Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea

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Abstract

We review recent accounts of the foraging ecologies of five species of small auklets found in the Bering Sea. These birds eat a wide variety of zooplankton and micronekton. Least Auklets *Aethia pusilla* and Whiskered Auklets *A. pygmaea*, as far as is known, primarily eat copepods, whereas Crested Auklets *A. cristatella* appear to specialize on euphausiids, at least during the breeding season. The diet of Parakeet Auklets *Cyclorrhynchus psittacula* is much broader than that of most other *Aethia* species, and includes many gelatinous species and their commensals. Little is known of the diet of Cassin's Auklet *Ptychoramphus aleuticus* in the Bering Sea, although elsewhere they take large copepods, euphausiids, and larval fish.

There are considerable differences in the at-sea distributions and foraging behaviours of these five species of auklet. Least Auklets in the northern Bering Sea concentrate their foraging activities over strongly stratified water and near fronts where pycnoclines may approach the surface. In the Aleutian Islands, Least Auklets forage where oceanic and tidal currents strike the shelf between the islands and rise toward the surface carrying plankton. Least Auklets and Crested Auklets are often found in large flocks, whereas Parakeet Auklets are rarely found in groups of more than three birds and are usually widely dispersed. The few at-sea observations of Whiskered Auklets have been of small flocks in turbulent waters of island passes. We relate prey types taken, foraging dispersion, and the use of hydrographic features by these auklet species.

Résumé

Les auteurs étudient les compte rendus récents sur l'écologie de l'alimentation de cinq espèces de petites alques, présentes dans la mer de Béring. Ces oiseaux se nourrissent de nombreux types de zooplancton et de micronecton. L'Alque minuscule *Aethia pusilla* et l'Alque barbue *A. pygmaea*, selon les connaissances actuelles, se nourrissent surtout de copépodes. L'Alque panachée *A. cristatella* semble privilégier les euphausiacés, du moins pendant la saison des amours. Le régime de l'Alque perroquet *Cyclorrhynchus psittacula* est beaucoup plus varié que celui de la plupart des autres alques planctonivores et comprend de nombreuses espèces gélatineuses et leurs commensaux. On connaît peu le régime de l'Alque de Cassin *Ptychoramphus aleuticus* dans la mer de Béring. Ailleurs, cet oiseau se nourrit de gros copépodes, d'euphausiacés et de larves de poissons.

Les cinq espèces d'alques mentionnées présentent de grandes différences de distribution en mer et de comportement d'alimentation. L'Alque minuscule, dans le nord de la mer de Béring, se nourrit surtout dans les eaux composées de couches de densité variable et près des fronts océaniques, où les pycnoclines peuvent être situées près de la surface. Dans les îles Aléoutiennes, l'Alque minuscule s'alimente là où les courants océaniques et de marée frappent la plate-forme continentale, entre les îles, et s'élèvent gorgés de plancton. L'Alque minuscule et l'Alque panachée forment des volées considérables, tandis que l'Alque perroquet recherche rarement la compagnie de plus de trois congénères. Habituellement, cette espèce est très dispersée. Les rares observations en mer de l'Alque barbue font état de petits groupes, dans les eaux troubles des passes entre les îles. Les auteurs étudient les espèces mentionnées, en fonction des proies capturées, de la dispersion à des fins d'alimentation et de l'utilisation des éléments hydrographiques.

1. Introduction

Five species of small auklets nest on islands of the eastern North Pacific. Species in the genus *Aethia*—Least Auklets *Aethia pusilla*, Whiskered Auklets *A. pygmaea*, and Crested Auklets *A. cristatella*—and the Parakeet Auklet *Cyclorrhynchus psittacula* are found most commonly from the Aleutian archipelago northward to the Bering Strait. Another species, Cassin's Auklet *Ptychoramphus aleuticus*, nests on islands from as far south as the central Pacific coast of Baja California northward to the Aleutian Islands. All of these small (70–320 g) birds feed on macroplankton and micronekton prey, and carry these prey to their young. Whereas other members of the Alcidae may take some plankton in their diets (Vermeer 1984), auklets, along with the Dovekie *Alle alle*, are primarily planktivorous and breed in ocean regions rich in planktonic organisms.

Auklets are small birds with high energy demands (Roby and Brink 1986; B. Obst, Z. Eppley, and Hunt, unpubl. data). For them to forage profitably on prey that are orders of magnitude smaller than themselves, it is probable that the prey must be concentrated (e.g., Brodie et al. 1978; Bradstreet and Brown 1985). Although the overall breeding distribution of auklets is related to the large-scale distribution of water masses and prey communities (Hunt et al. 1981b; Springer and Roseneau 1985; Springer et al., this volume), the foraging distributions at smaller scales probably depend on the interactions of physical processes and prey behaviour that result in localized and predictable aggregations of prey. One would therefore expect that the foraging distributions of these auklets would reflect locations where concentrations of prey could be

predicted. The largest prey taken by auklets are able to swim against weak currents; smaller species of prey may control their movements in the vertical dimension, but are unable to swim against even slight currents. Thus, at spatial scales of metres to tens of kilometres, the distribution of auklet prey should be strongly influenced by physical processes in the ocean such as upwelling events, fronts, and eddies (Haury et al. 1978).

When large aggregations of foraging seabirds are concentrated in restricted areas, they may be more vulnerable to natural or anthropogenic catastrophes than when they are dispersed (King and Sanger 1979). Thus, we review published information concerning the diets and at-sea distributions of small auklets in the eastern North Pacific Ocean and provide some previously unpublished observations of auklet responses to physical features of the ocean environment. Springer et al. (this volume) reviewed the larger-scale breeding and foraging distributions of these auklets. Therefore, we concentrate on small-scale events that may influence auklet foraging distributions. Our review focuses on the foraging ecology of breeding birds. There is little information on these birds when they are not associated with their colonies (but see Briggs et al. 1987, 1988). We discuss each species separately and then identify some phenomena that influence the small-scale foraging distributions of auklets.

2. Cassin's Auklet

Cassin's Auklets eat both micronekton (i.e., small fish) and macroplankton (i.e., large copepods) (Table 1). Throughout their breeding range from southern California to the Aleutians, euphausiids of the genera *Thysanoessa* and *Euphausia* are important, as are larval fish. Only in the Gulf of Alaska have Cassin's Auklets been recorded with copepods as the predominant prey, perhaps because large species of *Neocalanus* are abundant in these waters (Vermeer et al. 1985; Sanger 1986).

Although both Burger (1991) and Haney (1991) have developed estimates, based on regressing known maximal dive depths on body mass, for maximal diving depths for alcids, including the auklets, Cassin's Auklets are the only auklet species for which diving depths have been measured. Burger and Powell (1990) recorded the maximum diving depths of 22 Cassin's Auklets in the Queen Charlotte Islands and reported a mean of 28 m and a mode of 40 m. These depths were similar to those found by Croll and Carter (pers. commun. in Burger and Powell 1990) for auklets in the Farallon Islands off central California. Dolphin and McSweeney (1983) have indirect evidence for dives to similar depths, and theoretical calculations by Burger (1991) suggest that depths of 45 m may be near the maximum possible for a wing-propelled diving bird of the size of a Cassin's Auklet.

