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Tidal front affects the size of prey used by a top marine predator, the short-tailed shearwater (*Puffinus tenuirostris*)

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ABSTRACT

Oceanographic features are known to influence the distribution of marine predators by affecting the abundance and distribution of their prey. We tested the hypothesis that oceanographic features also affect predator distribution by enhancing the profitability of small-sized prey. During July and August 1999, short-tailed shearwaters feeding in Akutan Pass, Alaska (Aleutian Islands) fed upon small (11.6 ± 0.2 mm) euphausiids present in high density near the sea surface. Conductivity–temperature–depth (CTD) casts, hydroacoustic surveys, and net tows revealed that high densities of small euphausiids were associated with a tidal front on the north side of Akutan Pass. At most sites elsewhere in the Bering Sea, away from tidal fronts, shearwaters selected larger (14.2–20.1 mm) euphausiids, even when small euphausiids were present. This study provides evidence that, by promoting high densities of easily accessible prey, oceanographic features can broaden the range of prey sizes taken by marine predators.

Key words: Akutan Pass, Aleutian Islands, Bering Sea, foraging, oceanography, prey selection, seabirds, short-tailed shearwater, zooplankton

INTRODUCTION

Oceanographic features, such as upwelling, eddies and hydrographic fronts, are known to promote the formation of dense patches of marine plankton (Alldredge and Hamner, 1980; Yoder *et al.*, 1981; Le Fèvre, 1986; Franks, 1992a,b). They do so by advecting or mixing nutrients from depth, which enhances local production, or by accumulating biomass at regions of surface convergence (Wolanski and Hamner, 1988; Franks, 1992a,b; Strass, 1992). By aggregating plankton, oceanographic features enhance foraging opportunities for higher-level consumers, such as fish (Olson and Backus, 1985; Fiedler and Bernard, 1987; Lang *et al.*, 2000) and marine birds (reviewed by Schneider, 1990; Hunt *et al.*, 1999). In this study, we examined how one type of feature, a hydrographic front, may have enhanced foraging opportunities for seabirds by concentrating prey items that are usually too small to be fed upon profitably.

Hydrographic fronts are probably the most widely recognized type of oceanographic feature to influence the distribution of seabirds across ocean landscapes. Fronts occur where two physically distinct water masses meet, creating steep horizontal gradients in hydrodynamic properties, such as temperature, salinity, density and velocity (Owen, 1981; Fedorov, 1986). Traditionally, fronts are thought to enhance foraging opportunities for seabirds by making prey available to birds on a spatially and temporally predictable basis. Predictable food supplies would allow seabirds to reallocate time and energy otherwise spent searching for prey to other activities, such as reproduction (Vermeer *et al.*, 1987; Hunt, 1990; Hunt *et al.*, 1999). Hydrographic fronts are also thought to enhance foraging opportunities for seabirds by concentrating prey into high densities. Many seabirds are threshold foragers, which require prey to exceed a minimum density before they can forage successfully (Piatt, 1990). High prey densities are especially necessary for seabirds that invest a large amount of energy into capturing prey, such as by diving. During dives, birds expend energy to overcome buoyancy and drag, while losing heat (energy) to the environment (Lovvorn, 1999; Butler, 2000). Prey taken at depth

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must contain enough energy to offset these costs. Therefore, diving seabirds often take prey that occur in dense patches, such as euphausiid mating swarms, schooling fish or prey concentrated by oceanographic features (Hunt *et al.*, 1999).

Another factor that affects a predator's rate of energy intake while foraging is prey size (MacArthur and Pianka, 1966; Krebs, 1978). In general, large prey items contain more gross energy than small ones. This relationship appears to hold true for both zooplankton and forage fish, the main components of most seabird diets (e.g. Strel'nikova, 1985; Hislop *et al.*, 1991; Paul *et al.*, 1998). Because small prey may contain too little energy to offset dive costs, seabirds that dive for prey may not take prey items below a certain size. Consistent with this idea is the observation that seabirds and other top marine predators typically have diets consisting of prey that is larger than the mean size of prey available to them (Haney and Solow, 1992; Hill *et al.*, 1996; Tollit *et al.*, 1997). Benefits to seabirds of selecting relatively large prey may include not only enhanced foraging benefits for the consumer but also enhanced reproductive success for adults supplying food to dependent young (Lewis *et al.*, 2001). At some point, prey items may become too large for seabirds to capture and handle efficiently, but large prey size probably does not often limit foraging success among seabirds that specialize on dense patches of small prey, such as plankton.

Although seabirds foraging at sea may prefer relatively large prey items over small ones, the amount of energy per unit volume of water of small prey may equal or exceed that of large prey when oceanographic features cause small prey to occur in dense patches. These areas may therefore represent profitable foraging sites for seabirds, with birds exercising smaller minimum prey-size thresholds at those sites than they do where small prey are more widely dispersed. If so, oceanographic features that concentrate small prey would, in effect, broaden the range of prey sizes used by seabirds, turning otherwise unprofitable sections of the marine landscape into profitable foraging grounds. Although seabirds are known to use prey biomass concentrated at fronts (Schneider, 1990; Decker and Hunt, 1994; Hunt *et al.*, 1998; Russell *et al.*, 1999; Hyrenbach *et al.*, 2002), patterns in prey-size use are often not reported. Therefore, it is unclear to what extent oceanographic features concentrate large (typical) prey items versus the extent to which they enhance the profitability of consuming small prey.

In this study, we investigated conditions under which seabirds foraged upon especially small-sized prey concentrated at a hydrographic front. During July and August 1999, we encountered thousands of short-tailed shearwaters (*Puffinus tenuirostris)* feeding in long, well-defined lines in Akutan Pass, eastern Aleutian Islands. Short-tailed shearwaters are seabirds that spend their non-breeding season in the Bering Sea, where they number in the tens of millions (Schneider and Shuntov, 1993). In Bristol Bay, shearwaters feed mainly by 'plunge-diving', in which they initiate dives from the air (Hunt *et al.*, 2002). During plunge-diving, shearwaters remain submerged for periods up to 70 s (Hunt *et al.*, 1996) and reach depths up to 40 m (Ogi *et al.*, 1980; Hunt *et al.*, 1996). Shearwaters also capture prey by surface-seizing, hydroplaning and pursuit-diving (Ogi *et al.*, 1980; Morgan, 1982; terminology follows Ashmole and Ashmole, 1967). In surface-seizing and hydroplaning, shearwaters take prey at the surface from a sitting position or by skimming the surface with the lower mandible while in flight. In pursuit-diving, shearwaters initiate dives from the surface and propel themselves underwater with their wings. In contrast to shearwaters that forage by plunge-diving, shearwaters that forage by pursuit-diving appear to remain close to the sea surface (Sanger, 1972).

In the southeastern Bering Sea, those consume predominantly adult euphausiids, especially *Thysanoessa raschii* and *T. inermis* (Ogi *et al.*, 1980; Hunt *et al.*, 1996, 2002). They also take some fish (e.g. Pacific Sand lance, *Ammodytes hexapterus*) and squid (Ogi *et al.*, 1980; Hunt *et al.*, 2002). While foraging, shearwaters probably use bite-feeding to capture large prey items, such as fish and squid (Morgan and Ritz, 1982), and filter-feeding to capture relatively small prey items, such as euphausiids (Lovvorn *et al.*, 2001). Shearwaters filter prey through papillae that line the bill and tongue (Morgan and Ritz, 1982). Lovvorn *et al.* (2001) modeled the foraging energetics of shearwaters in Bristol Bay and calculated that shearwaters require adult euphausiids to occur in fairly high densities (>1550 adults m^{-3}) for foraging to be successful.

