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# Mass mortality of short-tailed shearwaters in the south-eastern Bering Sea during summer 1997

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## ABSTRACT

During summer 1997, hundreds of thousands of emaciated short-tailed shearwaters (*Puffinus tenuirostris*) died in the south-eastern Bering Sea. Using strip transect methodology, we documented the distribution and abundance of short-tailed shearwaters during cruises conducted prior to, during, and after the die-off, as well as the distributions and abundances of floating carcasses. The distributions and abundances of short-tailed shearwaters in 1997 were similar to those found during the 1970s and early 1980s. In August–September 1997, we observed 163 floating shearwater carcasses, most of which were between St Paul Island and Nunivak Island. We estimated  $\approx 190\,000$  carcasses were afloat in the study area, about 11% of the surveyed population. Between spring (June) and autumn (August/September), mean net body mass of shearwaters decreased by 19%, mean pectoral muscle mass decreased by 14%, and mean percentage body lipid content decreased by 46%, from 15.6% in spring to 8.4% in autumn. Compared with spring, short-tailed shearwater diets broadened in autumn 1997, to

include, in addition to adult euphausiids *Thysanoessa raschii*, juveniles of *T. inermis*, *T. raschii* and *T. spinifera*, crab megalops, fish and squid. We discuss how the ecosystem anomalies in the south-eastern Bering Sea during spring and summer 1997 relate to the mortality event and suggest possible implications of long-term climate change for populations of apex predators in the south-eastern Bering Sea.

**Key words:** Bering Sea, coccolithophorid, *Emiliana huxleyi*, euphausiid, *Puffinus tenuirostris*, seabird die-off, short-tailed shearwater, *Thysanoessa*

## INTRODUCTION

Short-tailed shearwaters (*Puffinus tenuirostris*) migrate annually from breeding grounds in south-eastern Australia and Tasmania to forage in the northern Pacific Ocean and Bering Sea during the austral winter. In the south-eastern Bering Sea, these seabirds have foraged primarily on the euphausiid *Thysanoessa raschii* (Ogi *et al.*, 1980; Hunt *et al.*, 1981; Hunt *et al.*, 1996). During spring 1997, unusual atmospheric and oceanographic conditions in the eastern Bering Sea initiated a variety of perturbations to the south-eastern Bering Sea marine ecosystem (Vance *et al.*, 1998; Overland *et al.*, 2001; Stabeno *et al.*, 2001; Stockwell *et al.*, 2001). Subsequently, thousands of short-tailed shearwater carcasses were found floating at sea or beachcast between early August and September, and runs of three salmon species fell well below expected returns (Kruse, 1998). Here, we report on the distribution and abundance of short-tailed shearwaters and their prey, and discuss potential causes of this unusually large shearwater mortality event in the Bering Sea.

Short-tailed shearwaters arrive in the south-eastern Bering Sea in May and June, finish their moult by August and depart in September and October (Shuntov, 1961; Schneider and Shuntov, 1993). During their summer dispersal, these shearwaters are the most numerous seabirds in the Bering Sea, with estimates for the entire region ranging from 8.7 million (Shuntov, 1972) to 20 million birds (Hunt *et al.*, 1981). Although they feed on a variety of fish, squid,

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and euphausiids throughout their range (Ogi *et al.*, 1980; Krasnow and Sanger, 1986; Montague *et al.*, 1986; Sanger, 1986; Skira, 1986; Weimerskirch and Cherel, 1998), the diet of short-tailed shearwaters over the south-eastern Bering Sea shelf in the past was apparently dominated by the euphausiid *Thysanoessa raschii* (96% of diet; Ogi *et al.*, 1980; Schneider *et al.*, 1986; Hunt *et al.*, 1996). Shearwaters capture prey by surface seizing, hydroplaning and pursuit diving to depths reaching 71 m (Weimerskirch and Cherel, 1998). In the south-eastern Bering Sea, shearwaters forage on shallow mating swarms of euphausiids, and by pursuit diving to depths of at least 35 m (Hunt *et al.*, 1996). It is likely that the ability to find concentrations of accessible euphausiids influences shearwater foraging success and survival in the eastern Bering Sea.

Euphausiids have dominated the herbivorous zooplankton community in the inner and middle shelf regions of the eastern Bering Sea (Vidal and Smith, 1986; Smith, 1991). *Thysanoessa raschii* is the most abundant euphausiid species there. In May and June, it forms mating swarms, and usually is associated with colder, less saline, coastal water (Smith, 1991). However, mating swarms have been observed as late as mid-August (Hunt *et al.*, 1996). *T. inermis* occurs farther offshore and dominates the outer shelf community (Vidal and Smith, 1986).

Short-tailed shearwaters are numerous in coastal waters of the North Pacific, and carcasses are deposited occasionally on beaches. Episodes of mortality in which unusually large numbers of carcasses were beachcast have been recorded in regions where their transequatorial migrations terminate in the Southern Hemisphere, along the eastern coast of Australia (Douglas and Setton, 1955; Serventy, 1967). In the Northern Hemisphere, die-offs have occurred along the Pacific coast of Japan in April to June (Kawaguchi and Marumo, 1964; Ozawa, 1964; Kuroda, 1967; Sugimori *et al.*, 1976; Oka and Maruyama, 1986; Toyohashi Wild Bird Club, 1978). Occasionally, mortality events have occurred in the Bering Sea, e.g. during the 1982–1983 El Niño (Nysewander and Trapp, 1984; Hatch, 1987; Vivian Mendenhall, unpublished data). The mortality event in 1983 ranged over an arc covering 2736 km from the northern and western Gulf of Alaska as far west as Dutch Harbor and into portions of the Bering and Chukchi seas as far north as Kotezbue Sound. In 1997, during the course of oceanographic studies of the foraging ecology of short-tailed shearwaters and the food web that supports them in the Bering Sea, we encountered an opportunity to investigate an exceptionally large die-off and

to observe the foraging conditions before and after the mortality event. In this paper, we present information on the status of shearwater populations within our study area, estimate the number of dead birds and report on body condition, diet trends, and the availability of prey to these birds during spring and autumn. Results are also discussed in Hunt *et al.* (1999a,b).

