

Patch Use

THE INFLUENCE OF HYDROGRAPHIC STRUCTURE AND PREY ABUNDANCE ON FORAGING OF LEAST AUKLETS

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Abstract. We investigated the foraging distribution of Least Auklets (*Aethia pusilla*) near their breeding colonies in the Chirikov Basin, northern Bering Sea, to determine the physical and biological aspects of the ocean important in their use of foraging areas. In this paper we report on a series of transects radiating out from colonies on St. Lawrence and King islands, along which we examined the importance to foraging Least Auklets of vertical structure in the water column. We counted birds, collected them for food samples, described the hydrography using conductivity-temperature-depth casts, and obtained data on the distribution and abundance of prey from net tows and high-frequency acoustic surveys. Copepods (*Neocalanus* spp.) were prominent in the diets, and auklets foraged in greatest numbers in waters where *Neocalanus* was present and where the water was strongly stratified. Auklet numbers were correlated more strongly with plankton biomass in the upper water column than with biomass in the water column as a whole. Within the upper water column, it appeared that these correlations were stronger at a scale of 9-22 km than at 1.8-4 km and that auklets select their foraging habitat in a coarse-grained fashion.

Key Words: Least Auklet; *Aethia pusilla*; foraging habitat; Bering Sea; predator-prey studies; stratified water.

The pattern of marine bird distribution at sea results from the selection and use of foraging areas. Ocean habitats vary in scale from major portions of ocean basins that may be occupied continuously for months or years, to tidal rips that are attended for, at most, hours at a time (Hunt and Schneider 1987). Descriptions of these marine foraging habitats have usually focused on the physical characteristics of the surface layer (sea surface temperature and salinity) (e.g., Pocklington 1979, Brown 1980, Ainley et al. 1984, Fraser and Ainley 1986). In the nearshore zone, features such as fronts separating stratified and well-mixed water (Pingree et al. 1974, Schumacher et al. 1979, Kinder et al. 1983), eddies at headlands and islands (Ashmole and Ashmole 1967, Pingree et al. 1978, Hamner and Hauri 1981), and sills that force currents to the surface (Vermeer et al. 1987, Brown and Gaskin 1988), are predictably attended by foraging seabirds. In the open ocean, physical features also act as foci to aggregate seabirds (Schneider 1982, Briggs et al. 1984, Schneider and Duffy 1985, Haney and McGillivray 1985, Briggs and Chu 1987). The strength of fronts in the Bering Sea is an important correlate of their attendance by seabirds (Schneider et al. 1987), and it is likely that topographically fixed inshore features, with steep gradients and high kinetic energy, are attractive for similar reasons (Roseneau et al. 1985, Schneider et al. 1986). Unfortunately, in many studies oceanographic and ornithological data have not been gathered simultaneously, and virtually no study has investigated how prey abundance or availability affects the linkage between physical features and birds.

Implicit in studies of seabird habitat preferences is the assumption that the birds aggregate where their preferred prey is most readily obtained. The rate of prey capture will depend not only on the number of prey present (abundance), but also on their degree of aggregation (density), and availability, which is a function of their accessibility (e.g., depth in the water column). Relatively few investigators, however, have been able to measure prey density or accessibility. Most investigators who have attempted to link bird abundance to prey availability have found either weak to moderate correlations (Schneider and Piatt 1986, Cairns and Schneider 1990, Safina and Burger 1988, Heinemann et al. 1989) or no correlation (Woodby 1984, Safina and Burger 1985, Obst 1985) at small and intermediate scales (but see Piatt [1987] and McClatchie et al. [1989]). At larger scales, from 100s of kilometers to whole ocean basins, strong positive correlations have emerged between bird numbers and the abundance of presumed prey or marine secondary productivity (Jespersen 1930, Heinemann et al. 1989, Erikstad et al. 1990). In studying seabird foraging, quantifying prey availability is even more difficult than measuring prey abundance. Foraging success is possibly the best indicator of prey availability, even though numerous factors other than prey availability may influence capture rates (Dunn 1973, Birkhead 1976, Searcy 1978, Morrison et al. 1978, Hunt et al. 1988).

The poor correlations often found between the abundance of marine birds (particularly subsurface foragers) and their prey may result from their inadequate knowledge of prey distributions. Surface cues may promote local, ephemeral corre-

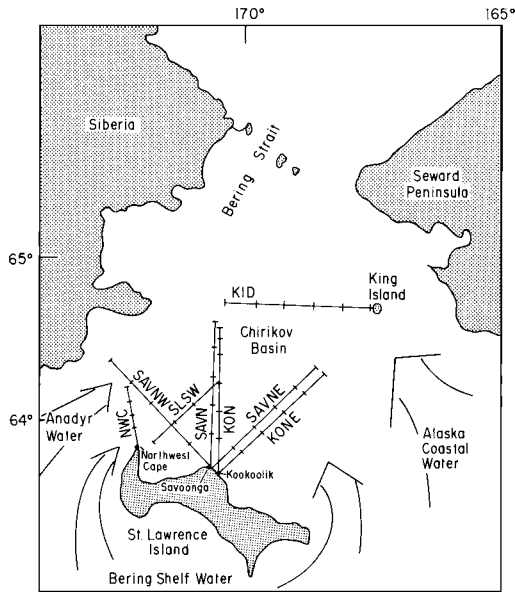


FIGURE 1. Study area and transect lines. Lines crossing transect lines indicate locations of stations. Stations were 18.5 km apart except on NWC where they were 9.8 km apart.

lations between birds and their prey. In some cases, prey are forced to the surface where they become apparent to flying birds. In other cases, surface characteristics, such as foam lines or narrow regions of choppy water, indicate the presence of subsurface processes that frequently concentrate prey (Hamner and Hauri 1981). However, subsurface foragers, such as alcids, may have few or no clues about the presence of prey many meters deep.

Although clues to the distribution of prey in the horizontal dimension may be lacking, prey distribution in the vertical dimension may be relatively predictable. Property gradients are often steep, resulting in stratification of the water column where marked changes in density (pycnoclines), due to rapid changes in salinity (haloclines) or temperature (thermoclines), impair vertical mixing. Plankton may be concentrated at or in these gradients (Harder 1968, Barroclough et al. 1969, Turner and Dagg 1983). As suggested by Briggs et al. (1987), when prey is concentrated at haloclines or thermoclines, particularly those near the surface, subsurface-foraging birds should be able to locate prey predictably and capture food more readily than when an equal abundance of prey is dispersed throughout an unstratified water column.

The Least Auklet (*Aethia pusilla*) is a small planktivorous alcid that specializes on various

species of copepods during the summer breeding season (Bédard 1969, Springer and Roseneau 1985, Hunt and Harrison 1990). Auklets obtain these prey while diving beneath the surface, and frequently take the large oceanic copepods *Neocalanus cristatus* and *N. plumchrus* (Springer and Roseneau 1985, Bédard 1969, Hunt and Harrison 1990). *Neocalanus* spp. are known to form dense layers in the ocean and respond to steep property gradients in the laboratory, which could lead to dense concentrations of these prey in the vertical dimension in a stable water column (Harder 1968, Barroclough et al. 1969). Thus, Least Auklets might be expected to concentrate their foraging in well-stratified water.

In this study we examined the foraging distribution of Least Auklets in the Chirikov Basin between St. Lawrence Island and King Island with respect to hydrographic structure and prey distribution in the vertical and horizontal planes. Using observations from transects that radiated from Least Auklet colonies on the north side of St. Lawrence Island and from King Island in the northern Bering Sea, we quantified bird distribution, water column structure, and the horizontal and vertical distribution of acoustically-determined biomass, the composition of which was determined by net tows.

STUDY AREA AND METHODS

Study area

The Chirikov Basin averages less than 50 m in depth and is bounded by St. Lawrence Island to the south, Siberia to the west, the Seward Peninsula of continental Alaska to the east and Bering Strait to the north (Fig. 1). Water enters the basin in two major currents: the Anadyr Current along the west side, and the Alaska Coastal Current along the eastern edge. Between these, Bering Shelf Water enters the basin from the south, passing primarily around the east end of St. Lawrence Island. The Anadyr Current originates in the deep Bering Sea, mixes with cold saline water in the Gulf of Anadyr, and sweeps northeasterly between Siberia and St. Lawrence Island into the basin and then out through Bering Strait (Coachman et al. 1975). The Alaska Coastal Current originates in Norton Sound. Compared to the Anadyr Current, the Alaska Coastal Current is a relatively warm, low salinity water mass that is similar to the coastal domain water of the southeastern Bering Sea (Coachman et al. 1975, Kinder and Schumacher 1981). Water in these currents is usually unstratified.

