Diets of short-tailed shearwaters in the southeastern Bering Sea

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Abstract

In the late 1990s, the southeastern Bering Sea exhibited a number of anomalous conditions, including a major die-off of short-tailed shearwaters (*Puffinus tenuirostris*), a trans-equatorial migrant that constitutes a major portion of the marine bird biomass in the southeastern Bering Sea. As part of a larger study of the ecological role of the inner or structural front over the southeastern Bering Sea shelf, in 1997–1999, we collected short-tailed shearwaters to determine diet composition. In spring 1997, we found that short-tailed shearwaters were consuming predominately the euphausiid *Thysanoessa raschii*, a diet expected on the basis of past studies. However, in subsequent years, short-tailed shearwater diets in spring contained increasingly larger proportions of fish, in particular, sandlance (*Ammodytes hexapterus*), as well as other species of euphausiids (*T. inermis* in 1999). In summer and fall collections, short-tailed shearwater diets were more varied than in spring, and included both fish (age-0 gadids, 21–35% by weight) and a wider variety of euphausiid species *(T. inermis* and *T. spinifera*). In summer and fall, crab zoea (August 1998) and copepods (August 1999) were eaten by shearwaters collected while feeding within the inner front. Diets in 1997–1999 were broader than those found in previous studies of short-tailed shearwaters over the inner shelf and Bristol Bay, which had documented diets composed almost solely of *T. raschii*. Our data are consistent with the hypothesis that euphausiids were less available to short-tailed shearwaters foraging over the middle and coastal domains of the southeastern Bering Sea in 1997–1999 than has previously been true. Our results are also consistent with hypothesis that the inner front can affect the availability of prey to shearwaters.
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1. Introduction

Each year millions of short-tailed shearwaters (*Puffinus tenuirostris*) migrate from their breeding colonies in Australia to spend the austral winter in the North Pacific (Shuntov, 1964; Tanaka and Kajihara, 1979; Guzman, 1981; Gould et al., 1982). As many as 16 million of these shearwaters forage in the Bering Sea between April and October (Schneider and Shuntov, 1993), where they have been recorded in flocks of tens to hundreds of thousands of birds (Guzman, 1981; Hunt et al., 1981b; Gould et al., 1982). The evolution of this annual trans-equatorial migration implies that extraordinary amounts of prey must be readily available to these birds in the Bering Sea.

The southeastern Bering Sea shelf is up to 500 km wide (Fig. 1). The inner and mid-shelf waters are differentiated by hydrographic structure associated with characteristic bottom-depth ranges (Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 2001). The coastal

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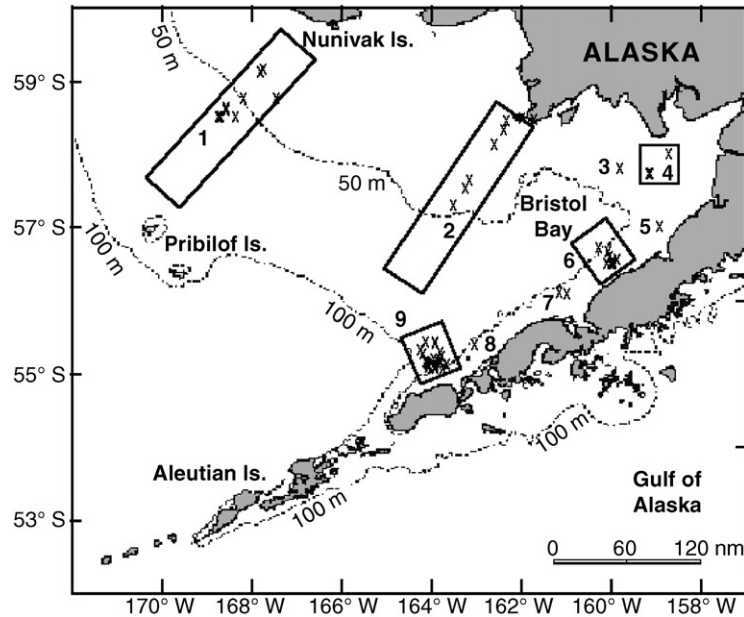
Fig. 1. Southeastern Bering Sea shelf, showing the locations of the collection sites (marked with an X), the main study grids in relation to depth contours (in m) and the coastline. The inner domain is shoreward of the 50-m isobath, and the middle domain is between the 50- and 100-m isobaths. The structural front is roughly co-incident with the 50-m isobath. Numbers refer to collection sites mentioned in Table 1: (1) Nunivak Island Grid; (2) Cape Newenham Grid; (3) Round Island Site; (4) Dillingham Sites; (5) Port Heiden Site; (6) Port Moller grid; (7) Nelson Lagoon Sites; (8) Amak Island Site; and (9) Slime Bank Grid.

