4) the food resources of seabirds away from colonies. We therefore made a more intensive investigation of seabird numbers, biomass, prey taken, and carbon flux, in Bristol Bay during 1980, 1981, and 1982 (Fig. 1).

METHODS

Spatial variation in seabird abundance was measured during 6 cruises in 1980 and 8 cruises in 1981 (Table 1). One cruise in 1982 was used primarily to collect birds for stomach samples.
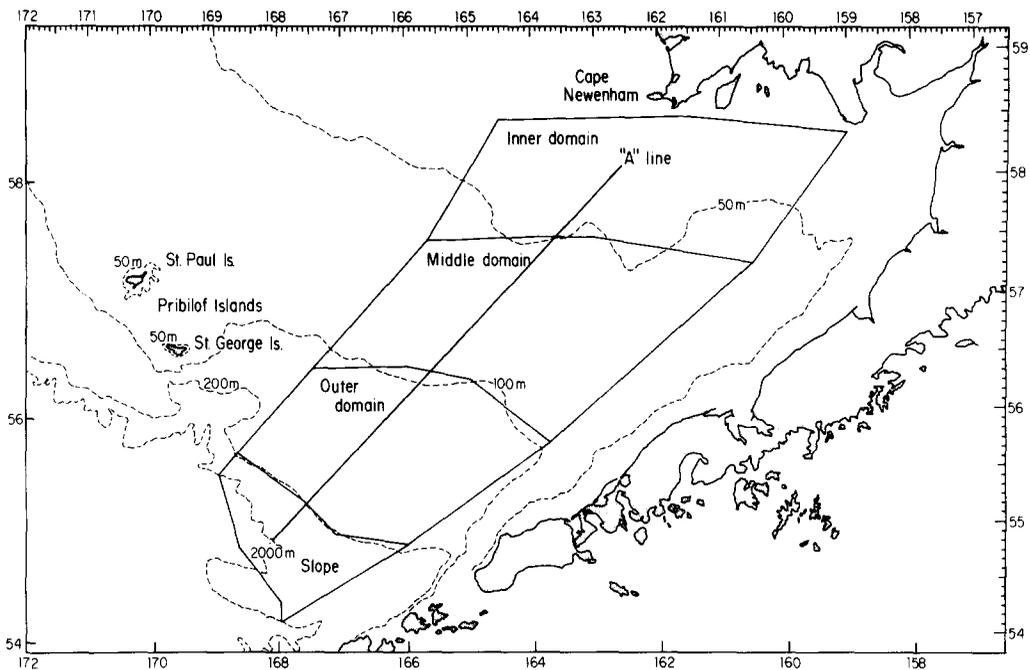
Fig. 1.   Areas used to classify bird counts by domain, central Bristol Bay.

Table 1.   Number of 10 min seabird counts and number of birds collected during cruises in Bristol Bay, 1980 to 1982

Year	Count dates	Ship (Cruise No.)	No. of counts	No. of birds collected
1980				
1.	18 March–3 April	T. G. Thompson (TT 149–1)	174	0
2.	5–23 April	T. G. Thompson (TT 149–2)	129	0
3.	26 April–19 May	T. G. Thompson (TT 149–3)	311	3
4.	21 May–12 June	T. G. Thompson (TT 149–4)	309	27
5.	16 Aug.–5 Sept.	Surveyor	441	0
6.	3–25 Oct.	Alpha Helix (HX 009)	281	0
1981				
1.	29 Jan.–17 Feb.	Surveyor	280	0
2.	11–27 April	T. G. Thompson (TT 159–1)	350	5
3.	29 April–25 May	T. G. Thompson (TT 159–2)	367	72
4.	23 May–2 June	Discoverer	468	0
5.	31 May–24 June	T. G. Thompson (TT 159–3)	452	43
6.	11–13 June	Alpha Helix (HX 014)	63	0
7.	24 June–3 July	Alpha Helix (HX 015)	393	2
8.	28 June–21 July	T.G. Thompson (TT 159–4)	598	70
1982				
1.	26 July–8 Aug.	Alpha Helix (HX 031)	183	231

Seabird abundance was estimated using a modified line transect technique (BURNHAM et al., 1980). Bird numbers were recorded nearly continuously while underway between hydrographic stations, which were typically spaced at 25 km intervals along straight cruise tracks. All birds within 300 m of the ship were counted, using a 90° arc extending directly forward and directly abeam on the side of the ship with the best visibility. Latitude and longitude were

recorded at the start and the end of each 10 min count, and environmental data (weather, sea state, visibility) were recorded at the start. Ship-following birds were noted and excluded from subsequent counts. We estimated density by dividing the number of each species recorded during 10 min by the area scanned during that period. The area scanned during 10 min varied, but at typical ship speeds a distance of 3 km was traversed and an area of 1 km^2 was scanned. Average abundance of numerically important species was computed in slope, outer shelf, middle shelf, and inner shelf regions of Bristol Bay (Fig. 1) using the coordinates listed in the Appendix. These coordinates include counts made along the PROBES "A", "B", and "D" lines, as well as counts made between lines. Counts made outside these boundaries (Fig. 1) were not included in computations.