Bering Shelf Water is of intermediate salinity, compared to Anadyr Current Water or Alaska Coastal Current Water, and is a mixture of water from the deep Bering Sea to the south and cold bottom water present on the seasonally frozen northern Bering Sea shelf. Bering Shelf Water forms a broad expanse of water that flows northward more slowly than the currents on either side, and it is usually strongly stratified in summer (Coachman et al. 1975, Hunt and Harrison 1990). Near

the northern shore of St. Lawrence Island, Bering Shelf Water may be diluted by freshwater runoff, and may be unstratified due to a combination of tidal and wind mixing, as seen elsewhere in the Bering Sea (Kinder and Schumacher 1981, Kinder et al. 1983).

The boundaries of these three water masses in the Chirikov Basin are not static. The area occupied by the stratified Bering Shelf Water varies greatly over short periods depending on the positions of the Anadyr and Alaska Coastal currents. Both currents meander, and large horizontal excursions on the order of tens of kilometers have been observed over the period of 2–4 days, as well as from year to year (Hunt and Harrison 1990).

The copepod community of the Anadyr Current is dominated by the very large *Neocalanus cristatus* (10 mm), *N. plumchrus* (5 mm), and *Eucalanus bungii* (8 mm) (Brodskii 1950; Smith and Vidal 1984; Springer et al. 1987, 1989). In contrast, the Alaska Coastal Current lacks these large species and is dominated by the smaller *Calanus marshallae*, *Acartia* spp. and *Pseudocalanus* spp. (Motoda and Minoda 1974, Cooney and Coyle 1982, Smith and Vidal 1984). The Bering Shelf Water contains representatives of both copepod communities, but in our experience, the larger oceanic forms predominate (Table 1, but note 1986, and Hunt and Harrison 1990). These oceanic copepods originate in the Anadyr Water and are advected into the Bering Shelf Water in the Chirikov Basin; their presence in the stratified waters of the basin is an indication of the mixture of oceanic water and Bering Shelf Water there (Springer et al. 1987, 1989).

Methods

We studied Least Auklets at St. Lawrence Island from 8 July to 10 July 1984, 4 August to 13 August 1985, and 11 August to 15 August 1986. In 1984, 1985, and 1986, one, seven and three transects, respectively, were run from the Savoonga-Kookoolik area. Of these 11 transects, nine had sufficient bird sightings on them to permit analysis and they are illustrated here, as are examples from the Northwest Cape area of St. Lawrence Island and from King Island. The proximal ends of transects at St. Lawrence Island were within 2–5 km of the nearest Least Auklet colonies. All transects but one (18 August 1986) were started no earlier than an hour after dawn and all were complete before dark. Times given are local time (GMT-10).

To determine the foraging distribution of Least Auklets, we counted birds from the bridge (eye height 7.7 m above the sea surface) of the R/V *Alpha Helix* while underway at speeds of 6–10 knots. All birds within an arc from 300 m ahead of the vessel to 90° off the beam were counted and data entered in a handheld micro-computer to the nearest 0.1 minute from time of entry for later processing. Time of entry was then used to correlate bird numbers with location and acoustic survey data. Distinction was made between birds on the water (assumed to be or have recently been foraging) and flying birds. Additionally, we recorded environmental conditions and the ship's position each half-hour, whenever we arrived at or departed an oceanographic station, or when significant changes were observed. For the analysis in this paper, for which changes along a transect line are more important than

absolute numbers or density, we used only counts of birds on the water, reported as birds per five- or ten-minute time interval.

Prey use was ascertained by collecting birds on the water along the transects in August 1985 and August 1986, the period when auklets were raising chicks. We also mist-netted auklets returning to the Kookoolik colony on St. Lawrence Island in August 1985 and recovered the regurgitated contents of the gular pouches. All samples were preserved in 85% ETOH for examination in the laboratory. Percent occurrence was calculated as the percentage of all birds containing a particular class of prey. Percent composition of prey was calculated as the percentage of individuals of a particular prey type in each food sample collected, averaged over all samples.

We obtained vertical profiles of water column structure by lowering a conductivity-temperature-depth (CTD) probe to within 3–5 m of the bottom at stations usually spaced 18.5 km apart along transects (Fig. 1). Although salinity is a more conservative marker for the various water masses, we have presented temperature profiles for this study as they indicated where the sharpest property gradients were located. Density profiles were similar, but gradients were less steep and the depth of the pycnocline was less easily determined.

We used two methods to determine zooplankton distribution and abundance. The species composition of the copepod community was determined using vertical tows of a 1-m, 505 μ m mesh plankton net at each CTD station, weather permitting. Plankton were identified to the lowest taxon possible in the laboratory. Identifications were complete prior to the description of *Neocalanus flemingeri* (Miller 1988, Miller and Clemons 1988) and therefore our taxon *N. plumchrus* includes an unknown number of *N. flemingeri*.

We investigated both the horizontal and vertical distribution of plankton biomass using a Biosonics® Model 101 echo-sounder (200 kHz) with the transducer towed in a V-fin depressor at about 6 knots. The calibrated system source level at maximum power was +224.8 dB re 1 μ Pa at 1 m. The receiver sensitivity under 20 log R time varied gain was -135.3 dB re 1 μ Pa at 1 m.

A Biosonics Model 120 scientific echointegrator was used to integrate measures of volume scattering in vertical intervals of two meters from 5 m below the surface to the bottom. At ship speeds of 6–8 knots, each integration sequence of 60 pings covered 0.1 to 0.2 nautical miles (0.185 to 0.37 km) of transect line. Individual integrations were read immediately by a micro-computer, which applied corrections for water temperature, salinity, and previously determined system calibration (source level and gain, transducer directivity). Estimates of acoustically determined biomass were obtained by using the results of Richter (1985) to estimate target strengths for the commonest large zooplankters in the Chirikov Basin. At a wavelength of 7.5 mm, the largest copepodid stages of *Neocalanus* spp. and *Eucalanus bungii* were expected to contribute significantly to the sound-scattering. The resulting conversion, -80 dB g⁻¹, was used to estimate the wet weight of plankton beneath the transect line. This was derived from an empirical relationship for target strength as a function of body size and frequency (Richter 1985). This procedure would overestimate the

TABLE 1. PREY IDENTIFIED IN LEAST AUKLETS NEAR ST. LAWRENCE ISLAND AND COMPOSITION OF PLANKTON IN VERTICAL NET TOWS

Prey type	1985		1985 at sea		1985 colony		1986		1986 at sea	
	\bar{X} % individuals in net tows	% occurrence in prey	\bar{X} % individuals in prey	% occurrence in prey	\bar{X} % individuals in prey	% occurrence in prey	\bar{X} % individuals in net tows	% occurrence in prey	\bar{X} % individuals in prey	% occurrence in prey
Sample size	12	37	37	25	25	9	25	24		
All <i>Neocalanus</i>	36.3	78	33.7	100	89.5	28.3	92	78.2		
<i>N. cristatus</i>	1.2	73	29.4	56	4.7	1.1	68	19.5		
<i>N. plumchrus</i>	35.1	24	4.3	100	84.8	27.2	72	58.7		
<i>Eucalanus bungii</i>	4.7	13	1.4	4	0.1	0.9	—	—		
<i>Calanus marshallae</i>	7.8	—	—	—	—	64.7	—	—		
<i>Pseudocalanus</i> spp.	12.8	—	—	—	—	1.6	—	—		
<i>Metridia</i>	1.3	—	—	—	—	0.8	—	—		
Pandalidae	0.3	78	33.5	80	4.8	—	—	—		
Hippolytidae	0.1	16	3.0	40	0.5	—	—	—		
Euphausiids	35.1	30	12.5	44	2.4	2.2	8	0.0		
Hyperiid	1.9	35	12.1	32	1.5	0.4	28	10.1		
Gammarids	—	—	—	4	0.3	0.4	8	3.0		
Crab larvae and zoea	1.3	16	2.2	60	1.5	0.7	—	0.0		
<i>Limacina</i>	1.1	—	—	4	0.0	—	—	0.0		
Other	—	—	1.6	—	—	0.3	—	8.7		

contribution to integrated biomass from the larger fishes in the area, but these fish were rarely encountered.