## METHODS

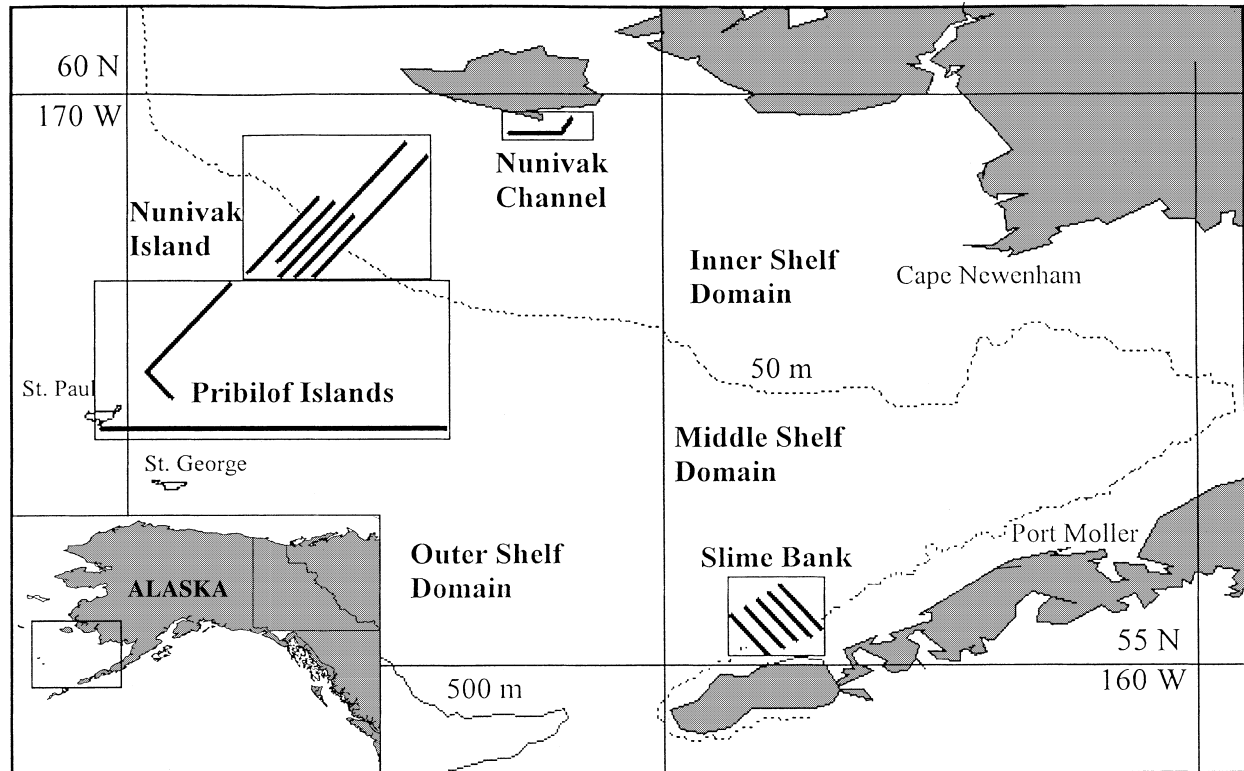
We studied the distribution, abundance, food habits, and mortality of short-tailed shearwaters during two research cruises to the south-eastern Bering Sea, in spring (27 May to 28 June) and autumn (27 August to 12 September) of 1997. Survey effort was concentrated in two areas adjacent to the inner or structural front that occurs near the 50 m isobath (Coachman, 1986): the Nunivak Island area in the north and the Slime Bank area in the south (Fig. 1). Additional observations were made along a transect from the outer edge of the Nunivak grid to north-eastern St Paul Island, Pribilof Islands. We also estimated the number of floating carcasses along the south-east coast of Nunivak Island during the autumn cruise. In spring 1997, observations were also made of short-tailed shearwaters in the Port Moller and Cape Newenham areas (Fig. 1).

### *Distribution and abundance of live and dead shearwaters*

We used standard strip transect methodology to estimate the distribution and abundance of short-tailed shearwaters (Burnham *et al.*, 1980; Tasker *et al.*, 1984) during systematic surveys when the vessel was under way at speeds of at least 2.57 m/sec (5 knots). All birds were counted continuously from the bridge (eye height = 7.7 m above sea surface) in a 300 m arc from directly ahead to 90° off the side with the best visibility (i.e. lowest glare) and logged into a portable field computer. When continuous lines of flying shearwaters (> 1000 individuals) were encountered crossing the bow of the vessel, observers switched to a snapshot method of counting birds to minimize the overestimate of numbers present (Tasker *et al.*, 1984). We did not employ the correction factors that account for the flux of flying birds within the transect (Spear *et al.*, 1992) because we wanted to compare our density estimates with historical records when such correction factors were not employed. Density was estimated in 3 km bins by dividing the number of shearwaters sighted by the area within each bin, and these were averaged to determine the density within a survey grid.

Shearwater distributions and abundances in the Nunivak Island and Slime Bank grids were compared

**Figure 1.** The study area in the south-eastern Bering Sea. Boxes indicate four regions in which transects were conducted and number of carcasses were estimated: Nunivak Channel, Nunivak Island, Pribilof Islands, and Slime Bank. Transect lines in which observations were used to calculate density estimates are indicated within each box. The inner shelf domain is inside of the 50 m isobath, the middle domain between the 50 and 100 m isobaths, and the outer domain between the 100 and 200 m isobaths.



with historical records of density compiled from a variety of sources of shipboard surveys from April 1975 to March 1981 (Glenn Ford, pers. comm.). Because the coverage of historical data taken within the grids during the same seasons as our study was low, we included historical data over a more extensive range in the Nunivak Island (100 km in the east–west direction of the 1997 grid) and Slime Bank (20 km to the west and 50 km to the east of the 1997 grid) areas. Densities of shearwaters were estimated from historical surveys for the months of June (spring) and September (autumn) for comparison with the 1997 records. We refrained from conducting statistical comparisons between density estimates for the 1997 season and those for the historical data sets, because the spatial and temporal coverage differed and because of the difficulty in estimating densities of highly aggregated birds.