Birds were collected for stomach analysis during 8 cruises (Table 1). During 1980 and 1981 birds were collected from a skiff while the ship was at a station, engaged in other activities. Birds were collected with a 12-gauge shotgun and tagged. Alcohol was injected down the throat to retard digestion. Birds were returned to the ship, stored in a freezer, and kept frozen until opened for examination in the laboratory.

During 1982 birds were collected whenever a large aggregation was encounted along the ship's track, which included the main PROBES line and a diversion to the Pribilof Islands. All birds were opened within an hour of collection and the contents of the crop and gizzard were placed in 80% alcohol in sealed plastic bags. Carcasses were frozen for shipment to museums.

Stomach contents were identified to the lowest possible taxonomic level using available taxonomic keys and a reference collection at the University of California at Irvine. The number of individuals of each prey group was recorded. No attempt was made to estimate the size of prey at ingestion. Percent occurrence of each prey group was computed within slope, outer, middle, and inner regions of Bristol Bay within each year.

Analysis was limited to the most frequently encountered bird genera in central Bristol Bay: northern fulmars (*F. glacialis*), fork-tailed storm petrels (*O. furcata*), shearwaters (primarily *P. tenuirostris*), *Larus* gulls (primarily *L. glaucescens*), kittiwakes (*R. tridactyla* and *R. brevirostris*), common and thick-billed murres (*Uria aalge* and *U. lomvia*), and tufted puffins (*Lunda cirrhata*). Genera were used because not all murres, shearwaters, and juvenile gulls could be identified to species. These 7 genera accounted for 81% of the birds encountered during a winter cruise in January 1981, and at least 90% of the birds encountered on all other cruises listed in Table 1.

An allometric model was used to estimate daily individual energy intake:

$$E_i = a\,b\,c\,M_i^{0.723}.$$

E_i is daily energy flux to individual of genus i (kcal bird^{-1} day^{-1}); $a = 1.33$ kcal ingested kcal^{-1} assimilated (COOPER, 1978); $b = 2.8$ kcal active kcal^{-1} at rest (KOOYMAN *et al.*, 1982); $c = 78.3$ kcal day^{-1} kg$^{-0.723}$ at rest (LASIEWSKI and DAWSON, 1967); and M_i is the average individual body mass (kg) of genus i. To include birds identified only to genus in the computations, E_i was estimated using the average mass of individuals of genus i collected in Bristol Bay. This procedure assumes that collection of birds was not biased toward large or small individuals.

Occupancy (days km^{-2} y^{-1}) was estimated from the functional relation between date and numbers developed by PRESTON (1966). Preston's function is based on three parameters, the mean annual date $\bar{x}$, the standard deviation around this date ($\tilde{x}$), and the maximum annual

density, D_{max}. Occupancy is then the integral of the normal curve, which is equal to:

$$0_i = \tilde{x} \, D_{max} \, \sqrt{2\pi}.$$

Mean dates, standard deviations, and maximum counts were determined for each of the 7 groups, in each domain, during the 1980 and 1981 seasons. The mid-point of each cruise was assigned a Julian date—1980 season (1 March 1980 = 61, 28 February 1981 = 425); 1981 season (1 September 1980 = 245, 31 August 1981 = 610). Note that data gathered between 1 September 1980 and 28 February 1981 were used for computations for both years due to the limited availability of autumn and winter crusies. Mean dates and standard deviations were computed by using D_{ij}, the number of individuals of genus i seen during cruise j, as a weighting factor. The procedure is the same as that used to compute a mean and a standard deviation from a frequency distribution, rather than from non-aggregated area. D_{max} was the maximum value of D_{ij} in each year. The accuracy of the model was checked by computing occupancy as the product of density and time elapsed between cruises, and summing these products over all cruises in a year: $0'_i = \Sigma w_j D_{ij}$; $0'_i$ is the occupancy by genus i (days km^{-2} y^{-1}); D_{ij} is the number of birds seen on cruise j, divided by the area scanned; and w_j is the number of days elapsed since the last cruise, plus the number of days until the next cruise, divided by 2.