Despite previous observations that shearwaters usually consume large euphausiids, we suspected that shearwaters feeding in Akutan Pass were taking small euphausiids, such as furcillids (i.e. those in the life stage preceding adolescence) and small juveniles, in near-surface patches at a tidal front. A number of observations supported these hypotheses. First, the linear shape of shearwater flocks suggested that prey also occurred in linear patches, which may have resulted from physical processes associated with a tidal front. Because they are poor swimmers, small euphausiids are more vulnerable to being entrained by local currents than are large euphausiids (Franks, 1992b). In addition, linear shearwater flocks occurred only on the north end of Akutan Pass, where water mixed in the pass met stratified water of the Bering Sea basin. Moreover, shearwaters initiated dives from the sea surface, not from the air, suggesting that shearwaters were feeding on near-surface prey.

In this study, we examined the distribution, foraging behavior, and diet of shearwaters relative to hydrographic structure and prey availability in Akutan Pass during two years with contrasting oceanographic conditions, 1999 and 2001. To place our observations in a broader context, we also compared the diets of shearwaters feeding in Akutan Pass with the diets of shearwaters feeding in Bristol Bay, away from tidal fronts, during 1997–99. This study provides empirical support for the hypothesis that oceanographic features not only influence the distribution of marine predators by affecting the abundance and distribution of large prey items, as shown in previous studies, but that oceanographic features can also enhance the profitability of small-sized prey.

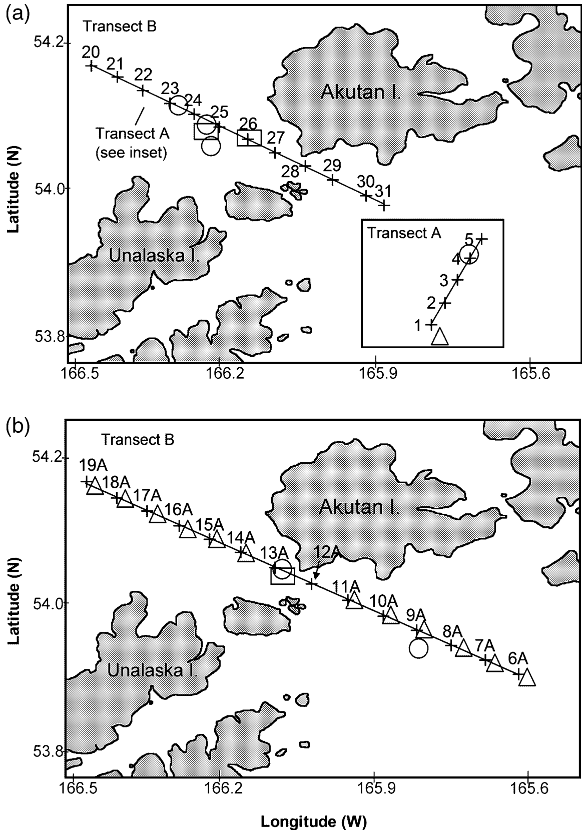
MARINE SETTING

Akutan Pass (54°01′N, 166°04′W) is located in the eastern Aleutian Island Archipelago, between Unalaska and Akutan Islands. Akutan Pass lies approximately 100 km southwest of Unimak Pass, the largest pass in the eastern Aleutian Islands in terms of both width and volume transport (Stabeno *et al.*, 2002). Akutan Pass, like other passes in the Aleutian Islands, connects the warmer, less saline water of the northern Gulf of Alaska with the cooler, more saline water of the eastern Bering Sea. North–south tidal currents dominate short-term variation in water flow through the pass. Relative to other passes in the region, Akutan Pass is shallow, with a maximum depth of roughly 80 m. During our study, current speed was 0–4 m s^{-1}.

METHODS

We visited Akutan Pass aboard the R/V *Alpha Helix* on July 25, 1999, August 18–19, 1999, and June 14–16, 2001. During July 25 and August 18–19, 1999, we measured shearwater distribution and diet, hydrography, and prey availability on two transects: A and B (Fig. 1a). Transect A was 1.7 km in length and ran perpendicular to a linear flock of feeding shearwaters. Transect B was 45.0 km in length and ran along the axis of Akutan Pass (Fig. 1a). Transect A was used to examine spatial relationships at small spatial scales, and Transect B was used to examine relationships at larger spatial scales. During June 14–16, 2001, we measured relationships among shearwater distribution and diet, hydrographic structure, and prey availability on Transect B only (Fig. 1b).

Figure 1. (a) Map of Akutan Pass, showing Transects A and B (solid line) sampled during July and August 1999. Transect A bisected a linear flock of shearwaters feeding by pursuit-diving. Transect B is positioned along the axis of Akutan Pass. (b) Map of Akutan Pass, showing Transect B (solid lines) sampled during June 2001. (A, B) The '+' symbol indicates CTD stations. Open triangles (△) indicate locations of MOCNESS sampling, and open rectangles () indicate locations of NIO net hauls. Open circles (○) indicate locations where birds were collected for diet analysis.



1999, Transect A

We determined the abundance and distribution of short-tailed shearwaters on Transect A by conducting systematic seabird surveys from the ship's bridge, while the ship was underway. During surveys, one observer noted the species, abundance, group size, and behavior (flying, on water, feeding, other) of each bird observed within a 300-m arc extending from the bow to the starboard side of the ship. If visibility was poor because of glare on the starboard side of the ship, observations were made from the port side. When flocks were observed beyond transect boundaries, the total number of birds in the flock was estimated. However, only birds within transect boundaries were included in our analysis. Foraging behaviour employed by shearwaters, such as plunge-diving, pursuit-diving, surface-seizing, or hydroplaning, was also recorded. An assistant entered each observation into a laptop computer equipped with software (FLOCK program) that tagged each sighting with time of day to the nearest 0.1 min. Shearwater abundance was grouped into 0.1-km bins for comparison with hydrographic structure and into 0.3-km (5.4-min) bins for comparison with hydroacoustic biomass (see below). Larger bins were used to compare shearwater distribution with hydoacoustic biomass because they minimized spatial autocorrelation in both backscatter and seabird abundance (see Results).

We used a Seabird 911-Plus conductivity–temperature–depth (CTD) probe with dual temperature and conductivity sensors to determine the presence, and if present, the location of tidal fronts in Akutan Pass. Hydrographic structure was measured in terms of sea temperature (°C), salinity, and density (σ). We used a Wetlabs fluorometer attached to the CTD to measure chlorophyll fluorescence (volts), which is a proxy measure of phytoplankton (Kolber and Falkowski, 1993). CTD casts were made at five fixed stations along the transect, with each cast made to within 3–5 m of the sea floor. Because physical features, such as density and salinity, were well represented by ocean temperature, we present transects of ocean temperature and fluorescence only.

We determined the presence of tidal fronts by locating strong horizontal gradients in sea surface temperature (SST). These regions were also characterized by vertical isotherms within the top 40 m of the water column, where water mixed by the pass met the more stratified water of the Bering Sea or Pacific Ocean.

We estimated the horizontal and vertical distribution of prey biomass in the water column below feeding shearwaters on Transect A by conducting a hydroacoustic survey and net sampling. The acoustic system employed a Hydroacoustic Technology Inc. (HTI) model 244 split-beam transducer towed on a hydrodynamic sled alongside the ship while underway at 1–2 m s^{-1}. We quantified potential prey biomass in terms of volume backscatter at 200 kHz. At this frequency, targets <2–3 mm in length should have been excluded from the analysis, leaving targets pertaining to plankton of the size consumed by shearwaters. The precision of our analyses may have been limited by the use of targets detected at only one frequency. However, we felt that this approach was sufficient because we were more interested in whether shearwaters were spatially aligned with scattering intensity more closely than expected by chance than we were in making precise estimates of euphausiid density. In addition, net tows were conducted through acoustically determined biomass to determine whether biomass represented shearwater prey. To avoid surface interference, we did not measure biomass at depths of 0–5 m.