To estimate the distribution and abundance of dead shearwaters (carcasses), standard line transect methodology was employed. The perpendicular distance to shearwater carcasses was estimated and then used to

determine an effective strip width based upon the drop-off in the probability of sighting with increasing perpendicular distance from the trackline (Buckland *et al.*, 1993; Laake *et al.*, 1994). The trackline was divided into 3 km bins and each bin was assigned an effective strip width based on water clarity; this width was 54.8 m in ‘milky’ waters within a coccolithophorid (*Emiliania huxleyi*) bloom, in which carcasses of dark birds were conspicuous against the lighter-coloured backgrounds, and 27.4 m in dark water outside the bloom.

Because the distribution of carcasses was highly variable and clumped in particular areas, we stratified our census estimates into four regions of relatively uniform distribution of carcasses, and generated density estimates for each region. These four regions were the Nunivak Channel, Nunivak Island area, the Pribilof Islands, and the Slime Bank area (Fig. 1). Density was estimated in 3 km bins by dividing the number of shearwaters sighted by the area within each bin, and these densities were averaged to determine the density within a survey grid. The estimates for each of the four

regions were added to produce a total estimate of the number of dead short-tailed shearwaters floating in the entire study area. The percentage of the population surveyed that had died was estimated by equation 1.

$$\% \text{ of population dead} = 100 \times (\text{estimated total dead shearwaters [4 regions]} / (\text{estimated total of live plus dead shearwaters [4 regions]})). \quad (1)$$

#### *Indices of body condition*

We used body mass, pectoralis (breast muscle) mass, and per cent body lipid content to determine the condition of short-tailed shearwaters. Shearwaters were collected both before and during the die-off. Measurements were made on birds collected in the Slime Bank, Port Moller, and Cape Newenham study sites in spring, and on birds collected in the Nunivak Island and Slime Bank study sites in autumn. Body condition was also measured on 12 'fresh' beachcast carcasses with feathers still waterproof (provided by the US Fish and Wildlife Service, Anchorage, Alaska). Fresh body mass was measured at sea using a Pesola scale ( $\pm 10$  g) and the mass of the pectoralis muscle from one side of the carcass was measured using a top-loading precision balance ( $\pm 0.01$  g; Acculab).

Lipid content was determined by thawing frozen birds (stored at  $-20^{\circ}\text{C}$ ) and defeathering the carcasses by hand plucking. Each bird was passed through a conventional meat grinder six times (twice through a wide-bore blade and four times through a small-bore blade), with hand mixing in between passes to homogenize the sample. Three subsamples of 30 g (wet mass) were measured from the homogenate, combined with 2–3 g of infusorial earth, and dried in a convection oven at  $60^{\circ}\text{C}$  ( $\pm 5^{\circ}$ ; Kerr *et al.*, 1982) for 24–48 h or until the dry mass stabilized. Dry samples were placed in tared extraction thimbles and weighed immediately before extraction in petroleum ether for  $20 \pm 1$  h (Christie, 1982; Dobush *et al.*, 1985; Roby, 1991). After extraction, samples were re-dried in an oven for 24 h or until a constant mass was achieved. Lipid content of each subsample was determined as the difference in dry mass of the sample prior to and after extraction. The average value of lipid content in the three subsamples was used to calculate the amount of body fat of the entire individual.

Body fat (g) was calculated by multiplying the mean per cent lipid content of the subsamples by dry carcass mass (excluding feathers). Per cent lipid content was calculated from equation 2:

$$\% \text{ lipid content}_{(\text{wet body mass})} = 100 \times (\text{body fat [g dry carcass mass]} / (\text{FBM} - \text{stomach contents})), \quad (2)$$

where FBM denotes fresh body mass upon capture. To compare between seasons, we wanted an estimate of body mass, lipid content, and breast muscle mass that accounted for overall body size. Thus, we tested for the covariance of these variables with a measure of body size, total length (Packard and Boardman, 1987). Because changes in body mass most often reflect changes in fat levels (Blem, 1981; Slagsvold, 1982; McEwan and Whitehead, 1984), we did not use a covariance-adjusted value with net body mass to compare lipid levels between seasons. We did not use any ratios of body size to structural measurements because ratios assume that variation owing to body size is eliminated by this transformation. Also, ratios can create misleading results if the structural indicator does not vary allometrically with body size (Packard and Boardman, 1987). Thus, for the interseasonal comparisons of net body mass, pectoralis mass, and lipid content, we used means that were adjusted for covariance with total length (body size).

#### *Food habits*

The food habits of short-tailed shearwaters in spring and autumn were determined from the stomach contents of birds that were collected while foraging or sitting on the water. Upon collection in the field, stomach contents were removed immediately, weighed, and preserved in 80% ethanol. Wet weight, displacement volume, and direct counts were used to determine the diets of individual birds. Stomachs containing  $> 50$  g (wet weight) biomass were split using a Folsom splitter, and a subsample of the entire contents was identified and enumerated. Particular attention was paid to species, age class, sex, and maturation state (containing spermatophores) of euphausiids; the size of euphausiids was determined by measuring the total length of  $\approx 15$  individuals of each species/age class within each sample. Additionally, the incidence of nematodes in the stomach contents was recorded.

#### *Prey distribution and abundance*

A MOCNESS (multiple opening and closing net environmental sensing system, Wiebe *et al.*, 1976) was deployed to sample zooplankton and other potential prey of short-tailed shearwaters. This system consisted of a series of nine 1 m nets with  $500 \mu\text{m}$  mesh size that allows for multiple opening and closing of nets, and thus allows sampling at discrete depth intervals in the

water column. Tows were made in the vicinity of the inner front with replicates collected inshore, offshore, and at the frontal area. Euphausiids are known to avoid nets and are typically difficult to sample during the day (Smith, 1991). Thus, sampling was conducted at night when the likelihood of catching euphausiids was greatest. A hydroacoustic system also was deployed in conjunction with the MOCNESS at night to identify layers to be fished by the nets. The MOCNESS samples were used to estimate the abundance of euphausiid prey items (number  $m^{-3}$ ), by species, sex, and age class. Because we were interested in the abundance of euphausiids in the entire water column, the eight quantitative nets collected within a single tow were combined and averaged to provide an abundance estimate for that particular tow in number  $m^{-2}$ .

Because the euphausiid abundance data were heteroscedastic and non-normally distributed at the Nunivak Island and Slime Bank study sites, two-way nonparametric versions of the Kruskal–Wallis (K–W) test were employed to determine if the distribution and abundance of major zooplankton taxa differed between spring (prior to) and autumn (during the mortality event). A posteriori, nonparametric versions of the Tukey multiple comparison test were conducted to determine which K–W factors differed significantly.