In southern California, Hunt et al. (1981c) obtained data on the foraging ecology of Cassin's Auklets near their colonies at San Miguel Island. There, Cassin's Auklets were found almost exclusively to the north and northeast of the island over shallow shelf waters. Because the location of foraging flocks varied greatly between surveys, Hunt et al. (1981c) speculated that auklets were attracted to concentrations of prey that resulted from aggregative behaviours of the prey rather than from physical forcing. Briggs et al. (1987, 1988) found concentrations of Cassin's Auklets off central California during the breeding season in the vicinity of the shelf break where they foraged in upwelled water on *Thysanoessa spinifera*. Prior to the upwelling season, this euphausiid was concentrated at or below the thermocline by day; after the onset of upwelling, the euphausiids were frequently observed swarming at the surface in daytime. In other seasons, Cassin's Auklets use the deeper waters of the continental slope both in California (Briggs et al. 1987, 1988) and off Oregon and Washington (K. T. Briggs, pers. commun.).

In the Queen Charlotte Islands, the diets of Cassin's Auklets appear to vary with location. At Frederick Island in the northwest, the copepod *Neocalanus cristatus* was a major portion of the diet, and fish were taken relatively rarely (Vermeer et al. 1985, 1987), a diet similar to that found in the Gulf of Alaska (Sanger 1986, 1987). *Neocalanus cristatus* aggregate near the pycnocline (Barnes Clough et al. 1969) early in the season before they migrate to deeper waters (Miller and Clemons 1988). Vermeer et al. (1985) found the auklets taking *N. cristatus* at a shelf edge front where the pycnocline approached the surface. At Reef Island in the eastern Queen Charlotte Islands, Burger and Powell (1990) found that Cassin's Auklets took predominantly fish and euphausiids, and few copepods, a diet more similar to that of auklets in California than of those nesting in the northwestern Queen Charlotte Islands. Burger and Powell suggest that the differences between colonies in the Queen Charlotte Islands may reflect differences in the plankton communities of Hecate Strait and the more exposed outer coastal areas. There are no data on the foraging ecology of the Cassin's Auklet from the southern extreme of its range in Baja California.

Piatt (unpubl. data) has observed Cassin's Auklets foraging over shallow shelf waters near the Shumagin and Samidi islands in the western Gulf of Alaska in summer. They were in loose aggregations, containing 2–10 individuals, that were spread over tens of kilometres. Neither the auklets nor

Table 1
Primary prey of Cassin's Auklets. Prey are listed in descending order of importance (N = number of samples collected)

Location	Prey type	Reference
Channel Is., southern California 1976 N = 95	larval *Sebastes* larval *Citharichthys* *Thysanoessa spinifera* *Euphausia pacifica*	Hunt et al. 1981c
Channel Is., southern California 1977 N = 102	*T. spinifera* larval *Sebastes* *Nyctiphanes simplex*	Hunt et al. 1981c
California Current, central California 1985 N = 65	*T. spinifera* *E. pacifica* *Sebastes* spp.	Briggs et al. 1988
Farallon Is., central California 1971 N = 22	*T. spinifera* *Phronema* amphipod squid spp.	Manuwal 1974
Queen Charlotte Is., British Columbia 1981 N = 62	*Neocalanus cristatus* *T. longipes* fish spp. *T. spinifera*	Vermeer et al. 1985 Vermeer 1984
Queen Charlotte Is., British Columbia 1987, 1988 N = 58	*Ammodytes hexapterus* *T. spinifera*	Burger and Powell 1990
Gulf of Alaska N = 8	calanoid copepods *T. spinifera* decapods larval fish	Sanger 1986
Shumagin Is., Alaska 1991 N = 21	*T. spinifera* *Limacina*	Piatt, unpubl. data
Semidi Is., Alaska 1990 N = 5	squid polychaetes *Limacina*	Piatt, unpubl. data
Buldir I., Alaska 1989 N = 7	euphausiids polychaetes	Piatt, unpubl. data

Table 2
Primary prey of Parakeet Auklets. Prey are listed in descending order of importance. These birds have a much more diverse diet than can be adequately represented here.

Location	Prey type	Reference
St. Lawrence I. 1961–66	*Parathemisto libellula*	Bédard 1969
N = 97	*Chaetognatha*	
	Neocalanus cristatus	
Chirikov Basin 1984–86	Ctenophora	Harrison 1987
N = 13	Scyphomedusae	
	fish spp.	
	N. cristatus	
St. Matthew I. 1983–86	Scyphomedusae	Harrison 1987
N = 39	*Theragra chalcogramma*	
Pribilof Is. 1975–78	fish spp.	Hunt et al. 1981a
N = 39	*Thysanoessa raschii*	
	Nereidae	
	P. libellula	
	Thysanoessa inermis	
Buldir I. 1976	*N. cristatus*	Day and Byrd 1989
N = 4	*P. pacifica*	

their presumed prey were concentrated in small patches of high density. Concurrent, high-frequency (120 kHz) echo-sounding surveys showed prey to be abundant in depths between 30 and 100 m over large areas of the shelf.

3. Parakeet Auklet

Parakeet Auklets take a greater variety of prey than other small auklets (Table 2). Bédard (1969) observed that this species feeds on a diversity of planktonic animals, many of which are at higher trophic levels than the herbivorous plankton eaten by other *Aethia* species. K.A. Hobson and Piatt (unpubl. data) using analysis of stable isotopes of nitrogen ($^{15}N/^{14}N$ ratios) found that Parakeet Auklets at the Shumagin Islands fed at higher trophic levels than Crested Auklets, Leach's Storm-Petrels *Oceanodroma leucorhoa*, or Fork-tailed Storm-Petrels *O. furcata*. Parakeet Auklets foraged at lower trophic levels than Black-legged Kittiwakes *Rissa tridactyla* or Marbled *Brachyramphus marmoratus* and Kittlitz's *B. brevirostris* murrelets. The higher diversity of prey taken by Parakeet Auklets relates to the use of gelatinous animals (Harrison 1984). Parakeet Auklets consume many jellyfish, ctenophores, and jellyfish commensals, such as amphipods and larval fish associated with Scyphomedusae (Harrison 1984, 1987, 1990).