Volume backscatter was converted from decibels (dB) to linear values for statistical analysis. Linear values were converted back to dB for graphic presentation. Acoustic backscatter was separated into 0.3-km horizontal bins and four vertical strata corresponding to depths of 6–10, 10–20, 20–30, and 30–40 m. Volume backscatter was integrated over each depth strata, then divided by area surveyed, to yield an estimate of volume backscatter per m^2 for each depth strata. Bin sizes pertained to distances that minimized spatial autocorrelation in backscatter and seabird abundance (see Results). Spatial autocorrelation in birds and acoustic backscatter was examined with the Spatial Autocorrelation Analysis Program (SAAP; Wartenberg, 1989). This program calculates the Moran's *I* statistic for each variable and its associated *P*-value. When $P < 0.05$ the variable was considered spatially autocorrelated.

We determined whether the distribution of shearwaters on Transect A was more closely aligned with scattering intensity than expected by chance by calculating Pearson's correlation coefficients (r) and associated *P*-values for abundances of shearwaters and backscatter for each 0.3-km bin along the transect.

We sampled the composition of acoustic biomass on Transect A with a multiple opening–closing net system (MOCNESS). The net was towed through the most dense patches of acoustic biomass, which were located at depths of 6–20 m. The contents of each net were preserved in formalin. In the laboratory, samples were weighed to the nearest milligram, and euphausiids were counted and identified to species. Euphausiids were also classified according to age and sex. Age and sex classes generally corresponded to two size classes: <15 mm (hereafter, small euphausiids) and >15 mm (hereafter, large euphausiids). Small euphausiids included furcillids, small juvenile and small adult female euphausiids. Large euphausiids included large juveniles, large female adults, and adult males.

We determined the type and size of prey consumed by shearwaters in Akutan Pass by collecting shearwaters that were actively feeding on Transect A. Shearwaters were collected immediately following MOCNESS surveys of prey availability. Shearwater collections were made by shooting in accordance with guidelines approved by the Institutional Animal Care and Use Committee of the University of California, Irvine and under U.S. Fish and Wildlife and State of Alaska scientific collection permits. Within minutes of collection, we removed the stomach of each bird and placed the contents in 80% ethyl alcohol. Contents were later weighed, identified to species (when possible), and enumerated. For samples containing fewer than 150 whole euphausiids, the total body length (mm) of each euphausiid was measured. For larger samples, a Folsom splitter was used to obtain a random subsample of 40 or more euphausiids, and the length of only euphausiids in the subsample was measured.

1999, Transect B

On August 18, 1999, we determined the abundance and distribution of short-tailed shearwaters on Transect B by conducting systematic seabird surveys. We followed the same procedure for seabird surveys as that described for surveys conducted on Transect A, July 25, 1999. Because Transect B was longer than Transect A, however, shearwater abundance on Transect B was grouped into 1.0-km bins for comparison with hydrographic structure (see below).

We measured hydrographic structure by conducting CTD casts at 11 fixed stations on Transect B. All CTD casts were made with a Seabird 911-Plus CTD probe equipped with a Wetlabs fluorometer. Each cast was made to within 3–5 m of the sea floor. We report hydrographic structure in terms of sea temperature and chlorophyll fluorescence only.

To determine the size of prey consumed by shearwaters, we collected shearwaters that were actively feeding on Transect B. Collections were made following the hydrographic survey. The stomach of each bird was removed immediately after collection, and the contents were preserved in 80% ethyl alcohol.

On August 19, we determined the size of euphausiids available to shearwaters feeding near the surface on the north end of Transect B by conducting surface tows with a 1-m^2 National Institute of Oceanography (NIO) net with 1-mm^2 mesh. Tows were made along three 10-min transects, with one transect located directly through the centre of a linear flock of feeding shearwaters and one transect located 0.8 km to either side of the flock. The net was towed with its bottom rim 0.5 m underwater. During tows, SST and fluorescence were measured by a Sea-Bird Electronics thermosalinograph and fluorometer installed on the ship. At 1-min intervals, an observer manually recorded these parameters, which were displayed on a ship's monitor. To assess whether tows were located in stratified water or water mixed by Akutan Pass, we compared SST on 10-min transects to SST measured on Transect B with the CTD on August 18, 1999. After each tow, net contents were preserved in 80% ethyl alcohol. In the laboratory, we used a Folsom splitter to obtain random subsamples containing at least 100 euphausiids. Each euphausiid in the subsample was identified to species, when possible. We also measured the total body length (mm) of each euphausiid in the subsample.

We also conducted a set of three 10-min tows in a region 5 km southeast of the first tow site. The second set was used to determine whether the size of euphausiids present at the water's surface where shearwaters foraged in linear flocks differed from the size of euphausiids in the middle of the pass, where shearwaters appeared consistently absent throughout the study. After each tow, net contents were preserved in 80% ethyl alcohol.

2001, Transect B

On June 14, 2001, we measured seabird abundance and distribution relative to hydrographic structure on Transect B. Systematic seabird surveys followed the same procedure as that described for seabird surveys conducted during July and August 1999. Shearwater abundance was grouped into 1.0-km bins for comparison with hydrographic structure.

Hydrographic structure on Transect B was measured with a Seabird 911-Plus CTD probe equipped with a Wetlabs fluorometer. CTD casts were made at 14 fixed stations along the transect, and each cast was made to with 3–5 m of the sea floor. As in July and August 1999, water density and salinity on June 14, 2001, were well represented by ocean temperature; therefore, we present transects of ocean temperature and fluorescence only.

Later on June 14, 2001, we determined the size of prey consumed by shearwaters foraging on Transect B by collecting shearwaters actively feeding on the transect. The contents of shearwater stomachs were preserved in 80% ethyl alcohol.

Two hours later, we measured potential prey availability to shearwaters on Transect B by conducting a hydroacoustic survey concurrent with a second systematic seabird survey. The hydroacoustic survey employed the HTI system used in Akutan Pass during 1999, but four transducers (420-kHz 6° single beam, and 43-kHz 7°, 120-kHz 6° and 200-kHz 3° split beam) were used as opposed to one. Volume backscatter (dB) was converted to estimates of euphausiid biomass density (g m^{-3}) using algorithms derived from night-time MOCNESS sampling (see below) and neural network analysis, a procedure described by Coyle (2005). Acoustic estimates of euphausiids biomass were separated into 1.0-km horizontal bins and integrated over four vertical strata corresponding to depths of 6–10, 11–20, 21–30, and 31–40 m. Shearwater abundance along Transect B was separated into 1.0-km bins for comparison with densities of euphausiid biomass. On this particular survey, shearwaters occurred in too few flocks to assess statistically their distribution relative to euphausiid biomass.

On June 15 and 16, 2001, we determined whether large (>15 mm) and small (<15 mm) euphausiids were present in Akutan Pass by conducting night-time MOCNESS tows on Transect B. Because euphausiids are dispersed in the upper water column at night, euphausiid densities estimated from night-time MOCNESS tows do not reflect densities available to seabirds during the day. Also, euphausiid densities are estimated by averaging the number of euphausiids caught over the distance that the net is towed, another reason that MOCNESS tows do not reflect densities of euphausiids encountered by shearwaters foraging during the day. Night-time surveys do, however, provide information on the presence and relative abundance of euphausiids of varying size in the water column during the day. These data can be used in combination with hydroacoustic surveys to estimate volume backscatter attributable to euphausiids in the water column (Coyle, 2005) and to determine whether both small and large euphausiids were present in Akutan Pass during the day. After each haul, net contents were preserved in formalin and later enumerated in the laboratory.

On June 16, 2001, we determined the size of euphausiids located at the sea surface directly below a flock of ~8000 shearwaters feeding by plunge-diving near the middle of Akutan Pass. We sampled euphausiids by conducting a set of three surface tows made with a 1-m^2 NIO net with 1-mm^2 mesh. One 10-min transect was located directly below the feeding flock, and one transect was located 0.8 km to either side of the flock. Net contents were preserved in 80% ethyl alcohol. Immediately following NIO net tows, shearwaters in the flock of ~8000 plunge-diving shearwaters were collected for diet analysis. Stomach contents were preserved in 80% ethyl alcohol.

