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Mass and Energy Transfer to Seabirds in the Southeastern Bering Sea

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## Abstract

The hypothesis that cross-shelf differentiation in food web structure results from seasonal differentiation of water masses across a wide continental shelf was tested with 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  $0.12 \text{ g-C m}^{-2} \text{ yr}^{-1}$  in 1980,  $0.18 \text{ g-C m}^{-2} \text{ yr}^{-1}$  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 surface foraging species, especially fulmars during the summer and fall, and Larus gulls in the fall and winter. Flux to seabirds in the inner domain was due to subsurface foraging birds, primarily murrelets in the spring and shearwaters during the summer. The euphausiid Thysanoessa raschii was the principal 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 fulmar 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. The replacement of surface foraging species in deep water by subsurface foraging species in shallower water may result from increased topographic control of prey patchiness in shallow water.

## 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. Birds are a convenient group for testing hypotheses concerning the role of apex predators in pelagic ecosystems for a number of reasons. First, birds can be censused readily while underway along extended transects. Second, energy intake can be modeled at the species rather than the individual level, since growth is determinate. Third, because adult mortality is on the order of  $10\% \text{ yr}^{-1}$  (Lack 1954, 1966), seasonal change in density can be modeled as a single process of periodic migration (Preston, 1966; Schneider, in press), rather than as the joint outcome of migration, birth, and death. Finally, a considerable amount of information on the behavior, energetic, and demography of marine birds already exists. By taking advantage of these circumstances, we have been able to use seabirds to test hypotheses about pathways of mass and energy transfer in the southeastern Bering Sea in conjunction with PROBES. The central hypothesis that we address is that mass and energy transfer to seabirds is a function of the system of 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 colony in the Southeastern Bering Sea, the Pribilof Islands was estimated at  $6.5 \times 10^{10}$  kcal during the 3-month breeding season (Wiens, Ford, Heinemann and Fieber, 1978). The most important prey brought to the islands was walleye pollock (Theragra chalcogramma), especially fish from the previous year class

(Hunt, Burgeson and Sanger, 1981a). This suggested that seabirds might be a major consumer of pollock, and might serve as a biological tracer of the passive migratory circuit hypothesized during the early stages of PROBES. Studies prior 1978 indicated that seabirds might be found feeding in substantial numbers away from breeding colonies. Shuntov (1972) estimated densities of 20 birds km<sup>-2</sup> over the eastern Bering Sea shelf in May-June, and densities of 18 birds km<sup>-2</sup> in July-August. Wahl (1978) found a 15 birds km<sup>-2</sup> in the vicinity of the Pribilof Islands in June-July, 1975. Irving, McRoy and Burns (1970) had reported feeding activity at the ice edge in March, 1968.

Counts during PROBES cruises in 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 (Rissa brevirostris) were not the most frequently encountered seabird species in central Bristol Bay away from island or mainland colonies. 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, Serventy and Burnham, 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 petrels and dark-phase fulmar (Hunt, Gould, Forsell and Peterson 1981c), suggested that birds away from colonies 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 over the middle shelf, relative to the outer shelf domain. Using 1975-1979 data, we found that aggregate 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 landward 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, carbon flux, and prey taken by seabirds in Bristol Bay in 1980, 1981, and 1982.

#### 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. Seabird abundance was estimated using a modified line transect technique (Burnham, Anderson and Laake, 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. Location was recorded at the start and the end of each ten minute count, and environmental data (weather, sea state, **visibility**) were recorded at the start. Ship following birds were noted and excluded from subsequent counts. Abundance was the number of each species recorded during a ten minute interval, divided by the area scanned during that interval. The

area scanned during ten minutes varied, but at typical ship speeds a distance of 3 km was traversed, and an area of one  $\text{km}^2$  was scanned. Average abundance of numerically important species was computed in slope, outer shelf, middle shelf, and inner shelf regions of Bristol Bay (Figure 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 (Figure 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, tagged, and injected with alcohol 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 encountered 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 Irvine. Skill in the identification of partially digested prey increased during the course of sorting samples, so samples examined at early stages were re-examined at a later stage. Volume and number 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 genera in central Bristol Bay--Fulmarus (1 species), Oceanodroma (1 species), Puffinus (primarily P. tenuirostris), Larus (primarily L. glaucescens), Rissa (2 species), Uris (both U. aalge and U. lomvia), and Lunda (1 species, L. cirrhata). Genera were used because not all murrelets, 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 intake:

$$E_i = a b c M_i^{.723}$$

$E_i$  is daily energy flux to individual of genera  $i$  (kcal  $\text{bird}^{-1}\text{day}^{-1}$ )

$a = 1.33$  kcal ingested  $\text{kcal}^{-1}$  assimilated (Kendeigh, Dolnik and Gavrilov, 1977).

$b = 2.8$  kcal active  $\text{kcal}^{-1}$  at rest (Kooyman, Davis, Croxall and Costa, 1982).