## RESULTS

### *Distribution and abundance of live and dead shearwaters*

A survey effort of 1186 km in spring (Slime Bank and Nunivak grids only) and 1282 km in autumn 1997 (four survey subareas) indicated that the abundance of live shearwaters in the Nunivak Island and Slime

Bank grids (combined) increased between spring 1997 (519 500) and autumn (1 579 000).

Shearwater densities in 1997 were within an order of magnitude of densities calculated for 1975–1981 (Table 1). Densities were greater at Slime Bank than at Nunivak Island in spring and autumn 1997 (Table 1), and a greater proportion of individuals were observed foraging in the Slime Bank study site than at Nunivak Island (binomial test, probability of birds sitting on the water and foraging at Nunivak and Slime Bank in spring and autumn 1997,  $P < 0.05$  for all significance tests; Table 1).

During autumn 1997, we encountered 163 shearwater carcasses floating at sea (Table 2), an observation unique in our experience. Most carcasses (128) occurred in the Nunivak Island area (25), and in the Nunivak Channel (103). We estimated that the total number of carcasses afloat in the study area was 191 500 ( $\pm 46 500$ ), or about 11% of the entire (live and dead) population surveyed.

### *Indices of body condition*

Pectoralis mass covaried significantly with total length (body size;  $n = 40$ ,  $F = 9.85$ ,  $P = 0.003$ ). The covariance between lipid mass and body size (total length) was not significant ( $n = 43$ ,  $F = 2.62$ ,  $P = 0.113$ ).

Mean net body mass (without stomach contents) decreased by 17% between spring and autumn (Fig. 2; Table 3). When adjusted for body size, mean net body mass was significantly lower in autumn than in spring (Table 3;  $n = 40$ ,  $F = 5.34$ ,  $P = 0.026$ ). By comparison, the mean net body mass of beachcast shearwater carcasses collected in August was significantly lower than that of birds collected alive in autumn (mean

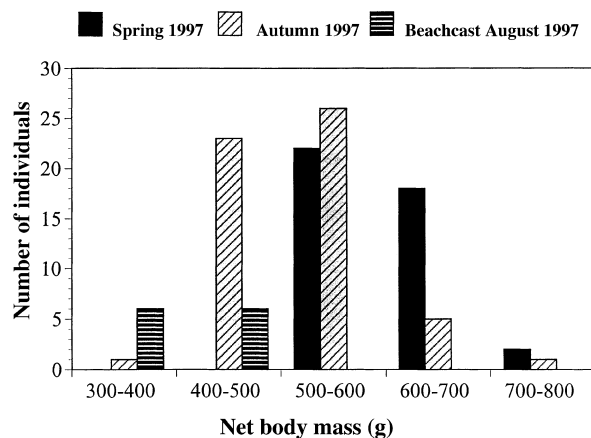
**Table 1.** Mean densities (birds  $km^{-2}$ ) of short-tailed shearwaters in the Nunivak Island and Slime Bank grids in spring and autumn during 1975–1981 and 1997. All behaviours (flying, sitting on the water, feeding) and only shearwaters feeding and sitting on the water are included. Historical data were combined from various sources (see Methods). Sample size ( $n$ ) indicates the number of 3 km transects surveyed in each area.

Site	Spring			Autumn		
	1975 to 1981 All behaviours	1997 All behaviours	1997 Feeding/ sitting on water	1975 to 1981 All behaviours	1997 All behaviours	1997 Feeding/ sitting on water
Nunivak Island						
Mean	0.67	0.19	0.01	39.09	32.61	3.53
SE	0.65	0.04	0.01	16.68	8.43	1.19
$n$	60	277	277	41	197	197
Slime Bank						
Mean	766.32	117.8	62.23	28.33	188.87	36.77
SE	623.87	24.4	17.85	0	50.08	11.59
$n$	32	94	94	1	70	70

Site (1997)	Live		Dead, autumn	
	Spring	Autumn	Actual number of carcasses sighted	Estimated number of carcasses floating
Nunivak Channel	NA	0	103	52 500 ± 17 000
Nunivak Island	2500 ± 500	402 500 ± 104 000	25	9 500 ± 2 000
Pribilof Islands	NA	348 500 ± 51 000	33	128 000 ± 26 500
Slime Bank	517 000 ± 107 000	828 500 ± 220 000	2	1 500 ± 1 000

**Table 2.** Estimated number of live and dead short-tailed shearwaters during spring and autumn 1997. Abundance of live and dead shearwaters was estimated in each of four subregions during autumn 1997, but only the number of live birds was estimated in two regions during spring 1997. Estimates include one standard error.

**Figure 2.** Frequency histogram of net body mass (without stomach contents) of short-tailed shearwaters in spring and autumn 1997 and beachcast short-tailed shearwaters from the south-eastern Bering Sea.



adjusted for body size,  $n = 66$ ,  $F = 14.99$ ,  $P < 0.001$ ; Table 3). The mean body mass of fresh beachcast carcasses collected during the die-off in 1997 (397 g) was similar to the mean body mass of beachcast carcasses collected during the 1983 mortality event in Alaskan waters (mean = 365 g; Nysewander and Trapp, 1984). Moreover, the mean net body mass in autumn 1997 was lower than that observed in the Bering Sea in previous, more typical years (historical mean for birds collected from July to August, 1970–1989, was 584 g,  $n = 129$ ; sources are Ogi *et al.*, 1980; Hunt *et al.*, 1996; and D.C. Schneider, unpublished data).

Lipid, as per cent fresh body mass, decreased by 46%, from 15.64% in spring, to 8.45% in autumn 1997 (Fig. 3). In autumn, 68% of shearwaters collected had lipid values  $\leq 10\%$ , whereas in spring, only 8% of

birds had  $\leq 10\%$  lipid content. There was also a significant decrease in lipid mass values after adjustment for body size (adj. mean spring = 87 g, adj. autumn mean = 54 g,  $n = 43$ ,  $F = 6.41$ ,  $P = 0.015$ ). Lipid values for beachcast carcasses were extremely low (mean = 0.76%), indicating that those individuals had completely consumed their lipid energy reserves (Fig. 3).