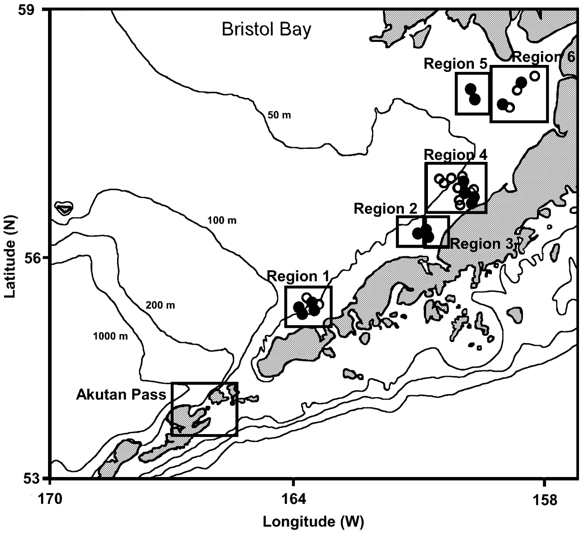
Regional comparison

We sought to determine whether shearwaters feeding in Akutan Pass consumed smaller prey than did those in pelagic settings that lacked tidal fronts. Information regarding shearwater foraging behavior and diet, hydrographic structure, and prey availability was obtained in Regions 1–6 in Bristol Bay (Fig. 2). This information was collected during a larger study conducted on the foraging ecology of short-tailed shearwaters in the southeastern Bering Sea during 1997–99. We used only data from shearwaters collected in water stratified to at least 40-m depth, or those in shallow (<35 m) mixed water, where temperature at the surface and at the bottom differed by <0.5°C.

The presence of small and large euphausiids in Regions 1–6 was determined by examining data from multiple MOCNESS hauls conducted in each region (Fig. 2). All MOCNESS hauls were conducted at night, between 00:00 and 06:00. We reemphasize that we used night-time tows to assess only the presence of euphausiids in each size class in each survey region. Following each haul, we treated the contents of each net in the same manner as that described for hauls conducted in Akutan Pass. In the laboratory, net contents were weighed and identified to species. Euphausiids were classified according to age and sex.

Seabird surveys were conducted in Regions 1–6, usually on the same day, or within 2 days of MOCNESS surveys. Observers conducting systematic

Figure 2. Map of eastern Bering Sea shelf showing location of MOCNESS hauls (○) and shearwater collections (●) made in Regions 1–6 during 1997–99. Circles may indicate more than one sampling event.



seabird surveys classified the primary foraging method of shearwaters as pursuit-diving, plunge-diving, surface-seizing, or hydroplaning. We examined the type and size of prey taken by three to five shearwaters collected in each region by quantifying shearwater diets with the same procedure described earlier for shearwaters collected in Akutan Pass.

RESULTS

1999, Transect A

On July 25, 1999, we observed 3000–6000 short-tailed shearwaters feeding on the north side of Akutan Pass. Shearwaters were situated in well-defined linear flocks, approximately 1–10 m in width and 0.1–5.0 km in length. Flocks were positioned parallel to one another, with birds departing and rejoining flocks every 5–30 min.

We counted a total of 1570 shearwaters on Transect A. Most (96%) of these birds belonged to two linear flocks located at km 0.4 (600 birds) and km 1.1 (900 birds; Fig. 3a). Linear flocks of shearwaters also contained hundreds of northern fulmars (*Fulmarus glacialis*), a surface-feeding seabird. However, the abundance of fulmars was not recorded until the second run of Transect A, when the hydroacoustic survey was conducted. We counted a total of 330 northern fulmars on the transect, with most ($N =$ 210) fulmars occurring at km 0.4 (Fig. 4a).

Five CTD casts (Stations 1–5) were conducted along Transect A to determine hydrographic structure below the two linear flocks (Fig. 3b). Sea surface temperature ranged from 6.7 to 7.3°C. The strongest horizontal temperature gradient was detected between km 1.3 and km 1.7 (Stations 4 and 5). The water column was weakly stratified to the ocean floor on the north side of the transect. On the south side, water was continuously stratified to 15-m depth, below which, it was well-mixed.

Potential prey availability to shearwaters feeding on Transect A was determined hydroacoustically immediately following the CTD survey. A region of high-intensity acoustic backscatter was located within 6–10 m of the water's surface (Fig. 4b). Shearwater density (Moran's $I = -0.147$, $P = 0.488$) and acoustic biomass in the four depth strata (6–10 m: Moran's $I = -0.310$, $P = 0.325$; 11–20 m: $I = -0.001$, $P = 0.325$; 21–30 m: $I = 0.005$, $P = 0.302$; 31–40 m:

Figure 3. Observations along Transect A on July 25, 1999, 15:40–16:17, of (a) abundance and distribution of short-tailed shearwaters observed feeding and resting on the water, and (b) sea temperature. Numbers along the top of the temperature plot represent station number.

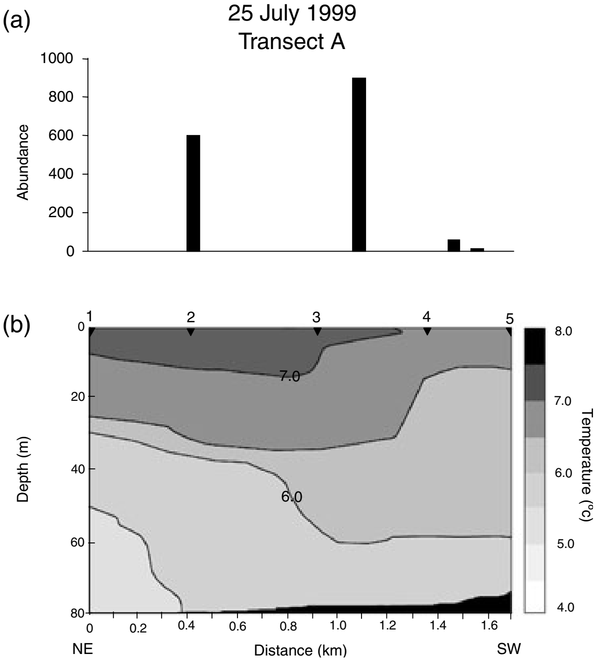
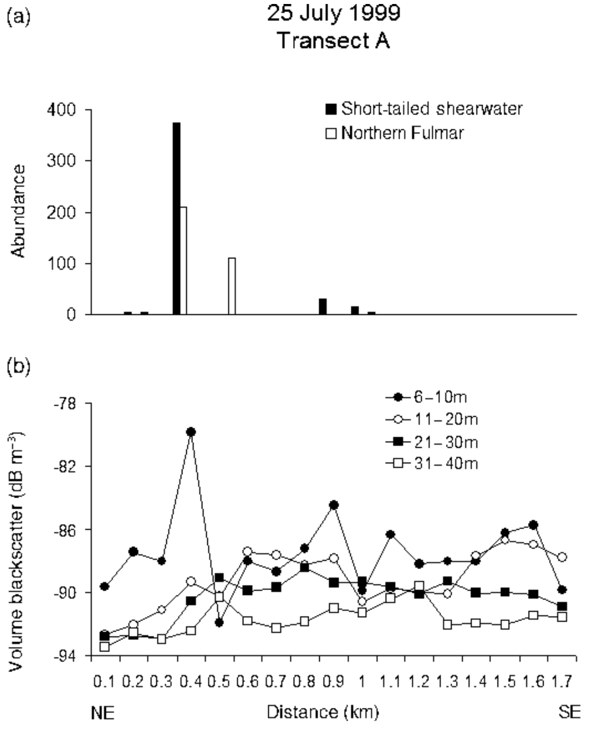


Figure 4. Observations along Transect A on July 25, 1999, 16:30–16:59, of (a) short-tailed shearwaters and northern fulmars feeding and resting on the water, and (b) integrated volume backscatter (dB) at four depth intervals.