$c = 78.3$  kcal  $\text{day}^{-1}$   $\text{kg}^{-.723}$  at rest (Lasiewski and Dawson, 1967).

$M_i$  = average individual body mass {kg} of genera  $i$

In order 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 ( $\text{days km}^{-2} \text{yr}^{-1}$ ) was estimated from the functional relation between date and numbers developed by Preston (1966). Preston's function is based on 3 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:

$$O_i = \bar{x} D_{\max} \sqrt{2\pi}$$

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 numerical date, as follows:

1980 season (1 March 1980 = 1, 28 February 1981 = 365)

1981 season (1 October 1980 = 1, 30 September 1981 = 365).

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 data.  $D_{\max}$  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:

$$O'_i = \sum w_j D_{ij}$$

$O'_i$  is the occupancy by genus  $i$  (days  $\text{km}^{-2} \text{yr}^{-1}$ )

$D_{ij}$  is the number of birds seen on cruise  $j$ , divided by the area scanned

$w_j$  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,  $w_j$ , 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 ( $O_i$ ) were then regressed against occupancy computed as a sum of products ( $O'_i$ ).

The annual energy flux to genus  $i$  was the **product** of  $O_i$  and  $E_i$ . Aggregate energy flux was the sum of energy **flux** over 7 genera. Conversion factors of 5  $\text{kcal g}^{-1}\text{dry}$  (Nishiyama, 1977; Cooper, 1978) and .4  $\text{g-C g}^{-1}\text{dry}$  (Curl, 1962) were used to convert energy transfer to mass transfer.

## Results

During 1980 and 1981 strong cross-shelf patterns in abundance were observed in 3 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 (Table 2). 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 genera, murrees and Puffinus shearwaters (Table 2). These birds were more abundant over the mixed waters of the inner domain than over the stratified waters of the middle and outer domains (Table 2). Cross-shelf variation was weak or absent in a less abundant subsurface forager, the Tufted Puffin (Table 2).

Comparison of mean dates of occupancy in 1980 and 1981 did not show any trend toward earlier or more extended occupancy in one year compared to the other year (Table 2). Mean dates ranged from spring (murrees) to fall (Larus gulls), with mean dates of most species occurring during the summer (Julian dates 180 to 270). The inner domain was occupied for relatively brief periods by large concentrations of shearwaters or murrees (Table 2). The outer domain was occupied for longer periods of time by lower concentrations of fulmars, large gulls, and storm petrels (Table 2). In all four regions, peak occupancy occurred well after the spring plankton bloom (Table 2).

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  $\text{km}^2 \text{yr}^{-1}$  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 fall**, and by shearwaters and **murres** inside the 50 m **isobath** (Table 2).

Mass-specific occupancy ( $\text{g-day m}^{-2} \text{yr}^{-1}$ ) 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 (Table 4). During 1980, and again in 1981, the slope and outer domains supported a greater biomass of surface than subsurface foraging birds (Table 4). At the same time, the **middle** and inner domains supported a greater biomass of subsurface than surface foragers.

A few species accounted for the bulk of the aggregate **flux**. 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 (Table 5). 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—murre in the spring, shearwaters in the summer, and fulmars and gulls in the fall 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 from elsewhere.

Aggregate flux to surface and subsurface foraging genera, as a function of hydrographic domain, is shown in Figure 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 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 (Table 5). The greatest difference in aggregate flux between years occurred in mixed water landward of the inner front (Figure 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 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 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). **Hyperiid**s were a regular component of **fulmar** diets in deep water. W. **Hammer** identified some of these **hyperiid**s as species **commensal on** jellyfish, which **also** occurred regularly in **fulmars** (Table 6). 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 (Table 6). **Fulmars** are known to feed on offal from fishing vessels (Fisher 1952), but we did not find large fish **bones**, as might be expected in **fulmars** feeding on offal. **Myctophid**s, a non-commercial species, were taken by the majority of **fulmars** collected in slope waters (Table 6). **Myctophid**s are a mid-water species, 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 stratified water **landward** of the inner front than in stratified **water** seaward of the front, due to a greater reliance on **euphausiids** by **shearwaters** in the inner domain (Table 6). All shearwaters collected were Slender-billed Shearwaters, based on bill lengths (Palmer, 1962). Predation on *T. raschii* by *P. tenuirostris* was the single greatest component of mass and energy transfer to seabirds away from colonies in the southeastern Bering Sea.

## Discussion

In our analysis of the 1975-1979 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, but was related to cross-shelf variation in carbon **flux** to grazing pressure (Cooney, 1981).

**Increased** flux to surface foraging birds in deep waters of **the** outer shelf was paralleled by increased flux to Large-bodied **copepods**, especially **Neocalanus cristatus**, **N. plumchrus**, and **Eucalanus bungii**, the major grazers in deep water in Bristol Bay (Cooney, 1981). Flux to surface foraging birds occurred after the movement of **copepods into** the surface waters of the outer domain (Smith and Vidal in prep). **Fulmar** prey such as jellyfish are known to feed on these **calanoids** (Hammer et al, in prep). Flux to surface foraging species in the outer domain was 3 times higher than flux to the same species in the middle domain, based on 1975-79 **data**. Flux to surface **foraging** species was 2.4 times higher in the **outer** than *in* the middle domain in 1980, 4.6 times higher in 1981.