The sum of the weights, Σw_j, over a year is 365 days. This procedure is equivalent to measuring the area of a histogram constructed from seasonal data (WINBERG, 1971). Estimates of occupancy from the seasonal model (0_i) were then regressed against occupancy computed as a sum of products ($0'_i$).

The annual energy flux to genus i was the product of 0_i and E_i. Aggregate energy flux was the sum of energy flux over 7 genera. Conversion factors of 5 kcal g^{-1}dry (NISHIYAMA, 1977; COOPER, 1978) and 0.4 gC g^{-1} dry (CURL, 1962) were used to convert energy transfer to mass transfer. Biomass and energy flux was calculated for two functional groupings—non-divers (fulmars, storm petrels, and gulls) and divers (murres and shearwaters).

RESULTS

During 1980 and 1981 strong cross-shelf patterns in abundance were observed in three surface foraging species—northern fulmar, fork-tailed storm petrel, and red-legged kittiwake. The maximum density of these species was greater over the deep water of the outer shelf domain than over shallower water of the middle and inner shelf domains (Table 2). Large gulls (*Larus* spp.), another surface foraging group, were also more abundant over the outer and slope domains than over shallower water. Cross-shelf variation was weak or absent in one surface foraging species, the black-legged kittiwake (Table 2). Cross-shelf variation was strong in two subsurface foraging groups, murres and shearwaters. These birds were more abundant over the mixed waters of the inner domain than over the stratified waters of the middle and outer domains. Cross-shelf variation was weak or absent in a less abundant subsurface forager, the tufted puffin.

Comparison of mean dates of occupancy in 1980 and 1981 did not show any trend toward earlier occupancy in one year relative to the other year (Table 2). Mean dates ranged from spring (murres) to autumn (*Larus* gulls), with mean dates of most species occurring during the summer (Julian dates 180 to 270). Comparison of standard deviations around mean date of

Table 2.   *Seasonal abundance of seabirds, by domain, southeastern Bering Sea*

	1980				1981			
	$\bar{X}$	$\tilde{X}$	D	O	$\bar{X}$	$\tilde{X}$	D	O
Non-divers								
Northern fulmar, *Fulmarus glacialis*								
slope	230	68.5	19.5	3348	212	57	20.6	2943
outer	229	66	19.6	3243	201	38	100	9525
middle	224	52	12.1	1577	187	43	15.3	1649
inner		0	0.09	0	146	34	2.3	196
Fork-tailed storm petrel, *Oceanodroma furcata*								
slope	203	60	1.8	271	179	19	4.4	210
outer	186	51	2.3	294	179	17	14.6	622
middle	237	24	2.0	120	170	35	1.4	123
inner		0	0.0	0		0	0.03	0
Large gulls, *Larus* spp.								
slope	263	74	19.8	3673	284	49	19.8	2432
outer	264	126	5.0	1579	315	96	5.0	1203
middle	190	137	1.5	515	251	148	1.2	445
inner		0	0.4	0	192	235	0.4	236
Red-legged kittiwakes, *Rissa brevirostris*								
slope	138	120	1.00	301	179	69	0.90	156
outer		0	0.14	0		0	0.31	0
middle		0	0.09	0		0	0.09	0
inner		0	0.32	0		0	0.32	0
Black-legged kittiwakes, *R. tridactyla*								
slope	134	133	0.98	327	182	67	2.4	403
outer	109	52	2.1	274	162	72	0.94	170
middle	119	86	1.1	237	144	66	0.88	146
inner		0	0.39	0	177	53	3.1	412
All kittiwakes, *Rissa* spp.								
slope	228	78	6.1	1193	230	74	6.1	1131
outer	209	76	6.8	1295	205	89	1.8	402
middle	194	76	3.1	591	160	70	1.3	228
inner	240	40	5.9	592	196	66	3.1	513
Divers								
Dark-bellied shearwaters, *Puffinus* spp.								
slope	216	48.8	2.5	306	162	32	7.6	610
outer	199	62	19.0	2953	194	55	16.0	2206
middle	252	37	17.4	1614	190	47	56.8	6692
inner	237	8	39.1	784	182	14	902	31654
Murres, *Uria* spp.								
slope	185	144	2.8	1011	185	90	3.6	818
outer	137	86	6.3	1358	166	73	5.6	1025
middle	158	87	6.1	1330	194	101	1.3	329
inner	105	11	178.4	4919	157	42	12.6	1327
Tufted puffin, *Lunda cirrhata*								
slope	249	72	2.0	361	184	77	1.3	251
outer	250	67	1.9	319	183	60	2.3	346
middle	257	44	2.9	320	255	86	1.5	323
inner	226	46	2.2	254		0	0.27	0