−0.065, $P = 0.352$) were not autocorrelated at the 0.3-km scale. At this scale, shearwaters were cross-correlated with acoustic biomass in the 6–10 m depth stratum ($N = 7$, $r = 0.86$, $P = 0.01$). They were not cross-correlated with acoustic biomass in the other strata (11–20 m: $r = 0.14$, $P = 0.756$; 21–30 m: $r = 0.10$, $P = 0.823$; 31–40 m: $r = 0.01$, $P = 0.989$).

The composition of acoustic biomass on the transect was sampled with the MOCNESS. Copepods (*Eucalanus* spp., *Calanus* spp., *Neocalanus* spp.) comprised most (96%) of the biomass (total = 1.45 kg) caught. Euphausiids, all of which were furcillids, comprised 1% of the biomass. Because the tow was conducted during the day (15:00–16:00), it was possible that adult euphausiids avoided the net. However, net contents were consistent with the size class of euphausiids found in the stomachs of shearwaters foraging on Transect A (see below), suggesting that the nets probably yielded accurate estimates of acoustic biomass composition. At the furcillid life stage, euphausiids lack distinguishing species characteristics, so individuals were not identified to species.

Following the MOCNESS survey, we collected seven shearwaters from a flock of ~600 shearwaters foraging on Transect A. Shearwaters contained, on average, 16.0 (±3.9) mL of food consisting entirely (100% by vol.) of euphausiids. Most (61%) of these euphausiids ($N = 367$) were <11 mm in length, including furcillids, and those unidentified to species, indicating that shearwaters were consuming relatively small euphausiids. Of those identified ($N = 106$), most (66%) were *T. raschii* and *T. inermis*. The remaining 33% were *T. spinifera*. Overall, consumed euphausiids averaged 11.6 (±0.2) mm in length.

1999, Transect B

On August 18, 1999, shearwaters displayed the same behaviour as those observed during the previous month – they formed linear flocks at the north end of Akutan Pass and foraged by pursuit-diving. Nearly all (96%) of the 4571 shearwaters observed on Transect B were located within the first 21 km of the transect (Fig. 5a), on the Bering Sea side of the front (see below). The largest flock (~2000 birds) was located at km 19.0, between Stations 24 and 25. We estimated that over half (58%) of the shearwaters observed between Stations 23 and 25 were foraging, all of which did so by pursuit-diving (Table 1). Because this foraging method involves birds diving underwater from the sea surface, it was sometimes difficult to distinguish foraging birds from those resting on the water, and we may have underestimated the proportion of birds foraging (versus resting) on this transect.

Figure 5. (a) Distribution of short-tailed shearwaters observed feeding and resting on the water, (b) sea temperature, and (c) fluorescence on Transect B on August 18, 1999. Numbers along the top of the temperature plot represent station number.

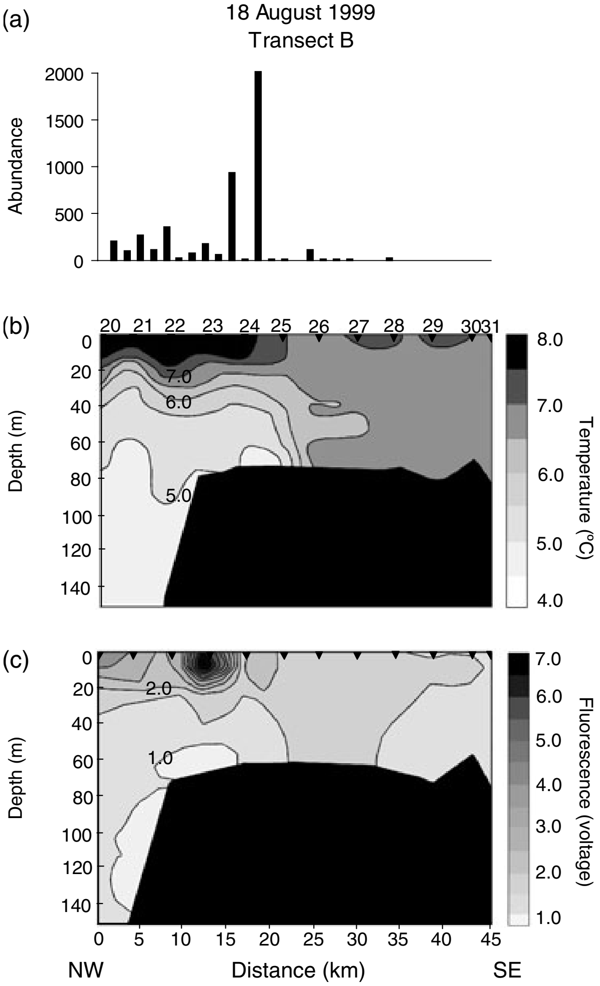


Table 1. Percentage of short-tailed shearwaters engaged in certain behaviours, Transect B, August 18, 1999, Akutan Pass. Most (99.9%) feeding shearwaters were observed between Station 23 and 25.

	Station		
	20–23	23–25	25–31
No. birds	3172	5054	303
Feeding			
Pursuit-diving	0.0	58.4	1.3
Plunge-diving	0.0	0.0	0.0
Resting on water	34.2	9.3	19.5
Flying w/o feeding	65.8	32.3	78.9
Other	0.0	0.0	0.3

During seabird surveys, 11 CTD casts (Stations 20–31) were made on Transect B. Sea surface temperature in the pass ranged from 6.6 to 7.8°C. A front was detected on the north end of the pass, between km 19 and km 23 (Stations 24–25; Fig. 5b). The front was expressed as isotherms descending to the seafloor from approximately 30 m depth, as well as isotherms ascending from 30 m to the surface. Mixed water on the opposite side of the front was approximately 6.6–6.8°C and extended into Akutan Pass (Fig. 5b). There was a patch of exceptionally high surface fluorescence in the warm, stratified water near Station 23 on the Bering Sea side of the front (Fig. 5c).

On August 19, 1999, we collected four pursuit-diving shearwaters from a flock consisting of ~1000 birds feeding over stratified water (see below). They contained, on average, 1.9 mL (±0.5) of food. Diets were composed of predominantly small euphausiids (99% by vol.), averaging 11.5 (±0.3) mm in length (Fig. 8). Many (45%) euphausiids ($N = 71$) were <10 mm in length and could not be identified to species. Of those identified ($N = 39$), 97% were *T. raschii* and *T. inermis*. The remainder was *T. spinifera*.

Potential prey availability to shearwaters feeding near the sea surface was estimated by conducting two sets of three surface tows with the NIO net on the north end of Transect B. The first set of tows was conducted directly through the flock from which shearwaters had been collected (see above). Sea surface temperature during the tows ranged from 7.1 to 7.9°C, indicating that tows were located in stratified water. The second set of tows was conducted where shearwaters appeared consistently absent during the study. Sea surface temperature during tows was 6.9°C, indicating that tows were located in water mixed by Akutan Pass. Euphausiids caught in tows conducted in stratified water, where shearwaters foraged by pursuit-diving, were larger (8.4 ± 0.05 mm) than those caught in mixed water, where foraging shearwaters were consistently absent (6.9 ± 0.1 mm; $t^2 = 9.34$, $P < 0.001$; Fig. 6).

2001, Transect B

We estimated that over 12 000 shearwaters were present in Akutan Pass during June 14–16, 2001. Shearwaters behaved in a manner different from those observed during July and August 1999. They travelled in large cohesive flocks and foraged by plunge-diving near the middle of Akutan Pass (Table 2). On June 14, 2001, ~9000 shearwaters fed by plunge-diving on Transect B. Most (89%) shearwaters ($N = 9500$) were located between km 42 and km 44, near the south end of Akutan Pass (Fig. 7a). Only four northern fulmars were observed on Transect B during 2001. These birds were located on the north side of the transect, between km 0 and km 1, and were not associated with shearwater flocks.

