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Distribution of foraging shearwaters relative to inner front of SE Bering Sea

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ABSTRACT: We examined the hypothesis that short-tailed shearwaters *Puffinus tenuirostris* aggregate to forage at the inner front of the SE Bering Sea because of enhanced production there. We tested this hypothesis by comparing primary production, the distribution of euphausiids and the distribution of shearwaters relative to the front during late spring and late summer/early fall of 1997, 1998 and 1999. We found enhanced primary production at the front and offshore of the front during summer but not during spring. Primary production varied between seasons and years. Major differences were related to anomalous conditions in 1997 and 1998. The density of euphausiids was higher at the front and offshore of the front during summer, but there were no differences among regions during spring. Foraging shearwaters aggregated in high densities at the front during summer, but foraged close to shore during spring. At the front, shearwaters foraged on euphausiids *Thysanoessa raschii* and *T. inermis* as expected, and on copepods that accumulated in the area. The proportion of zooplankton consumed at the front decreased from summer 1997 to summer 1999, while consumption of sandlance *Ammodytes hexapterus* at this feature increased. Our results show that, during summer, the inner front supports aggregations of euphausiids and their seabird predators. The means by which the frontal system supports enhanced production and the subsequent trophic transfers is dependent on the availability of nutrients at depth in the frontal region and the aggregation of small zooplankton organisms in this feature.

KEY WORDS: Short-tailed shearwater · *Puffinus tenuirostris* · Euphausiids · *Thysanoessa raschii* · *Thysanoessa inermis* · Seabird foraging · Fronts · Bering Sea

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INTRODUCTION

Seabirds and other higher trophic-level organisms are known to aggregate and make use of the enhanced production that usually occurs at tidal fronts (Pingree et al. 1974, Schneider 1982, Hunt et al. 1996, 1999c, Begg & Reid 1997, Durazo et al. 1998). Increased production at fronts may not always be the case, and at least 1 front has been shown to have decreased production and not to be important for the successful foraging of seabirds and other predators (Caldeira et al. 2001). The purpose of this paper was to test the hypothesis that foraging short-tailed shearwaters *Puffinus tenuirostris* aggregate at the inner front of the

SE Bering Sea to prey on euphausiids aggregating to feed on the enhanced primary production expected to occur in this feature during summer.

Millions of short-tailed shearwaters migrate each year across the equator from their breeding grounds in southern Australia and Tasmania to winter in the North Pacific and the Bering Sea (Marshall & Serventy 1956, Warham 1990). Birds arrive in the SE Bering Sea early in the spring, and by mid-May (Schneider & Shuntov 1993, Shuntov 1993) thousands are found in Bristol Bay (see Fig. 1), where they are the most abundant seabird during summer (Hunt et al. 1981b). Short-tailed shearwaters are often associated with areas of strong tidal shears (Schneider & Shuntov 1993). This

species congregates in high numbers in the vicinity of the 50 m isobath (Hunt et al. 1981b, Schneider & Shuntov 1993), which corresponds to the location of a tidal front (i.e. the inner front; Schumacher et al. 1979, Coachman 1986, Stabeno et al. 2001, Kachel et al. 2002). In the past, shearwaters in Bristol Bay foraged primarily on the euphausiids *Thysanoessa raschii* and *T. inermis* (Ogi et al. 1980, Hunt et al. 1981a, 1996, 2002, Schneider et al. 1986), which are abundant in this area (Vidal & Smith 1986, Smith 1991, Coyle & Pinchuk 2002a). The predominately coastal distribution of short-tailed shearwaters in Bristol Bay and the SE Bering Sea has been hypothesized to be the result of birds being attracted to large surface concentrations of euphausiids feeding on phytoplankton patches associated with the inner front (Hunt et al. 1996).

The inner front is a structural front that separates the stratified waters of the middle domain from the mixed waters of the coastal domain of the SE Bering Sea (Kachel et al. 2002). The stratification of middle domain water is maintained by heating and wind-mixing of the top layer and tidal-mixing of the bottom layer (Iverson et al. 1979a, Kachel et al. 2002). Surface and tidal-mixing depths converge shoreward of the 50 m isobath, producing a well-mixed water mass where bottom waters are constantly stirred upwards (Iverson et al. 1979a, Kachel et al. 2002).

The abundance of nutrients and incident radiation over the SE Bering Sea supports high levels of primary production early in the spring (Iverson et al. 1979a,b). After the spring bloom, nutrients become limiting and the phytoplankton maximum occurs at 30 m where a chlorophyll maximum persists into the fall (Iverson et al. 1979a, Kachel et al. 2002). Early in summer, nutrients are usually exhausted in the upper mixed layer, although a large reservoir exists below it (Kachel et al. 2002). Nutrients are replenished in the euphotic zone by intense storms that break down the stratification of the water (Iverson et al. 1974, Sambroto et al. 1986, Kachel et al. 2002), and tidally induced vertical mixing at the inner front that supports local phytoplankton blooms in the summer (Iverson et al. 1974, Sambroto et al. 1986, Hunt et al. 1996, Kachel et al. 2002).

Tidal currents over shallow topography provide a continuous source of nutrients that are mixed back into the water column and can stimulate phytoplankton production (Holligan 1981, Mann & Lazier 1996). Tidally generated fronts, such as the inner front, separate well-stratified waters from well-mixed waters over shallow continental shelves during summer (Holligan 1981, Mann & Lazier 1996, Maguer et al. 2000). Offshore of these fronts, primary production nearly ceases after nutrients are depleted by the spring bloom (Pingree et al. 1976). Inshore of these fronts, a nutrient-rich system develops if the well-mixed water is suffi-

ciently deep, and light-limited phytoplankton never fully depletes its nutrients (Holligan 1981). A nutrient-poor system, such as that in the Bering Sea, develops if the well-mixed water is shallow and nutrients are depleted by the phytoplankton (Holligan 1981, Walsh & McRoy 1986). Characteristically, there is a higher biomass of phytoplankton at tidal fronts than in well-stratified or well-mixed waters (Pingree et al. 1975, Holligan 1981, Maguer et al. 2000). Vertical mixing processes and the relative stabilization of the water column offshore of the front maintain favorable conditions for maximum phytoplankton growth rates in these areas (Pingree et al. 1974, Fogg 1984, Fogg et al. 1985, Le Fevre 1986). The high productivity characteristic of tidal fronts is reflected by an abundance of higher trophic-level organisms such as predatory fishes, seabirds and marine mammals (Pingree et al. 1974, Schneider 1982, Hunt et al. 1996, 1999c, Begg & Reid 1997, Durazo et al. 1998).

In this study, we investigated the role of the inner front of the SE Bering Sea as a feature of the marine environment important for successful foraging by shearwaters. We predicted that foraging short-tailed shearwaters would aggregate at the inner front of the SE Bering Sea to prey on euphausiids feeding there on the enhanced primary production that is expected to occur in this physical feature subsequent to the spring bloom. To test this hypothesis, we measured the distribution and abundance of shearwaters, euphausiids and primary production at and away from the inner front of the SE Bering Sea.

MATERIALS AND METHODS

Study area. We studied the distribution of foraging short-tailed shearwaters relative to the inner front of the SE Bering Sea by conducting multiple crossings of the front in 4 predetermined grids located off Slime Bank, Port Moller, Cape Newenham and Nunivak Island (Fig. 1). Grid areas consisted of 1 to 5 transect lines running perpendicular to the bathymetry from nearshore to beyond the 50 m isobath. Cruises were carried out in late spring (May to June), and late summer/early fall (July to September), during 3 consecutive years (1997 to 1999). During each cruise, the physical structure of the water, primary productivity, euphausiid distribution and shearwater distribution and diet were determined.