$\bar{X}$ is mean date (days from 1 January). $\tilde{X}$ is 1 S.D. (days). D is maximum density (birds km^{-2}). Occupancy $(O) = \tilde{X}D\sqrt{2\pi} =$ bird-days km^{-2} y^{-1} (see text). Occupancy in 1980 based on the following number of 10 min counts: slope (135), outer (374), middle (392), inner (79). In 1981: slope (234), outer (783), middle (796), inner (148).

occupancy did not show any trend toward more extended occupancy in one year relative to the other. The inner domain was occupied for relatively brief periods by large concentrations of shearwaters or murres. The outer domain was occupied for longer periods by lower concentrations of fulmars, large gulls, and storm petrels. In all four regions, peak occupancy occurred well after the spring plankton bloom.

Parametrically derived estimates of annual occupancy (Table 2) were in reasonable agreement with empirically derived estimates. Model estimates explained 79% of the variation in the empirical estimates. The slope of the regression line was 1.033, close to the expected value of unity. The largest discrepancy between model and empirically derived estimates occurred for shearwaters in the inner domain in 1981, with an empirical value that was twice that of the parametrically derived value. Thus, the largest model estimate was conservative with respect to the largest empirical estimate.

Occupancy in excess of 3000 bird-days $km^{-2} y^{-1}$ was observed in only a few species in a few regions of the shelf. Occupancy of the outer shelf and slope waters by fulmars regularly exceeded this value; large values were also observed in *Larus* gulls in deep water in the autumn, and by shearwaters and murres inside the 50 m isobath (Table 2).

Mass-specific occupancy (g-day $m^{-2} y^{-1}$) was estimated as the product of individual occupancy (Table 2) and average individual mass (Table 3), summed over 7 genera. Mass-specific occupancy (Table 4) was highest in the inner domain, and lowest in the middle domain. Mass-specific occupancy was similar in the outer and slope domains. During 1980,

Table 3.   *Average mass of birds collected in the southeastern Bering Sea in 1981. Values are grams per bird*

	Mean	Standard deviation	Number weighed
Non-diving species			
Fulmarus glacialis	704	105	38
Oceanodroma furcata	65	7	19
Larus glaucescens	1501	114	6
Rissa brevirostris	405	60	4
Rissa tridactyla	420	26	6
Diving species			
Puffinus tenirostris	646	56	21
Uria lomvia	1105	91	6
Uria aalge	999	8	2
Lunda cirrhata	883	5	2

Table 4.   *Mass-specific occupancy by seabirds in central Bristol Bay, 1980 and 1981*

Domain	1980		1981	
	Non-diving species	Diving species	Non-diving species	Diving species
Slope	8.4	1.6	6.2	1.5
Outer	5.2	3.7	8.7	2.8
Middle	2.1	2.8	1.9	5.0
Inner	0.24	5.7	0.71	21.9

Values are g-day $m^{-2} y^{-1}$, computed from data in Tables 2 and 3. Divide by 365 to obtain average daily standing stock.

Table 5. Energy flux to seabirds, central Bristol Bay. Values are Kcal m^{-2} y^{-1} × 10^3

	Slope		Outer		Middle		Inner	
	1980	1981	1980	1981	1980	1981	1980	1981
Non-diving species								
F. glacialis	759	667	736	2160	358	374	0	44
O. furcata	11	9	12	25	5	5	0	0
Larus spp.	1440	954	619	472	202	174	0	93
Rissa spp.	185	175	200	62	91	35	92	7?
Diving species								
Puffinus sp.	65	130	629	470	344	1426	167	6747
Uria spp.	312	253	419	317	411	102	1519	419
L. cirrhata	96	67	85	92	85	86	68	0
Total (Kcal m^{-2} y^{-1})	2.9	2.3	2.7	3.6	1.5	2.2	1.8	7.3
Total (gC m^{-2} y^{-1})	0.23	0.18	0.22	0.28	0.12	0.18	0.15	0.59

and again in 1981, the slope and outer domains supported a greater biomass of non-divers than divers. During 1980 and 1981 the middle and inner domains supported a greater biomass of divers than non-divers.

A few species accounted for most of the flux to birds. Large gulls (primarily *Larus glaucescens*) made the greatest contribution in slope waters—50% of the flux in 1980, and 42% in 1981 (Table 5). Fulmars made the greatest contribution in the outer domain—27% in 1980 and 60% in 1981. During 1980, murres accounted for 27% of the flux in the middle domain and 82% of the flux in the inner domain. In contrast, during 1981, shearwaters accounted for 65% of the flux in the middle domain, and 92% of the flux in the inner domain.