Figure 6. Total body length (mm) of euphausiids caught in NIO net hauls conducted at the sea surface through a flock of feeding shearwaters on Transect B (grey bars), and in water mixed by Akutan Pass (white bars), where shearwaters appeared to be consistently absent. Abundance of euphausiids caught in NIO net hauls represents the total number of individuals caught during three 10-min tows. Black bars represent euphausiids taken by shearwaters foraging by pursuit-diving on Transect B. Sampling was conducted on Transect B on August 19, 1999.

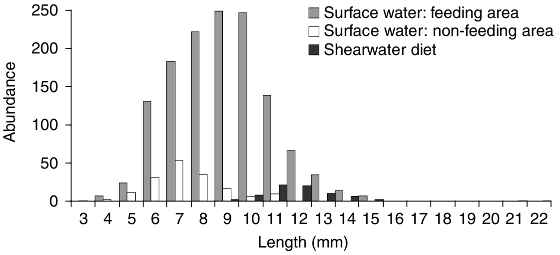
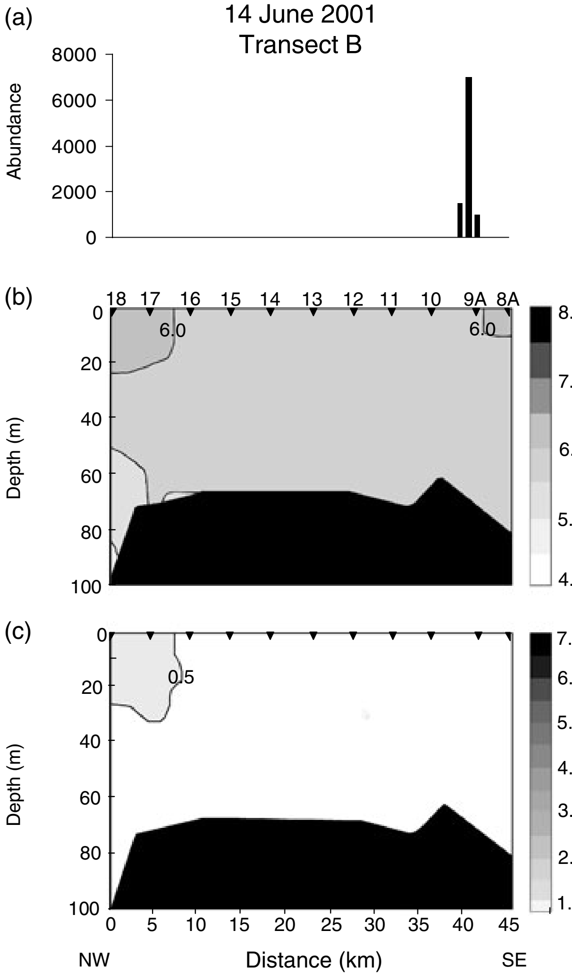


Table 2. Percentage of short-tailed shearwaters engaged in certain behaviours, Transect B, June 14, 2001, Akutan Pass. All (100.0%) feeding shearwaters were observed between Station 9A and 10.

	Station		
	8A–9A	9A–10	10–18
No. birds	251	9500	95
Feeding			
Pursuit-diving	0.0	0.0	0.0
Plunge-diving	0.0	94.7	0.0
Resting on water	1.2	5.3	7.4
Flying w/o feeding	98.8	0.0	92.6
Other	0.0	0.0	0.0

During seabird surveys, we conducted 11 CTD casts on Transect B (Fig. 7b). Sea surface temperature in Akutan Pass ranged from 5.8 to 6.2°C (Fig. 7b). We detected a front between km 5 and km 10 (Stations 17A–18A; Fig. 7b). We also detected a front between km 40 and km 45 (Stations 8A–9A), where water mixed in the pass met stratified water of the Gulf of Alaska (Fig. 7b). These fronts were weak compared with the front observed at the north end of Akutan Pass during August 1999. In June 2001, the difference in water temperature at stations at either side of the front was 0.4°C on the north end of Akutan Pass and 0.2°C on the south end. During August 1999, this

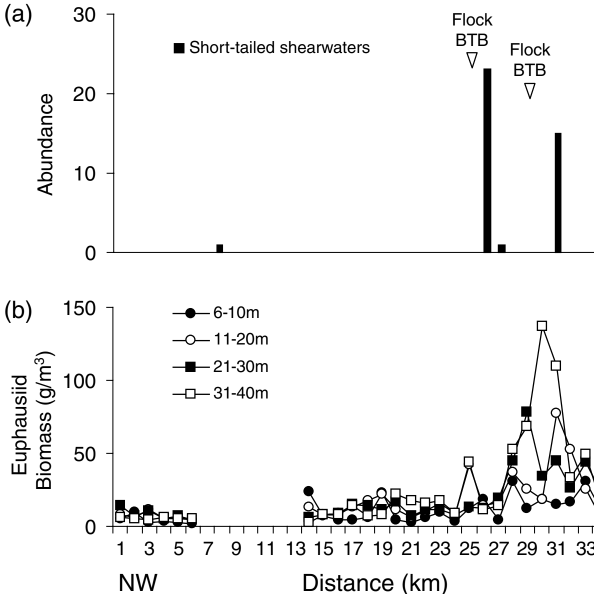
Figure 7. (a) Distribution of short-tailed shearwaters feeding and resting on the water, (b) sea temperature, and (c) fluorescence on Transect B on June 14, 2001, 12:45–17:40. Numbers along the top of the temperature plot represent station number.



difference was 1.0°C. In June 2001, surface fluorescence on Transect B did not exceed 1.5 V (Fig. 7c).

We collected four shearwaters from a flock containing ~10 000 plunge-diving birds on Transect B. Shearwaters contained more food than those collected during 1999, with stomachs averaging 185.6 (±6.8) mL of food per bird. Diets were dominated by euphausiids (99–100% by vol.), averaging 16.9 (±0.1) mm in length. None of these euphausiids were furcillids. Nearly 99% ($N = 345$) were *T. inermis*. Seventy-nine percent of the euphausiids in shearwaters diets carried spermatophores, suggesting that euphausiids had recently mated.

Figure 8. Observations along Transect B on June 14, 2001, 19:35–22:13, of (a) short-tailed shearwaters feeding and resting on the water, and (b) euphausiid biomass (dB) integrated over four depth intervals. Acoustic data for km 22–28 were removed because of environmental noise. Large flocks of shearwaters, up to 4.3 × 0.8 km in size and containing several thousand birds, were observed during this survey, but they were located beyond transect boundaries (BTB).



Immediately following shearwater collections, we measured potential prey availability to shearwaters by conducting hydroacoustic measurements from Station 8A to Station 15 on Transect B. Volume backscatter from km 23 to km 29 was removed from our analysis because it contained background noise. Mean (±SE) density of euphausiid biomass along the transect was 19.0 (±2.0) g m^{-3}, with a marked peak in density (136.5 g m^{-3}) at km 30 (Stations 9–10; Fig. 8b). Peak densities pertained to euphausiids at depths of 31–40 m.

During the hydroacoustic survey, we observed only 41 shearwaters feeding or resting on Transect B. Most (93%) of these shearwaters occurred at km 26 and km 32 (Stations 9–10). More striking, however, was the observation of two enormous shearwater flocks, each containing thousands of plunge-diving shearwaters, beyond the 300-m transect boundary. One flock, located adjacent to km 25, was approximately 4.3 km long and 0.8 km wide. The other flock, located adjacent to km 28, was approximately 2.4 km long and 0.8 km wide.

We estimated the relative abundance of small and large euphausiids in the water column by conducting six MOCNESS hauls at Stations 14A–19A between 00:00 and 06:00 on June 15, 2001, and six MOCNESS hauls at Stations 6A–11A between 00:00 and 06:00 on

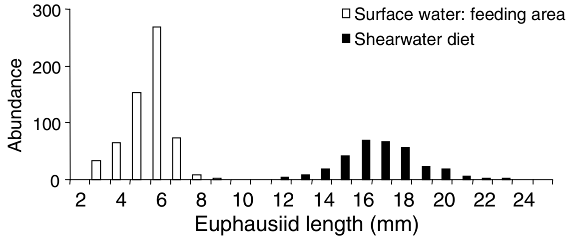
June 16, 2001. Both small and large euphausiids were present at depth in Akutan Pass, with biomass from large euphausiids being approximately three times greater than that of small euphausiids (Table 3).