domain (depth < 50 m) typically is either weakly stratified or well mixed as a result of a combination of tidal and wind mixing. The middle shelf domain (depth between 50 and 100 m) is two-layered in summer because mixing energy is not sufficient to stir the entire water column in the presence of a positive buoyancy flux. A structural front (the inner front) 5–30 km wide separates the middle and coastal domains (Schumacher et al., 1979; Kachel et al., 2002). It is present along the entire southeastern shelf to north of Nunivak Island. A similar feature exists around the Pribilof Islands (Kinder et al., 1983). Advection across the structural front is minimal (Coachman, 1986; Kachel et al., 2003).

Between May and September, major concentrations of short-tailed shearwaters occur in an arc from the eastern passes of the Aleutian Islands into Bristol Bay and northwestward over the nearshore waters to Nunivak Island (Bartonek and Gibson, 1972; Guzman, 1981; Hunt et al., 1981b; Gould et al., 1982). These large aggregations appear to be associated with the 50-m isobath throughout the eastern and western Bering Sea, as well as in the shallower passes of the Aleutian Islands (Schneider and Shuntov, 1993).

Previous studies have shown that in Bristol Bay and adjacent areas of the southeastern Bering Sea, short-tailed shearwaters forage primarily on euphausiids (in particular, *Thysanoessa raschii* and *T. inermis*) (Ogi, 1973; Ogi et al., 1980; Hunt et al., 1981a; Schneider et al., 1986; Troy and Bradstreet, 1991). At the Pribilof Islands in July–August 1989, short-tailed shearwaters foraged almost exclusively on adult *T. raschii* (Hunt et al., 1996). In the Bristol Bay region, Ogi et al. (1980) estimated that short-tailed shearwaters consume at least 30,000 metric tons of euphausiids annually, a consumption roughly equivalent to the consumption of euphausiids by sockeye salmon during the month that these salmon reside in Bristol Bay before ascending rivers to spawn (Nishiyama, 1974).

Short-tailed shearwaters forage by pursuit diving from the surface, plunging from above the

surface, seizing prey at the surface, and by hydroplaning, a foot-propelled movement at the surface in which the head and back may be beneath the surface while the wings are held out of the water (Ogi et al., 1980; Morgan, 1982). Short-tailed shearwaters also may obtain prey by filter feeding (Morgan and Ritz, 1982; Lovvorn et al., 2001). Maximum dive depths have been estimated to be between 20 and 40 m (Skira, 1979; Hunt et al., 1996). Thus, short-tailed shearwaters must seek euphausiids either in near-surface swarms, or in epibenthic layers less than 40 m deep. Recent modeling studies suggest that these shearwaters must use filter-feeding in dense near-surface euphausiid aggregations if they are to meet their daily energy requirements with this type of prey (Lovvorn et al., 2001).