Perhaps because of their use of jellyfish, Parakeet Auklets are less clumped at sea than other auklets (Harrison 1990; Hunt, unpubl. data). Like Bédard (1969), Hunt et al. (unpubl. data) found these auklets widely scattered throughout the areas they surveyed. At sites where Parakeet Auklet diets included a large proportion of jellyfish, typically only two or three Parakeet Auklets were encountered per kilometre of 300-m-wide transect in the Chirikov Basin. Gelatinous zooplankton were abundant and ubiquitous in the areas surveyed, and it is possible that Parakeet Auklets benefit by scattering widely when using this resource. At St. Matthew Island, where Parakeet Auklets took a larger proportion of euphausiids and the free-swimming *Parathemisto libellula*, their distribution at sea was more clumped (Harrison 1990; Hunt, unpubl. data). In the western Aleutians, Parakeet Auklets are typically well dispersed at sea and rarely form flocks of more than two or three individuals (Piatt, unpubl. data).

We suggest that physical processes that concentrate jellyfish might influence Parakeet Auklet distributions. Jellyfish migrate to the sea surface at dusk and their attempts to remain near the surface make them vulnerable to concentration in downwelling convergences, such as those formed by Langmuir circulation cells (Hamner and Schneider 1986). Whether Parakeet Auklets use these concentrations of potential prey is not known.

4. Whiskered Auklet

The foraging ecology of Whiskered Auklets in the eastern Bering Sea is not well known. They are frequently encountered in passes between the islands of the Aleutian chain, where planktonic prey might be concentrated by eddies and tidal fronts (Pingree et al. 1974, 1978). Recent information on the diet of Whiskered Auklets includes that of Day and Byrd (1989) who found the copepod *Neocalanus plumchrus* to be the principal prey in 25 birds sampled at Buldir Island; the amphipod *Parathemisto pacifica* was also important for birds during the early chick-rearing period at Buldir Island. Additional data come from Troy and Bradstreet (1991) who found *Thysanoessa inermis* and *T. spinifera* important prey in 23 auklets sampled in Unimak Pass in 1986 and 1987, and from Piatt (unpubl. data) who found *T. inermis* was the prey taken by 16 auklets sampled in Baby Pass, Aleutian Islands, in 1991. Dietary information from seven adults collected in winter near the Commander Islands showed amphipods to be the principal prey taken (Stejneger 1885). The recent dietary observations are of interest because, in their centre of abundance, Whiskered Auklets are taking species of euphausiids, one of which is a deep-water species, and not copepods as their principal prey.

Flocks of 10–25 Whiskered Auklets have been observed off Buldir Island in upwelled waters over seamounts, and thousands of Whiskered Auklets sometimes aggregate off Buldir Island in the evening (Piatt, unpubl. data). Whether these birds were staging or foraging is unknown. Day and Byrd (1989) suggested that convergent tidal fronts near the islands are more important foraging areas than the open waters of the inter-island passes. Piatt (unpubl. data) in 1991 saw thousands of Whiskered Auklets concentrated in tide rips and feeding over dense concentrations of plankton observed with the aid of a 120-kHz echo sounder. Flocks of 10–50 individuals were typical, and extended single-species aggregations (comprising thousands of birds) were spatially segregated from other species of seabirds.

Whiskered Auklets apparently remain in the inshore waters of the Aleutian Islands throughout the year. Stejneger (1885) reported them inshore at the Commander Islands in winter, and Troy and Bradstreet (1991) report wintertime concentrations of up to 1337 birds/km^2 in the passes of the eastern Aleutian Islands.

5. Crested Auklet

Most studies have shown that euphausiids of the genus *Thysanoessa* are the principal prey of Crested Auklets, although *Parathemisto libellula* and copepods occasionally form a significant portion of the diet (Table 3). At St. Lawrence Island, Bédard (1969) found that Crested Auklets early in the season had a diversified diet that included mysids, hyperiids, and gammarids. However, while raising chicks, the diets of adults and chicks were dominated by *Thysanoessa*. Although most seabird species in the Bering Sea feed on euphausiids when they are abundant (Hunt et al. 1981a; Harrison 1987), the high frequency of euphausiids in the Crested Auklet's diet,

Table 3
Primary prey of Crested Auklets. Prey are listed in descending order of importance.

Location	Prey type	Reference
St. Lawrence I. 1964–66 N = 242	*Thysanoessa* spp. *Calanus marshallae* Gammaridae Mysidacea *Parathemisto libellula*	Bédard 1969
St. Lawrence I. 1987 N = 54	*Thysanoessa* spp. *Neocalanus plumchrus*	Piatt et al. 1990
Chirikov Basin 1984–86 N = 22	*T. raschii* Pandalidae *P. libellula* *N. plumchrus*	Harrison 1987
St. Matthew I. 1983–86 N = 6	*T. raschii* *Theragra chalcogramma* *P. libellula*	Harrison 1987
Pribilof Is. 1975–78 N = 21	*P. libellula* *Thysanoessa inermis* *T. raschii*	Hunt et al. 1981a
Buldir I. 1976 N = 7	*N. cristatus*	Day and Byrd 1989
Big Koniuji I. 1990 N = 62	*T. inermis* *N. cristatus* *T. chalcogramma*	Piatt, unpubl. data

especially when feeding chicks, indicates a greater degree of specialization on this prey than is true for other auklets. When foraging on vertically migrating euphausiids, diurnally foraging Crested Auklets should choose locations where bottom waters are forced upward. In these locations one would expect the accumulation of downward-swimming euphausiids as they swam against the upward-moving water (Simard et al. 1986). Schneider et al. (1990) and Coyle et al. (in press) postulated this mechanism for murres feeding on *T. raschii* at a subsurface front near the Pribilof Islands.

Crested Auklets are abundant breeders in the eastern Bering Sea; hence there should be considerable data on their at-sea distribution and on the mechanisms that determine the availability of euphausiids to them. This is not the case; compared to the data available for Least Auklets *A. pusilla* (see below), we know relatively little about the biology of Crested Auklets at sea. At St. Lawrence Island and at King Island, Crested Auklets were underrepresented on shipboard surveys that extended up to 55–110 km to sea from the colonies (Table 4). However, Hunt et al. (unpubl. data) saw numerous flocks of Crested Auklets flying to or from the colony, which suggested that many Crested Auklets were foraging at least 55 km and in some cases over 110 km from their colonies. Piatt (unpubl. data) has observed Crested Auklets foraging at the border between the Anadyr and Bering Sea shelf waters, 30–60 km west-southwest of breeding colonies on the Diomede Islands. The birds were in large, extended aggregations (up to 10 km), but flocks were small (10–50 birds) and dispersed compared to the concentrations seen in the passes of the Aleutian Islands.