The major problem with the use of single frequency acoustic observations is associated with converting measures of volume scattering to estimates of biomass, due to the relationship between body size and characteristics and backscattering efficiency (i.e., target strength). The use of 200 kHz probably eliminated detectable acoustic returns from most organisms <2–3 mm long. Thus, although we present our data in terms of g of zooplankton, our results are primarily useful as relative estimates of large zooplankters beneath the transect line and not of absolute levels of total plankton biomass.

To quantify the use of stratified waters by foraging auklets near St. Lawrence Island, we used two approaches, one focusing on the location of peaks in the number of foraging auklets, the other on whether more auklets foraged over stratified water than expected by chance. Stratified water was defined as having a thermocline in which there was a change of $\geq 4^\circ\text{C}$ in a five meter depth-interval. A peak was defined as a 10 min sampling period in which the number of foraging auklets exceeded the mean for the whole transect plus 1.96 times the standard deviation for the transect.

To examine the relationship between auklet numbers and the strength of the thermocline, we standardized data to allow combining of data from several transects. For auklets, the standardized number was computed by dividing the mean for the four ten-minute counts nearest a station by the maximum number for any ten-minute count on a particular transect; for the thermocline we divided the change in temperature per unit depth for the thermocline at the station by the maximum thermocline strength observed on the transect in question.

RESULTS

Data on prey obtained from Least Auklets at sea and at the Kookoolik colony are presented in Table 1, as are data from vertical plankton tows. For both 1985 and 1986, *Neocalanus* spp. were prominent in the diet. The occasional use of other prey, such as euphausiid larvae and shrimp larvae (Pandalidae), probably results from year-to-year changes in their relative abundance. Pandalid larvae were relatively large and were apparently a preferred prey of Least Auklets in 1985, as the larvae were relatively rare in our net samples of zooplankton (Table 1). Auklets took euphausiids in the year that they were abundant in net tows, but to a lesser extent than would have been expected based on their relative abundance. Evidently euphausiids were less preferred than *Neocalanus* spp. Least Auklets at King Island fed primarily on *Neocalanus* spp. (Hunt and Harrison 1990).

There were striking differences between 1985 estimates of auklet diets based on birds shot and birds mist-netted in the colonies. The prey collected in the colony was exclusively the regurgitated contents of gular pouch-loads destined for chicks. The at-sea collections, including many subadults in heavy primary moult that were unable to take flight, or did so only with great difficulty, usually yielded small numbers of items. The use of calanoid copepods would likely be underestimated in these birds, as many of these birds contained a large proportion of unidenti-

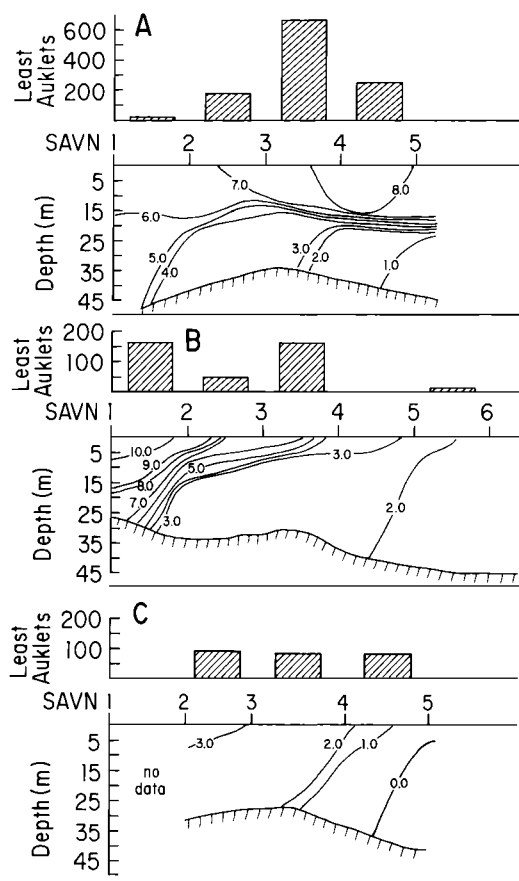


FIGURE 2. Temperature profiles and numbers of foraging Least Auklets on a series of lines north of Savoonga, St. Lawrence Island for (A) 13 August 1986, 11:45 to 16:30, (B) 4 August 1985, 05:00 to 12:00 and (C) 8 July 1984, 11:19 to 16:45. Variations in bottom profile represent soundings for each line or date run. Stations were 18.5 km apart.

fiable mush that was almost certainly derived from copepods. The difference in the species composition of the *Neocalanus* identified in the two sets of samples is of interest but we have no explanation for it.

We encountered three different classes of physical profiles on the transects at St. Lawrence Island (Fig. 2). The commonest pattern showed a relatively warm, well-mixed water inshore and stratified water with a strong thermocline between 18.5 and 37 km offshore (Fig. 2A). In these cases, the water inshore and on the surface was slightly fresher than the offshore, deeper water (32.2 vs. 32.6‰). Less commonly, we found poorly stratified water at the distal end of the transect (Figs. 2B and 3A), in areas where exten-

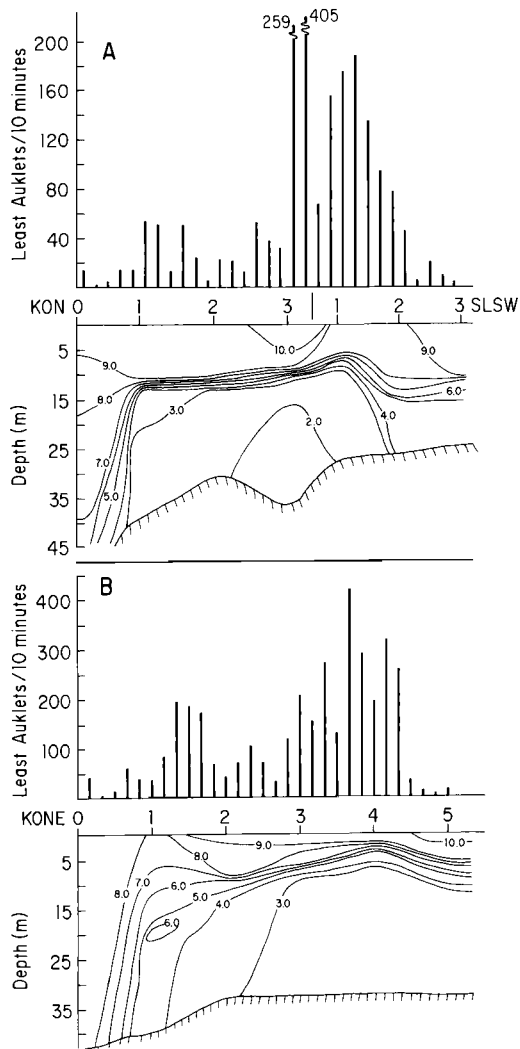


FIGURE 3. Temperature profiles and numbers of foraging Least Auklets per 10 min of counting north of St. Lawrence Island. A. A line due north from Kookoolik starting at 05:44 for 56 km in stormy weather, with a change in course at KON-3 (at 12:32) toward the southwest toward Northwest Cape on 7 August 1985. B. A line to Kookoolik from the northeast on 11 August 1985 between 05:00 and 10:43. On both lines auklet numbers reach their maximum where a strong thermocline is near the surface.

sions of the Anadyr Current had intruded eastward close to the north side of St. Lawrence Island. In these cases, the long, sloping thermoclines indicate the breakdown (or setting up) of structure offshore. At times the thermocline was absent and the offshore region had cold water mixed top to bottom, with a thermal front marking the