A recognizable inner front was found in 41% out of 83 CTD transects occupied during the inner front project (Kachel et al. 2002). In these cases the location of the inner front was taken from Kachel et al. (2002), who defined the inner edge of the front as 'the seawardmost location where the maximum gradient in

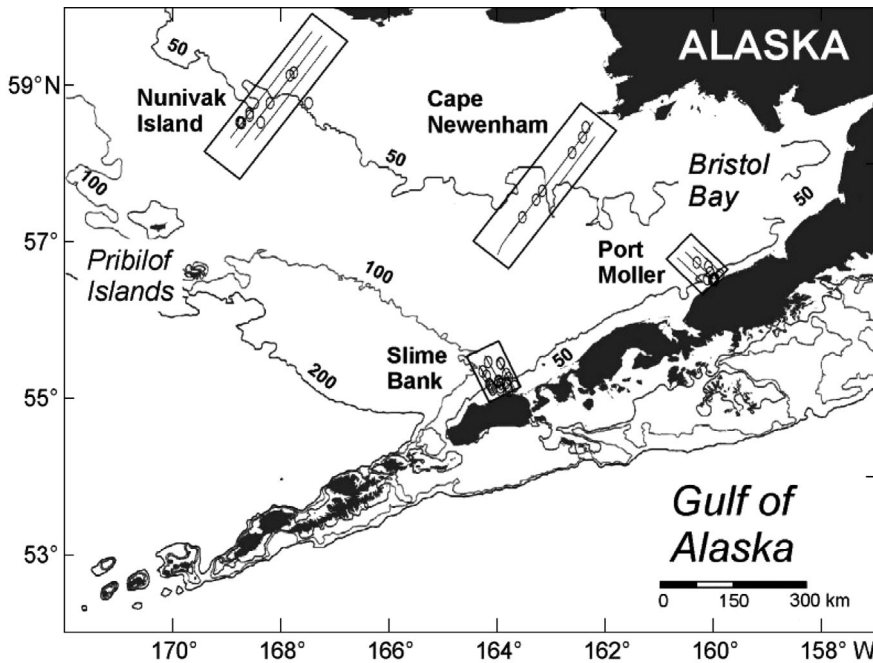


Fig. 1. SE Bering Sea, showing location of study areas at Nunivak Island, Cape Newenham, Port Moller and Slime Bank. Transect lines surveyed in each grid area are shown; (o) locations where shearwaters *Puffinus tenuirostris* were collected for stomach-content analysis

temperature by depth was less than $0.05^{\circ}\text{C m}^{-1}$ and the outer edge of front as the location where the maximum gradient in temperature by depth becomes less than one-half the greatest value observed on that grid of stations and less than 1°C m^{-1} . The mean distance from the coast and depth of the outer and inner edges of the inner front in each grid area are shown in Table 1. We used both the mean location and the precise location of the front to divide transects into regions (i.e. inshore, mean front, offshore) and to study the importance of processes at the front relative to the nearby non-frontal regions.

Primary productivity. Primary production was measured using ^{14}C uptake rates from a combination of incubator and *in situ* experiments. Water samples were collected using Niskin bottles at multiple depths. Primary productivity rates were estimated using ^{14}C -labelled bicarbonate. Incubations were carried out in triplicate under controlled temperature and different light intensities (Zeeman & Jensen 1990a,b). Primary production rates were calculated using light-dark counts, and normalized to chlorophyll *a* concentrations (Parsons et al. 1984). Water-column productivity rates were estimated from the uptake mea-

surements, chlorophyll profiles, and light attenuation in the water column using a numerical integration model (Zeeman & Jensen 1990a,b). Daily *in situ* production was estimated using chlorophyll-specific production as a function of light from the incubations plus *in situ* measurements of irradiance and chlorophyll (Zeeman 1992). Photosynthesis versus irradiance functions and chlorophyll *a* determinations were obtained as described by Stockwell et al. (2001). *In situ* experiments consisted of duplicate light and dark bottles, identical to those used in the incubator experiment, suspended in groups of 4 at 6 depths from the surface to 40 m. These bottles contained 5 to 10 μCi of ^{14}C . Incubations proceeded for 1 h or less, and then the bottle string was retrieved and samples filtered and counted in a manner similar to that used for the incubator samples. The *in situ* measurements were used as independent measurements to verify the incubator estimates.

Distribution of euphausiids. Euphausiid abundance and distribution were determined with acoustic surveys using a Hydroacoustic Technology (HTI) Model 244 split-beam digital system. Data were collected using a 43 kHz 7° split-beam and 120 kHz 6° split-beam transducers. The transducers were towed beside the vessel at about 3 m s^{-1} in a dead-weight tow body about 4 m from the hull and 2 m below the surface. Sampling was mostly done during the day and restricted to calm conditions when noise due to surface bubbles and waves were not observed in the data. These data were first processed to eliminate noise and to scale the volume-scattering at 43 and 120 kHz to biomass using sound-scattering models (Coyle & Pinczuk 2002a). Euphausiid density in mg m^{-3} was then

Table 1. Mean (\pm SD) distance from coast and depth of outer and inner edges of inner front of SE Bering Sea. Numbers in parentheses: number of times edges of inner front were observed during transect runs

Area	Outer edge		Inner edge	
	Distance (km)	Depth (m)	Distance (km)	Depth (m)
Slime Bank	26 \pm 11 (15)	73 \pm 17 (15)	15 \pm 12 (12)	48 \pm 17 (12)
Port Moller	29 \pm 9 (6)	56 \pm 8 (6)	7 (1)	24 (1)
Cape Newenham	146 \pm 22 (9)	50 \pm 4 (9)	110 \pm 49 (9)	44 \pm 6 (9)
Nunivak Island	169 \pm 14 (25)	54 \pm 5 (25)	132 \pm 33 (16)	44 \pm 7 (16)

determined for every 180 m interval in 1997, and for 45 m intervals in 1998 and 1999, at vertical intervals of 1 to 2 m. We transformed densities into biomass and integrated it from the bottom to the surface, producing estimates of the total amount of euphausiids in the water column.

Distribution of shearwaters. Counts of shearwaters and other birds were made from the bridge of the RV 'Alpha Helix' (eye level = 7.7 m above the sea surface) while the ship was underway. Vessel speed varied from about 11 km h⁻¹ while conducting acoustic surveys to about 19 km h⁻¹ when cruising between oceanographic stations. Birds were counted continuously during daylight hours in a 300 m arc from directly ahead of the vessel to 90° off the side with best visibility (i.e. lowest glare) and logged into a portable computer. Each separate entry in the computer of 1 or more birds was considered a flock. 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). Shearwater behaviors were recorded as flying, sitting on the water, and feeding; for the purpose of this analysis, we assumed that birds sitting on the water had previously fed in the vicinity of where they were resting.

Seabird counts were carried out during CTD and acoustic transects, and unless one of the transects was at night, a minimum of 2 seabird data sets existed for each transect line. Seabird counts during CTD transects were interrupted every 25 min, for about 30 min after arriving at oceanographic stations. Acoustic transects were carried out without interruption and may provide a better representation of seabird distribution along the transect lines. Seabird counts from CTD transects were included when counts from acoustic transects were not available (i.e. transects were done at night). Seabird density (birds km⁻²) was determined by dividing the number of seabirds and flocks by the number of kilometers surveyed.

Diet composition of shearwaters. We determined the diet composition of shearwaters by shooting 3 to 8 birds per flock from flocks of birds that were foraging within each grid area. We limited our collections to foraging birds so that we could be certain that the birds had obtained their prey near to the place at which we collected them. Upon collection, proventriculus contents were removed, weighed and preserved in 80% ethanol. Wet weight of alcohol-preserved specimens, their displacement volume, and direct counts were used to determine the diet of individual birds, as described in Hunt et al. (2002). We assumed that individuals shot at the same location were not independent, and estimated diet composition by averaging the prey-

type volumes and prey-item numbers for birds from the same collection. We determined the proportion of prey types by volume and the proportion of zooplankton organisms by number for each bird collection. We transformed all data into proportions to avoid the possibility that a few individual birds with large amounts of one particular prey would disproportionately influence the assessment of overall diet composition.

Data analysis. We divided all transects into regions, determined by the location of the edges of the front, and calculated the euphausiid biomass and number of shearwaters in each region to examine whether prey and birds were being attracted to the front. We used (1) the mean distance from the coast to the outer and inner edges of the inner front to divide all transects into regions (i.e. mean frontal region, MFR), and (2) the exact location of the edges of the front (Kachel et al. 2002) to divide the corresponding transects into regions (i.e. precisely defined fronts, PDF). The latter include seabird surveys conducted while towing acoustic equipment along the same transect within 2 d of the date when the exact location of the front was determined. In these cases we assumed that oceanographic conditions and the location of the front had not changed. We also assigned primary production estimates and bird-diet collections to regions determined by the mean location of the front (Table 1).