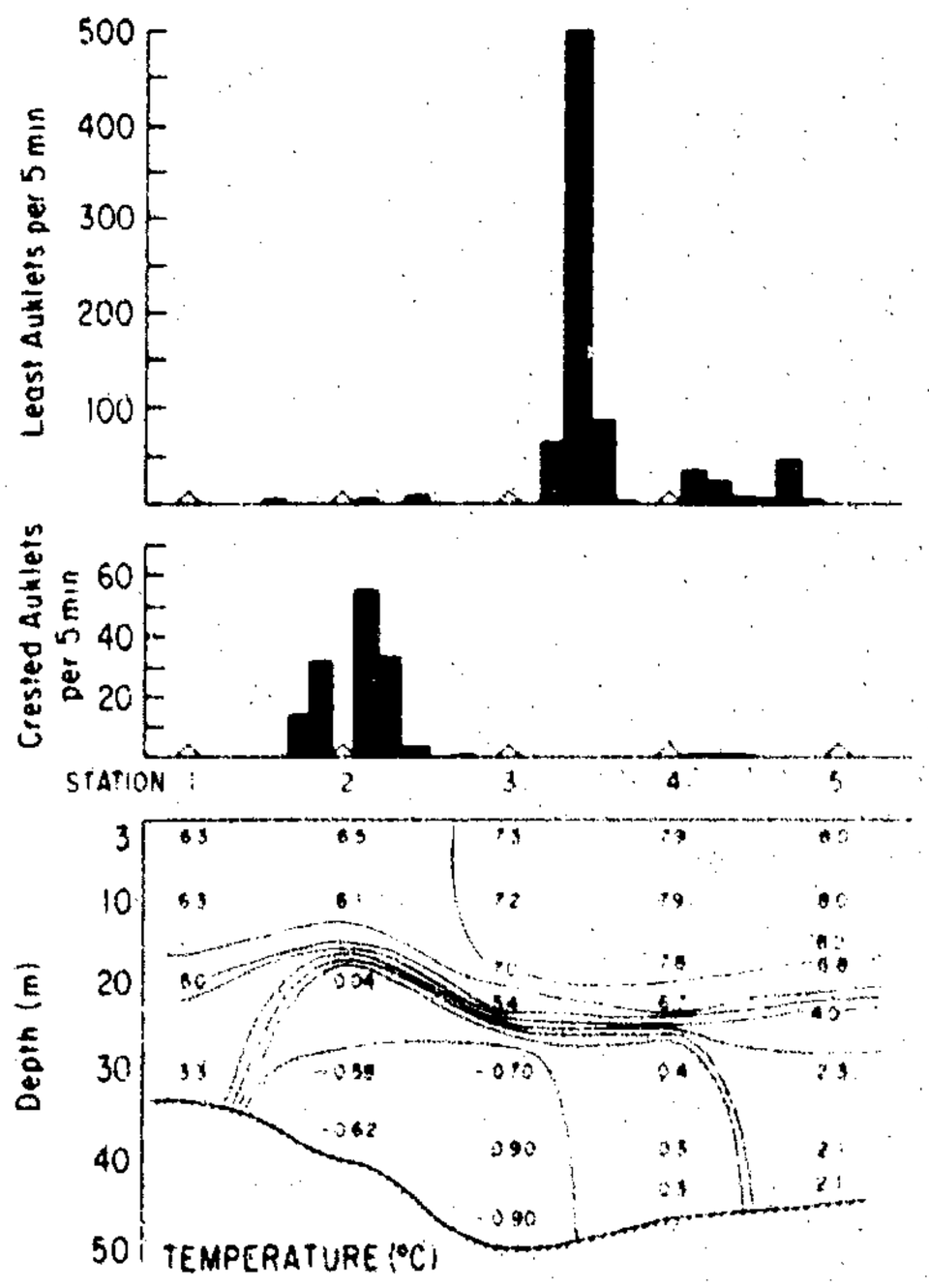
Crested Auklets in the Bering Sea at least occasionally forage close to their colonies. Bédard (1969) found flocks of Crested Auklets foraging near the west end of St. Lawrence Island, possibly near the edge of the Anadyr Current. Figure 1 shows the distribution of Crested and Least auklets with respect to bathymetry and water temperatures on a 37-km transect northwest from Gambell on St. Lawrence Island, 11 August 1986 (Hunt et al., unpubl. data). An oceanic current passes from the Gulf of Anadyr by the west end of St. Lawrence Island and north through the Bering Strait (Coachman et al. 1975). The

Table 4
Proportions of auklet species in colonies and observed foraging on transects radiating out from the colonies at King Island and St. Lawrence Island

	Total numbers of birds	Proportion of auklets		
		Least	Crested	Parakeet
Nesting on King I.[a]	144 000	0.55	0.15	0.29
Observed on surveys near King I.	3 137	0.85	0.04	0.11
Nesting on north side St. Lawrence I.[a]	980 000	0.66	0.34	0.00
Observed on transects at St. Lawrence I.	7 262	0.77	0.23	0.01

[a] Data on numbers of nesting birds from Sowls et al. (1978).

Figure 1
Distribution of Least and Crested auklets with respect to water temperature on a 38-km ship transect running NNW from Gambell, St. Lawrence Island, on 11 August 1986. Start position 63° 51′ N, 171° 47′ 0″ W; end position 64° 11′ N 171° 57.7′ W. The deep, cold water is part of the Anadyr Current, which flows northward.



water of the Anadyr Current is extremely dense and cold compared to Bering Sea shelf water. The Anadyr Current is evident in the figure as a dense, cold (<0 °C), deep, 20–30 m tongue below stations 2 and 3, moving off the page. The strength of the current was not measured; however, the strong thermocline in Figure 1 is the position of a strong flow gradient, with the Anadyr Current moving faster than both the surface water and the inshore water near Gambell (station 1).

The plankton community changed along the transect, with *Calanus* dominant near the island, and a diverse "Anadyr" community dominant at stations 3, 4, and 5 (Table 5a). At station 3, *Neocalanus* of the "Anadyr" community was present

Table 5a
Mean number of individual plankters under 1-m^2 surface, based on a station where two tows were made with a 1-m diameter 505-µm net. Water depth is in metres. Station numbers correspond to those in Figure 1.

	Station number				
	1	2	3	4	5
Water depth (m)	29	33	54	46	41
Calanus marshallae	1440	576	448	192	288
Neocalanus plumchrus	32	64	1824	1952	1312
N. cristatus	0	0	96	32	64
Calanoid copepods	2976	8032	3680	384	512
Eucalanus	0	0	224	228	320
Eucalanoid copepods	32	64	5792	2272	3040
Metridia	32	0	96	74	1472
Euphausiid larvae	0	160	1792	0	160

Table 5b
Mean number of individual plankters under 1-m^2 surface at two depths, at station 3

	Water depths	
	0–25 m	0–54 m
Calanus marshallae	0	448
Neocalanus plumchrus	0	1824
N. cristatus	0	86
Calanoid copepods	2424	3680
Eucalanus	16	224
Eucalanoid copepods	192	5792
Euphausiid larvae	24	1792

only in the colder deep waters (Table 5b), and Crested Auklets were abundant where there was evidence of euphausiids in the water present below 25 m. On a transect run for 75 km north from St. Lawrence Island (in August 1985), Crested Auklet numbers peaked on either side of an aggregation of Least Auklets, over a shallow thermocline (Fig. 2). Collections of birds in these flocks showed both Crested and Least auklets feeding on *Neocalanus* (Harrison 1987).