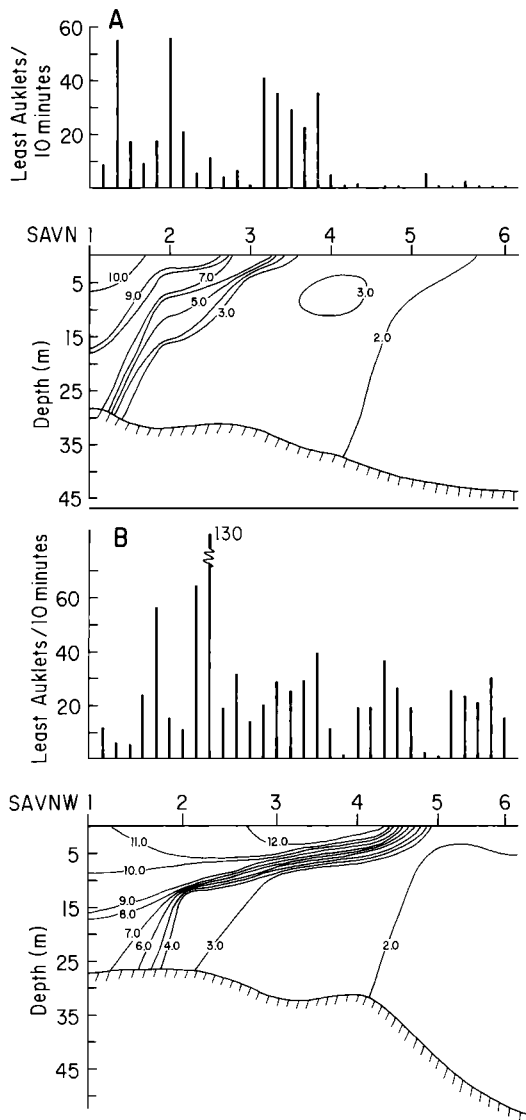


FIGURE 4. Temperature profiles and numbers of foraging Least Auklets per 10 min of counting along two lines on 4 August 1985 (A) to the south to Savoonga, run between 05:00 and 12:00 and (B) to the NW from Savoonga, run between 12:30 and 18:45. Stations were 18.5 km apart.

region where the thermocline surfaced (Figs. 2B, 3A, 3B). The offshore thermal front varied in its distance from the island and in its strength (Figs. 2B and 3A vs. 3B), presumably in response to the extent of the Anadyr Current intrusion. In one instance (Fig. 2C), cold unstratified water was found for the entire length of the transect and there was no evidence of a thermocline.

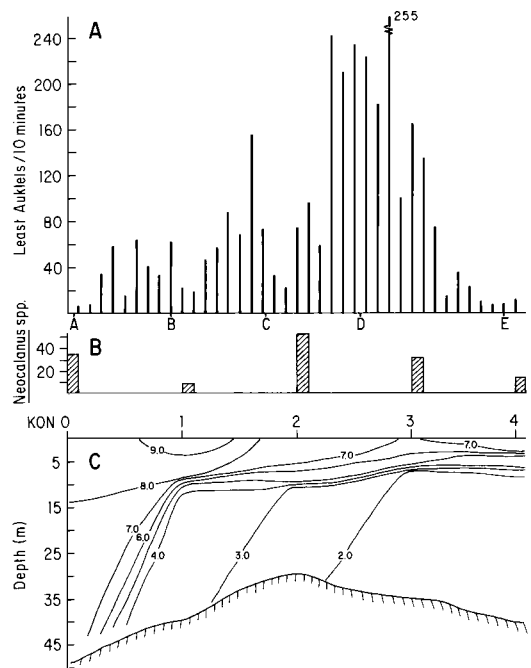


FIGURE 5. Temperature profiles, counts of *Neocalanus* spp. and Least Auklet numbers per 10 min of counting on a line north from Kookoolik, 10 August 1985 between 13:20 and 19:56, in calm weather. Stations were 18.5 km apart. Letters at the base of Figure 5A show location of profiles given in Figure 7B.

The distribution of Least Auklets varied with the type of temperature profile encountered (Fig. 2). When there was a strong thermocline offshore, peak numbers of auklets were found, although not necessarily where it was strongest (Fig. 2A). Concentrations above the thermocline, particularly where it bent toward the surface, were particularly striking on 7 and 11 August 1985 (Figs. 3A,B). In contrast, where the thermocline was closer inshore, with a front marking its offshore transition to unstratified water, we found two relatively small peaks in auklet numbers, one inshore near the commencement of the stratified layer, and one offshore at the outer end of the stratified layer (Figs. 2B, 4A, and for the inner end, 4B). On two of these three transects, numbers dropped immediately when auklets encountered the unstratified water offshore (Figs. 2B, 4A). Their distributions were relatively even over the unstratified water encountered in July 1984 (Fig. 2C).

Foraging auklets were most abundant in regions where *Neocalanus* spp. were present, and where the water was also strongly stratified. The transect north from Kookoolik on 10 August 1985,

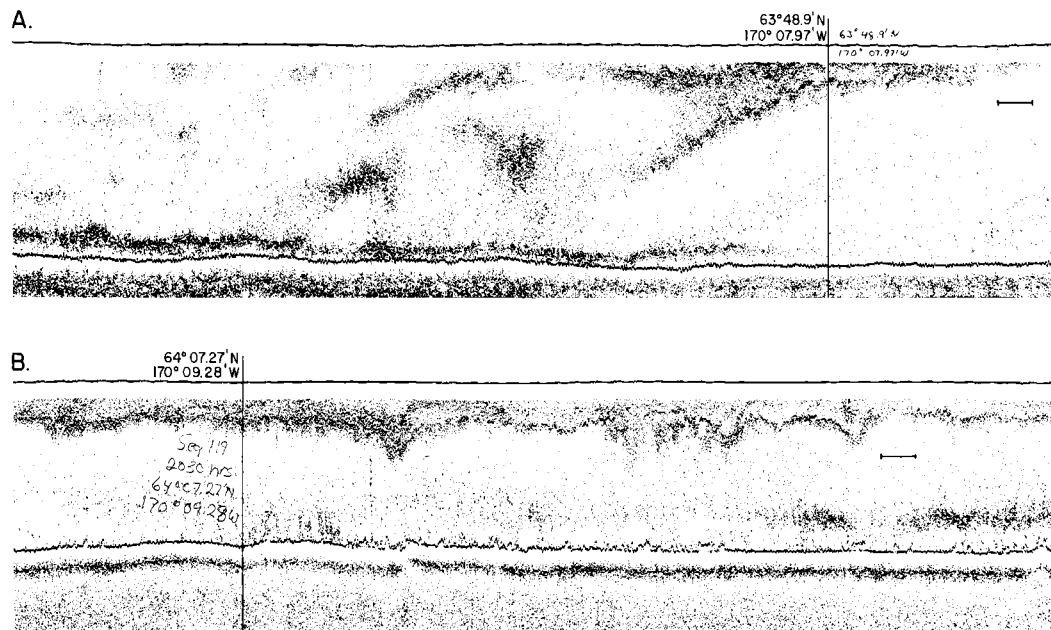


FIGURE 6. A. Echogram of acoustically determined biomass in the region of the inner front as seen in Figure 5 just inshore of station KON-1. The scale bar equals 1.85 km. B. Echogram of acoustically determined biomass between stations KON-2 and KON-3 where the plankton is in dense layers at and above the thermocline.

for example (Fig. 5A), revealed large concentrations of auklets between stations KON-2 and KON-3, approximately 40–65 km from shore. *Neocalanus* spp. were present in net tows at all stations (Fig. 5B). Acoustic estimates taken concurrently with the bird counts showed that total plankton biomass, inshore where few birds were present, was widely dispersed in the upper water column, with evidence of concentrations rising toward the surface in the vicinity of the inshore front (Fig. 6A). In contrast, beneath the offshore concentration of Least Auklets, plankton in the upper water column was concentrated above the thermocline (Fig. 6B). Plankton distribution along the transect was extremely patchy, with numerous biomass peaks in the upper 9–15 m of the water and in the water column as a whole (Fig. 7A). Acoustically determined biomass showed peak abundances near the bottom inshore, and at 7–10 m depth offshore, where the auklets were most abundant (Fig. 7B). A strong thermocline was present offshore starting near station KON-1, which appeared to rise from about 10 m depth at station KON-2 to 5–7 m depth at KON-3 (Fig. 5B). Thus, the birds were most concentrated where a strong, shallow thermocline coincided with an accumulation of plankton.