Much of the flux to seabirds in central Bristol Bay was to non-breeding populations—murres in the spring, shearwaters in the summer, and fulmars and gulls in the autumn and winter. The breeding status of fulmars in central Bristol Bay in the summers of 1980 and 1981 was not determined. Fulmars collected in the outer and middle domains in July and August of 1982 were virtually all in breeding condition, as indicated by brood patches. The majority of the fulmars were dark phase individuals, but the nearest breeding colony of any size, at the Pribilof Islands, consists primarily of light phase individuals (HUNT *et al.*, 1981b). Thus, flux to fulmars over the outer shelf during the summer was either due to breeding fulmars commuting from colonies at substantial distances from the area, or it was due to an influx of failed breeders.

Aggregate flux to divers and non-divers, as a function of hydrographic domain, is shown in Fig. 2. Patterns of cross-shelf variation in carbon flux were similar in the 1980 and 1981 seasons. Aggregate flux in the outer domain was 1.8 times that in the middle domain in 1980, 1.6 times that in the middle domain in 1981, based on figures from Table 5. Aggregate flux in the inner domain was 1.2 times higher than flux in the middle domain in 1980, 3.3 times
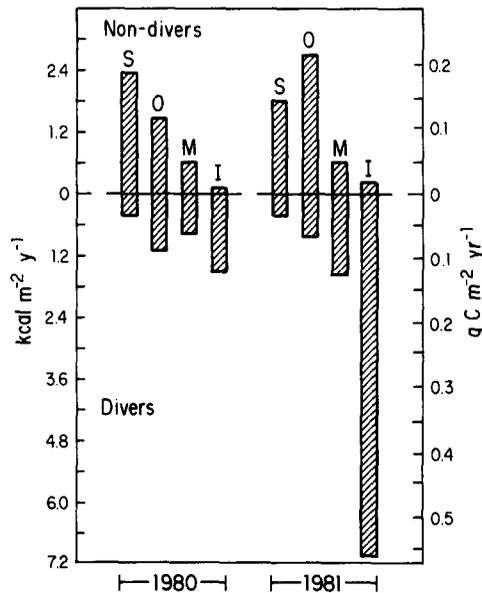
Fig. 2. Annual mass and energy transfer to seabirds in 1980 and 1981. Non-diving species are: *Fulmarus glacialis, Oceanodroma furcata, Larus* sp., *Rissa tridactyla*, and *R. brevirostris*. Diving species are: *Puffinus griseus, P. tenuirostris, Uria aalge, U. lomvia*, and *Lunda cirrhata*. S, O, M, I are slope, outer, middle, and inner domains.

higher in 1981. There was no consistent difference in flux between the outer domain and adjacent slope waters. Flux was lower in the outer domain than in the slope in 1980, higher in 1981. The greatest difference in aggregate flux between years occurred in mixed water landward of the inner front (Fig. 2).

Carbon flux to fulmars was localized near the shelf break, while flux to shearwaters was localized near the inner front. Figure 3 shows the distribution of fulmars and shearwaters along the PROBES "A" line in late July 1982. Similar patterns of localization were observed during cruises in 1980 and 1981. Carbon flux to large gulls, the third major avian consumer, was localized near the shelf break (Table 2).

Prey species taken by fulmars and shearwaters are listed, by domain, in Table 6. Fulmars captured a diverse set of prey in slope, outer, and middle shelf waters. Squid remains (mostly
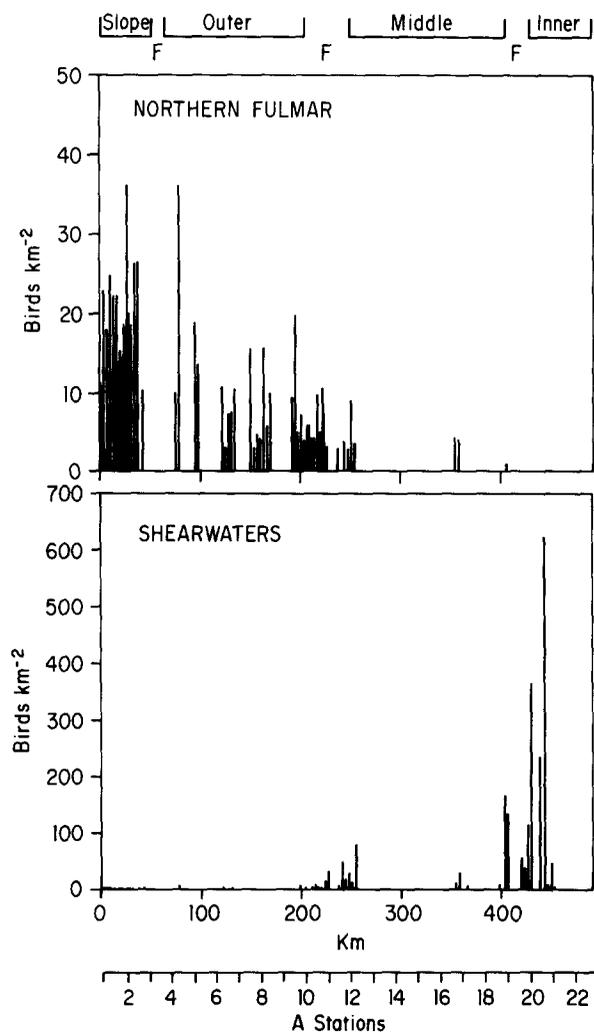
Fig. 3. Distribution of fulmars (*F. glacialis*) and dark-bellied shearwaters (*Puffinus* spp.) along PROBES "A" line, 26 to 28 July 1982. Number of birds seen during each 10 min count was divided by the area scanned during the count. Station 1A = 54° 51.1' N, 167° 53.5' W. Sta. 23A = 58° 10' N, 162° 22.5' W.