We used Kruskal-Wallis 1-way analysis of variance to compare the rate of primary production between regions determined by the mean location of the front. We used the Wilcoxon matched-pairs signed-ranks test to compare the density of euphausiids and seabirds among inshore, front and offshore regions. We used the euphausiid biomass in a 1 m² column of water and the number of shearwaters feeding and sitting on the water in 1 km², averaged over the whole length of the region, as the measure of euphausiid and shearwater density, respectively. We used regression analysis to examine whether euphausiids (log-transformed) aggregate in larger densities at the narrower fronts, and Kruskal-Wallis 1-way analysis of variance and Mann-Whitney *U*-tests to compare distance from the coast of large aggregations of foraging shearwaters and the diet composition of shearwaters in habitat regions determined by the location of the front. We sampled the location of the large aggregations of shearwaters by sorting all 1 km bins within each grid area by their number of shearwaters, and separated all bins with highest values needed to account for 90% of the total number of shearwaters observed each season, this comprised 133 of 5701 bins in spring and 131 of 4333 bins in summer.

We used the utilization test to examine the significance of euphausiid and shearwater aggregations in 3 habitat regions—offshore of the front, within the

frontal area and inshore of the front (Haney & Solow 1992). We compared the non-overlapping transect regions previously determined using the MFR and PDF. The width of the frontal region was determined by Kachel et al. (2002). The length of the non-frontal region varied according to the location and length of transects. Assuming a uniform distribution of shearwaters along each transect, we calculated an expected value for the number of shearwaters and flocks of shearwaters that should have occurred within each transect region. This expected value was based on the total number of shearwaters and flocks of shearwaters counted along the transect and the amount of survey effort (k surveyed) spent in each region. Observed values were compared to expected values and 95% confidence intervals were constructed according to the methods of Neu et al. (1974) for the observed proportions of birds for a Type I error rate of $\alpha = 0.05$. We conducted these analyses on data pooled by season, year and grid area.

We used a permutation analysis (Riehle et al. 2001) to determine the location of the significant aggregations of euphausiids along the transects, and determined the observed density of euphausiids within a 5 km sliding window that moved throughout the series of data. Expected density of euphausiids and confidence intervals were obtained by a permutation testing procedure. The mean, variance and 95% confidence intervals in the expected density of euphausiids were calculated over 500 random permutations of the order of 500 bins sampled from the remaining length of the transect.

RESULTS

Late spring conditions

Neither enhanced primary production nor euphausiid aggregations were found at the inner front during late spring (Table 2). The rate of primary production at the mean front was not significantly different than elsewhere along the transect (Kruskall-Wallis statistic = 0.754, $df = 2$, $n = 52$, $p = 0.686$). Although the density of euphausiids at the MFR was significantly higher than elsewhere along-transect in 10 out of 21 (48%) transects, and at the PDF in 9 out of 11 (82%) fronts (uti-

Table 2. Mean (\pm SE) primary production, density of euphausiids (*Thysanoessa* spp.) and abundance of shearwaters *Puffinus tenuirostris* relative to inner front of SE Bering Sea, analyzed using mean frontal regions or precisely defined fronts. Numbers in parentheses: number of transect lines included in analysis

Region	Primary production (mg C m ⁻² d ⁻¹)	Euphausiid density (g m ⁻²)	Shearwater abundance (birds km ⁻²)	Flock abundance (flocks km ⁻²)
Mean frontal region				
Spring				
Inshore	256±68 (19)	3.36±0.81 (19)	25.3±14.7 (22)	2.3±1.0 (22)
Front	437±181 (14)	4.68±1.21 (21)	6.1±2.8 (34)	0.5±0.2 (34)
Offshore	437±124 (19)	6.28±1.25 (19)	0.1±0.03 (34)	0.1±0.02 (34)
Summer				
Inshore	262±86 (11)	0.50±0.12 (8)	26.4±17.0 (16)	2.1±1.3 (16)
Front	789±251 (12)	1.60±0.29 (8)	72.0±59.9 (22)	1.9±0.7 (22)
Offshore	1106±303 (18)	1.85±0.34 (8)	9.2±6.5 (17)	0.5±0.3 (17)
Precisely defined front				
Spring				
Inshore	–	4.25±1.20 (9)	32.9±32.1 (8)	0.7±0.4 (8)
Front	–	4.55±1.14 (11)	7.6±4.8 (10)	0.5±0.3 (10)
Offshore	–	5.66±1.25 (10)	0.0±0.0 (7)	0.0±0.0 (7)
Summer				
Inshore	–	0.42±0.20 (6)	31.0±22.3 (8)	4.1±1.8 (8)
Front	–	1.62±0.30 (8)	21.0±10.4 (14)	1.3±0.5 (14)
Offshore	–	1.80±0.36 (8)	10.4±7.6 (13)	0.6±0.3 (13)

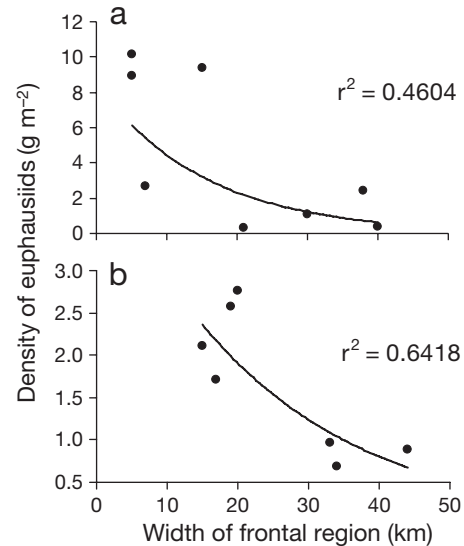


Fig. 2. *Thysanoessa* spp. Density as function of width of precisely defined fronts (PDF) identified in (a) spring and (b) summer cruises

lization test, $p < 0.05$), no statistical differences in density of euphausiids were found between regions in the spring, whether we used MFR or PDF for analyses (Wilcoxon matched-pairs signed-ranks statistic, $p > 0.05$). The density of euphausiids was not significantly higher in the narrower PDF (Fig. 2a, $r^2 = 0.460$, $F = 5.119$, $p = 0.064$, $n = 8$). Significant aggregations of euphausi-