The transect on 14 August 1986, NE from Savoonga, provided a similar association. We saw virtually no auklets until just before we reached station SAVNE-3, approximately 40 km offshore (Fig. 8A). Between SAVNE-3 and SAVNE-4 numbers increased and then dropped off as we progressed toward SAVNE-5. Plankton hauls indicated that *Neocalanus* spp. were scarce or absent inshore (stations SAVNE-1 and 2), but were present at SAVNE-3, 4, and 5. The physical structure of the system also changed at SAVNE-3. Farther inshore the water column was relatively well mixed from top to bottom; offshore a strong thermocline developed. Again, the presence of *Neocalanus* spp. coincided with the presence of a stratified water column.

To examine in detail the relationship between the distribution of auklets and plankton we returned down the transect from station SAVNE-5 to SAVNE-3 with counts of birds and an acoustic survey of plankton (Fig. 9). The bird distribution had shifted somewhat inshore from the previous survey that day, but there was still a major peak near where we had taken station SAVNE-4 four hours earlier (Fig. 9A). Biomass also showed a broad peak in the vicinity of station SAVNE-4 (sections C, D), with a large portion of the de-

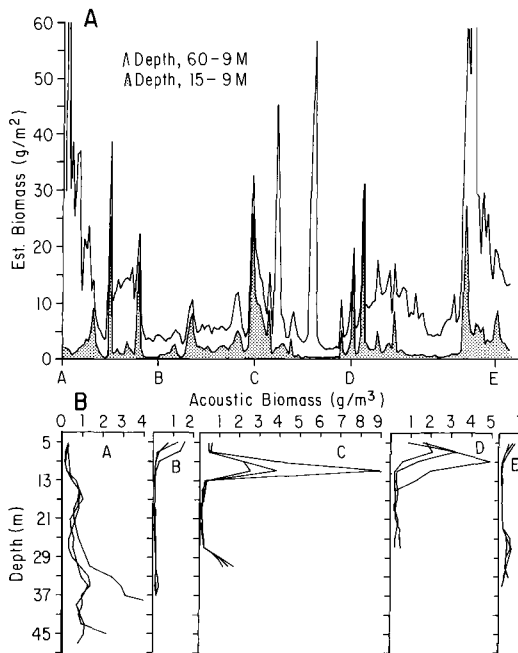


FIGURE 7. A. Horizontal profile of acoustically determined biomass obtained concurrently with bird counts reported in Figure 5 on 10 August 1985. B. Selected vertical profiles of acoustic biomass at the positions indicated. For each section, three adjacent profiles are presented to give a sense of the variation in vertical plankton distribution.

tected biomass above 24 meters (Figs. 9B,C). Although birds and plankton biomass were not well matched up over the smallest measurable scales, over larger scales (5.5–9.3 km) there was greater concordance.

We used two approaches to examine the small-scale distribution of plankton within the stratified zone offshore. First, we obtained acoustically determined vertical profiles of the prey distribution between SAVNE-5 and SAVNE-3 (Fig. 9). Peaks in biomass were found consistently 13 to 17 m below the surface in the area where foraging auklets were most abundant (C and D). Similar but smaller biomass peaks were present at A and B, where birds were less abundant. These patches of biomass were all apparently above the thermocline (See Fig. 8C). Second, we conducted net tows with single replicates at five stations, 3.7 km apart, between SAVNE-3 and -4 (Fig. 10). We found that tows taken at the same position, one immediately after another, often differed as much as those from stations 18.5 km apart. There were individual tows that sampled biomass peaks, and their results supported those

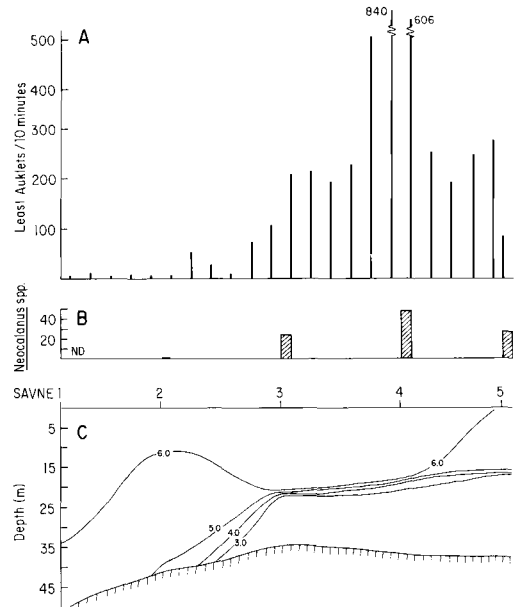


FIGURE 8. The distribution of Least Auklets, *Neocalanus* spp., and sea temperature along a transect NE from Savoonga, St. Lawrence Island, 14 August 1986 between 05:15 and 12:04. The stations are 18.5 km apart.

from the acoustic survey that high plankton biomass occurred near SAVNE-4.

The 8 August 1985 transect northeast from Kookoolik also showed most auklets foraging over stratified water, but without a single strong peak (Fig. 11). All plankton tows along this line contained *Neocalanus* spp., including the inshore station where there was no thermocline. Thus, in this case most auklets overflowed unstratified water containing appropriate prey to forage in more distant, stratified water, and missed the area of greatest prey concentration.

We conducted an acoustic survey concurrently with the bird counts depicted in Figure 11 and found that the distribution of plankton differed strikingly from that of the birds (Fig. 12A). For the water column as a whole, biomass was extremely patchy. Plankton was scarce in the upper layers for most of the transect of the offshore stratified water. In contrast, in the unstratified water inshore, there were dense small patches of plankton in the upper layers. However, vertical profiles showed that most of the biomass was near the bottom throughout the transect (Fig. 12B). Inshore, biomass in the upper water column was widely dispersed in depth, with great km-to-km variability (A); offshore the small amount of biomass present in the upper water

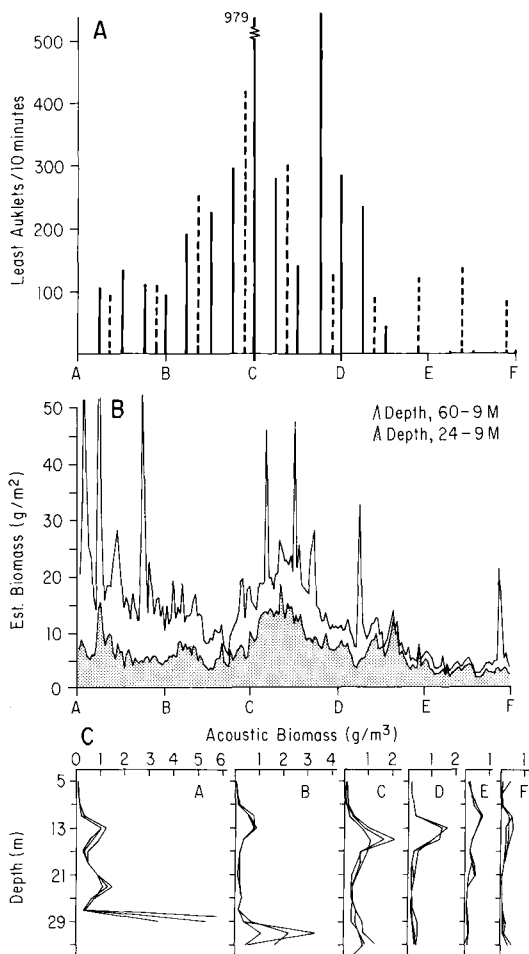


FIGURE 9. Comparison of the distribution of (A) Least Auklets over 10 min of counting and (B) acoustically determined biomass between stations SAVNE-5 and SAVNE-3, 14 August 1986 immediately after completing the run in Figure 8 (10:30 to 13:45). Dotted lines in (A) represent numbers of auklets seen on the first run, with stations; the solid lines represent auklet numbers on the repeat run. C. Vertical profiles of acoustically determined biomass. Three adjacent profiles are presented for each section. Acoustic profiles (A–F) are each 9.3 km apart.

column was concentrated at or above 9 m, with less small-scale variability (B, C, D, E and F).