There are several observations of Crested Auklets foraging in areas of strong tidal currents. Near St. Matthew Island and in the Pribilof Islands, large flocks of Crested Auklets forage in areas of intense tidal mixing (Hunt et al., unpubl. data). At St. George Island, Crested Auklets concentrated where tidal currents carried euphausiids onto a shallow sill (Hunt et al., unpubl. data). Similarly Piatt (unpubl. data) observed large flocks of foraging Crested Auklets in tidally driven upwellings of the western Aleutians and near Big Koniuji Island in the Shumagins, where they were feeding on *Thysanoessa inermis*. Although it is clear that Crested Auklets take advantage of upwellings that concentrate euphausiids, our observations of foraging Crested Auklets are too few and the circumstances too diverse to provide a clear picture of the hydrographic features important to their foraging.

6. Least Auklet

Least Auklets forage mainly on large copepods, although other small zooplankters are also taken (Table 6). The small-scale spatial distribution of Least Auklet prey is likely to be determined by hydrographic processes to a greater extent than for other species of auklets taking larger prey. Hence, one might expect Least Auklet foraging distributions to be more sensitive to physical processes than those of other auklets whose prey have more control of their movements.

Figure 2
Distribution of Least and Crested auklets with respect to water temperature and copepod abundance on a 75-km transect running south toward Kookoolik Point, near Savoonga, St. Lawrence Island, on 10 August 1985. Start position 64°22′N, 170°09′W; end position 63°42′N, 170°09′W. The stations are 18.5 km apart. Modified from Hunt et al. (1990).

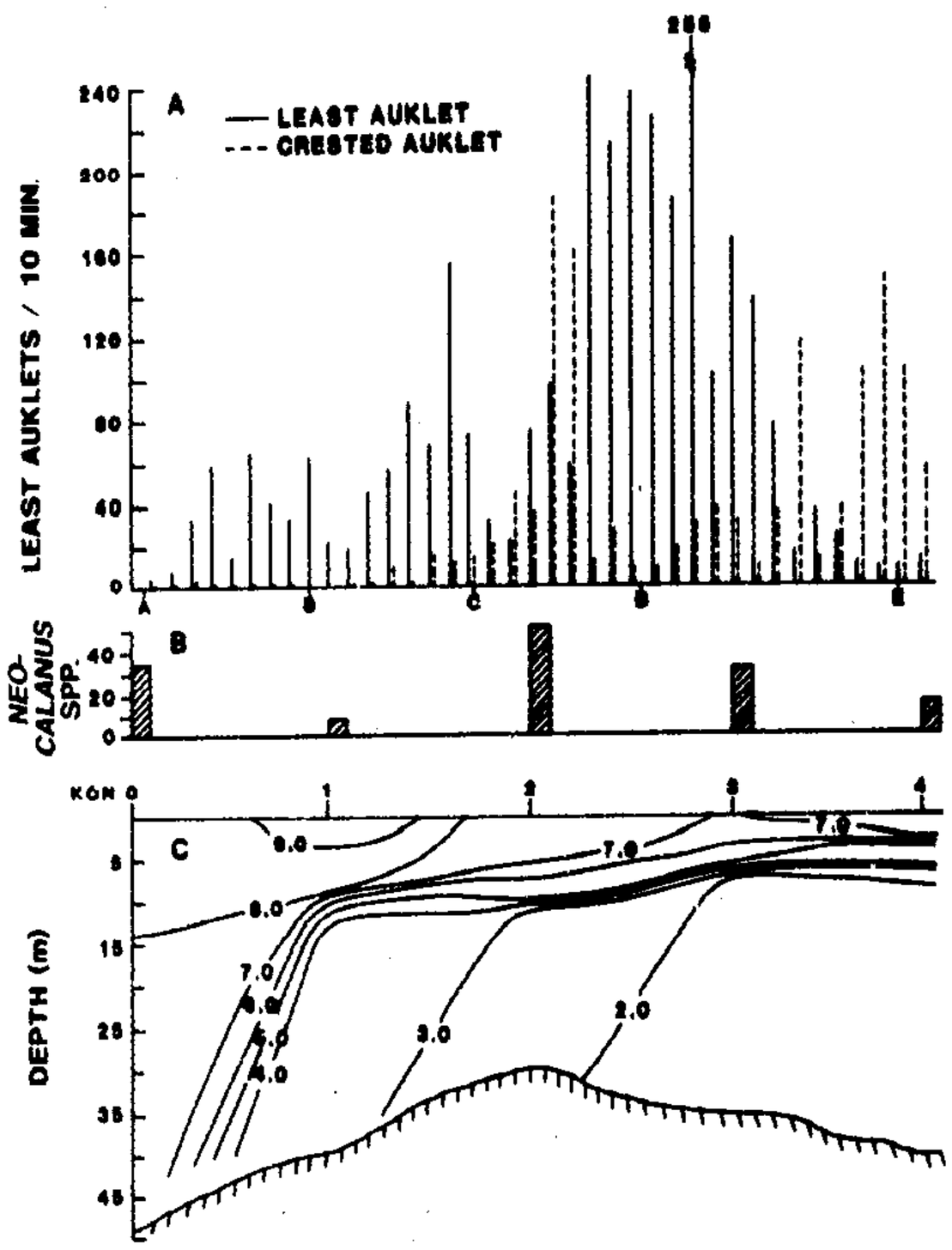


Table 6
Primary prey of Least Auklets. Prey are listed in descending order of importance (N = number of birds sampled).

Location	Prey type	Reference
Big Diomede I. 1991 N = 17	*Neocalanus plumchrus* *Thysanoessa* spp. *N. cristatus*	Piatt, unpubl. data
St. Lawrence I. 1964–66 N = 124	"*Calanus finmarchicus*"[a] Gammaridae Caridea	Bédard 1969
St. Lawrence I. 1976 N = 12	*N. plumchrus*	Searing 1977
St. Lawrence I. 1981 N = 24	*N. plumchrus* *Calanus marshallae*	Springer and Roseneau 1985
Chirikov Basin 1984–86 N = 83	*N. plumchrus* pandalid shrimp larvae	Harrison 1987
St. Lawrence I. 1987 N = 74	*N. plumchrus* *C. marshallae* *N. cristatus*	Piatt et al. 1990
St. Matthew I. 1982–83 N = 69	*C. marshallae*	Springer and Roseneau 1985
St. Matthew I. 1984–86 N = 58	*C. marshallae* *Thysanoessa raschii*	Harrison 1987
Pribilof Is. 1975–78 N = 258	*N. cristatus* *C. marshallae*	Hunt et al. 1981a
Pribilof Is. 1984 N = 49, 15 sorted	*N. plumchrus* *C. marshallae*	Bradstreet 1985 in Roby and Brink 1986
Buldir I. 1976 N = 3	*N. plumchrus*	Day and Byrd 1989

[a] Probably *Neocalanus plumchrus*.