Breast muscle mass decreased by 16% between spring and autumn (Table 3). However, when adjusted for body size (using total length), mean pectoralis mass did not differ significantly between spring and autumn (Table 3; adjusted mean for spring and autumn,  $n = 40$ ,  $F = 0.19$ ,  $P = 0.663$ ).

The incidence of nematodes found in the stomach contents increased by 294% between spring and autumn collections (Fisher's exact test,  $n = 88$ ,  $P < 0.001$ ; Table 3).

#### Food habits and prey distribution and abundance

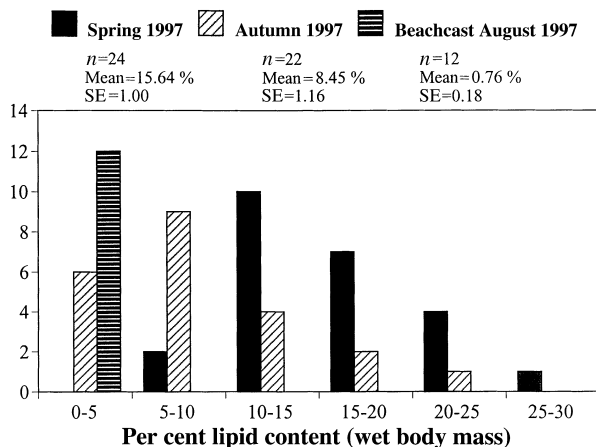
The diet of short-tailed shearwaters in the Slime Bank study area was broader in autumn than in spring 1997 (Table 4). In spring, adult euphausiids (*T. raschii*) occurred in 100% of the stomach contents collected (Table 4), most of them being mature females with spermatophores. In autumn 1997, however, the diet was dominated by juveniles of *T. inermis* and *T. spinifera*, and contained a variety of prey items including adult, mature *T. raschii* females, squid beaks, and crab megalops (Table 4). There were no foraging shearwaters available for collection at Nunivak Island in spring 1997, therefore no comparison was made between spring and autumn for the Nunivak Island grid. However, in autumn, female *T. raschii*, although rare, were more important at Nunivak Island than at Slime Bank.

**Table 3.** Net body mass, pectoralis mass, and frequency of nematodes in the stomach contents of short-tailed shearwaters during spring and autumn 1997, and beachcast 1997. Values presented are means, with sample sizes in parentheses. Values that are significantly different ( $P < 0.05$ ) between spring and autumn 1997, and spring and beachcast 1997, have an asterisk (\*).

Variable	Spring 1997 3–14 Jun	Autumn 1997 28 Aug–11 Sep	% Change, spring vs autumn	Beachcast
Net body mass (g) <sup>a</sup> (without stomach contents)	600 ± 9.0 (42)	515* ± 9.0 (54)	–17%	397* ± 12.3 (12)
Adjusted net body mass (g) (for variation owing to body size)	574 (9)	530* (33)	–8%	412*
Pectoralis mass (g) (one side of pectoralis muscle)	30.22 (10)	26.03* (33)	–16%	18.06*
Adjusted pectoralis mass (g) (for variation owing to body size)	28.76 (9)	27.92 (33)	–3%	19.28*
Frequency of nematodes in stomach	0.17 (42)	0.67* (46)	+ 294%	

<sup>a</sup>Standard errors are reported for net body mass values.

**Figure 3.** Frequency histogram of per cent lipid content (wet body mass without stomach contents) of short-tailed shearwaters in spring and autumn 1997, and in beachcast short-tailed shearwaters from the south-eastern Bering Sea.



The distribution and abundance of euphausiid prey changed dramatically between spring and autumn 1997 (Table 5, Fig. 4). In spring, adult *T. raschii* (males and females) were moderately abundant ( $> 90 \text{ m}^{-2}$ ) at Slime Bank, in nearshore surface waters. In autumn, adult *T. raschii* were scarce at both study sites ( $< 10 \text{ m}^{-2}$ ), although modest numbers were found in middle domain waters offshore of the Nunivak site. In autumn, most euphausiids captured were juveniles, especially *T. inermis* (Fig. 4). A striking exception was in autumn at Slime Bank, where we encountered a surface aggregation of *T. inermis* juveniles with a density of  $1000 \text{ km}^3$  at which 300 short-tailed shearwaters were

foraging. In 1997, we detected few epibenthic layers or patches of swarming euphausiids of any species using 43 kHz and 120 kHz echosounders.

Because there was an interaction in the trends of euphausiid abundance between Nunivak and Slime Bank, each area was treated separately for statistical comparisons between spring and autumn (overall euphausiid abundance decreased between spring and autumn at Slime Bank and increased at Nunivak). At Slime Bank, the abundance of euphausiids for the entire water column (number  $\text{m}^{-2}$ ) was significantly greater in spring (mean = 18.93) than in autumn (mean = 2.79; Table 5, posthoc nonparametric Tukey multiple comparison test,  $P < 0.01$ ). At Nunivak, euphausiid abundance (number  $\text{m}^{-2}$ ) for the entire water column was significantly less in spring (mean = 2.21) than in autumn (mean = 6.11; Table 5), and the abundance of euphausiid taxa differed significantly between spring and autumn (Fig. 4b). A posthoc Tukey test indicated that the abundance of juvenile *T. raschii* (mean = 10.77) was greater than that of *T. inermis* and *T. spinifera* juveniles combined (mean = 0.45  $\text{m}^{-2}$ ) in both spring and autumn ( $P < 0.002$ ). The abundance of *T. raschii* adults (mean = 4.55  $\text{m}^{-2}$ ) was also significantly greater than that of *T. inermis* and *T. spinifera* juveniles combined (both seasons) in the Nunivak grid (posthoc nonparametric Tukey multiple comparison test,  $P < 0.001$ ).

## DISCUSSION

In this paper, we used strip and line transect methods to estimate short-tailed shearwater abundance in



Table 4. Summary of prey items found in the stomach contents of short-tailed shearwaters collected in spring and autumn, 1997.