Two transects at King Island on 16 and 18 August 1986 also illustrated the importance of the vertical position of plankton concentrations. On 16 August, auklets foraged 55–75 km from their colony, in a region where acoustic data indicated the plankton was more abundant above 20 m than it was in surface waters closer to the island (Fig. 13). Due to rough weather, we ob-

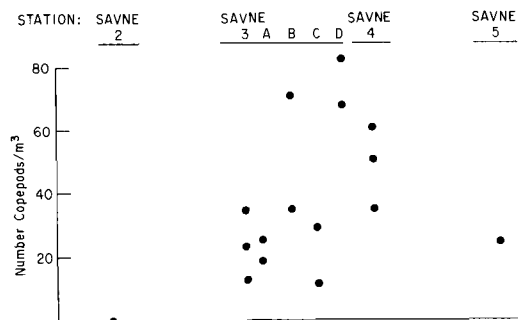


FIGURE 10. Number of *Neocalanus plumchrus* per m^3 in vertical net hauls along SAVNE transect, 14 August 1986. Stations were at 3.7 km intervals between SAVNE-3 and SAVNE-4.

tained no CTD profiles or net tows along this transect. However, past experience (Hunt and Harrison 1990) would suggest that the large copepods would have been absent within 18 km of King Island but common 18–55 km to the west. Vertical profiles along this line showed peaks

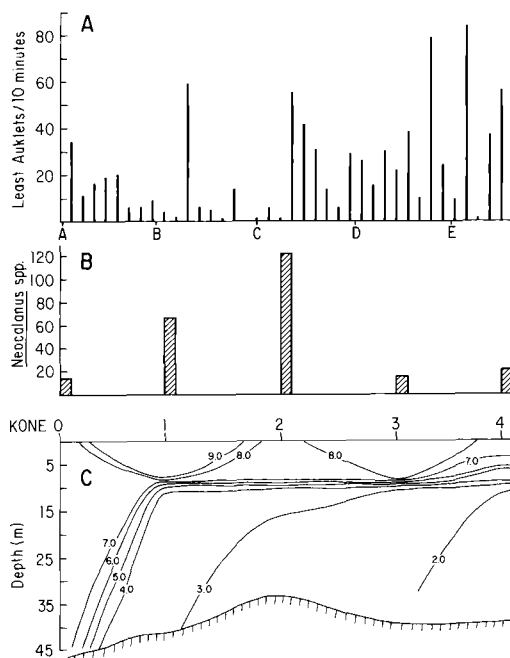


FIGURE 11. The distribution of (A) Least Auklets over 10 min of counting, (B) their *Neocalanus* spp. prey and (C) sea temperatures along a transect NE from Kookoolik, St. Lawrence Island, 8 August 1985 between 05:40 and 13:15, the day after a major storm. Stations were 18.5 km apart. Letters at the base of Figure 11A show the location of profiles given in Figure 12B.

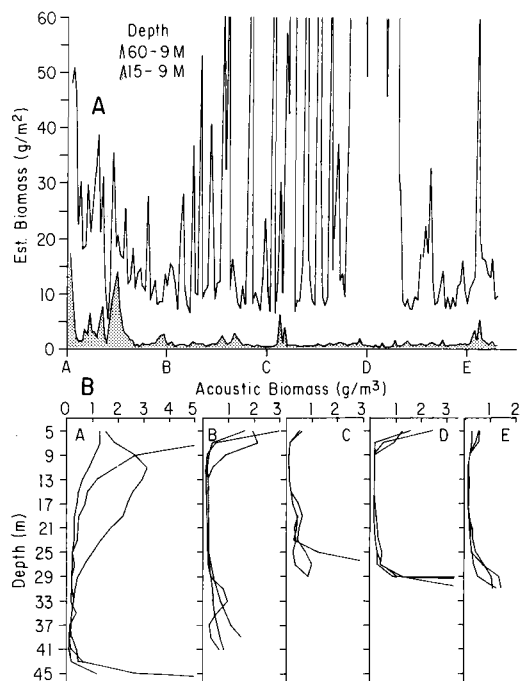


FIGURE 12. A. Horizontal profile of acoustically determined biomass along the same transect as depicted in Figure 11. B. Vertical profiles of the distribution of acoustically determined biomass at the positions indicated. Three adjacent profiles are presented for each station.

in plankton biomass between 9 and 13 m depth (interference from entrained bubbles obliterated the record above 7–9 m). Two days later, most foraging auklets were near KID-4, well within the region with a strong thermocline (Fig. 14). Biomass was patchily distributed along the whole transect, but concentrated near the bottom. Several broad areas of concentration were evident in the upper water column, one of which coincided with the concentration of auklets near KID-4. Vertical plankton tows showed *Neocalanus* spp. at all stations, but more abundant west of KID-2 (Table 2). Vertical profiles from the acoustic measurements showed that in the region where the thermocline was strong (KID-3 to KID-5), most biomass in the upper water column was concentrated at 11–16 m (Fig. 15), above the top of the thermocline at 16–20 m (Fig. 14).

Structures, such as thermoclines, that rise toward the surface sometimes (Figs. 4, 5 and 11), but not always (Fig. 3), had foraging auklets above them. This relationship can be particularly striking in the vicinity of fronts where prey may become available near the surface (Fig. 16). A tran-

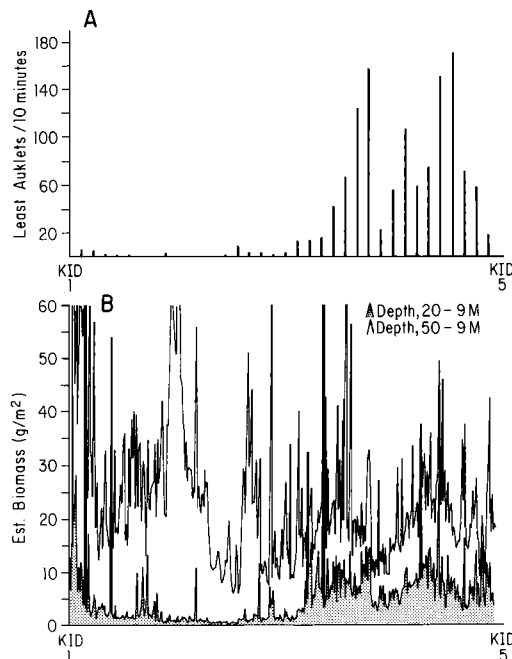


FIGURE 13. Distribution of Least Auklets (A) and acoustically determined biomass (B) along a transect west of King Island on 16 August 1986, 05:45–11:35, during stormy weather. The distance between KID-1 and KID-5 is 74 km.

sect run 12 August 1986, from Northwest Cape to the boundary between United States and Soviet-controlled waters, encountered a remarkable peak in foraging auklets as we approached a front between Bering Shelf Water and the Anadyr Current. In the region of the front, the isohalines bent toward the surface (between NWC-4 and NWC-5), and Least Auklet numbers increased from ≤ 10 to over 2500 in 5-min counts (Fig. 16).

Least Auklets occurred more frequently over stratified water than was expected by chance. Of the 24 transect segments between stations over stratified water, 42% contained peaks in auklet numbers, as contrasted with only 7% over unstratified water ($\chi^2 = 5.60$, $P < 0.05$). Data from interstation observations provided similar results (unpubl.). When we compared total counts of auklets over stratified and unstratified water near St. Lawrence Island, we found that although only 50% of the transects were over stratified water, 82% of all foraging auklets were seen over this habitat (unstratified $\bar{X} = 139.75 \pm \text{SD } 154.23$; stratified $\bar{X} = 649.79 \pm 642.58$, $N = 24$ for both).

The number of foraging auklets in the vicinity of a station was positively correlated with the

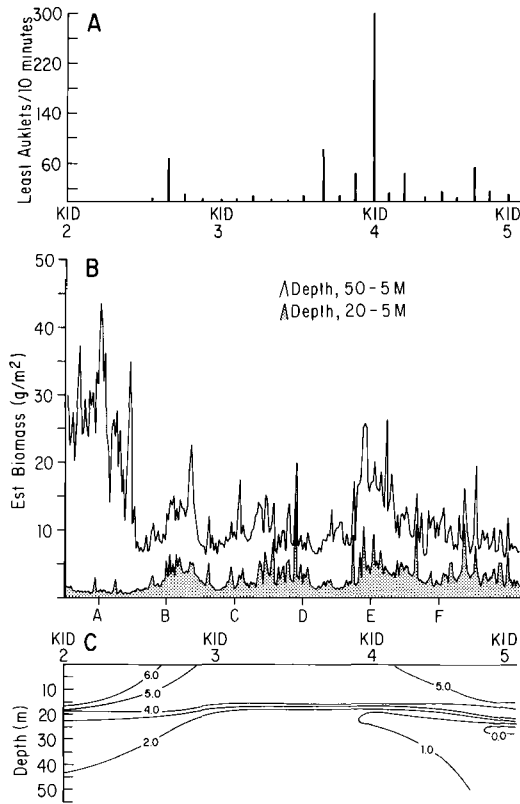


FIGURE 14. Distribution of (A) Least Auklets over 10 min of counting, (B) acoustically determined biomass and (C) sea temperatures along a line from 18.5 km west of King Island to 74 km west of the island, 18 August 1986, 04:18 to 12:08. Letters along the bottom of (B) refer to the patterns of vertical profiles in Figure 15.

steepness of the thermocline at that station, when both auklet numbers and thermocline strength were standardized (Fig. 17, Spearman Rank Correlation $r_s = 0.34$, $P < 0.05$). The lack of auklets in the upper left hand and lower right hand portions of the figure shows that the correlation is driven by both the auklets' avoidance of weakly stratified water and their use of the most stratified water available on a given transect. A similar examination revealed no significant negative correlation of auklet numbers with thermocline depth.