Flux to subsurface foraging birds was localized in shallow water, and was not associated with **the** distribution of large **copepods**. **Much** of the flux to subsurface foraging **shearwaters in** the inner domain was from a single species,

T. raschii, the major grazer **in the shallow** waters of inner Bristol Bay (Smith and Vidal, in prep). Flux to subsurface foraging species 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.

Why should subsurface foragers not exploit **copepod--based** food resources in the outer domain, and why should surface foragers not exploit **euphausiids** in shallow water? We hypothesize that strong topographic control of fronts (Schumacher, Kinder, **Pashinski**, and **Charnell**, 1979) and eddies (Brown, 1980) in **shallow** water results **in** horizontally predictable prey concentrations that may move vertically through a well mixed water column. This distribution of prey would favor subsurface foragers which have relatively high wing loading, because prey would be horizontally restricted **in** distribution, thus requiring less wide-ranging search, and subsurface foragers **could** pursue them throughout the **water** column. Conversely, reduced topographic **control** of prey patchiness in outer shelf waters, replete with large eddies (Kinder and Coachman, 1978), favors surface foraging species with reduced costs of travel needed **to** locate laterally unpredictable concentrations of vertically migrating prey.

Predictions from this hypothesis are:

- (1) Large foraging **ambits** by birds in deep water, and smaller foraging **ambits** **in** shallow water.
- (2) Large foraging **ambits** by other mobile predators, such **as** fish, in deep water, and reduced foraging **ambits** in shallow water.
- (3) Concentration of **mobile** predators into smaller areas **in** shallow water and less concentration in deep water.

These predictions remain to be tasted.

Our estimates of carbon flux to seabirds in 1980 and 1981 were higher than our 1975-1979 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, **Kooyman** and **Croxall** (1983). Both of these studies were with penguins, but in the Bering Sea **Roby (unpublished)** found that **free-living 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 1975-1979 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 1980, and 9 **July 1981** (Table 3). Mean date of occupancy of the outer domain by large gulls was 23 August 1980 and 11 October 1981 (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 method of estimating occupancy did not contribute significantly to **the** higher estimates in 1980-81, 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.

$$\text{If } E = aM^b$$

$$\text{then } dE / da = M^b$$

$$\text{and } dE / db = aM^b \ln M$$

( $\ln M$  = natural logarithm of  $M$ ). Our estimates assume **that** total **daily** energy expenditure scales to body mass raised **to** a power of .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 .6052, **below** the standard physiological scaling of .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 greater than .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 **under-**represented **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 .7 kg **fulmar** the **Walsberg** estimate is the same as the estimate we used.

The 1980-81 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  $78.3 \text{ kcal kg}^{-.723} \text{ day}^{-1}$  appears to be low for boreal **seabirds**, based on the measured SMR of Uris lomvia (Johnson and West, 1975), Oceanodroma furcata (Iversen and Krog, 1972), and Aethia pusilla (Roby, unpublished). 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 birds collected in deep water away from breeding colonies (Bédard, 1969; Ogi and Tsujita, 1973; Sanger and Baird, 1977; Sanger, in press). **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, MS). **Pollock**, the most important prey at the **Pribilof** Island colonies in outer Bristol Bay (Hunt et al, 1981a) were notably less important. **We** also discovered an increase in dietary diversity of seabirds in deep water seaward of the inner front. We could not estimate food web connectivity (Pimm, 1981) from stomach samples alone, but it is interesting to note the frequency of general carnivores (jellyfish, squid,

hyperiid) in the diet of fulmars, which are also general carnivores. The increase in dietary diversity in deep water suggests that food web connectivity may be high in the "pelagic" food web in the outer domain, while connectivity is lower in shallow water. This needs to be tested with other species, and in other locations.

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Table 1. Number of ten minute seabird counts and number of birds collected during cruises in Bristol Bay, 1978-1982.

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

Table 2. Seasonal abundance of **seabirds, by domain, southeastern Bering Sea.**  $\bar{X}$  is mean date (days from 1 January).  $\tilde{X}$  is one standard deviation (days). D is maximum density (birds km<sup>-2</sup>). Occupancy (O) =  $\bar{X} \cdot D \cdot \tilde{X}$  = bird-days km<sup>-2</sup> yr<sup>-1</sup> (see text). Occupancy in 1980 based on the following number of 10-minute counts: Slope (135), Outer (374), Middle (392), Inner (79). In 1981: Slope (234), Outer (783), Middle (796), Inner (148).