In the late 1990s, the southeastern Bering Sea exhibited a number of anomalous conditions, including unusually warm surface temperatures in 1997 and a recurring coccolithophore bloom that increased turbidity in the water column (Vance et al., 1998; Hunt et al., 1999; Napp and Hunt, 2001; Stabeno et al., 2001; Stockwell et al., 2001). In the Bering Sea in fall 1997, hundreds of thousands of short-tailed shearwaters starved, and in fall 1998, short-tailed shearwaters were emaciated, though moribund birds were not encountered (Baduini, 2000; Baduini et al., 2001a). In spring 1999, short-tailed shearwaters in Bristol Bay had body masses intermediate between those in 1997 and 1998, and in summer 1999, body masses were greater than those measured in either fall 1997 or fall 1998 (Baduini et al., 2001b). In comparison to past studies of short-tailed shearwater foraging ecology in the southeastern Bering Sea, in August and September 1997, short-tailed shearwater diets included a wider variety of prey than expected (Baduini et al., 2001a). Baduini et al. hypothesized that the more diverse diets than expected were a response to the unavailability of adult euphausiids, the previously dominant prey of short-tailed shearwaters over the middle and inner shelf domains. In this paper, we examine the spatial and temporal variability of short-tailed shearwater diets in the southeastern Bering Sea, and relate changes to factors that may have affected the availability of euphausiid prey.

2. Methods

Between June 1997 and August 1999, we studied the food habits of short-tailed shearwaters during six research cruises to the southeastern Bering Sea (Table 1). To determine food habits, we shot foraging shearwaters or birds sitting on the water that were assumed to have been foraging in the recent past. On each cruise, collections were made in each of our sampling grids (Fig. 1, Table 1) where foraging short-tailed shearwaters were seen. Although we were not able to collect birds from

Table 1
Timing and distribution of sampling effort

Year		Dates	Location	Sample size
1997	Spring	1–6 June	Slime Bank	23
		9–11 June	Port Moller	7
		12–15 June	C. Newenham	12
		16–21 June	Nunivak Is.	0
	Fall	8–11 September	Slime Bank	34
		28 August–5 September	Nunivak Is.	20
1998	Spring	26–28 May	Slime Bank	4
		18–20 June	Amak Is.	5
		28 May–1 June	Port Moller	19
		1–4 June	Dillingham	20
		5–11 June	C. Newenham	7
		13–17 June	Nunivak Is.	0
	Fall	21 August	Slime Bank	10
		2 September	C. Newenham	26
		28 August	Nunivak Is.	4
1999	Spring	20–23 May; 14 June	Slime Bank	19
		28–29 May; 13 June	Nelson Lagoon	9
		25–28 May; 13 June	Port Moller	14
		12 June	Port Heiden	6
		11 June–12 June	Round Is.	5
		31 May–3 June	C. Newenham	5
		4 June–8 June	Nunivak Is.	0
	Summer	27–29 July	Slime Bank	8
		30 July–2 August	Port Moller	7
		5–10 August	C. Newenham	11
		11–15 August	Nunivak Is.	13

every foraging group encountered, we attempted to collect birds from each area of each grid where birds were foraging. At each collection site, between 3 and 8 birds were shot.

After collection, proventriculus (the fore-stomach of birds where chemical digestion begins) contents were removed immediately, weighed, and preserved in 80% ethanol. Wet weight of alcohol-preserved specimens, their displacement volume, and direct counts were used to determine the diets of individual birds. Proventriculus contents containing more than 50 g (wet weight) biomass of zooplankton were split using a Folsom splitter, and a subsample of the prey present was identified and enumerated. Although squid beaks occurred occasionally, we did not include them in the present analysis because we were unable to determine whether they were recently ingested, or had been carried in the alimentary canal for some time, and thus represented prey ingested outside the study area.

To assign short-tailed shearwater collections to habitat regions with respect to water depth, we identified four habitat categories: offshore (water depth $= z > 55$ m); the region of the inner front (45 m $< z < 55$ m); the central region of the inner domain (25 m $< z < 45$ m); and the inshore region ($z < 25$ m). The lengths of these regions varied greatly depending on the slope of the bottom. At Slime Bank and Port Moller, grids were only about 40 km long, whereas at Cape Newenham and Nunivak Island, grids were up to 120 km long. Thus, division into four habitat categories reflected the ease with which short-tailed shearwaters might have been able to reach epibenthic prey, rather than distance from shore. We identified the frontal region separately because we wished to know if it was a feature in determining the types of prey taken.