We examined the extent to which the correlation of numbers of foraging Least Auklets with acoustic estimates of biomass depended on the depth interval over which biomass was estimated, and on the horizontal scale at which correlations were sought. At horizontal scales of 1.9–3.7 km and 9.4–22.2 km, we found that auklets

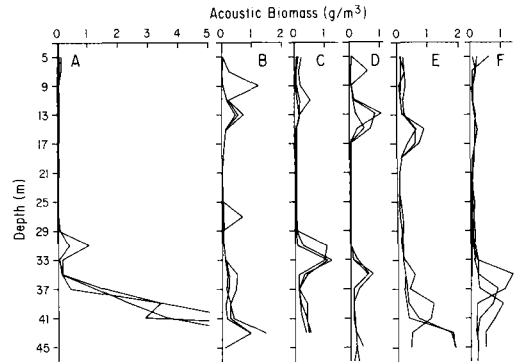


FIGURE 15. Vertical profiles of the distribution of acoustically determined biomass at the positions indicated along the transect of 18 August 1986 in Figure 14. Three adjacent profiles are presented for each section.

may be better correlated with estimates of prey biomass at and above the thermocline than within the whole water column (Tables 3A,B). For the upper water column, there is also some evidence that correlations were stronger at 9.3–22.2 km (4 of 5 cases). Since at the small measurement scales (1.9–3.7 km) autocorrelation is a problem, effective sample sizes are smaller than the number of segments compared. Therefore, acceptance of the null hypothesis is conservative, and apparently significant P values can lead to a false rejection of H_0 . When auklet numbers were compared with plankton biomass over 1.9–3.7 km intervals for the 9.3–22.2 km runs between stations, values of r_s were consistently low (Table 4).

Although small sample sizes and autocorrelations make establishing the statistical significance of differences in the strength of correlations at different spatial scales difficult, our data suggest that Least Auklets show their strongest correlations with presumed prey when correlations are based on biomass estimates for the upper water column over relatively long distances. We can assert with considerable certainty that cor-

TABLE 2. PRESENCE OF CALANOID PREY OF LEAST AUKLETS AS SAMPLED BY VERTICAL PLANKTON TOWS ALONG A LINE WEST OF KING ISLAND, 18 AUGUST 1986. DATA ARE EXPRESSED AS INDIVIDUALS/M³

Species	Station			
	KID-2	KID-3	KID-4	KID-5
<i>Calanus marshallae</i>	11.9	6.1	41.1	21.3
<i>Neocalanus plumchrus</i>	1.5	36.6	86.8	42.7
<i>N. cristatus</i>	—	0.9	4.9	0.7
<i>Eucalanus bungii</i>	3.0	0.8	0.6	—

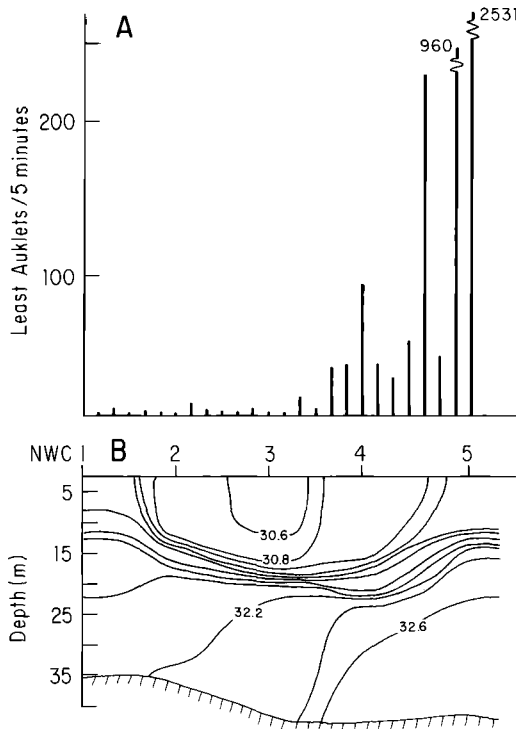


FIGURE 16. Distribution of (A) Least Auklets per 10 min of counting and (B) salinity along a line northward from Northwest Cape to the International Date-line, 12 August 1986 between 05:00 and 08:10. At station NWC-5 we were close to, but not yet in, Anadyr Current Water. Stations are 9.8 km apart.

relations between Least Auklets and acoustically estimated biomass are weak when estimates of biomass are based on the whole water column.

Quantification of the relationship between the numbers of Least Auklets and *Neocalanus* spp. is limited by the paucity of net hauls in unstratified water. However, for the 10 suitable stations at St. Lawrence Island we obtained *Neocalanus* spp. at eight. On at least two dates, 8 and 10 August 1985, *Neocalanus* spp. were present in unstratified water but there were no concentrations of Least Auklets nearby (Figs. 4, 5). We do not know whether *Neocalanus* spp. were less abundant in the unstructured water because we are unable to partition acoustically-measured biomass among the various species of plankton in the water column. However, distinct layers of biomass in the unstructured water were unusual (Fig. 7B, section A, but see Fig. 12), and concentration of biomass (g/m^3) may be more important to the auklets than overall abundance in the water column as a whole (g/m^2).

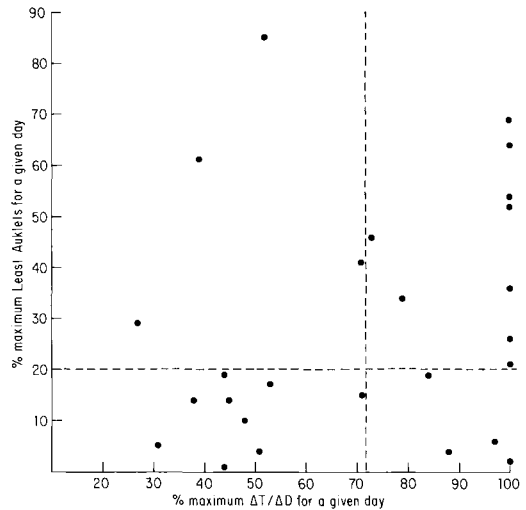


FIGURE 17. The relationship between the percent of the maximum number of Least Auklets seen on a given transect and the strength of the thermocline as defined by the percent of the maximum change in temperature per change in depth for a given transect. Dotted lines represent position of median values.

DISCUSSION

We think three aspects of the marine environment operate simultaneously to influence selection of foraging areas by Least Auklets in the Chirikov Basin: the presence of preferred types of prey (e.g., *Neocalanus* spp. copepods), their abundance in the water column, and their availability as determined by their vertical distribution in the water column. The relative contribution of the three elements is difficult to assess.

At King Island, Least Auklets overfly Alaska Coastal Water to forage in Bering Shelf Water (Hunt and Harrison 1990, this study). Two variables, water stratification and the prey community present, vary in parallel. Near King Island, Alaska Coastal Water is unstratified and lacks *Neocalanus* spp., and farther offshore the Bering Shelf Water is stratified and contains *Neocalanus*. Still farther from King Island, where Bering Shelf Water abuts the Anadyr Current, there is a change from stratified shelf water to unstratified Anadyr Current Water, with both water masses containing *Neocalanus* spp. Auklets foraged more commonly in the stratified water (Hunt and Harrison 1990), suggesting that they prefer foraging areas with a stable vertical structure.