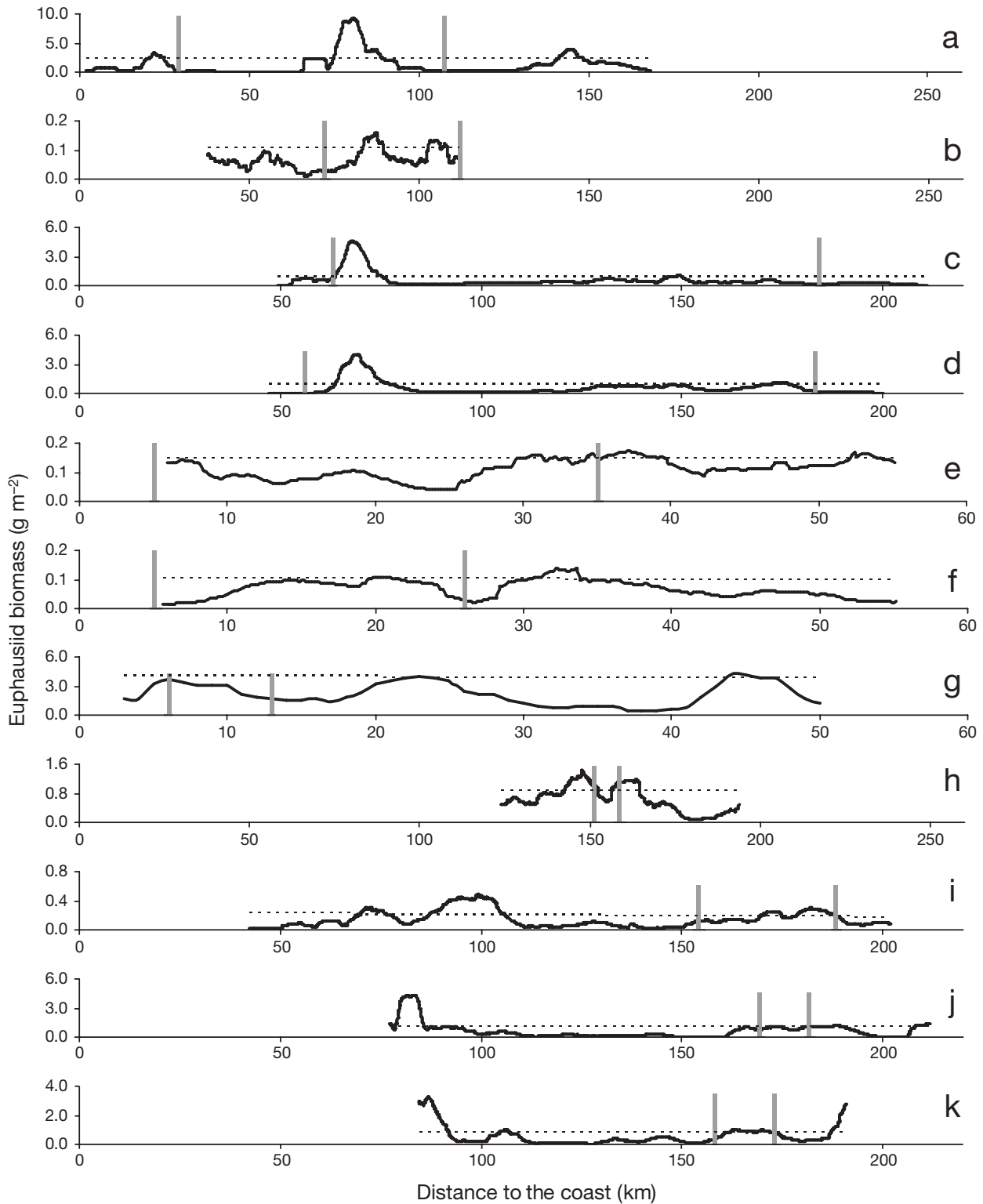


Fig. 3. *Thysanoessa* spp. Distribution of biomass in spring of (a–g) 1997, (h,i) 1998, and (j,k) 1999 along transects in which inner and outer edges of frontal region (as defined by Kachel et al. 2002) were observed. Shaded bars represent inner (on left) and outer (on right) edges of front; dotted line: 95% confidence interval (data above this line are considered significant aggregations). (a) Cape Newenham C; (b) Cape Newenham E; (c) Nunivak Island C2; (d) Nunivak Island E; (e) Port Moller A; (f) Port Moller C; (g) Slime Bank C; (h) Cape Newenham C; (i) Nunivak Island C; (j) Nunivak Island C; (k) Nunivak Island E

ids occurred within the PDF in 5 out of 11 transect lines (45%); no clear spatial pattern in the location of these aggregations was found (Fig. 3).

Aggregations of foraging short-tailed shearwaters were found inshore of the inner front during late spring (Table 2). The mean density of shearwaters feeding and sitting on the water inshore of the MFR was 4 times the density of shearwaters found foraging at the MFR. The number of birds and flocks at the MFR was significantly higher than elsewhere along transect in 24 and 22% of the 41 transects and at the PDF in 20% of the 10 fronts, respectively (utilization test, $p < 0.05$). No statistical differences in density of foraging shearwaters were found between the inshore and the MFR (Wilcoxon matched-pairs signed-ranks statistic = 0.314, $n = 41$, $p = 0.754$), and significantly higher densities of foraging shearwaters were found inshore and at the MFR than offshore of this feature (Wilcoxon matched-pairs signed-ranks statistic, $n = 41$, $p < 0.05$). The numbers of flocks of shearwaters showed similar patterns (Wilcoxon matched-pairs signed-ranks statistic, $n = 41$, $p < 0.05$).

Zooplankton, particularly euphausiids, were the main prey consumed by short-tailed shearwaters foraging in the inner domain of the SE Bering Sea during late spring. Zooplankton represented, on average, 75% by volume of the prey consumed in spring, the remainder of their prey was fishes. The proportion of zooplankton in the diet decreased from 100% by volume in spring 1997 to 50% by volume in spring 1999 (Fig. 4a); conversely, the proportion of sandlance *Ammodytes hexapterus* increased during the same period. The most important zooplankton consumed were euphausiids, representing 95% by number of the items consumed (Fig. 4b). The euphausiid *Thysanoessa raschii* was the most common prey item found in the diet, and its consumption decreased from 96% by number in spring 1997 to 38% in spring 1999. The proportion of *T. inermis* in the diet increased over the same period to 38% by number during spring 1999.

Late summer and early fall conditions

We found enhanced primary production at the inner front and offshore of the front during late summer and early fall (Table 2). However, the mean rate of primary production at the MFR was not significantly different than elsewhere along the transect (Kruskall-Wallis statistic = 4.143, $df = 2$, $n = 41$, $p = 0.126$). Primary production rates at the MFR were intermediate compared to the low production observed inshore of the front and the high production observed offshore of this feature. Significant differences in the rate of primary production between years confounded our results (Kruskall-

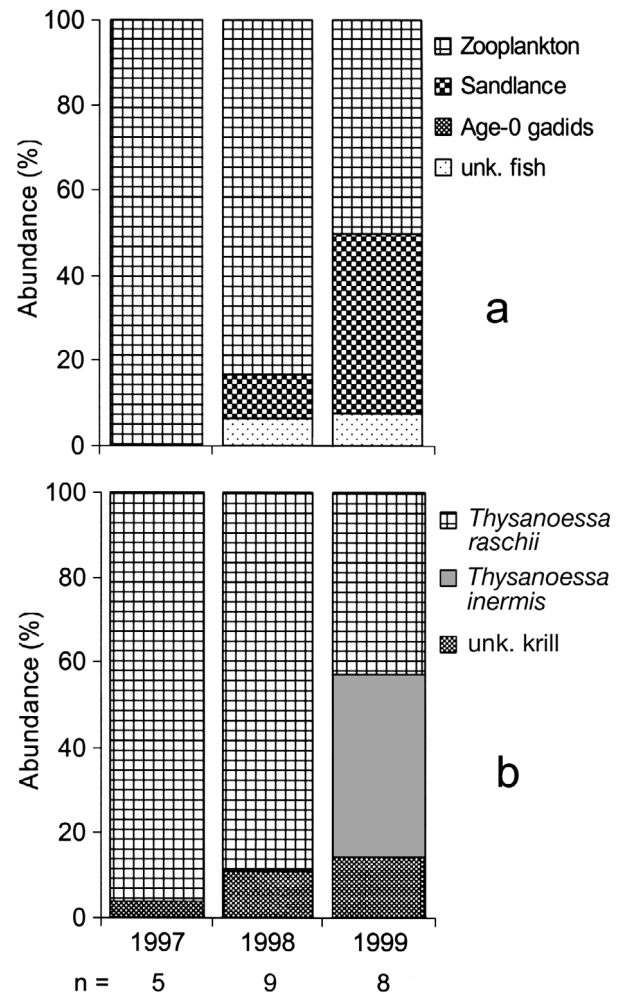


Fig. 4. *Puffinus tenuirostris*. Diet composition in spring. (a) Relative consumption of major prey types (by volume); (b) consumption of main zooplankton organisms (by number). n: sample size for each year; unk: unknown (i.e. unidentified)

Wallis statistic = 26.045, $df = 2$, $n = 41$, $p < 0.001$). In the summers of 1997 and 1998, no significant differences in the rate of primary production were found between regions (Kruskall-Wallis statistic, $df = 2$, $p > 0.05$); in summer 1999, the rate of primary production was significantly higher at the front and offshore of the front than inshore of this feature (Kruskall-Wallis statistic = 8.697, $df = 2$, $n = 16$, $p = 0.013$).

Aggregations of euphausiids were found at the inner front and offshore of the front during late summer and early fall (Table 2). The density of euphausiids at the MFR was significantly higher than elsewhere along-transect in 6 out of 8 (75%) transects surveyed, whether we used MFR or PDF for analyses (utilization test, $p < 0.05$). The density of euphausiids inshore of the front was significantly lower than in the MFR and offshore regions (Wilcoxon matched-pairs signed-

ranks statistic, $n = 8$, $p < 0.05$) and there were no significant differences in density of euphausiids between the MFR and the offshore region (Wilcoxon matched-pairs signed-ranks statistic = 0.280, $n = 8$, $p = 0.779$). The density of euphausiids was significantly higher in the narrower PDF (Fig. 2b, $r^2 = 0.713$, $F = 12.420$, $p = 0.017$, $n = 7$). Aggregations of euphausiids were found near the offshore end of the PDF in 6 out of the 8 transects for which acoustic data were available (Fig. 5).