In assessing diet composition for different time- × location categories (e.g., year, season, cruise, grid or habitat), we determined the proportion of a prey type in a particular bird in terms of both the proportion by displacement volume, and for zooplankton, the proportion by number of prey items present. We then averaged proportions across birds in a category. This approach avoided the possibility that a few birds with particularly

large amounts of prey would have disproportionate influence on our assessment of the diet composition of short-tailed shearwaters in our study.

To test for differences between seasons, years and locations, we performed Kruskal–Wallis one-way analyses of variance. Diet data were aggregated into 63 groupings of birds to avoid pseudo-replication. Each group of birds was composed of all the birds shot at a given time and place, and the proportions of prey taken by the individuals in the group were averaged to provide the proportion of prey from that sample. This decision criterion for independent sample units was based on the assumption that birds foraging in a given flock were not independent samples of short-tailed shearwater diets. Most birds taken from a flock contained the same foods. However, occasionally in a flock of birds feeding on a particular prey, we would find an individual that contained not only the prey being taken by others in the flock, but an additional type of prey as well. Thus, our estimate of independent sampling units is conservative. In the tables we present the numbers of birds sampled in each category, as is common practice, whereas in the text, where statistical tests on differences in diets are presented, we use the more conservative sample size based on grouped birds.

3. Results

The biomass of prey present in the proventriculus of short-tailed shearwaters varied among cruises (Table 2). The mass of prey present in stomachs was generally greater in spring than in fall (Mann–Whitney $U = 15293$, $n = 288$ birds, $p < 0.001$). The mean displacement volumes of proventriculus contents varied among prey types (euphausiids, 33 ml, to age-0 gadids, 56 ml), as did the maximum volumes recorded (euphausiids, 155 ml, sandlance, 180 ml and age-0 gadids, 198 ml) (Table 3). The maximum for euphausiids was almost double the maximum stomach load of 89 g recorded by Ogi et al. (1980).

Prey use varied both seasonally and annually (Table 4). In all years, the predominant prey in

Table 2
Mean net body mass (gross body minus mass of proventriculus contents) and mean volume of proventriculus contents of short-tailed shearwaters in the main study grids

Grid sampled											
	Slime Bank		Port Moller		C. Newenham		Nunivak Is.		All	
	Spr.	Fall	Spr.	Fall	Spr.	Fall	Spr.	Fall	Spr	Fall
Body mass (g)										
1997	596	512	622	ND	593	ND	ND	520	600	515
1998	473	468	549	ND	588	525	ND	433	557	501
1999	536	591	549	553	594	575	ND	564	554	568
Proventiculus. Vol. (ml)										
1997	75	13	39	ND	34	ND	ND	29	59	19
1998	2	9	41	ND	91	44	ND	1	56	41
1999	49	13	51	64	55	2	ND	18	48	27

ND: No data.

Table 3
Short-tailed shearwater proventriculus volume (ml) as a function of prey type used

Prey type									
Year	Zooplankton			Sandlance			Gadidae		
	Mean	±sd	Max.	Mean	±sd	Max.	Mean	±sd	Max
Spring									
1997	59	41	155	Not used			Not used		
1998	45	34	150	61	54	180	Not used		
1999	37	30	115	41	33	115	Not used		
Fall									
1997	20	25	120	Not used			Not used		
1998	3	6	25	48	28	78	77	54	198
1999	7	10	34	69	36	102	24	12	39

Table 4
Diet composition (percent by volume) of short-tailed shearwaters by year and season based on proportion of prey type in individuals, where *n* is the number of individuals for which the proportion of prey type by volume was determined

Year	1997		1998		1999	
Season	Spring	Fall	Spring	Fall	Spring	Summer
N	42	54	55	40	58	39
# empty	0	1	1	1	3	3
Zooplankton	100	97	78	33	59	46
Sandlance	0	0	15	14	29	15
Gadidae (age-0)	0	0	0	35	0	21
Unident. Fish	0	1	5	18	12	13
Total	100	98	98	100	100	95