Figure 3
Distribution of Least Auklets with respect to water temperature, sea surface temperature, and sea surface salinity on a 140-km transect from 180 km N of Little Diomede Island ENE across the southeastern Chukchi Sea toward Cape Thompson on 24 August 1988. Start position 67°22.31'N, 168°51.51'W; end position 67°59.8'N, 165°57.1'W. The cold saline water between 15 km and 90 km is a tongue of Bering Sea shelf water that intrudes from the NW and extends southeastward toward Kotzebue Sound. On either side of this tongue is Alaska Coastal water.

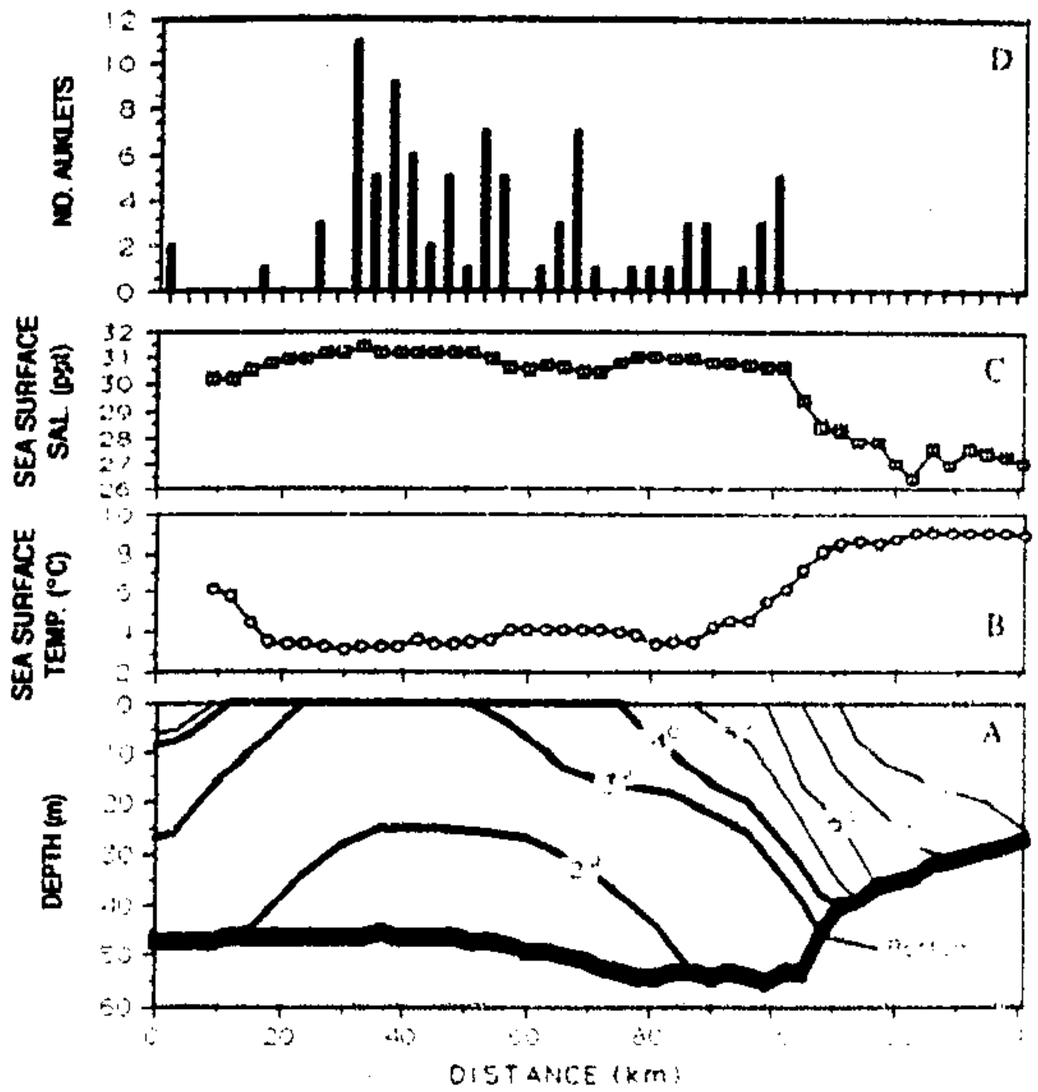
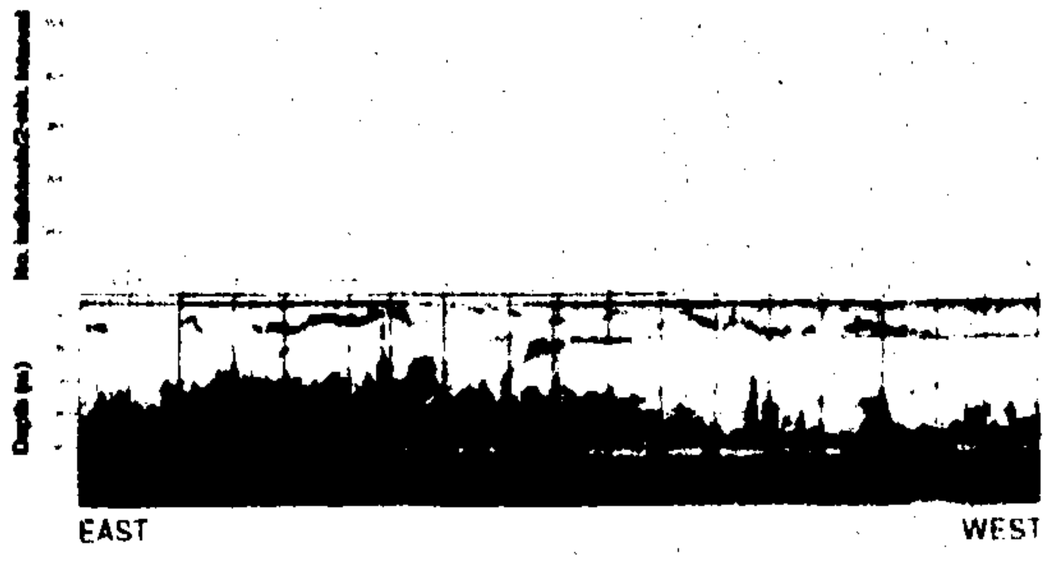


Figure 4
The distribution of Least Auklets with respect to plankton distribution as measured by a 200-kHz echo sounder using a transducer towed in a V-fin depressor, towed at 6 knots (11 km/h) on a 37-km portion of a transect west of King Island, 20 August 1986. The figure covers the portion of a 75-km transect in which Least Auklets were concentrated over stratified Bering Sea shelf water. Acoustic data were gathered by R.T. Cooney and K.O. Coyle of the Institute of Marine Sciences, University of Alaska.