Table 6. *Prey found in stomachs of F. glacialis and P. tenuirostris, southeastern Bering Sea. Values are percent of birds with prey*

Domain (year)	Slope (1982) F. glacialis	Outer (1982) F. glacialis	Middle (1982) P. tenuirostris	Middle (1982) F. glacialis	Inner (1982) P. tenirostris	Inner (1981) P. tenuirostris
Number of birds	9	61	17	32	7	22
Fish		30	29	25		
Myctophid	56	3				
Gadid		2	24	3		
Squid	100	97	29	94		5
Nereids		8				
Jelly fish		44	29	34		
Crustacean	22	28	24	25		9
Copepods	22				29	5
Hyperiids			19			
Gammarideans	33	31	6			
Mysids		7				
Crab Larvae		5	12			
Euphausids		2	18		29	14
Thysanoessa raschii		5	29		71	68

beaks) were found in nearly all fulmars collected in slope waters, and in a smaller proportion of the fulmars collected in shallower water (Table 6). Hyperiids were a regular component of fulmar diets in deep water. William Hamner (University of California, Los Angeles, CA) identified some of these hyperiids as species commensal on jellyfish, which also occurred regularly in fulmar stomachs. During August 1982, predation on jellyfish was most noticeable during the extended twilight when jellyfish became visible near the surface. Fish were also a regular component of fulmar diets. Fulmars are known to feed on offal from fishing vessels (FISHER, 1952), but we did not find bones from large fish, as might be expected in fulmars feeding on offal. Myctophids, a non-commercial group of species, were taken by the majority of fulmars collected in slope waters. Myctophids are mid-water fishes and like squid and jellyfish, migrate toward the sea surface at night.

The diet of shearwaters was lower in diversity than the diet of fulmars. The euphausiid *Thysanoessa raschii* was the major dietary item of shearwaters collected in the inner domain in 1981 and 1982 (Table 6). Dietary diversity of shearwaters was lower in unstratified water landward of the inner front than in stratified water seaweed of the front, due to a greater reliance on euphausiids by shearwaters in the inner domain. All shearwaters collected were slender-billed shearwaters, based on bill lengths (PALMER, 1962). Predation on *T. raschii* by *P. tenuirostris* was a major component of mass and energy transfer to seabirds away from colonies in the southeastern Bering Sea, based on the relatively brief summer occupancy of shearwaters (Table 2) and the importance of *T. raschii* during the summers of successive years (Table 6).

DISCUSSION

In our analysis of the 1975 to 1979 data from central Bristol Bay (SCHNEIDER and HUNT, 1982), we found that aggregate carbon flux to seabirds in the outer shelf domain was 1.6 times greater than flux to seabirds in the middle shelf domain during spring and early summer. In 1980 and 1981, we found similar ratios, using a 12-month rather than 5-month budget. Aggregate flux was 1.8 times higher in the outer than middle domain in 1980, 1.6 times higher in 1981. Aggregate flux to seabirds in mixed waters of the inner domain was variable, and on the whole, greater than aggregate flux in stratified waters of the middle domain. Flux in the inner domain was 1.2 times higher than in the middle domain in 1980, 3.3 times higher in 1981. Cross-shelf variation in carbon flux to birds was not related to known patterns of cross-shelf variation in primary productivity or algal standing crop.