Prey species	Slime Bank						Nunivak		
	Spring			Autumn			Autumn		
	Percent number	Frequency of occurrence	Mean length (mm)	Percent number	Frequency of occurrence	Mean length (mm)	Percent number	Frequency of occurrence	Mean length (mm)
Euphausiids	1.00	1.00	19.23	0.78	0.76	13.13	0.99	0.69	23.17
<i>T. raschii</i>									
Females with spermatophores	0.75	1.00	20.18	0.006	0.21	19.37	0.75	0.69	24.01
Females without spermatophores	0.24	0.85		0.01	0.21		0.24	0.69	
Males	0.006	0.43	18.28	0.007	0.24	17.93	0.006	0.38	22.33
Juveniles	0	0		0.017	0.14	10.75	0	0	
<i>T. inermis</i>									
Juveniles	0	0		0.44	0.62	11.54	0	0	
<i>T. spinifera</i>									
Juveniles	0	0		0.30	0.41	11.83	0	0	
Other zooplankton									
Crab megalops	0	0		0.19	0.39		0	0	
Calanoid copepods	0	0		0.006	0.07		0	0	
Amphipods	0	0		0.004	0.18		0	0	
Squid beaks	0.004	0.43		0.004	0.29		0.01	0.38	
Fish remains									
Otoliths (pollock)	0	0		0.001	0.07		0	0.07	
Tissue and bones	0	0		0.07 <sup>a</sup>	0.1		0.01 <sup>a</sup>	0.15	
Sample size		21			29			13	
Wet weight (g), entire contents		77			12			56	

<sup>a</sup> Fish tissue quantified as percent weight of entire contents.

**Table 5.** Results of statistical analyses for euphausiid abundance at (a) Slime Bank and (b) Nunivak Island grids.

(a) Two-way nonparametric extension of Kruskal–Wallis abundance data (number per m <sup>2</sup> ) for euphausiids, Slime Bank					
Model:					
Independent variables	Season (autumn, spring)				
	Taxa ( <i>T. raschii</i> adults, <i>T. spinifera</i> juveniles, <i>T. inermis</i> / <i>T. raschii</i> juveniles combined)				
Dependent variable	Abundance (number per m <sup>2</sup> )				
	SS	d.f.	Total MS	H	P
Cells	74 962	5	540		
Factor 1 (season)	2 557	1		4.74	0.05
Factor 2 (taxa)	37 729	2		69.87	< 0.001
1 × 2 <sup>a</sup>					

(b) Two-way nonparametric extension of Kruskal–Wallis abundance data (number per m <sup>2</sup> ) for euphausiids, Nunivak Island					
Model:					
Independent variables	Season (autumn, spring)				
	Taxa ( <i>T. raschii</i> adults, <i>T. raschii</i> juveniles, <i>T. inermis</i> / <i>T. spinifera</i> juveniles combined)				
Dependent variable	Abundance (number per m <sup>2</sup> )				
	SS	d.f.	Total MS	H	P
Cells	75 132	5	414		
Factor 1 (season)	16 046	1		38.74	< 0.001
Factor 2 (taxa)	73 748	2		178.06	< 0.001
1 × 2 <sup>a</sup>					

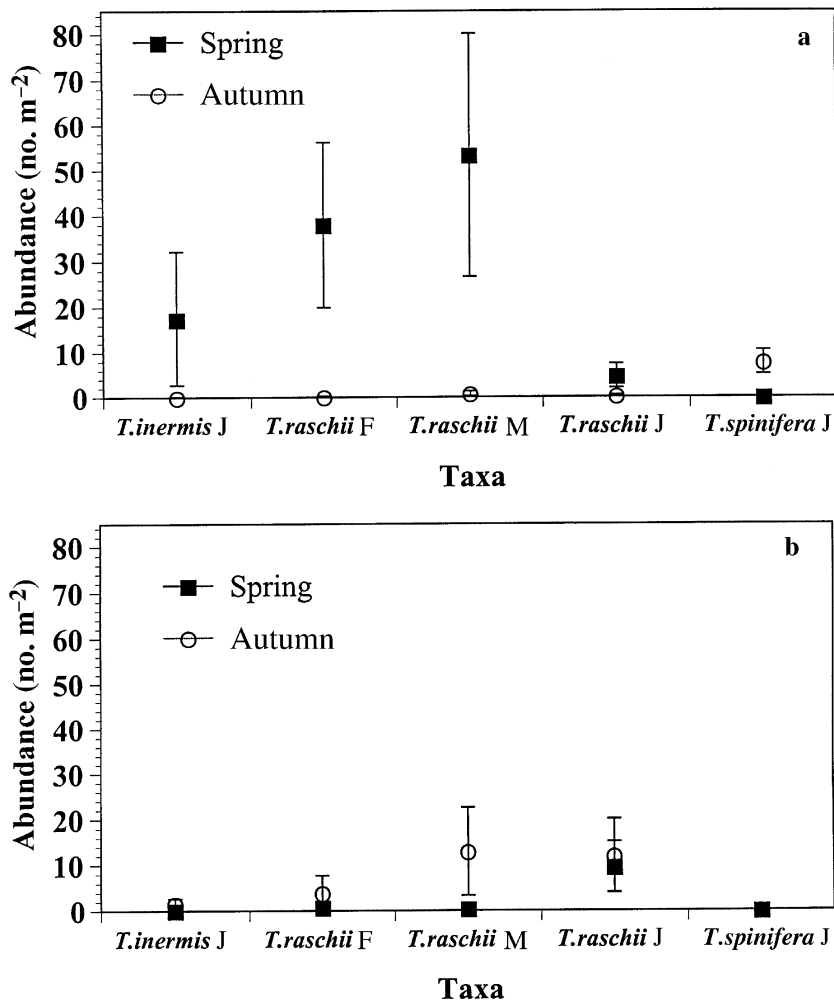
<sup>a</sup>Cannot test interactions in K–W ANOVA (Seaman *et al.*, 1994).

spring and autumn 1997, compared these estimates with historical records, and estimated the numbers of dead shearwaters afloat in our survey area during the autumn die-off. The strip transect observations of shearwaters were collected to determine short-term foraging patterns in relation to physical oceanographic features, and thus the data were not collected specifically for making a population estimate. The observations included flying birds, as well as birds that were feeding and on the water. Inclusion of flying birds in strip transect counts is a measure of bird flux and usually leads to an overestimation of the absolute density (Spear *et al.*, 1992). However, our data were collected using methods similar to those used in 1975–1981 and thus are appropriate for making interdecadal comparisons of population densities within the vicinity of our study grids.