The foraging distributions of Least Auklets appear to be strongly influenced by hydrography. Studies in the Chukchi Sea (Fig. 3) and King Island (Hunt and Harrison 1990) showed that Least Auklets avoided the relatively low salinity, warm Alaska Coastal Current water and foraged in colder, saltier Bering Sea shelf and Anadyr Current waters in which their preferred prey, *Neocalanus* spp., was abundant. These prey apparently aggregate at thermoclines and Least Auklets crossed well-mixed water containing *Neocalanus* to forage in the stratified water (Figs. 1, 2, and 4; see also Hunt et al. 1990). Within stratified waters, Least Auklets preferred regions with strong thermoclines, or areas where upwelling brought the thermocline to the surface (Hunt et al. 1990; Hunt and Harrison 1990; but see Haney 1991 for a different view). Figure 4 is an acoustic record taken west of King Island where auklets were abundant. The concentration of acoustically detected biomass at the pycnocline near 15-m depth is evident. Net samples taken later in this area showed the biomass to be dominated by *Neocalanus plumchrus*, an important prey of Least Auklets (Springer and Roseneau 1985; Hunt and Harrison 1990).

The pattern of Least Auklet foraging at a shallow pycnocline is illustrated in Figure 1 (Table 5b). All copepod prey except young stages were in Anadyr water at or below the thermocline at station 3 (Table 5b). It is likely that the birds in this flock were foraging in Anadyr water and diving 25 m or more to obtain prey. The hydrography and plankton sampling indicated that few, if any, prey would have been present at a shallower depth. It is possible that the strong flow gradient between the Anadyr Current and the Bering Sea shelf water resulted in turbulence that concentrated prey just beneath the thermocline, but data to demonstrate this are lacking.

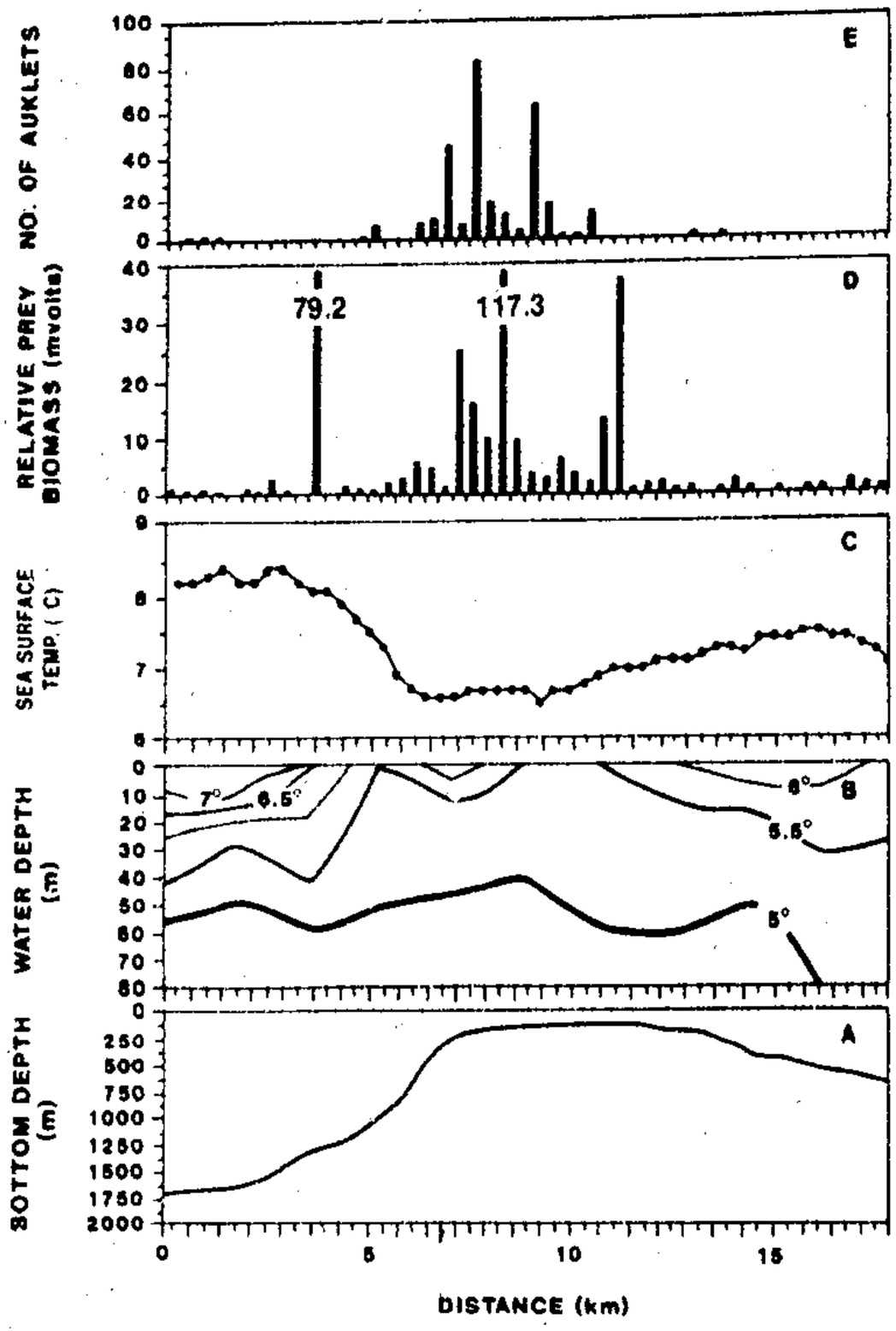
The importance of frontal areas to foraging Least Auklets is not confined to the northern Bering Sea. In the Aleutian Islands near Buldir Island, Piatt (unpubl. data) found that Least Auklets concentrated their foraging along a northeast–southwest transect where cold, plankton-rich water from the North Pacific upwelled against the island shelf (Fig. 5). Least Auklets were foraging at the edge of the shelf in a region where plankton biomass was high.

7. Discussion

The auklets can be divided into three groups on the basis of foraging ecology: 1) Parakeet Auklets at sea are scattered at low density, possibly in response to the distribution of jellyfish, and their diet is more diverse than that of other planktivorous auklets. 2) Least Auklets and Cassin's Auklets forage in small to large flocks, and they are almost always associated with physical features that would facilitate the concentration of prey. These features include pycnoclines and fronts where pycnoclines surface. 3) Crested Auklets are generally underrepresented in sampling near their colonies (at least in the central eastern and northern Bering Sea), indicating that they are foraging at more distant sources. They feed upon prey that swarms and schools, but we know little about the physical processes that may affect the availability to birds of these aggregations of prey.