Foraging short-tailed shearwaters aggregated at the inner front of the SE Bering Sea during late summer

and early fall (Table 2). The mean density of shearwaters feeding and sitting on the water at the MFR was about 3 times the density of shearwaters foraging inshore of the front. The number of birds and flocks was significantly higher at the MFR in 25 and 17% of the 24 transects and at the PDF in 47 and 20% of the 15 fronts, respectively (utilization test, $p < 0.05$). There were no statistically significant differences in density of foraging shearwaters between the inshore and the MFR (Wilcoxon matched-pairs signed-ranks statistic = -6.222 , $n = 24$, $p = 0.539$). The density of foraging

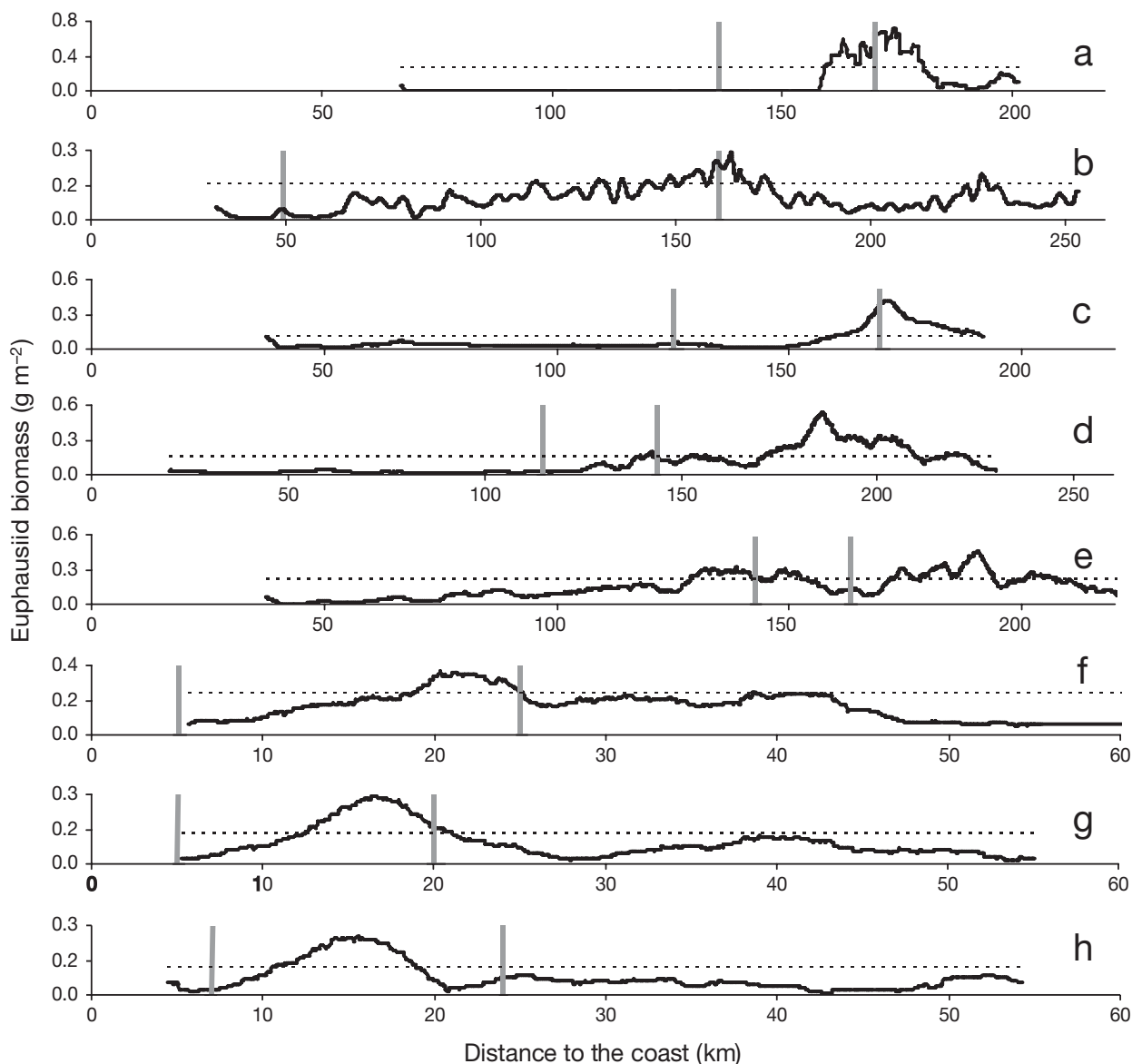


Fig. 5. *Thysanoessa* spp. Distribution of biomass in summer of (a) 1997, (b,c) 1998 and (d–h) 1999 along transects in which inner and outer edges of frontal region (as defined by Kachel et al. 2002) were observed. (a) Nunivak Island C2; (b) Cape Newenham C2; (c) Nunivak Island C2; (d) Cape Newenham C1; (e) Nunivak Island C1; (f) Port Moller A; (g) Port Moller C; (h) Port Moller E. Further details in Fig. 3 legend

shearwaters at the MFR was 8 times that of birds foraging offshore of the front and this difference was significant (Wilcoxon matched-pairs signed-ranks statistic = -1.956 , $n = 24$, $p = 0.05$). The number of flocks of shearwaters showed patterns that were similar to that of densities among regions (Wilcoxon matched-pairs signed-ranks statistic, $n = 24$, $p < 0.05$).

Short-tailed shearwaters foraged at greater distances from the coast during late summer and early fall (Fig. 6). The seasonal differences in distance from the coast of foraging aggregations were statistically significant in Nunivak Island, Cape Newenham and Slime

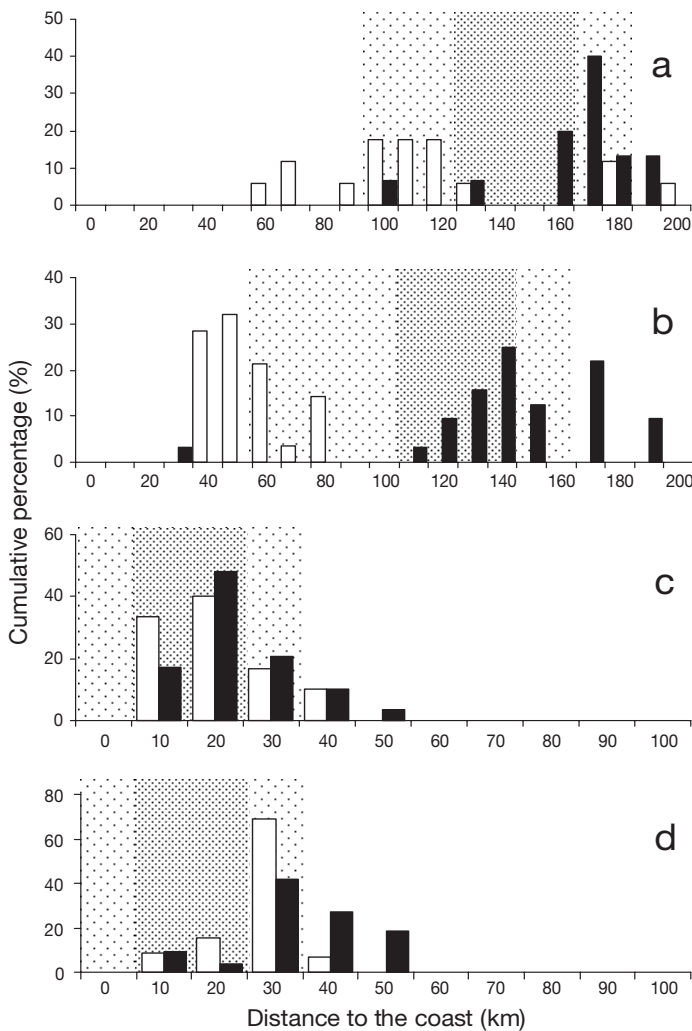


Fig. 6. *Puffinus tenuirostris*. Distance to coast of large aggregations (90% of total foraging seabirds) in spring (open bars) and summer (black bars). Dark-shaded area: extent of mean frontal region; light-shaded area: extent of maximum frontal region which includes 1 SD added at each edge (Table 1). (a) Nunivak Island ($n_{spring} = 17$, $n_{summer} = 15$); (b) Cape Newenham ($n_{spring} = 28$, $n_{summer} = 32$); (c) Port Moller ($n_{spring} = 30$; $n_{summer} = 29$); (d) Slime Bank ($n_{spring} = 58$; $n_{summer} = 55$)

Bank (Mann-Whitney U -test, $p < 0.05$), where short-tailed shearwaters foraged closer to the coast in spring and away from the coast in the summer. The location of foraging aggregations in summer coincided with the MFR, with a peak in bird numbers near the outer edge of the front (Fig. 6).