	1980				1981			
	$\bar{X}$	$\tilde{X}$	D	O	$\bar{X}$	$\tilde{X}$	D	O
Surface foragers.								
<b><u>Fulmarus glacialis</u></b>								
slope	230	68.5	<b>19.5</b>	3348	212	57	20.6	2943
outer	229	66	19.6	3243	201	38	<b>100</b>	9525
middle	224	52	12.1	<b>1577</b>	<b>187</b>	43	15.3	<b>1649</b>
inner		0	.09	0	146	34	2.3	196
<b><u>Oceanodroma furcata</u></b>								
slope	203	60	<b>1.8</b>	271	179	19	4.4	210
outer	186	51	2.3	294	179	<b>17</b>	14.6	622
middle	237	24	<b>2.0</b>	<b>120</b>	170	35	1.4	<b>123</b>
inner		0	0.0	0		0	.03	0
<b><u>Larus sp.</u></b>								
slope	263	74	19.8	3673	284	49	19.8	2432
outer	264	126	5.0	1579	<b>315</b>	96	5.0	1203
middle	190	137	<b>1.5</b>	515	251	<b>148</b>	1.2	445
inner		0	.4	0	<b>192</b>	235	.4	236

Table 2. (Continued)

	x	$\tilde{x}$	D	o	x	$\tilde{x}$	D	o
<b><u>Rissa brevirostris</u></b>								
slope	138	120	1.00	301	179	69	.90	156
outer		0	.14	0		0	.31	0
middle		0	.09	0		0	<b>.09</b>	0
inner		0	.32	0		0	<b>.32</b>	0
<b><u>R. tridactyla</u></b>								
slope	134	<b>133</b>	.98	327	182	67	2.4	403
outer	109	52	2.1	274	162	72	.94	170
middle	119	86	1.1	237	144	66	.88	146
inner		0	.39	0	177	53	3.1	412
<b><u>Rissa sp. (all)</u></b>								
slope	228	78	6.1	<b>1193</b>	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

Table 2. (Continued)

	<b>x</b>	$\bar{x}$	D	o	x	$\bar{x}$	D	o
Subsurface foragers								
<b><u>Puffinus</u> sp.</b>								
slope	<b>216</b>	48.8	2.5	306	<b>162</b>	32	7.6	<b>610</b>
outer	<b>199</b>	62	19.0	2953	<b>194</b>	55	16.0	2206
middle	252	37	17.4	1614	190	47	56.8	6692
inner	237	8	39.1	784	182	14	902	3 1 6 5 4
<b><u>Uris</u> sp.</b>								
slope	185	144	2.8	1011	185	90	3.6	818
outer	137	86	6.3	<b>1358</b>	<b>166</b>	73	5.6	1025
middle	158	87	6.1	1330	<b>194</b>	101	1.3	329
inner	105	<b>11</b>	<b>178.4</b>	4919	157	42	12.6	<b>1327</b>
<b><u>Lunda cirrhata</u></b>								
slope	249	72	2.0	361	184	77	1.3	251 -
outer	250	67	1.9	<b>319</b>	183	60	2.3	346
middle	257	44	2.9	320	255	86	1.5	323
inner	226	46	2.2	254		0	.27	0

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

	Mean	Standard Deviation	number Weighed
Surface foraging species			
<u>Fulmarus glacialis</u>	704	105	3a
<u>Oceanodroma furcata</u>	65	7	19
<u>Larus glaucescens</u>	1501	114	6
<u>Rissa brevirostris</u>	405	<b>60</b>	4
<u>Rissa tridactyla</u>	420	26	6 -
Subsurface foraging species			
<u>Puffinus tenuirostris</u>	646	56	21
<u>Uria lomvia</u>	1105	91	6
<u>Uria aalge</u>	999	8	2
<u>Lunda cirrhata</u>	883	5	2

Table 4 Mass-specific occupancy by seabirds in central Bristol Bay, 1980 and 1981. Values are g-day  $M^{-2} \text{yr}^{-1}$ , computed from data in Tables 2 and 3. Divide by 365 to obtain average **daily** standing stock.

Domain	1980		1981	
	Surface	Subsurface	Surface	Subsurface
	foragers	foragers	foragers	foragers
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	.24	5.7	.71	21.9

Table 5. Energy Flux to Seabirds, central Bristol Bay. Values are  $\text{Kcal M}^{-2} \text{yr}^{-1} \times 10^3$ 

	<u>                    </u>		<u>Outer</u>		<u>Middle</u>		<u>Inner</u>	
	1980	1981	1980	1981	1980	1981	1980	1981
<b>Surface foragers</b>								
<u>F. glacialis</u>	759	667	736	2160	358	374	0	44
<u>O. furcata</u>	11	9	12	25	5	5	0	0
<u>Larus spp.</u>	1440	954	619	472	202	174	0	93
<u>Rissa spp.</u>	185	175	200	62	91	35	92	79
<b>Subsurface foragers</b>								
<u>Puffinus sp.</u>	65	130	629	470	344	1426	167	6747
<u>Uria spp.</u>	312	253	419	317	411	102	1519	410
<u>L. cirrhata</u>	96	67	85	92	85	86	68	0
Total ( $\text{Kcal M}^{-2} \text{yr}^{-1}$ )	2.9	2.3	2.7	2.6	1.5	2.2	1.8	7.3
Total ( $\text{g-C M}^{-2} \text{yr}^{-1}$ )	.23	.18	.22	.28	.12	.18	.15	.59