Surface tows conducted on Transect B during June 16, 2001 revealed that euphausiids directly below a flock of ~8000 plunge-diving shearwaters were small, averaging 5.0 (±0.05) mm in length (Fig. 9). From this flock, we collected seven shearwaters. Their stomachs contained an average of 158.1 (±26.8) mL of food, consisting of 99–100% euphausiids by volume. Euphausiids averaged 16.9 (±0.1) mm in length ($N = 319$; Fig. 9). Most (79%) were *T. inermis*. The remainder was *T. rachii* and *T. spinifera*. Fifty-five percent of the euphausiids carried spermatophores. Overall, euphausiids consumed by plunge-diving shearwaters in Akutan Pass during June 2001 were significantly larger (16.6 ± 0.1 mm) than euphausiids consumed by pursuit-diving shearwaters in Akutan Pass during July and August 1999 (11.6 ± 0.2 mm; Student's *t*-test: $t^2 = 32.3$, $P < 0.001$).

Regional comparison

Outside of Akutan Pass, in Regions 1–6, shearwaters were collected in water that was either continuously stratified to at least 40 m depth (Region 1 in 1997, Regions 3 and 6) or in shallow (<35 m) mixed water of the inner Bering Sea shelf (Region 1 in 1998 and 1999, Region 2, and Region 4 in 1998 and 1999, Region 5), where temperature at the surface and at the bottom differed by <0.5°C.

Figure 9. Total body length (mm) of euphausiids caught in NIO net hauls conducted at the surface (white bars) below a flock of shearwaters feeding by plunge-diving, and euphausiids eaten by shearwaters ($N = 7$) in the flock (black bars). Abundance of euphausiids caught in NIO net hauls represents the total number of individuals caught during three 10-min tows. Sampling was conducted on Transect B, June 16, 2001.



We examined densities of small and large euphausiids in the water column in Regions 1–6, where shearwaters were also collected (Fig. 3). In most cases, euphausiids of both size classes were present. Exceptions were Regions 2 and 4 during 1999, where small euphausiids were absent (Table 3).

Shearwaters in most regions contained large euphausiids, averaging between 14.2 and 20.1 mm in length (Table 4). Exceptions were shearwaters in Region 1 during 1997 and 1998, which foraged by

Table 3. Biomass of euphausiids sampled at depths ranging from 0 to 105 m during MOCNESS tows in Akutan Pass and Regions 1–6 in Bristol Bay, Alaska, 1997–2001.

		Sampling effort			Density of euphausiid biomass (mg m^{-3})[†]	
Region	Year	Period	No. hauls	Total vol. (m^3) water sampled	Small (<15 mm)	Large (>15 mm)
Akutan Pass	1999	Day	1	1944	7.5	0.0
	2001	Night	12	7445	14.6	63.7
SE Bering Sea*						
1	1997	Night	6	6068	9.8	523.0
1	1998	Night	3	3269	<0.1	20.0
1	1999	Night	4	3838	0.1	88.2
2	1999	Night	4	4868	0.0	24.0
4	1998	Night	6	5633	4.5	1.3
4	1999	Night	3	2922	0.0	0.1
6	1998	Night	3	2370	0.1	29.9

*Region 1 = Slime Bank, Region 2 = Port Moller South, Region 3 = Nelson Lagoon, Region 4 = Port Moller North, Region 5 = Round Island, Region 6 = Dillingham.

[†] Euphausiids <15 mm include furcillids, small juveniles and small adult female euphausiids (<50 mg). Euphausiids >15 mm include large juveniles, large adult females and adult males (>50 mg).

Table 4. Foraging method and length of euphausiids taken by short-tailed shearwaters in Akutan Pass and Regions 1–6, Bristol Bay, Alaska, 1997–2001.

			Sampling effort			Shearwater diet
Region	Year	Shearwater foraging behaviour	No. birds sampled	Mean food vol. (mL)	Total no. euphausiids sampled	Mean (±SE) euphausiid length
Akutan Pass	1999	Pursuit dive	11	16.0	438	11.6 (0.2)
	2001	Plunge dive	15	172.8	664	16.5 (0.1)
SE Bering Sea*						
1	1997	Pursuit dive	5	25.4	354	9.4 (0.1)
1	1998	Pursuit dive	1	25.0	60	8.8 (0.2)
1	1999	Plunge dive	5	46.0	413	14.2 (0.1)
2	1999	Plunge dive	4	69.8	201	19.5 (0.1)
3	1999	Plunge dive	5	47.2	227	19.5 (0.1)
4	1998	Hydroplane	5	61.0	210	18.1 (0.1)
4	1999	Plunge dive	3	70.2	86	17.2 (0.2)
5	1999	Plunge dive	4	36.3	113	20.1 (0.2)
6	1998	Plunge dive	5	51.8	291	20.1 (0.1)

*Region 1 = Slime Bank, Region 2 = Port Moller South, Region 3 = Nelson Lagoon, Region 4 = Port Moller North, Region 5 = Round Island, Region 6 = Dillingham.

pursuit-diving and took euphausiids averaging 8.8 and 9.4 mm in length, respectively (Table 4). Overall, shearwaters that foraged by pursuit-diving contained smaller euphausiids than did shearwaters that foraged by plunge-diving or hydroplaning ($t^2 = 63.00$, $P < 0.001$).

DISCUSSION

During July and August 1999, short-tailed shearwaters in Akutan Pass formed linear feeding flocks on the Bering Sea side of tidal fronts. Most, if not all, of the shearwaters captured prey by near-surface pursuit-diving. Shearwaters in linear flocks were spatially concordant with high densities of acoustic backscatter attributable to small euphausiids near the sea surface. Diets of shearwaters feeding at the tidal front consisted of smaller euphausiids than did the diets of shearwaters collected in Akutan Pass during 2001, when only weak fronts were present. Shearwaters in Akutan Pass during 1999 also consumed smaller euphausiids than did shearwaters feeding by plunge-diving in large cohesive flocks elsewhere in the Bering Sea. Collectively, these observations support the hypothesis that shearwaters feeding in linear flocks in Akutan Pass consumed small prey associated with tidal fronts. They also suggest that oceanographic features can make small, otherwise unusable prey profitable to top marine predators.

We did not attempt to characterize in detail the mechanism by which small euphausiids may have become concentrated at tidal fronts in Akutan Pass during 1999. However, we did observe high levels of fluorescence on the stratified side of the front. Fluorescence is a proxy measure for chlorophyll and is an indicator of phytoplankton abundance. Regions of enhanced primary production are often associated with the stratified side of tidal fronts (Simpson *et al.*, 1979; Holligan, 1981; Franks, 1992a), where mixed water adjacent to the front delivers nutrients, either by diffusion or vertical mixing, across the pycnocline and into the euphotic zone of the stratified water (Loder and Platt, 1985; Dewey and Moum, 1990). This process is especially likely to occur in shallow passes with strong currents, such as Akutan Pass, where turbulence mixes the entire water column in the pass (Franks, 1992a).

Primary production associated with tidal fronts can support extensive food webs that include organisms at lower trophic levels, such as microbes (Floodgate *et al.*, 1981), zooplankton (Alldredge and Hamner, 1980; Smith *et al.*, 1986; Pakhomov *et al.*, 1994), and forage fish (Lang *et al.*, 2000). These organisms, in turn, support organisms at higher trophic levels, such as fish (Fiedler and Bernard, 1987; Sims and Quayle, 1998), seabirds (Schneider, 1990; Decker and Hunt, 1994; Hunt *et al.*, 1998, 1999; Russell *et al.*, 1999; Hyrenbach *et al.*, 2002; but see Spear *et al.*, 2001), and marine mammals (Kingsford and Choat, 1986). Such multi-trophic-level interactions were associated with the tidal front in Akutan Pass during 1999. On the stratified side of the front were high levels of fluorescence (i.e. phytoplankton), dense patches of small euphausiids near the sea surface and thousands of feeding shearwaters and other seabirds.