Our work near St. Lawrence Island provided the opportunity to test the importance of vertical structure. There we found Least Auklets overflying nearshore unstratified water containing *Neocalanus* spp. to forage in stratified water offshore.

TABLE 3. RESULTS OF SPEARMAN RANK CORRELATIONS BETWEEN FORAGING LEAST AUKLETS AND ACOUSTICALLY DETERMINED BIOMASS OVER TWO DEPTH RANGES AT A, A HORIZONTAL SCALE OF 1.85–3.7 KM AND B, A HORIZONTAL SCALE OF 9.3–22.2 KM

Transect	Date	km over which biomass integrated	N	r_s , bottom to 5 m	r_s , thermocline to 5 m
A.					
KONE	8 Aug 85	3.7	17	0.24	-0.24
KON	10 Aug 85	3.7	18	-0.12	-0.07
SAVNE	14 Aug 86	1.85	20	0.47*	0.46*
KID	16 Aug 86	3.7	35	-0.20	0.77***
KID	18 Aug 86	1.85	26	-0.07	0.64***
B.					
KONE	8 Aug 85	18.5	4	0.40	-0.60
KON	10 Aug 85	18.5	4	-0.80	0.80
SAVNE	14 Aug 86	9.3	4	0.40	1.00*
KID	16 Aug 86	18.5	4	-0.54	0.77
KID	18 Aug 86	18.5	5	-0.40	0.90*

* P < 0.05.

*** P < 0.001.

And, as at King Island, relatively few Least Auklets foraged over unstratified Anadyr Current Water. Along transects, the large feeding flocks nearest shore usually occurred when we first encountered stratified water. Frequently additional feeding flocks were encountered up to 90 km offshore in areas where the thermocline was strong and shallow. In virtually all cases, Least Auklets were the only species present on the water. Although the occasional Parakeet Auklet (*Cyclorhynchus psittacula*) or small numbers of Crested Auklets (*A. cristatella*) were encountered, we rarely observed mixed-species foraging aggregations.

We have too few samples of prey biomass in unstructured water in which *Neocalanus* spp. occurred to determine whether the abundance of Least Auklets foraging in stratified water was due to differences in food availability (density and accessibility) or differences in food abundance in the two habitats. Therefore, we cannot rule out the possibility that the auklets were responding to differences in prey biomass. However, two types of evidence suggest that Least Auklets selected their foraging areas in a coarse-grained fashion on the basis of vertical stratification (and prey availability) and only secondarily on the basis of local prey abundance. First, correlations between the presence of foraging Least Auklets and presence of stratified water were stronger than correlations between auklet numbers and estimates of local prey abundance. Second, within the stratified water Least Auklet numbers tended to be greatest where the stratification was strongest. The vertical profiles of acoustically-estimated prey biomass revealed consistent peaks in the concentration of biomass at or above the

thermocline, and *Neocalanus* spp. are known to form dense layers 20–40 m below the surface in the open ocean (Barroclough et al. 1969); *N. plumchrus* occurs mostly above the seasonal thermocline (C. Miller, pers. comm.), while *N. cristatus* occurs mostly below the thermocline (see also R. Le Brasseur in Vermeer 1981). Thus, stratification partitions the water column vertically and sets up the potential for “vertical compression” and increased density of plankton biomass. Data from our net tows indicate that the biomass in the surface waters was dominated by *Neocalanus* spp. Our replicate net tows showed a consistent species composition in the plankton over scales of up to 19 km, despite considerable local patchiness. Thus, we tentatively conclude that auklets are foraging in the stratified water because prey is more likely to be concentrated at or above the thermocline there. Auklet use of fronts or areas where the thermocline approaches the surface is the extreme expression of this pattern.

TABLE 4. SPEARMAN RANK CORRELATIONS BETWEEN FORAGING LEAST AUKLETS AND ACOUSTICALLY DETERMINED BIOMASS AT A SCALE OF 1.85–3.7 KM WITHIN INTERSTATION SEGMENTS (9.3–22.2 KM)

Transect	Date	No. inter-station segments	Mean r_s , bottom to 5 m	Mean r_s , thermocline to 5 m
KONE	8 Aug 86	4	0.43	0.08
KON	10 Aug 86	4	-0.15	-0.28
SAVNE	14 Aug 86	5	0.00	0.18
KID	16 Aug 86	5	0.54	0.48
KID	18 Aug 86	4	0.25	0.30

In the Southern California Bight, vertical stratification of the water column has been shown to be important to Xantus' Murrelets (*Synthliboramphus hypoleuca*). Murrelets delayed reproduction in a year when storms increased the depth of the mixed surface layer of the water column (Lasker 1979, Hunt and Butler 1980). The murrelets' apparent dependence on a stable water column involves a different, though related, phenomenon to that found in Least Auklets. Xantus' Murrelets prey extensively on larval northern anchovies (*Engraulis mordax*) (Hunt et al. 1979). The anchovies in turn depend upon high concentrations of phytoplankton if they are to survive the first-feeding stage; if turbulence in the upper water column disperses their prey, they fail to survive (Lasker 1979, Peterman and Bradford 1987). Thus, in the murrelet-anchovy system, the importance of a stable upper water column is mediated through an additional link in the food chain.

These instances in which a stable vertical structure enhances food availability differ from those in which more dynamic physical processes are involved. In the case of vertically stable systems, prey are aggregating in a narrow zone to enhance their own energy intake and growth. In systems with high kinetic energy, currents may cause the passive accumulation of prey in eddies (Aldredge and Hamner 1980, Hamner and Hauri 1981) or the active accumulation of organisms resisting either upwelling or downwelling (Pingree et al. 1974, Brown 1980, Barstow 1983).

The relatively poor correlation between Least Auklets on the water and the distribution of acoustically determined plankton biomass at scales of 2–5 km may be the result of the methods we used, or an important aspect of the foraging biology of these birds. Three aspects of our methods could have contributed to an apparently weaker correlation between the auklets and their prey than actually existed. First, we could not obtain data on plankton distributions in the top 5–7 m of the water, and we do not know if it held significant prey populations that were not correlated with deeper, measured prey populations. However, the four (of a possible five) strong positive correlations between auklets and biomass in the upper water column at a scale of 9–22 km suggest that acoustically-estimated biomass in the upper water column was a reasonable indicator of potential prey abundance. Second, the transect width over which we counted birds was considerably wider than the cone-shaped area beneath the ship that was scanned by the echosounder. Given our evidence for patchiness in the plankton at very small scales, the birds may have been responding to different distributions of prey than we could detect. Third, we assumed

that birds on the water were foraging or had been foraging in the recent past. If long periods elapsed since their foraging, auklets could have drifted away from the food patch, especially since the water mass below the thermocline may have been moving with respect to the surface waters. At present, we cannot eliminate or even estimate the magnitude of these sources of error.

There exist, however, at least two related reasons why auklets might not be well correlated with small-scale variations in the abundance of their prey. First, overall prey abundance may be sufficiently high that it would not pay auklets to search out the peak concentrations, as suggested by Woodby (1984) for murrets (*Uria* spp.) in the southeastern Bering Sea. An alternative, though not mutually exclusive, hypothesis is that seabirds are not particularly good at locating the best prey patches, and instead of searching for such patches, they join birds already foraging (Hoffman et al. 1981, Obst 1985). In this scenario, the first bird to find an adequate, "threshold" concentration of prey would have a disproportionate effect on the distribution of foraging birds with respect to prey. Piatt (1990) has found evidence for threshold densities of prey necessary to attract foraging Common Murres (*U. aalge*) and Atlantic Puffins (*Fratercula arctica*), and observations of seabirds joining others already on the water are commonplace.

We suggest that Least Auklets locate suitable foraging areas by using a combination of physical and biological cues. Sea surface temperature in some instances is indicative of water column structure in the Bering Sea (Schumacher et al. 1979, Kinder et al. 1983). Near St. Lawrence Island, cool surface temperatures offshore indicate unstratified water, as is also frequently the case close to the island. We suggest that Least Auklets may seek areas with the warmer surface temperatures that can indicate subsurface stratification. The auklets commence foraging either when they encounter some minimum "threshold" concentration of plankton by chance, or by joining other birds already engaged in foraging. We interpret the stronger correlation of predators and presumed prey at larger scales as due to the auklets' being better at locating generally rich foraging areas than at locating specific prey patches.

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