The line transect methodology used to determine the number of floating carcasses in the study area was one of the first attempts to quantify mortality at sea using these methods. Because there are several fates of seabird carcasses at sea, including sinking, washing ashore, removal by scavenging, as well as floating (Bibby and Lloyd, 1977; Bibby, 1981; Threlfall and Piatt, 1983; Piatt *et al.*, 1990), we believe our estimates

of floating carcasses were conservative and probably underestimated the number of short-tailed shearwaters that died in our study area. Oceanographic currents and wind conditions also probably influenced the distribution of carcasses by concentrating or dispersing them in different areas. We attempted to account for this discrepancy by stratifying our effort and estimates into subregions of unique distribution. In particular, the Nunivak Channel was an area of exceptionally high density of floating carcasses, with 103 birds counted in the 55 km of strip surveyed. It is possible that this was the result of a convergence or of wind-driven concentration. In August 1998, in which another coccolithophorid bloom occurred and during which there was no die-off of shearwaters (Hunt *et al.*, 1999a), few carcasses were observed floating in the light-coloured, coccolith-filled waters in the same study area.

The first reports of dead shearwaters in the southeastern Bering Sea in 1997 occurred on about 1 August, and our at-sea observations began on 28 August. If the persistence-time of birds floating in the Bering Sea ranges from 10 to 20 days (Glenn Ford, pers. comm.), then a significant proportion of the carcasses may have sunk or washed ashore by the time our observations



**Figure 4.** Seasonal trends in mean abundance of euphausiid taxa collected in MOCNESS tows for (a) Slime Bank and (b) Nunivak Island. Taxa: *T. inermis* J, juvenile *T. inermis*; *T. raschii* F, adult female *T. raschii*; *T. raschii* M, adult male *T. raschii*; *T. raschii* J, juvenile *T. raschii*; and *T. spinifera* J, juvenile *T. spinifera*.

began. Indeed, the total count of beachcast short-tailed shearwater carcasses was  $\approx 400,000$ , double our estimate of 190 000 floating carcasses. The total for beachcast birds was obtained from a more extensive area with birds washing ashore on both sides of the Alaskan Peninsula, the Aleutians Islands as far west as Adak, Bristol Bay, the Pribilof Islands, and Cape Anadyr (Russia) as well as the eastern Chukchi Sea (unpublished data, USFWS, Anchorage, Alaska). At a minimum, the two estimates of mortality are additive ( $\approx 600\,000$ ). If 10% of all short-tailed shearwaters in the south-eastern Bering Sea died, the total mortality could have been as great as 2 million. Additional years of data will be necessary to determine if there has been a significant decrease in the numbers of shearwaters foraging over the inner shelf of the south-eastern Bering Sea.

Past mortality events of short-tailed shearwaters reported from the Japanese coast comprised mostly young-of-the-year individuals (Serventy, 1967; Oka

and Maruyama, 1986). In contrast, limited data on the ages of beachcast short-tailed shearwaters collected in the Bering Sea during summer 1997 suggest the majority were older than young-of-the-year. Of 46 birds examined, only 9 (19.6%) had detectable bursa (the presence of which indicates a young-of-the-year individual). Although the age of bursa regression in shearwaters is unknown, the age-structure of dead shearwaters in the Bering Sea clearly differed from that reported along the Japanese coast, with adults affected as well as immature birds.

The observed die-off of short-tailed shearwaters in the south-eastern Bering Sea in 1997 is unusual not only for its magnitude, but also for its timing and location. Most mortality events of short-tailed shearwaters have been documented from Japan and south-eastern Australia, when individuals had just completed a long transequatorial migration. Large-scale die-offs of short-tailed shearwaters in the south-eastern Bering Sea are infrequent, as this area usually provides

foraging opportunities for shearwaters once they have completed their migration. When die-offs have occurred in the Bering Sea and Gulf of Alaska, they were usually associated with warm water events, such as El Niño. Although indirectly related to an El Niño that began in the same year (Overland *et al.*, 2001), the warm water in 1997 was associated with an anomalous high atmospheric pressure system over the area which led to a blockage of storm events, insolation, and subsequent warming of the water column (Stabeno *et al.*, 2001). Our estimates of mortality in the south-eastern Bering Sea in 1997 were within the same order of magnitude as the 1983 die-off (tens of thousands to hundreds of thousands) and an order of magnitude greater than estimates made during die-offs that occurred along the Japanese coast during 1983–1985 (Oka and Maruyama, 1986).

It is probable that the die-off of short-tailed shearwaters in 1997 was caused by starvation. The lower body mass and lipid values, as well as the greater incidence of nematodes in the stomach contents observed during August/September, suggest that birds collected alive during the die-off were in poor condition and had difficulty obtaining their daily energetic requirements (Cherel *et al.*, 1988). The mean body mass of individuals captured alive during the die-off (515 g) was less than that observed for adults (559 g) first arriving at the breeding grounds in September after having completed migration (Lill and Baldwin, 1983). The mean body mass observed in autumn 1997 was also less than that observed for breeding adults in Tasmania in March (mean =  $652 \pm 56.2$  SD; Weimerskirch and Cherel, 1998).

The arrival of short-tailed shearwaters in the Bering Sea in early spring coincides with the timing and distribution of spawning adult euphausiids, especially *T. raschii*. Based on naupliar abundance in zooplankton tows collected across the south-eastern Bering Sea shelf, Smith (1991) suggested that the timing of euphausiid spawning progresses across the shelf coincident with the seasonal increase in temperature. Spawning begins 4–6 weeks earlier along the outer shelf than it does along the middle shelf. *T. raschii* does not begin spawning along the middle shelf until mid or late May, and initiates spawning along the inner shelf by late May or early June. The general anticlockwise pattern of shearwater movements once they reach the south-eastern Bering Sea follows the timing of surface swarms of spawning euphausiids (Guzman, 1981). Therefore, it is likely that the timing of arrival of short-tailed shearwaters in the Bering Sea would influence opportunities to forage on surface mating swarms of adult *T. raschii*.