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

Domain (year)	Slope (1982)	Outer (1982)	Middle (1982)	Middle (1982)	Inner (1982)	Inner (1981)
	<u>F. glacialis</u>	<u>F. glacialis</u>	<u>P. tenuirostris</u>	<u>F. glacialis</u>	<u>P. tenuirostris</u>	<u>P. tenuirostris</u>
Number of birds	9	61	17	32	7	22
Fish		.30	.29	.25		
Myctophid	.56	.03				
Gadid		.02	.24	.03		
Squid	1.00	.97	.29	.94		.5
Nereids		.08				
Jelly fish	.22	.44	.29	.34		
Crustacean	.22	.28	.24	.25	.29	.09
Copepods						.05
Hyperiid	.3	.3		.19		
Gammarideans			.06			
Mysids		.07				
Crab Larvae		.05	.12			
Euphausids		.02	.18		.29	.14
<u>Thysanoessa raschii</u>		.05	.29		.71	.68

Appendix. Coordinates used to classify seabird counts by domain.

Domain	Latitude ( $^{\circ}$ 'N)	Longitude ( $^{\circ}$ 'w)
<b>Inner</b>		
	57 $^{\circ}$ 30 '	<b>165<math>^{\circ}</math></b> 40 '
	58 $^{\circ}$ 30 '	164" 30 '
	58 $^{\circ}$ 30 '	162 $^{\circ}$ 30 '
	58" 30 '	<b>161<math>^{\circ}</math></b> 30 '
	58" 20 '	159 $^{\circ}$ 0'
	57 $^{\circ}$ 20 '	160 $^{\circ}$ 30 '
	57 $^{\circ}$ 30'	163 $^{\circ}$ 0'
	57" 30 '	<b>164<math>^{\circ}</math></b> 0'
<b>Middle</b>		
	57 $^{\circ}$ 30 '	<b>165<math>^{\circ}</math></b> 40 '
	56" 25 '	167" 30'
	<b>56<math>^{\circ}</math></b> 25 '	166" 0'
	56 $^{\circ}$ 18 '	165" 0'
	55 " 45 '	163 $^{\circ}$ 45 '
	57 $^{\circ}$ 20 '	160 $^{\circ}$ 30 '
	<b>57<math>^{\circ}</math></b> 30 '	163" 0'
	57 $^{\circ}$ 30'	<b>164<math>^{\circ}</math></b> 0'

Appendix Continued.

**Outer**

<b>56°</b> 25'	167' 30"
56" 25'	<b>166'</b> 0'
560 28'	165" 0'
55° 45'	<b>163°</b> 45'
540 50'	<b>166°</b> 0'
54" 57'	167° 10'
<b>55°</b> 15'	<b>167°</b> 40'
55° 40'	168° 40'

## Slope

55" 40'	168" 40'
55* 15'	167° <b>40'</b>
540 57'	167" 10'
54° 40'	166° <b>10'</b>
<b>54°</b> 10'	168" 0'
54° 20'	168° 0'
540 50'	<b>168°</b> 40'
55" 30'	169" 0'