The use of the inner front by foraging short-tailed shearwaters during late summer and early fall varied greatly between years. There were more shearwaters foraging at the MFR than expected by chance in 1997 and 1999 and less than expected in late summer and early fall 1998 (utilization test, $p < 0.05$). There were no differences in the number of flocks of shearwaters between regions in 1997 and 1999, and significantly fewer flocks foraging at the front in 1998 (utilization test, $p > 0.05$).

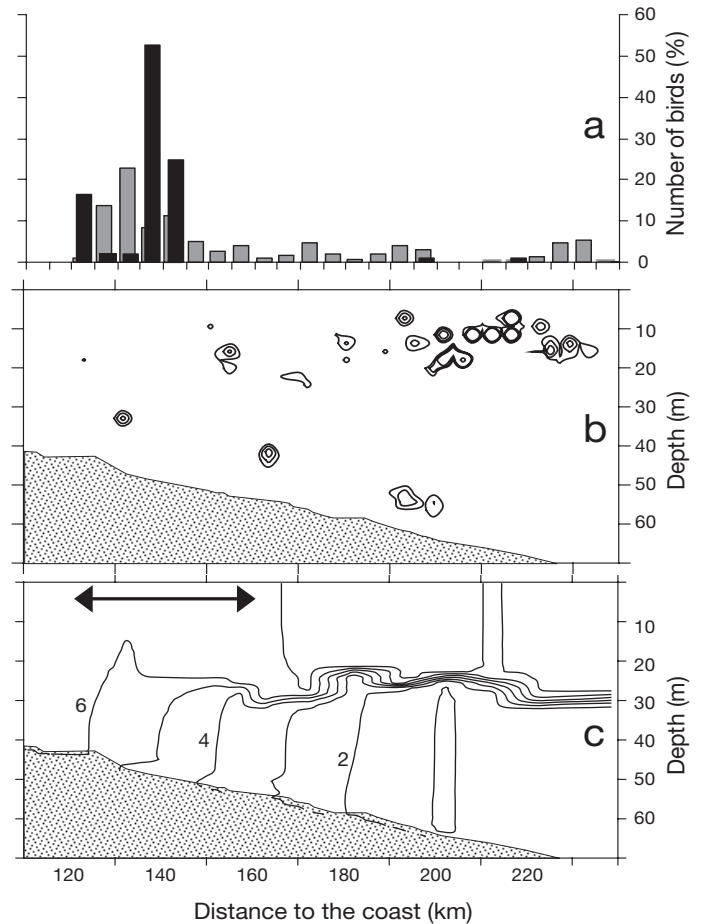


Fig. 7. (a) Distribution of flying (light bars) and foraging (dark bars) *Puffinus tenuirostris* as proportion of total number displaying each behavior; (b) distribution of acoustically estimated biomass of euphausiids (*Thysanoessa* spp.) >100 mg m⁻³; (c) temperature contours (°C) along Transect C off Cape Newenham in summer 1999, arrow indicates precise position of front (after Kachel et al. 2002)

We chose 2 examples of foraging shearwaters associated with the inner front—in summer 1999 in Cape Newenham and Port Moller. In Cape Newenham we found more shearwaters than expected by chance foraging at the inner front (utilization test, $p < 0.05$); 95% percent of the birds and 80% of the flocks were foraging in this area (Fig. 7). We found birds flying all along the 130 km transect surveyed; 70% of them were located at the front. The density of euphausiids in this particular transect was higher offshore of the front (acoustically determined biomass, $ADB = 2.6 \text{ g m}^{-2}$) than in the frontal region ($ADB = 1.0 \text{ g m}^{-2}$). However, the stratified waters offshore of the front were green or milky-green inside the densest part of the cocco-

lithophore bloom (Stockwell et al. 2001). In Port Moller, the number of shearwaters and flocks of shearwaters foraging at the inner front were also higher than expected by chance (utilization test, $p < 0.05$) (Fig. 8). All birds and flocks of foraging birds were at the front. The density of euphausiids in this case was higher at the front ($ADB = 1.7 \text{ g m}^{-2}$) than offshore of the front ($ADB = 0.7 \text{ g m}^{-2}$).

Zooplankton, particularly euphausiids and crab larvae, were the main prey consumed by short-tailed shearwaters foraging at the SE Bering Sea during late summer and early fall. Zooplankton represented, on average, 70% by volume of the prey consumed, the remainder was fishes. The proportion of zooplankton in the diet decreased from 100% by volume in late summer and early fall 1997 to about 40% by volume of prey consumed in the same period in 1998 and 1999

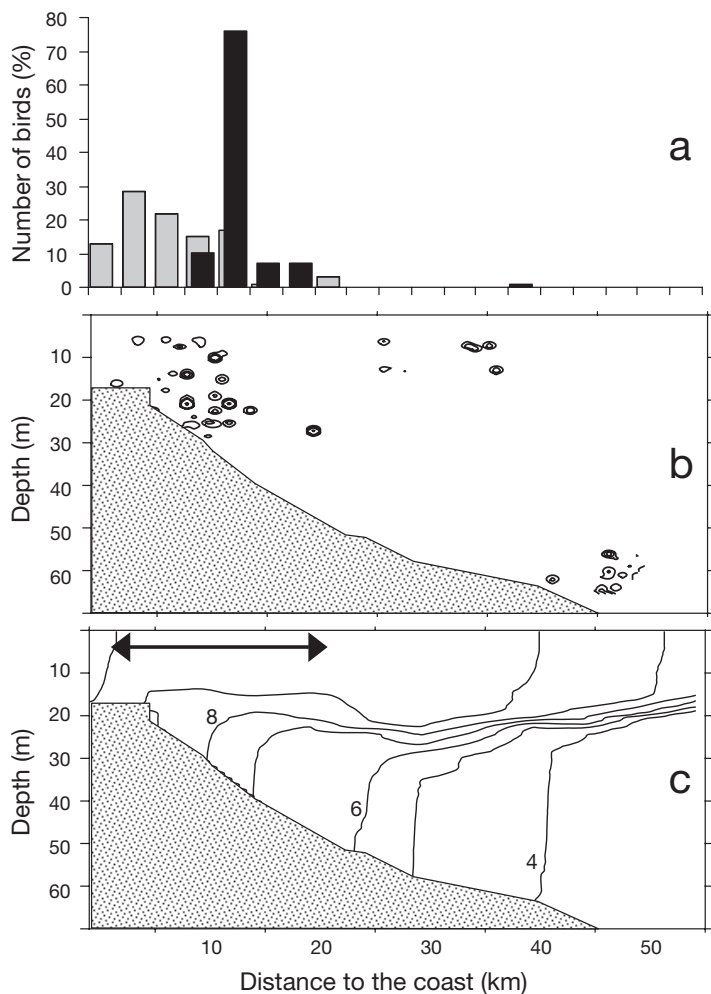


Fig. 8. (a) Distribution of flying (light bars) and foraging (dark bars) *Puffinus tenuirostris* as proportion of total number displaying each behavior; (b) distribution of acoustically estimated biomass of euphausiids (*Thysanoessa* spp.) $>100 \text{ mg m}^{-3}$; (c) temperature contours ($^{\circ}\text{C}$) along Transect E off Port Moller in summer 1999; arrow indicates precise position of front (after Kachel et al. 2002)