A scarcity or unavailability of euphausiids in nearshore surface waters may have contributed to the starvation of short-tailed shearwaters. Although there was an increase in *T. raschii* from spring to autumn at Nunivak Island, the absolute numbers were trivial compared with their abundance at Slime Bank in spring and in areas where birds were foraging. Because adult *T. raschii*, and usually mature females with spermatophores, have dominated the diet of short-tailed shearwaters in the south-eastern Bering Sea (85% of the diet, Ogi *et al.*, 1980;  $\approx 100\%$  of diet, Hunt *et al.*, 1996), we expected to find a majority of adult *T. raschii* in the diet. However, in autumn, the diet broadened to include *T. inermis* juveniles, fish remains, and crab megalops. The lack of observations of foraging birds, particularly at Nunivak, supports the hypothesis that prey were less accessible, although some birds at Nunivak Island were eating *T. raschii* almost exclusively (Table 4).

Despite greater euphausiid abundance around the Pribilof Islands in 1997 than in 1995 and 1996 (Table 4; Stockwell *et al.*, 2001), significant mortality of short-tailed shearwaters occurred there. Three observations lead us to believe that euphausiids probably were unavailable to foraging shearwaters in the Pribilof Islands. Firstly, observations from acoustic surveys (120 kHz echosounder) conducted in the vicinity of the Pribilofs demonstrated that euphausiids were deeper in the water column in 1997 than in the previous 3 years (G. Swartzman, pers. comm.). Also, there was no evidence of surface concentrations of euphausiids or swarms in the upper water column in this region during daytime. Thirdly, water clarity inside the coccolithophore bloom was low (visibility 1–2 m) and turbidity extended to the bottom at inshore stations (R. Brodeur, pers. comm.). This turbidity would have made it difficult for shearwaters to see prey from the surface, and few birds were observed foraging there in August/September 1997.

Unusually high surface temperatures in 1997 may have caused a shift in the vertical distribution of euphausiids in the water column and influenced the timing of spawning, thereby affecting the availability of euphausiids to shearwaters. In the past, warm surface temperatures have been associated with reduced observations of euphausiids in the Bering Sea and in surface waters off Japan. During the anomalously warm, calm year of 1981 in the south-eastern Bering Sea (sea surface temperature had reached 10°C), euphausiid biomass was less ( $150 \text{ mg m}^{-2}$ ) on the inner shelf than at the same time in 1980 ( $400 \text{ mg m}^{-2}$ ; Smith, 1991), which was a year of cool water

temperatures. The Japanese fishery for *T. inermis*, a closely related species, operates actively in water temperatures between 4°C and 6°C, and stops when temperatures reach 7–8°C, presumably because swarming behaviour for mating ceases at that point (Hanamura *et al.*, 1989). Surface temperatures at mooring site M2 (fig. 1 in Stabeno *et al.*, 2001) on the Bering Sea middle shelf ranged between 10°C and 15°C during July and August 1997, compared with 7–11°C in 1995 and 1996 at the same site (Stabeno *et al.*, 2001). If *T. raschii* mating activity is also sensitive to high surface temperatures, then surface temperatures > 10°C in the south-eastern Bering Sea in summer 1997 may have caused an early termination of daytime, near-surface swarms, thus affecting availability of euphausiids to foraging shearwaters. However, warm surface temperatures (8–9°C) did not inhibit euphausiids from moving to the surface for nocturnal feeding in nearshore surface waters around the Pribilof Islands (Stockwell *et al.*, 2001).

Most shearwater carcasses were observed in the Nunivak Island area, within the extent of the coccolithophorid bloom (Vance *et al.*, 1998; Stockwell *et al.*, 2001). These small phytoplankton (5–20 µm) are surrounded by calcium carbonate plates (coccoliths), which reflect light and when abundant (Voss *et al.*, 1998), turn the water a milky white (Brown and Yoder, 1994). Although the relationship between shearwater mortality and the bloom remains unknown, there is evidence that light properties within the bloom probably had little influence on the ability of shearwaters to capture prey once swarms were located. Lovvorn *et al.* (in press) modelled underwater vision of short-tailed shearwaters and demonstrated that capture time and capture probability had a greater influence on intake rates than the amount of available light (PAR – photosynthetically active radiation) or the scattering and attenuation of light. Thus any change or reduction of light that occurred within the bloom probably did not influence the ability of shearwaters to capture prey, once found. However, the ability to see euphausiid swarms from the air, as opposed to feeding on them underwater, may still have been affected by optical properties of the bloom. Additionally, it is unlikely that the bloom itself was a source of shearwater mortality. There is no evidence that coccolithophorids are toxic to vertebrates, and the mortality event extended into waters unaffected by the bloom. Necropsies performed by a veterinary pathologist on fresh beachcast carcasses around the Pribilof Islands found low levels of microbial infection, and starvation was believed to be the most likely cause of death (Dr Terry Spraker, pers. comm.).

The unprecedented changes in the marine environmental conditions of the Bering Sea during 1997 may have affected other top predators in addition to short-tailed shearwaters. Unexpectedly poor runs and lower weights of sockeye salmon (*Oncorhynchus nerka*) returning to Bristol Bay also occurred in summer 1997 (Kruse, 1998). Sockeye salmon feed on euphausiids during the month they spend in the Bering Sea prior to spawning, and based on Nishiyama's (1972) determination of energetic requirements, 2.2 year-old sockeye are estimated to have a daily intake of euphausiids of 30–90 g day<sup>-1</sup> in Bristol Bay. The lower weights of sockeye salmon returning to Bristol Bay and the die-off of short-tailed shearwaters that occurred in 1997 may be related to a lack of available prey on the south-eastern Bering Sea shelf.

In 1997, anomalous weather patterns (Overland *et al.*, 2001) forced changes in the physical regime of the south-eastern Bering Sea (Stabeno *et al.*, 2001) that resulted in changes not only in hydrography, but also in the timing and fate of primary production (Stockwell *et al.*, 2001). These changes resulted in an early burst of near-surface primary production followed by late spring and summer production at depth (Stockwell *et al.*, 2001), conditions likely to favour the benthic community over the pelagic community (Grebmeier *et al.*, 1988). We do not know why euphausiids and other potential prey were absent in daytime from nearshore surface waters on the inner shelf of the south-eastern Bering Sea in summer 1997, but the result was starvation of one apex predator, the short-tailed shearwater, and possibly a lack of prey for salmon. If the unusually warm oceanographic conditions that occurred during summer 1997 are similar to conditions that may result from global climate change, our findings suggest that the ability of the south-eastern Bering Sea ecosystem to support large populations of migrating shearwaters, and possibly other predators of euphausiids, may be reduced.

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