Although there is considerable variation in secondary types of prey consumed by different auklet species and within auklet species at different locations, there is a high degree of overlap in the principal types of prey taken. Copepods of the genus *Neocalanus* are of widespread importance, as are euphausiids and to a lesser extent larval fish and *Calanus marshallae*. The behaviour of these plankters and their interactions with physical processes are important for understanding why auklets forage where they do. *Neocalanus* spp. are known to aggregate at pycnoclines in stratified water, and euphausiids form schools, have diel migration from near the bottom during the day to the surface at night, and may also form daytime surface swarms when breeding (e.g., Boden et al. 1955). The extent of vertical migration varies between euphausiid species; *Thysanoessa raschii* is a shelf species that undertakes smaller vertical migrations than do other.

Figure 5
The distribution of Least Auklets with respect to water temperature and plankton distribution as measured by a 120-kHz dual-beam hull-mounted transducer on an 18-km transect perpendicular to the Aleutian Arc near Buldir Island, 24 August 1988. Start position 52°29′N, 175°55′E; end position 52°24′N, 175°43′E. Tidally modified surface currents normally flow from south to north (right to left in the figure) in summer, causing fronts over the shallow Buldir Shelf, but current direction may reverse with ebbing tides (Favorite 1974).



deep-water species such as *Euphausia pacifica*. Both the preference for steep gradients and vertical migration, when combined with appropriate hydrographic conditions, can result in the concentration of organisms (Simard et al. 1986; Schneider et al. 1990). In many cases, these aggregations would not have occurred if the organisms acted as passive particles. Thus the behaviour of prey may be as important as physical processes in providing prey concentrations profitably exploited by birds.

Oceanographic features with which concentrations of foraging auklets have been associated are summarized in Table 7. The emphasis on physical events of short periodicity, high energy, and small scale (e.g., various tidal rips and pumps) may be the result of the bias in where we have looked for phenomena to study. It is easier to emphasize work on large aggregations of birds close to colonies than it is to run long transects over areas of relatively barren ocean in search of the foraging areas used by birds. Some of these flocks have been followed, and the importance to Least Auklets of frontal areas and areas with strong thermoclines was discovered in this way (e.g., Hunt and Harrison 1990; Hunt et al. 1990). However, a similar description of foraging habitat for Crested Auklets will be more difficult. The Crested Auklet is more patchily

Table 7
Oceanographic features with which foraging auklets have been associated

Species	Region	Features used	Reference
Cassin's Auklet	southern California	shallow bank	Hunt et al. 1981c
	central California	convergences near edge of California Current	Briggs et al. 1987
	Queen Charlotte Is.	seamounts, shelf-edge front	Vermeer et al. 1985
Parakeet Auklet	Bering Sea	jellyfish; use of physical features not yet shown	Bédard 1969 Harrison 1987
Crested Auklet	Bering Sea	tidal pumps at ends of islands	Hunt et al., unpubl. data
Least Auklet	Chirikov Basin	fronts shallow, strong pycnoclines	Hunt and Harrison 1990 Hunt et al. 1990
	St. Matthew I.	tidal rip, over shallow sill	Hunt et al., unpubl. data
	Aleutian Is.	tidal pumps	Piatt, unpubl. data
Whiskered Auklet	Aleutian Is.	tidal rips	Day and Byrd 1989 Troy and Bradstreet 1991 Piatt, unpubl. data

distributed at sea, and larger-scale patterns are difficult to identify. Our data on Crested Auklets feeding at sea form a small collection of special cases, with few habitat features in common. It may be profitable to compare Crested Auklet foraging distribution to that of Least Auklets. For instance, Crested Auklets may benefit from the same hydrographic features that have been shown to be important for Least Auklets. However, we would expect differences in how their preferred prey (copepods for Least Auklets and euphausiids for Crested Auklets) would respond to the hydrography. The two species of auklets may also respond differently to concentrations of prey. Hunt et al. (1990) found that small-scale peaks in Least Auklet numbers were not closely matched with peaks in prey distribution. The overall habitat appeared to provide adequate foraging conditions for this species, and the selection of foraging habitat by Least Auklets appeared to be coarse grained at a mesoscale. The Crested Auklet may be more closely tied to aggregations of its preferred prey, in which case its more patchy distribution reflects a smaller scale of habitat selection.

The duration of some prey concentrations and their locations may be more predictable than others. Large patches may persist for longer duration than small patches (Haury et al. 1978) and so may be followed by the birds longer and/or used repeatedly. Small plankton patches are likely to be available only for short periods and to be difficult to relocate if contact is lost. Thus, we may expect foraging flocks to vary in size depending upon prey patch size, prey species composition, and the physical processes that are at work.

The predictability of the location of prey concentrations is likely to be a function of the extent to which the patch is caused by bathymetrically driven physical processes. Physically forced concentrations of prey are more predictable in both time and space than concentrations dependent solely on the aggregative behaviour of prey. Hence, the locations of auklet flocks foraging at physical features are more predictable than those of Parakeet Auklets feeding on jellyfish and associated commensals. When Parakeet Auklets shift to prey similar to those taken by Least or Crested auklets, their foraging distribution becomes similar to that of the other auklet species (Harrison, unpubl. data).

We know little about the extent to which present competition influences diet choices or foraging distribution of auklets. Bédard's (1969) early work was predicated on the assumption of competitive interactions and their effect on diet and foraging behaviour, though he was far more cautious in his assessments than was Cody (1973, see Bédard 1976). Although Bédard found different auklet species taking different prey to chicks, there was considerable overlap in prey species taken by adults at St. Lawrence Island prior to chick hatching. Likewise the three northern species of auklet (Least, Crested, and Parakeet) are often found together at sea. Bédard (1969) mentions that on only three of 30 transects did he encounter partial or complete segregation of foraging Least and Crested auklets. In contrast, the transect counts shown in Figures 1 and 2 are the only ones out of many transect counts that we did in the Chirikov Basin in which we found sizable numbers of the two species together on the same transect. In both of these cases there was small-scale separation of the species. These separations may be because of interactions between the auklet species, or may be the result of taking prey that vary spatially in their availability. The latter explanation appears to account for the distribution and dispersion of Parakeet Auklets. Two decades after Bédard's pioneering work, we still do not know the role of competitive interactions in the foraging ecology of auklets.

In summary, we have learned much about the kinds of locations where auklets seek food during the breeding season. However, with the exception of the Cassin's Auklet in the California Current region, we know very little about how auklets find food when they are away from their colonies. Particularly in the winter, it is probable that many species move to deep oceanic water where bathymetrically fixed physical processes are unlikely to be of importance. We need more information on how individuals search for food and about how they decide where they will stop to forage. We suspect that social interactions between birds play an important role in the choice of foraging areas (Hunt et al. 1990), but we have no data. Methods to follow individual birds and methods to probe prey abundance in the upper 10 m of the water column are needed if this next generation of questions is to be answered.

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