May/June was zooplankton, as was also true in August/September 1997. However, in both August/September 1998 and July/August 1999, fish constituted the major portion of the diets. Sandlance (*Ammodytes hexapterus*) was used predominately in spring ($U = 639$, df $= 1$, $n = 63$ groups, $p = 0.012$), whereas age-0 gadids, most likely walleye pollock (*Theragra chalcogramma*) (see Coyle and Pinchuk, 2003), were consumed only in summer and fall ($U = 391.5$, df $= 1$, $n = 63$ groups, $p = 0.01$). The percent volume of zooplankton consumed varied significantly by year (Kruskal–Wallis statistic $= 21.975$, df $= 2$, $n = 63$ groups, $p < 0.001$), as did the proportion of sandlance used (Kruskal–Wallis statistic $= 13.854$,

Table 5
Types of zooplankton (percent by number) in the diets of short-tailed shearwaters in the Bristol Bay region of the southeastern Bering Sea

Year	1997		1998		1999	
Season	Spring	Fall	Spring	Fall	Spring	Summer
# Proventriculi examined	42	54	55	40	58	39
# items	33,469	14,323	22,128	1,392	19,894	2,283
Thysanoessa raschii	100	41	99	19	49	0.0
T. inermis	0	35	0	1	51	0
T. spinifera	0	15	0	9	0	0
Crab Zoea	0	8	0	61	0	1
Copepods	0	0	0	0	0	96
Total	100	99	99	90	100	97

$df = 2$, $n = 63$ groups, $p = 0.001$). The proportion of age-0 gadids consumed varied significantly by cruise (Kruskal–Wallis statistic $= 23.450$, $df = 5$, $n = 63$ groups, $p < 0.001$) but not by year (Kruskal–Wallis statistic $= 4.978$, $df = 2$, $n = 63$ groups, $p = 0.083$). Of the zooplankton eaten, the euphausiid *T. raschii* was the dominant prey in June 1997 and May/June 1998 (Table 5). In May/June 1999, both *T. raschii* and *T. inermis* were important components of the diet. Most euphausiids taken were adults, and many of them were females with spermatophores. An exception occurred in September 1997, when 93% of the euphausiids eaten were juveniles. The use of *T. raschii* varied significantly by season ($U = 762$, $df = 1$, $n = 63$ groups, $p =, 0.001$), but not by year (Kruskal–Wallis statistic $= 3.230$, $df = 2$, $n = 63$ groups, $p = 0.199$). In summer and fall, other small zooplankton were eaten. In fall 1998, crab zoea constituted a small percentage of the zooplankton items consumed, whereas in July/August 1999, copepods were the dominant zooplankton used and made up 46% by volume of the prey found in short-tailed shearwater stomachs (Tables 4 and 5).

The types of prey consumed varied with respect to the location within the grids where foraging short-tailed shearwaters were collected (Table 6). Foraging short-tailed shearwaters that had eaten sandlance were collected primarily from waters shoreward of the inner front (Kruskal–Wallis statistic $= 11.617$, $df = 3$, $n = 63$ groups, $p = 0.009$). In contrast, age-0 gadids were found

Table 6
Distribution of prey taken as a function of water depth (habitat region)

	Inshore $z < 25$ m	Central inner domain 25 m $< z < 45$ m	Frontal region 45 m $< z < 55$ m	Offshore (middle domain) $z > 55$ m
# Proventriculi examined	48	121	49	70
Zooplankton	74	73	74	60
All Fish	25	27	20	39
Sandlance	19	19	7	1
Gadidae (age-0)	0	1	5	27
Unknown fish	6	7	8	11

Note: Percent by volume using proportion per individual.

almost exclusively in short-tailed shearwaters collected in middle domain waters deeper than 55 m (Kruskal–Wallis statistic $= 7.832$, $df = 3$, $n = 63$ groups, $p = 0.050$). Likewise, there was striking spatial segregation in the locations where various kinds of zooplankton were encountered in foraging short-tailed shearwaters (Table 7). In particular, *T. raschii* was found primarily in birds collected inshore of the front (Kruskal–Wallis statistic $= 13.273$, $df = 3$, $n = 63$ groups, $p = 0.004$). Smaller zooplankton, such as crab zoea and copepods were consumed by shearwaters collected while foraging in the frontal region.