Energy flux to non-diving birds (fulmars, gulls, and storm petrels) was greater in the seaward domains than it was in the middle or inner domains and showed a stronger pattern of energy flux with respect to domains than was true for all birds when considered together. Flux to non-divers in the outer domain was 3 times higher than flux to the same species in the middle domain, based on 1975 to 1979 data. Flux to non-diving species was 2.4 times higher in the outer than in the middle domain in 1980, 4.6 times higher in 1981. Increased flux to non-divers in deep water of the outer domain occurred in the same region where energy flux to large bodied calanoid copepods, especially *Neocalanus cristatus, N. plumchrus*, and *Eucalanus bungii* (COONEY, 1981) was greatest. Flux to non-divers occurred after the spring movement of copepods into surface waters of the outer domain (SMITH and VIDAL, 1984). The diet of fulmars during mid-summer in deep water consisted of potentially important predators on copepods, including jellyfish, myctophids, and small squid.

Energy flux to diving birds (murres and shearwaters) was greater in the shoreward domains

than in the outer and shelf edge domains. Flux to divers in the inner domain was 2.1 times higher than flux in the middle domain in 1980, 4.4 times higher than the middle domain in 1981. *T. raschii*, an important grazer in shallow water in Bristol Bay (S. SMITH, personal communication), was a major component of the diet of shearwaters in shallow water in 1980 and 1981.

Why should non-divers account for most of the flux in deep water, while divers account for most of the flux in shallow water in Bristol Bay? This difference cannot be a function of distance to breeding colonies, because much of the flux is to non-breeding birds, nor can it be solely a function of the distribution of preferred prey, because fulmars feed on a variety of prey. We hypothesize that strong topographic control of fronts (SCHUMACHER *et al.*, 1979; KINDER and COACHMAN, 1978) and eddies (BROWN, 1980) in shallow water results in horizontally predictable prey concentrations that may occur anywhere in the water column. Horizontally predictable and vertically unpredictable prey concentrations would favor divers, which can pursue prey throughout the water column. In outer shelf waters, the presence of large eddies and reduced topographic control would result in a lack of horizontally predictable prey concentrations. These circumstances would favor non-diving species with highly efficient flight mechanisms needed to locate laterally unpredictable prey concentrations of vertically migrating prey (SMITH and VIDAL, 1984). A testable prediction of this hypothesis is greater daily foraging range by birds in deep water than in shallow water. A second prediction is greater correspondence between patches of divers and their prey in shallow than in deep water. WOODBY (1984) reported non-correspondence of murre and potential prey patches in the outer domain of the southeastern Bering Sea, but did not investigate the inner domain, where we found the highest energy flux to murres.

Our estimates of carbon flux to seabirds in 1980 and 1981 were higher than our 1975 to 1979 estimates, even after multiplying the 5-month budget by 12/5 to make it comparable to the 12-month budget in 1980 and 1981. There are several reasons for this difference. First, in this paper we used a slightly higher multiple of the standard metabolic rate (2.8 rather than 2.5) based on recent work by KOOYMAN *et al.* (1982) and DAVIS *et al.* (1983). Both of these studies were with penguins, but in the Bering Sea, Daniel Roby (personal communication) found that free-living least auklets (*Aethia pusilla*) metabolized at 3 times the standard metabolic rate, so an upward adjustment is warranted. A second factor contributing to higher estimates in 1980 and 1981 is that the 5-month budget constructed from 1975 to 1979 data did not include the substantial food requirements of shearwater and gull populations after July. Mean date of occupancy of the middle domain by shearwaters in 1980 was 9 August, and in 1981, 9 July (Table 3). Mean date of occupancy of the outer domain by large gulls was 23 August 1980 (Table 3). Third, we did not attempt to correct for ship attraction by applying a constant (SCHNEIDER and HUNT, 1982). Ship attraction can vary considerably with factors such as time of day (LACOCK and SCHNEIDER, 1982). Attraction of fulmars and gulls to ships can raise the observed density of birds in the immediate vicinity of a research vessel, but may also lower the observed density near fishing fleets. Our calculations are based on the assumption that behavioral responses to ships are independent of domain and hence that our figures are valid on a relative, rather than absolute scale.

Our method of estimating occupancy did not contribute significantly to the higher estimates in 1980 to 1981, based on regression analysis. Previous estimates of energy flux to seabirds have used total population size (EVANS, 1973; HUNT *et al.*, 1981a), the sum of monthly averages (SCHNEIDER and HUNT, 1982) or demographic projections based on linear arrival and departure rates (WIENS and SCOTT, 1975; FURNESS, 1978). We had no way of

estimating arrival and departure rates, so we approximated seasonal abundance as a normal curve (PRESTON, 1966) and then integrated underneath this curve for each species in each domain.