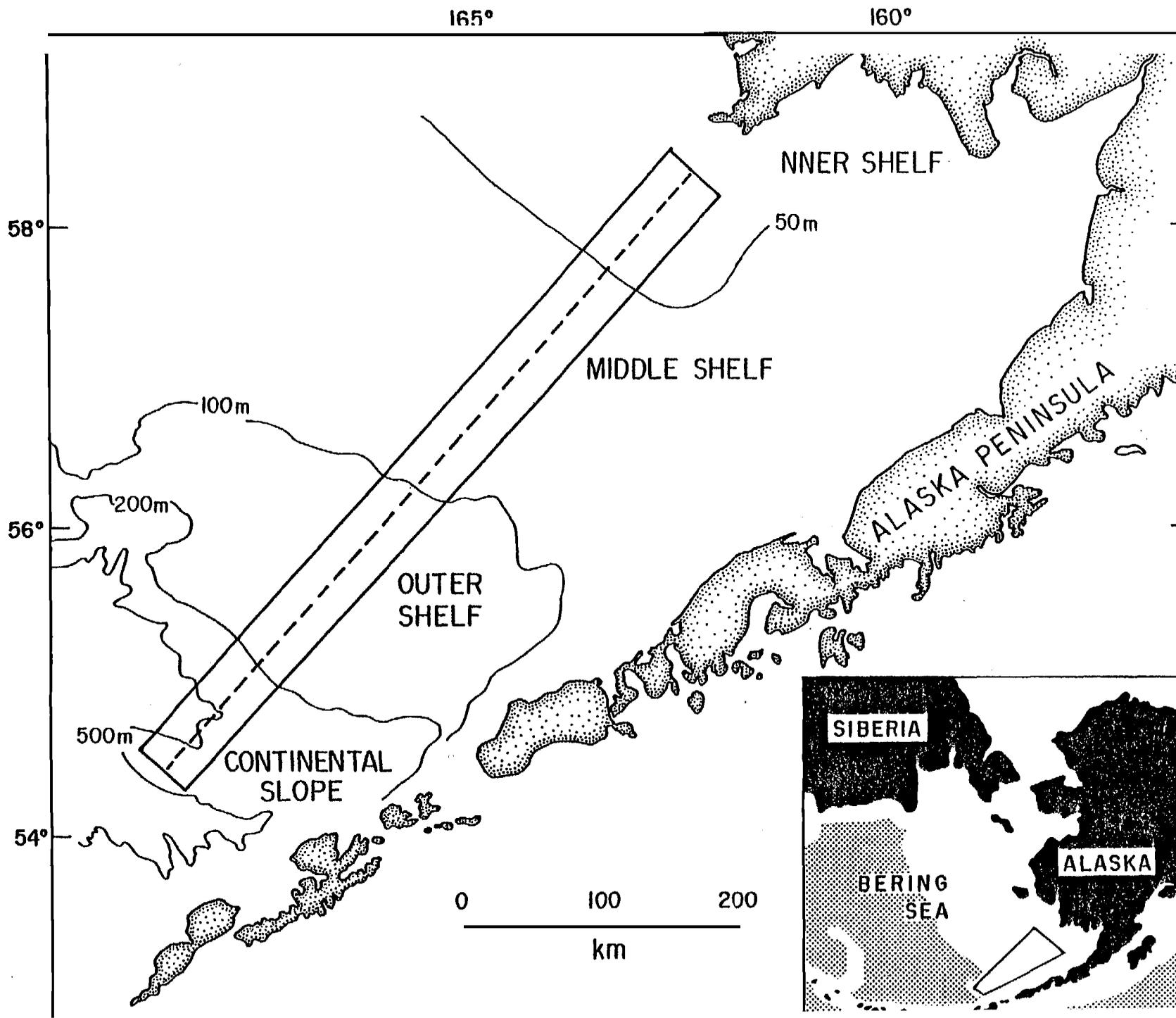
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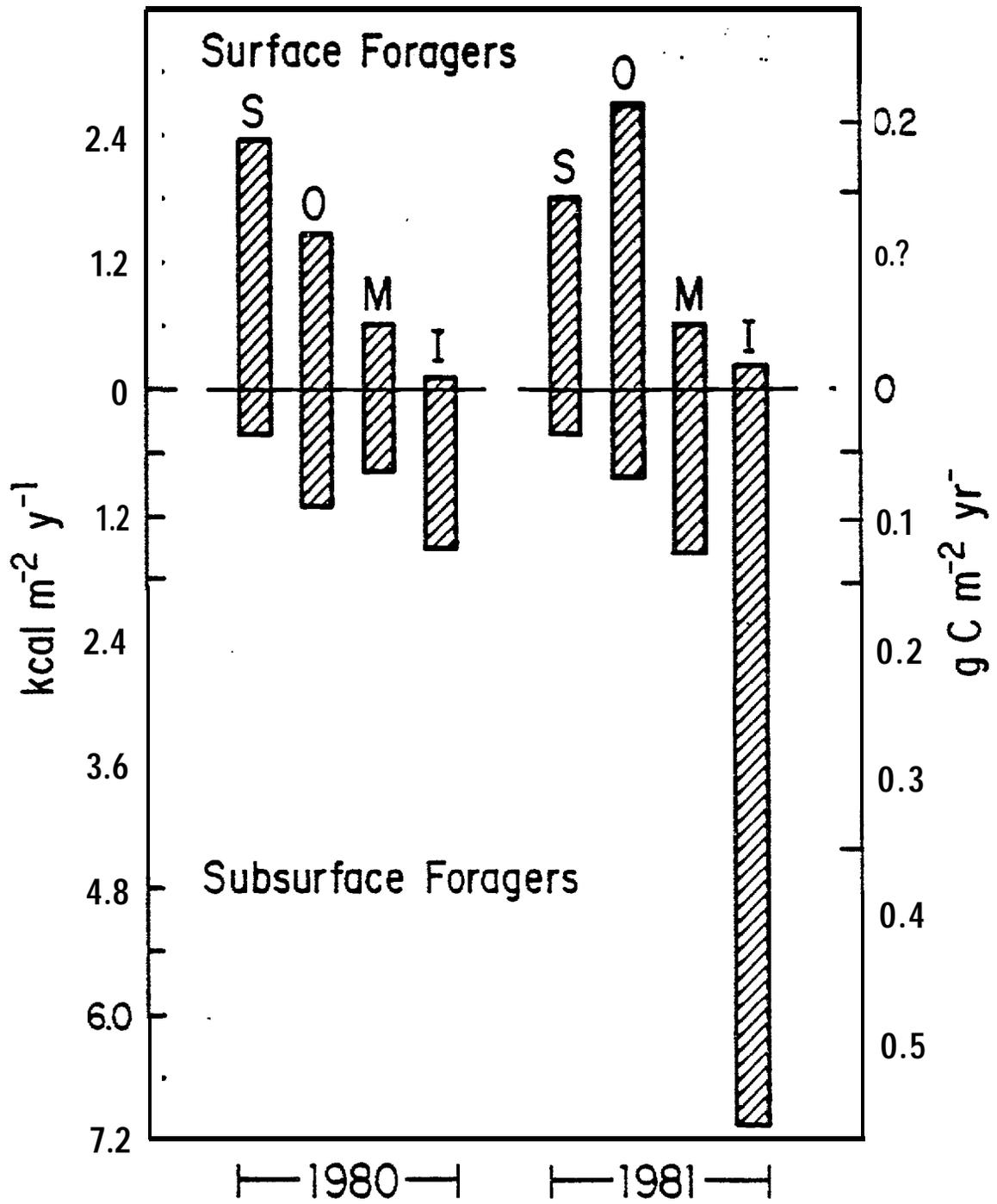
Figure 1. Areas used to classify bird counts by domain, central Bristol Bay.