Table 7
Types of zooplankton (percent by number) taken as a function
of location within the grids

	Inshore $z < 25$ m	Central inner domain 25 m $< z < 45$ m	Frontal region 45 m $< z < 55$ m	Offshore (middle domain) $z > 55$ m
# Proventiculi examined	48	121	49	70
# Prey items	20,053	49,343	11,937	12,157
All Euphausiids	100	97	83	95
T. raschii	96.2	83.3	47.9	42.5
T. inermis	3.3	12.7	33.7	34.3
T. spinifera	0.0	0.3	0.2	17.2
Crab Zoea	0.0	0.7	11.5	2.7
Copepods	0.0	2.8	5.1	1.8

4. Discussion

In the present study, approximately 70% by
weight of short-tailed shearwater prey was zoo-
plankton, 13% sandlance, 8% age-0 gadids, and
8% unidentified fish. Of the zooplankton con-
sumed, 76% by number were *T. raschii*, 20% were
other species of or unidentified euphausiids, 2%
were crab zoea and 2% were copepods. Our
summer and fall data were collected primarily in
July and August in the coastal domain, and in
middle domain waters close to the inner front,
seasons and places similar to those in which the
earlier studies had been conducted. Thus, we
expected to find that the euphausiid *T. raschii*
would have made up almost 100% of the shear-
waters' diet, as was found by Ogi et al. (1980)—
99.4% euphausiids, Schneider et al. (1986)—82%
in 1981, 100% in 1982, and Hunt et al. (1996)—
100% in 1989. Diets from spring and fall 1997, and
to a lesser extent June 1998, conformed to this
expectation, although the euphausiids used in
August/September 1997 included considerable
numbers of *T. inermis* and *T. spinifera*, species
that had not previously been important constitu-
ents of short-tailed shearwater diets in the region.
What was unexpected was the heavy reliance on
fish in August/September 1998, and throughout
the spring and summer of 1999. Likewise, the use
of crab zoea in fall 1998, and copepods in summer
1999, was not anticipated.

In other shelf regions of the Bering Sea from
Cape Navarin around the northern shelf to the
Pribilof Islands, short-tailed shearwater diets
contained a wide mix of prey, and *T. raschii* was
not the most important prey species. For example,
Ogi et al. (1980), collected 69 samples in June and
July of 1973, 1976 and 1977 around the outer rim
of the eastern Bering Sea (their "shelf area"). In
these samples, the hyperiid amphipod *Parathemis-
to (Themisto) libellula* was the most important
prey (66.7% by weight, Ogi et al., 1980, Table 1),
followed by euphausiids (20.5%) and fish (12.6%).
Excluding two stations that they classified as
atypical, the distribution of prey types by weight
was: amphipods, 88.1%; fish, 11.2%; euphausiids
0.5%; squid, 0.1% (Ogi et al., 1980, Table 5). Fish
species included both walleye pollock and capelin
(*Mallotus villosus*). Ogi et al. concluded that short-
tailed shearwaters had "flexible feeding habits that
probably varied according to the distribution of
planktonic and neustonic organisms in the surface
layer". Thus, we interpret the use of prey other
than euphausiids in our study as evidence that this
type of prey was less accessible to short-tailed
shearwaters foraging in our study areas than was
true in the past.

The increase in the use of prey other than *T.
raschii* by short-tailed shearwaters after spring
1997 could be the result of a decrease in the
availability but not the abundance of *T. raschii*, a
decrease in the abundance of *T raschii*, or the
result of an increase in the availability of
alternative prey. The short-tailed shearwaters
turned to a number of different species of
alternative prey, some of which, such as copepods
and crab zoea, are smaller or with lower energy
density than adult *T. raschii*. It seems unlikely that
these alternative prey were more profitable to take
than *T. raschii* had been. As an alternative, we
hypothesize that after June 1997, the availability of
T. raschii decreased in the inner and middle shelf
domains where we were sampling short-tailed
shearwater diets.