Allometric estimates of daily intake are likely to be sensitive to small changes in an exponent, especially in massive birds. If $E = aM^b$, then $dE/da = M^b$ and $dE/db = aM^b \ln M$ ($\ln M = $ natural logarithm of M). Our estimates assume that total daily energy expenditure scales to body mass raised to a power of 0.723, comparable to other physiological rate functions. A recent review by WALSBERG (1983) suggests that this scaling may be too high. Walsberg found that daily energy expenditure was proportional to body mass raised to a power of 0.6052, below the standard physiological scalings of 0.7 or greater. However, the reported metabolic rates of free-living penguins, as measured by water turnover (KOOYMAN *et al.*, 1982; DAVIS *et al.*, 1983) are above the values predicted by Walsberg's equation; the measured rates are consistent with a scaling factor >0.7. Water turnover can overestimate metabolic rate if birds ingest appreciable quantities of seawater (KOOYMAN *et al.*, 1982), alternatively, Walsberg's scaling may be sensitive to the fact that large species are underrepresented in the set of studies used for the regression. The difference between scalings is small in birds less massive than 2 kg. For a 1.5 kg gull, the Walsberg estimate will be 90% of the estimate that we used. For a 0.7 kg fulmar the Walsberg estimate is the same as the estimate we used.

The 1980 to 1981 estimates, while higher than our previous estimate, still do not include several potentially important components of energy transfer to seabirds. First, our estimates do not include the energetic costs of producing eggs or of accumulating fat for migration, since the multiple of SMR that we used was based on birds that were not undergoing changes in mass (DAVIS *et al.*, 1983). Pre-migratory fat deposition may be substantial in shearwaters, which migrate annually from the Bering Sea to Australian breeding grounds; these migrants are not known to feed en route (SERVENTY *et al.*, 1971). Second, our estimates do not include food exported from central Bristol Bay to feed nestlings at colonies. During August 1982, virtually all of the fulmars and storm petrels collected in Bristol Bay were in breeding condition. It is not known whether these birds were returning food to chicks at the time. Third, our estimates do not include feeding by seabirds along the ice edge during the winter (IRVING *et al.*, 1970; DIVOKY, 1981). Fourth, the standard conversion factor of 78.3 kcal $kg^{-0.723}$ day^{-1} appears to be low for boreal seabirds, based on the measured SMR of *Uria lomvia* (JOHNSON and WEST, 1975). *Oceanodroma furcata* (IVERSEN and KROG, 1972), and *Larus hyperboreus* (SCHOLANDER *et al.*, 1950). We could not quantify these four factors, but we suspect that these factors, leading to underestimation of energy transfer to seabirds, are at least as important as the effects of ship attraction on counts made from research vessels not engaged in trawling.

Our analysis of seabird diets was one of the few attempted on northern seabirds collected in deep water away from breeding colonies (BÉDARD, 1969; OGI and TSUJITA, 1973; SANGER and BAIRD, 1977; SANGER, 1985). The most surprising result was the frequency of jellyfish in the diet of both fulmars and shearwaters. The importance of jellyfish in seabird diets may have gone unrecognized in previous work because of the rapid breakdown in tissue in preserved samples (HARRISON, 1984). We found that the northern fulmar, a major avian consumer in the southeastern Bering Sea, preys on a variety of planktonic and nektonic species. This diversity suggests that energy flux to the fulmar is a function of some common feature of these prey, such as vertical migration. The spatial lability that we observed in the diets of two major avian consumers, fulmars and shearwaters, suggests that pelagic birds may be useful for investigating trophic diversity and the dynamics of prey choice in marine food webs.

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APPENDIX

Coordinates used to classify seabird counts by domain

Domain	Latitude (°N)	Longitude (°W)
Inner	57° 30'	165° 40'
	58° 30'	164° 30'
	58° 30'	162° 30'
	58° 30'	161° 30'
	58° 20'	159° 0'
	57° 20'	160° 30'
	57° 30'	163° 0'
	57° 30'	164° 0'
Middle	57° 30'	165° 40'
	56° 25'	167° 30'
	56° 25'	166° 0'
	56° 18'	165° 0'
	55° 45'	163° 45'
	57° 20'	160° 30'
	57° 30'	163° 0'
	57° 30'	164° 0'
Outer	56° 25'	167° 30'
	56° 25'	166° 0'
	56° 18'	165° 0'
	55° 45'	163° 45'
	54° 50'	166° 0'
	54° 57'	167° 10'
	55° 15'	167° 40'
	55° 40'	168° 40'
Slope	55° 40'	168° 40'
	55° 15'	167° 40'
	54° 57'	167° 10'
	54° 50'	166° 0'
	54° 10'	168° 0'
	54° 20'	168° 0'
	54° 50'	168° 40'
	55° 30'	169° 0'