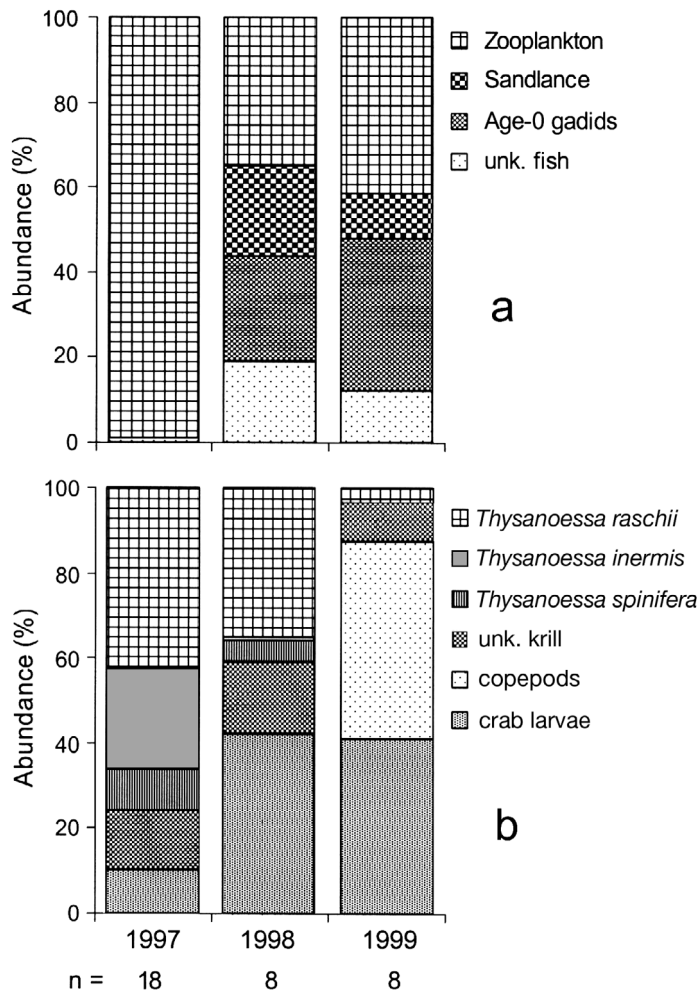


Fig. 9. *Puffinus tenuirostris*. Diet composition in summer. (a) Relative consumption of major prey types (by volume); (b) consumption of main zooplankton organisms (by number). n: sample size for each year

(Fig. 9a), the proportion of sandlance and Age-0 gadids (most probably walleye pollock *Theragra chalcogramma*) increased during the same period. The most important zooplankton were the euphausiid *Thysanoessa raschii* (with about 40% by number consumed in summer 1997 and 1998), crab larvae (about 40% in summer 1998 and 1999) and copepods (about 50% in summer 1999) (Fig. 9b).

Diet of shearwaters in relation to inner front

Zooplankton was the main prey consumed by short-tailed shearwaters foraging at the inner front (Fig. 10a), representing 82 to 93% by volume of the pooled sample of consumed prey, depending on whether we used the MFR or the PDF for analyses, respectively. However, the proportion of zooplankton in the diet was not significantly higher at the MFR (Kruskall-Wallis statistic = 2.125, $df = 2$, $n = 56$, $p = 0.346$) or at the PDF (Kruskall-Wallis statistic = 1.209, $df = 2$, $n = 16$, $p = 0.546$) than elsewhere along-transect. The most important zooplankton organisms found in the diet were 3 species of euphausiids, crab larvae and copepods (Fig. 10b). The euphausiids *Thysanoessa raschii* and *T. inermis* were consumed in all 3 regions (Kruskall-Wallis test, $df = 2$, $n = 44$, $p > 0.05$); *T. spinifera* was found mainly in the stomachs of birds collected at the MFR (Kruskall-Wallis statistic = 9.864, $n = 2$, $n = 44$, $p = 0.007$). The proportion of crab larvae (Kruskall-Wallis statistic = 7.484, $df = 2$, $n = 44$, $p = 0.024$) and copepods (Kruskall-Wallis statistic = 3.473, $df = 2$, $n = 44$, $p = 0.176$) was higher offshore of the MFR. Adult stages of *T. raschii* and *T. inermis* were consumed in spring; in summer, juvenile euphausiids contributed a large fraction (35%) to the diet, as did other small zooplankton such as crab larvae and copepods (39%). The proportion of zooplankton consumed at the MFR decreased from 99 to 78% in summer 1997 and 1998, respectively, to 49% in summer 1999. The proportion of sandlance in the stomachs of birds collected at the MFR increased in the same period. Sandlance was consumed mainly at and inshore of the MFR (Kruskall-Wallis statistic = 6.22, $df = 2$, $n = 56$, $p = 0.045$). Age-0 gadids, most probably walleye pollock, were consumed predominately offshore of the MFR (Kruskall-Wallis statistic = 12.131, $df = 2$, $n = 56$, $p = 0.002$).

DISCUSSION

In this study we found large interannual differences in primary production at the inner front related to the anomalous conditions in the Bering Sea during 1997 and 1998 (Hunt et al. 1999a,b, Overland 2001, Stabeno

et al. 2001). In 1997, calm weather and a shallow mixed-layer produced conditions that allowed phytoplankton to grow below the thermocline (Stabeno et al. 2001, Kachel et al. 2002). The inner front moved closer to shore than previously recorded (Kachel et al. 2002). Nutrients were depleted early in spring, and few remained into the summer (Stockwell et al. 2001, Kachel et al. 2002). No nutrients were available to be carried to the surface at the inner front; hence primary production did not occur there or was very low (Kachel et al. 2002). In 1998 and 1999, stormy weather and a deeper mixed-layer isolated a reservoir of nutrients in the bottom layer (Stabeno et al. 2001, Kachel et al. 2002). The inner front moved offshore to near the seaward end of the study grids (Kachel et al. 2002). Frequent strong winds throughout spring and summer sustained mixing and delayed the onset of the spring bloom (Kachel et al. 2002). The spring cruises in 1998

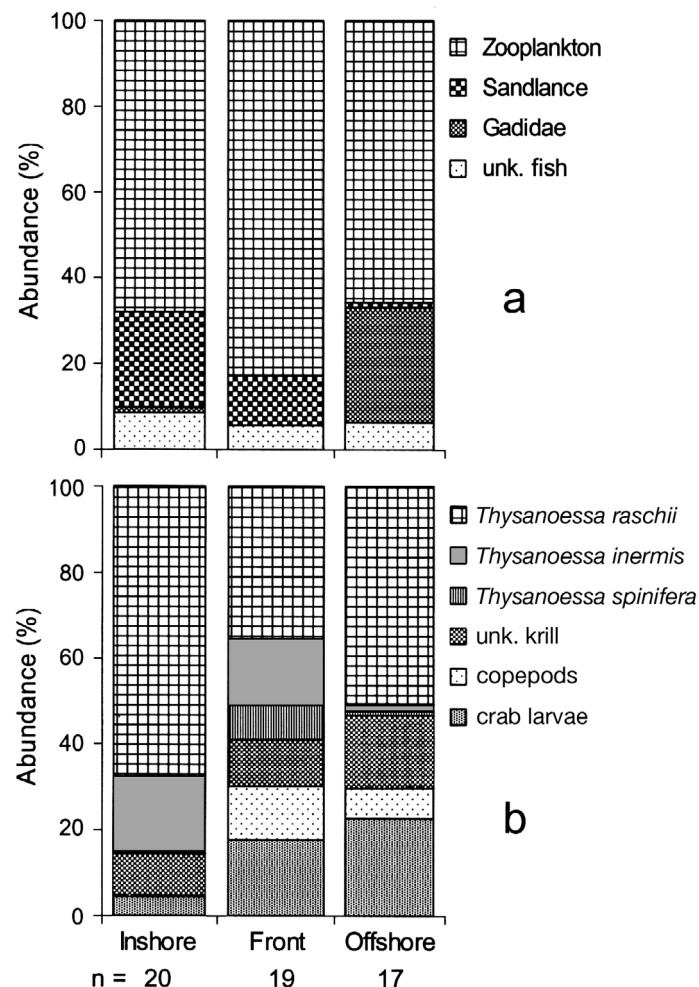


Fig. 10. *Puffinus tenuirostris*. Diet composition in relation to mean frontal region. (a) Relative consumption of major prey types (by volume); (b) consumption of main zooplankton organisms (by number). n: sample size for each region

and 1999 took place early in the season, when stratification of the water was just beginning and the bloom was yet to occur (Kachel et al. 2002). Stormy conditions in 1999 delayed the formation of the 2-layered system during spring, and the inner front developed later in the season with colder temperatures and higher nutrient concentrations than the surrounding waters (Kachel et al. 2002).

Primary production during late summer and early fall was higher at the inner front and offshore of the front than inshore of this feature. This was particularly clear in late summer 1999, when abundant cold, nutrient-rich water below the pycnocline led to the conditions required for the inner front to supply nutrients to the upper layers of the water, thus enhancing primary production (Kachel et al. 2002). However, stormy weather played an important role in replenishing nutrients to the upper layer of the well-stratified waters as well; high levels of fluorescence and elevated nutrients were found after storms over the stratified waters and near the inner front in summer 1999 (Kachel et al. 2002, see also Sambroto et al. 1986).