A decrease in the availability of *T. raschii* could
result from one or more of the following reasons:
(1) a change in horizontal distribution (e.g., a

move offshore); (2) a change in vertical distribution, such that fewer euphausiids were available near the surface; (3) a change in the ability of the short-tailed shearwaters to locate euphausiid swarms because of the extensive coccolithophore blooms over the middle and inner shelf (Stockwell et al., 2001); or (4) a decrease in abundance, possibly because of an increase in the biomass of species that may compete with short-tailed shearwaters for euphausiid prey.

For the most part, we lack sufficient data, particularly the historical data, necessary to test these hypotheses. Elsewhere (Baduini et al., 2001a), we have argued that the warm surface water in fall 1997 may have inhibited surface swarming of adult euphausiids. While this explanation may be relevant for 1997, it is not adequate to explain why there was an apparent lack of near-surface swarms in 1998 and 1999, when surface temperatures were cooler. Alternatively, the presence of the coccolithophore bloom (Sukhanova and Flint, 1998; Vance et al., 1998; Napp and Hunt, 2001) may have reduced the ability of short-tailed shearwaters to find swarms of euphausiids from the air (Baduini et al., 2001a). The presence of dense coccolithophore blooms could reduce the ability to find swarms and thus diminish the region of ocean available for foraging (see also Coyle and Pinchuk, 2002). However, this explanation does not account for the increased use of alternative prey, such as sandlance, early in 1999 in areas distant from the incipient bloom.

It is also possible that the abundance of euphausiids in the inner domain has decreased since the 1980s. During our surveys and transits between sampling grids, we frequently observed both minke (*Balaenoptera acutorostrata*) and humpback whales (*Megaptera novaeangliae*) foraging in shallow coastal waters, often in association with foraging short-tailed shearwaters that were consuming euphausiids (G. Hunt, Unpublished data). Each spring from 1997 to 1999, we encountered between 9 and 12 humpback whales foraging together in the shallow waters of inner Bristol Bay. In addition to potential competition from baleen whales, the number of sockeye salmon returning to the rivers of Bristol Bay has increased greatly since the 1970s (Kruse, 1998). However,

data presented by Coyle and Pinchuk (2002) show that there is an overlap between the 95% confidence intervals around MOCNESS samples of euphausiid abundance in the 1990s and the estimates of euphausiid abundance from MOCNESS tows from the 1980s. Therefore, they conclude that there has been no decrease in the abundance of euphausiids over the shelf since the early 1980s. Alternatively, foraging whales and salmon may disrupt the patch structure of the euphausiids, and decrease their availability to the shearwaters, but we lack data with which to test this hypothesis.

Short-tailed shearwater diets showed small-scale variation in composition that reflected the different habitats present in the study areas. In particular, consumption of age-0 gadids was found mostly in birds shot while foraging at or offshore of the inner front. These data are consistent with the observation that these fish were confined primarily to the stratified waters of the middle domain and the frontal region (Coyle and Pinchuk, 2002). In contrast, sandlance were taken mostly in shallow waters inshore of the front. Observations from the ship suggested that short-tailed shearwaters foraging on sandlance did so primarily when the fish were schooling near the surface. Thus, the inshore distribution of shearwaters that had consumed sandlance most likely reflects where sandlance are found in near-surface schools, rather than the depth range to which short-tailed shearwaters can dive.

The distribution of zooplankton obtained from foraging short-tailed shearwaters also indicated that there was considerable small-scale variation in the distribution of zooplankton species. The euphausiid *T. raschii* was obtained primarily from short-tailed shearwaters foraging inshore of the frontal region, whereas *T. inermis* and *T. spinifera* were found primarily at and offshore of this region. Although Pinchuk and Coyle (2002) found little evidence that the inner front influenced the distribution or abundance of copepods, our findings are similar to those reported by Smith (1991) and Coyle and Pinchuk (2002, Fig. 6) for euphausiids species, and are consistent with the hypothesis that the structural front can influence

the distribution of fauna (Coachman, 1986; Kachel et al., 2002).

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