Figure 2. Annual. mass and energy transfer to seabirds in 1980 and 1981.

Surface feeders were: Fulmarus glacialis, Oceanodroma furcata,  
Larus sp., Rissa tridactyla, R. brevirostris. Subsurface feeders  
were: Puffinus griseus, P. tenuirostris, Uris aalge, U. lomvia,  
Lunda cirrhata.

Figure 3. Distribution of fulmar (F. glacialis) and dark-bellied shearwaters  
(Puffinus spp.) along PROBES "A" line, 26-28 July, 1982. Number  
of birds seen during each 10-minute count was divided by the area  
scanned during the count.





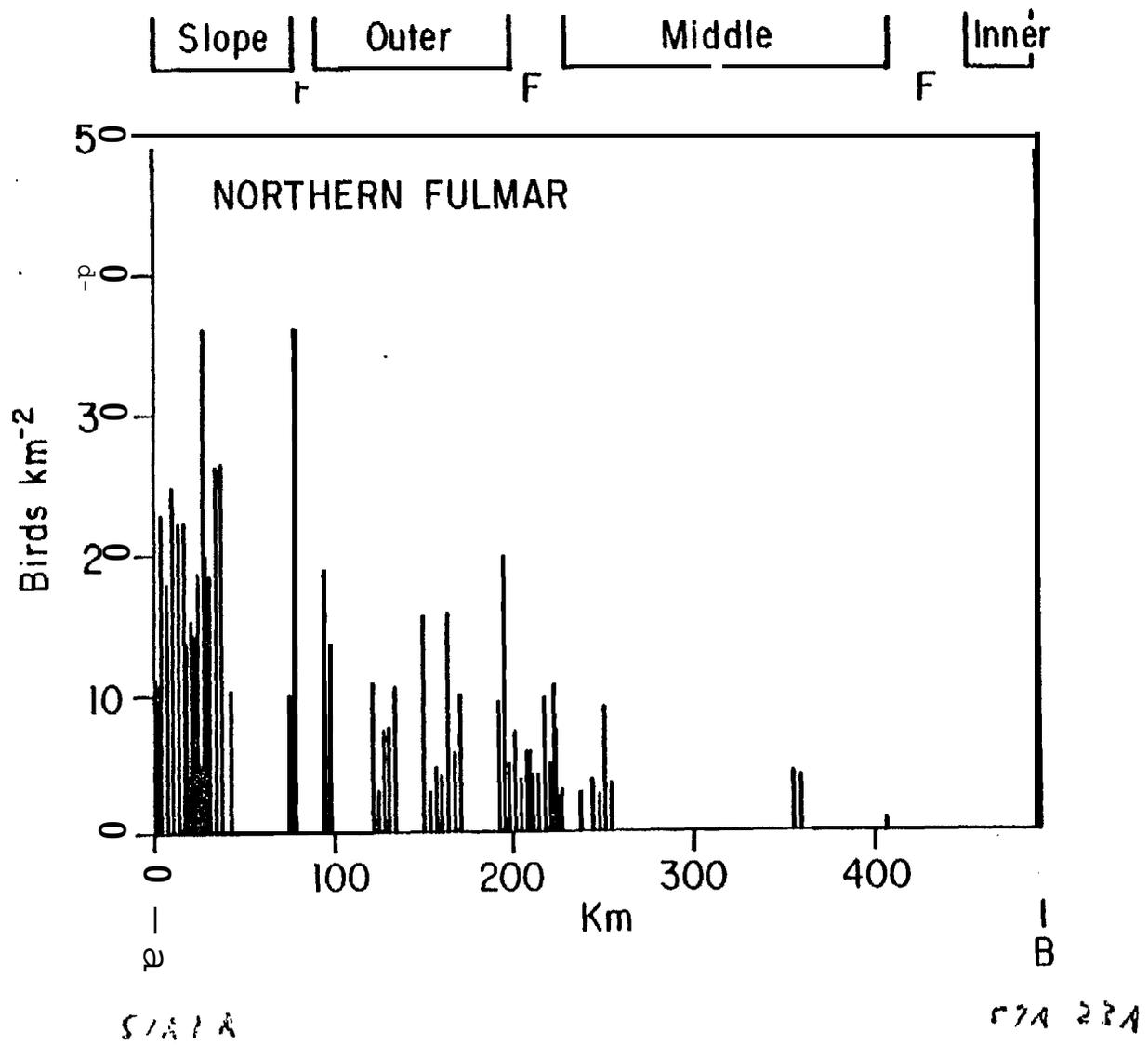
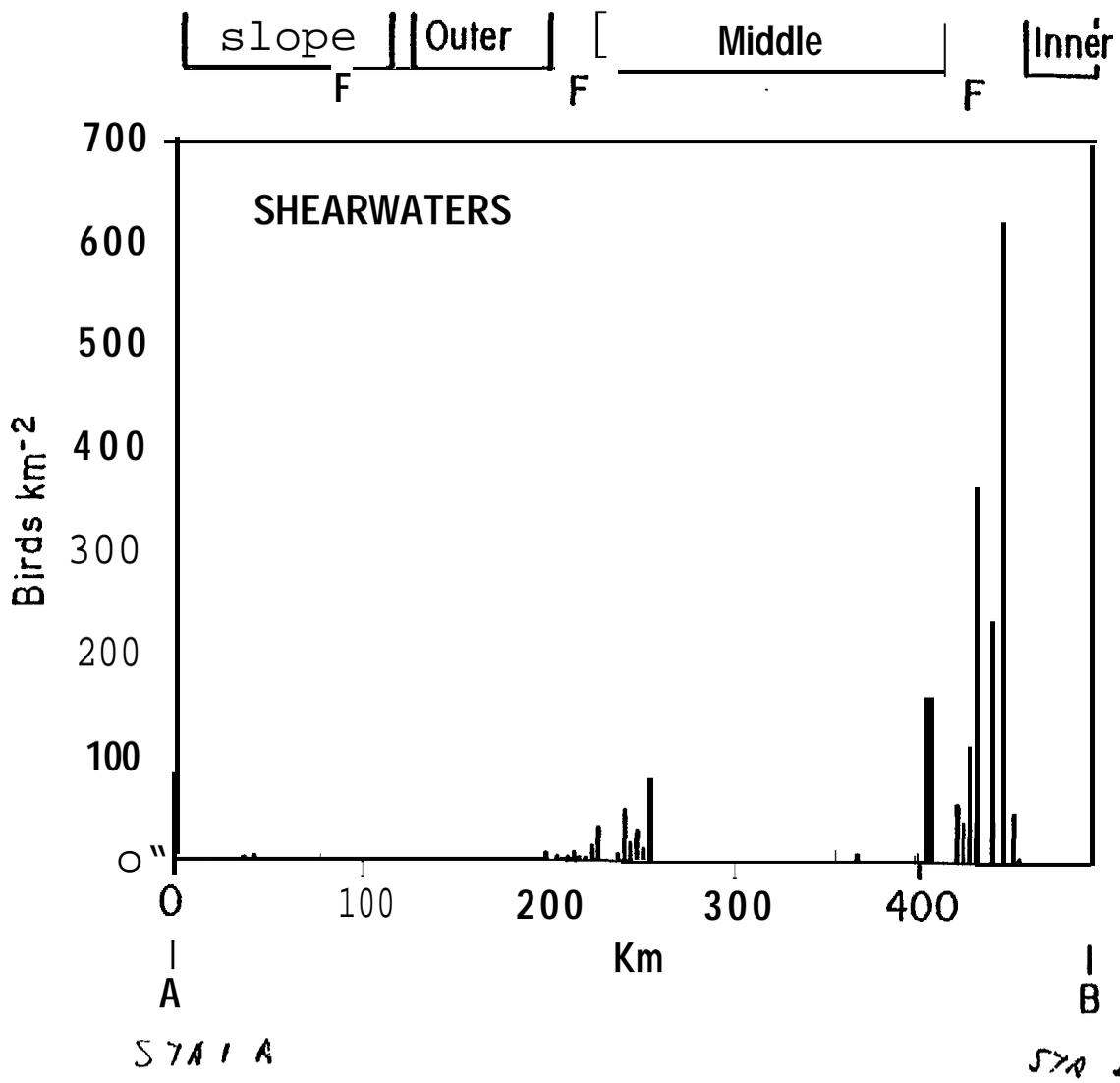


Fig 3A



57A 23A