The density of euphausiids in late summer and early fall was higher at the inner front and offshore of the front than inshore of this feature. The presence of Age-0 pollock may have caused an underestimate of euphausiids in these 2 habitats, since their acoustic signal masks the acoustic signal of euphausiids (Coyle & Pinchuk 2002a). Age-0 pollock were distributed near the thermocline and at the front, and dominated the acoustic record over much of the stratified portion of the study area during late summer and early fall (Coyle & Pinchuk 2002a). The density of euphausiids was higher at the front in 50 to 80% of the transects we analyzed using the MFR and PDF, regardless of season. Furthermore, shearwaters foraging at the front were consuming zooplankton and sandlance; Age-0 pollock was consumed predominantly offshore of the frontal region. Shearwaters are opportunistic in their diet and consume the prey most readily available in their foraging range (Ogi et al. 1980). Shearwaters in Bristol Bay have been known to prey almost exclusively on euphausiids (Ogi et al. 1980, Hunt et al. 1981a, 1996, 2002, Schneider et al. 1986). However, their diet changes to mostly fishes in the North Pacific Ocean and mostly squid near the Bering Sea shelf-break area (Ogi et al. 1980). In the present study, prey consumption by shearwaters suggests high availability of euphausiids and sandlance at the inner front, and Age-0 gadids offshore of this feature. If readily available offshore of the front, euphausiids would probably have been present in larger amounts in the diet, as was observed in 1997.

Euphausiids concentrate at fronts as a consequence of biological (mating or feeding) or physical (conver-

gence or divergence) processes. Flow at the inner front has been shown to produce the divergence of the upper layers and convergence of the lower layers of the water column, suggesting a frontal upwelling (Coachman 1986). Frontal upwelling was evidenced by vertical, finger-like structures with elevated nitrate concentration associated with high standing stocks of phytoplankton during summer (Kachel et al. 2002). Areas of enhanced production often attract zooplankton; swarms of *Thysanoessa raschii* have been observed at the structural front north of St. Paul Island (Pribilof Islands) during July and August (Coyle & Cooney 1993). Aggregations of euphausiids at the front were probably the result of attraction to ephemeral patches of high primary production. Euphausiids can detect phytoplankton patches (Price 1989), and breeding occurs in the presence of elevated primary production (Paul et al. 1990). Euphausiids form daytime near-surface and surface mating-swarms when spawning during summer (Smith & Adams 1988, Hanamura et al. 1989), even though most spawning usually occurs during spring (Smith 1991). The presence of juvenile stages of euphausiids in the diet of the birds was probably the result of spring breeding events; juvenile stages were more abundant over the shelf break in the summer than in the spring (Stockwell et al. 2001), as may have occurred in other areas of the Bering Sea shelf.

Some enhancement of zooplankton biomass could occur as consequence of directed swimming behavior, which would physically increase the accumulation of organisms independent of their physiological response to increased production (Franks 1992a). Vertically migrating zooplankton may become concentrated at the surface when swimming against a current (Simard et al. 1986, Coyle et al. 1992). The aggregation of other smaller zooplankton organisms may be due to any physical or/and biological process(es). The aggregation of copepods at a front in the Ligurian Sea was attributed to directive active swimming (Boucher 1984), while aggregations of copepods at fronts in the Irish Sea were associated with high surface chlorophyll *a* concentrations at the front (Scrope-Howe & Jones 1985).

Primary production, the aggregation of euphausiids and their later consumption by seabirds and other higher trophic-level predators occur at different spatial and timescales. Nutrient transport at tidal fronts is associated with the periodic effect of tides that break down the stratification of the water, thereby carrying nutrients to the surface (Pingree et al. 1974, 1976, Holligan 1981, Le Fevre 1986). Cyclonic eddies of 20 to 40 km in diameter that may form along the front and persist for 3 to 4 d are important in the transfer of heat, salt and nutrients across the stratified regions during summer (Pingree 1978). It takes about 10 d for nutri-

ents to build up after the initial formation of the physical feature (i.e. the front) and about 5 more days for phytoplankton to reach maximum levels (Franks 1992b). Nutrients forced into the euphotic zone are incorporated into phytoplankton over a period of days and into zooplankton in a matter of weeks (Franks 1992b). Fronts and other physical features of comparable extent may last for weeks (or months), while seabird aggregations may only last for a few hours (Schneider et al. 1987). The probability of encountering zooplankton aggregations at the front is likely to be much higher than the probability of finding large aggregations of foraging seabirds. Also, while all seabird aggregations at sea are likely to be associated with prey, not all prey aggregations need be exploited by seabirds at a given time (Heinemann et al. 1989).

Shearwaters foraged primarily in shallow inshore waters during late spring and shifted to deeper offshore waters in late summer and early fall. Possible explanations for this shift from coastal to offshore foraging habitats include nutrient depletion in inshore waters and depletion of prey inshore of the front by foraging shearwaters and humpback whales during spring (Hunt et al. 2002). Foraging in the coastal region during spring is advantageous for shearwaters because euphausiid aggregations will be trapped near the bottom and thus easier to locate and exploit in these shallow waters (Genin et al. 1988, Hunt et al. 1996). As nutrients are depleted and production ceases in the coastal domain (Kachel et al. 2002), zooplankton and fishes (i.e. sandlance) will move and aggregate at the front or offshore of this feature, where production continues during summer (Kachel et al. 2002). As the season progresses to summer and fall, the diurnal daylight cycle changes to longer periods of darkness and euphausiids spend more time in the upper layers providing more foraging opportunities for shearwaters over deeper waters (K. O. Coyle unpubl.). The occurrence of these surface patches of euphausiids is somewhat unpredictable, as most aggregations will concentrate near the pycnocline where the chlorophyll maximum is located. Foraging at the front is advantageous during summer because surface aggregations of euphausiids are more easily detected by flying birds. At the front, the pycnocline bends upwards, and patches of phytoplankton that attract euphausiids are closer to the surface than they are farther offshore.

Shearwaters at the inner front foraged on euphausiids and a large fraction of smaller zooplankton. The proportion of zooplankton consumed at the front decreased from summer 1997 to summer 1999, while the consumption of sandlance increased in this area. Calm weather conditions (Stabeno et al. 2001, Kachel et al. 2002) and water turbidity due to the presence of a coccolithophore bloom (Vance et al. 1998, Stockwell

et al. 2001) contributed to high mortality of shearwaters in 1997 (Baduini et al. 2001a). Light attenuation resulting from the coccolithophore bloom probably had a negligible influence on underwater foraging; however, greater turbidity and backscatter of light may have impaired the birds' ability to locate prey from the air (Lovvorn et al. 2001), thus increasing their in-flight energy demand (Baduini et al. 2001a). Our results support the idea that birds may not be able to forage successfully inside a coccolithophore bloom even when prey is readily available in the area. In summer 1998, shearwaters were feeding on euphausiids, and more nutrients were available to enhance production at the inner front; however, we did not find more birds and flocks of shearwaters in this area. Stormier conditions (Stabeno et al. 2001, Kachel et al. 2002) probably decreased energy demand for flight in 1998, but the coccolithophore bloom was still there (Napp & Hunt 2001), reducing their ability to find prey (Baduini et al. 2001a). There was but a minor die-off of shearwaters in 1998 (Hyrenbach et al. 2001), even though their overall body condition was lower than in 1997 (Baduini et al. 2001b). Age-0 pollock were abundant at the outer ends of the transects in 1998 and 1999 late in the season, and shearwaters made use of this prey offshore of the inner front (Baduini et al. 2001b). In summer 1999, the water was colder (Coyle & Pinchuk 2002b) and there were more nutrients to enhance production at the front (Kachel et al. 2002). More birds and flocks used the inner front this year, consuming euphausiids and sandlance. The overall body condition of the birds in 1999 was better than in 1997 and 1998 (Baduini et al. 2001b) and there was no shearwater die-off (Hyrenbach et al. 2001). However birds were still taking Age-0 pollock as prey.

This paper has shown that there is a clear seasonal change in the foraging habitats of short-tailed shearwaters in the inner domain of the SE Bering Sea, where the inner front is likely to produce an aggregation of zooplankton organisms and higher trophic-level predators during summer and fall. The means by which this aggregation occurs remain obscure, as we found no clear evidence of enhanced production at the front. The inner front has been shown to be an ephemeral feature that forms in spring and recurs 'intermittently' (depending on storm activity) throughout the summer (Kachel et al. 2002). When present, the inner front is likely to prolong primary production into summer, favoring the aggregation of zooplankton and their seabird predators.

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