Observations of zooplankton near the sea surface in Akutan Pass were somewhat unusual because most euphausiids migrate from the surface to depth during the day (Mauchline and Fisher, 1969a; Godlewska, 1996). However, young (i.e. small) euphausiids tend to have shorter migration cycles, lower migration amplitudes, and shallower submergence depths than do larger, older euphausiids. This difference may be related to age-specific differences in motile capability (Mauchline and Fisher, 1969b; Nordhausen, 1994). Euphausiids also tend to remain near the surface when local foraging conditions are especially profitable relative to regional conditions (Nordhausen, 1994; Godlewska, 1996; Hernández-León *et al.*, 2001). Shallow daytime depth distributions have been observed in young *T. inermis* and *T. raschii* (Mauchline and Fisher, 1969b), species that constituted the primary prey of shearwaters in Akutan Pass. We do not know the mechanism responsible for the high chlorophyll concentrations at the tidal front in Akutan Pass; however, it is possible that the small euphausiids we observed may have been exploiting phytoplankton associated with nutrient availability on the stratified side of the front. Similarly, Hunt *et al.* (1996) hypothesized that enhanced production associated with a tidal front near the Pribilof Islands was responsible for attracting adult euphausiids to the sea surface, which were also preyed upon by short-tailed shearwaters.

Akutan Pass was not the only site where we observed dense patches of small euphausiids near the surface during the day. Small euphausiids occurred in Region 1 during 1997 and 1998, the only other site where shearwaters foraged by pursuit-diving. Surveys in this region indicated relatively high levels of fluorescence in surface water, and observers looking over the side of the ship could see dense patches of small euphausiids swimming at the sea surface (G. Hunt, University of California, Irvine, USA, personal communication). Here, shearwaters consumed small euphausiids. They also fed in mixed water, away from any front or other concentrating mechanism.

High abundances of zooplankton near the sea surface may also enhance foraging opportunities for marine predators other than seabirds. On June 19, 2001, approximately 5 km north of Akutan Pass, we encountered a small ($\sim$500 m^2) area where we could see dense patches of large euphausiids near the surface by looking over the side of the ship. The patch also contained thousands of fish 'roiling' at and slightly below the sea surface, apparently feeding on the euphausiids. We opportunistically sampled euphausiids by conducting one 13-min haul with the 1-m^2 NIO net, directly through the patch. Approximately 66 kg (12.5 L) of euphausiids were caught and identified as adult *T. inermis* ($N = 129$), averaging 18.4 (±1.7) mm in length. Two Pacific herring (*Clupea pallasi*), with stomachs packed with adult *T. inermis*, were caught. Within minutes, a minke whale (*Balaenoptera acutorostrata*) approached the ship and began feeding, clearly targeting prey at and slightly below the sea surface. There were no other signs of subsurface predators. It is unclear why these euphausiids occurred in such high density near the surface north of Akutan Pass. The ship's continuous data recorder indicated that chlorophyll was not unusually high in this region. While traveling through the area numerous times in the past, we had not observed such an event. It is possible that euphausiids were mating near the surface, as nearly half (45%) of the euphausiids we sampled carried spermatophores. Regardless of the mechanism, it seems clear that dense patches of zooplankton near the surface can provide a variety of predators with a profitable, but probably intermittent, food source.

In addition to biological factors, such as enhanced foraging opportunities for zooplankton, physical processes may accumulate prey biomass at tidal fronts. For example, mixed (cool) water may be subducted below stratified (warm) surface water at the front (Hill *et al.*, 1993). Where the upward swimming or floating motion of zooplankton in the subducted water is counterbalanced by the downward force of the water, zooplankton become aggregated. These aggregations usually occur along the pycnocline or, for weak swimmers such as small euphausiids, on the stratified side of the front. The result is a band of zooplankton along the pycnocline, at or slightly below the water surface (Wolanski and Hamner, 1988; Franks, 1992b). This effect may have accounted for the linear orientation of shearwaters at the front in Akutan Pass. Because we did not measure surface currents in the pass, we cannot confirm nor rule out the possibility that physical mechanisms, such as surface convergence, may have aggregated small euphausiids at the tidal front.

Other studies suggest that physical processes operating within island passes do indeed play important roles in determining the distribution of short-tailed shearwaters over larger spatial scales, such as that of the Aleutian Island Archipelago. Shearwaters are more abundant in the narrow, shallow passes of the eastern Aleutian Islands than in the deeper, wider passes of the western Aleutians. This pattern may be the result of physical processes specific to shallow passes, such as upslope advection and associated surface convergence, which together may enhance prey availability to shearwaters and other birds that feed, at least occasionally, on near-surface prey (Jahncke *et al.*, 2005; Ladd *et al.*, 2005).

At smaller spatial scales, tidal fronts have been shown to concentrate plankton and influence the distribution of other seabirds elsewhere in the Aleutian Islands, and one study suggests that island passes may represent especially profitable foraging grounds for seabirds during certain times of year. For example, Hunt *et al.* (1998) showed that tidal currents influenced prey availability to three auklet (*Aethia* spp.) species feeding on zooplankton in a pass through the Delarof Islands, central Aleutian Islands. During certain tidal phases, copepods were concentrated near the sea surface, where they were available to near-surface-feeding least auklets (*Aethia pusilla*). The authors hypothesized that prey concentrations associated with the tidal fronts were important sources of food for auklets during times of year when most copepods had undergone ontogenetic migration to depth.

Similarly, we predict that near-surface patches of euphausiids occur more often in Akutan Pass during mid or late summer than during other times of year. In 2001, we visited Akutan Pass during June (i.e. early summer), and the water column was well mixed along most of Transect B, with only weak fronts near the ends of the pass. Even though euphausiids may breed in early summer, feeding-stage larvae and furcillids may not be abundant near the surface until mid or late summer, when surface heating has led to thermal stratification. Paul *et al.* (1990) found that calyptopes (the life stage preceding the furcillid stage) in Auke Bay, Alaska, initiated feeding following the spring bloom, when the water column was stratified. Consistent with the idea that Akutan Pass is most profitable for foraging seabirds during mid to late summer is the fact that our first and second visit to Akutan Pass, when shearwaters foraged on small euphausiids at the tidal front, occurred during July and August. During June 2001, when the water column was well-mixed, shearwaters exhibited behavior typical of those feeding in pelagic environments – they foraged in cohesive flocks and captured prey by plunge-diving. Moreover, shearwaters did not feed upon very small (<9 mm) euphausiids that were present at the sea surface, but instead consumed large euphausiids, presumably abundant at depth (31–40 m).

It is unclear to what extent oceanographic features influence prey-size use by seabirds on a day-to-day basis. When small prey is concentrated, seabirds may still prefer large prey items when they are available because, although small prey may offset the immediate cost of foraging, patches of large euphausiids may be required for seabirds to acquire sufficient prey to store fat necessary for migration or reproduction. At colonies off the coast of British Columbia, seabirds with diets containing a high proportion of 'large' copepod and euphausiid species had greater reproductive success than did seabirds that consumed relatively 'small' species (Bertram *et al.*, 2001). In Prince William Sound, Alaska, seabirds exhibited relatively poor reproductive success during years in which their main prey, age-0 sandeels (*Ammodytes marinus*), were relatively small (Lewis *et al.*, 2001). If seabirds make foraging decisions based on maximizing their long-term foraging returns as opposed to meeting short-term foraging requirements, then concentrations of small prey associated with tidal fronts may be of most importance to seabirds at times and in places where large prey is unavailable.

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