

Diets in Relation to Prey Resources

GELATINOUS ZOOPLANKTON IN THE DIET OF THE PARAKEET AUKLET: COMPARISONS WITH OTHER AUKLETS

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Abstract. I studied the diet and foraging habits of the Parakeet Auklet (*Cyclorhynchus psittacula*), Least Auklet (*Aethia pusilla*) and Crested Auklet (*A. cristatella*) in the northern Bering Sea from 1983 to 1986. Parakeet Auklets frequently fed on gelatinous zooplankton (e.g., jellyfish and ctenophores) and jellyfish symbionts such as hyperiid amphipods and fish larvae. In the Chirikov Basin 54% of the Parakeet Auklets collected (N = 13) had eaten jellyfish and 69% had eaten ctenophores (some birds with both prey); near St. Matthew Island 54% (N = 39) had eaten jellyfish, with no ctenophores in evidence. Euphausiids and other zooplankton, which live independently of jellyfish, were abundant at the latter site and were eaten by all three auklet species. I found greater dietary overlap between Parakeet Auklets and the *Aethia* species at St. Matthew Island than in the Chirikov Basin. The unique upturned bill of the Parakeet Auklet may be a specialization for handling slippery gelatinous zooplankton. In the Chirikov Basin Parakeet Auklets were more dispersed than were Least Auklets, which were usually aggregated. The dispersed foraging distribution of the Parakeet Auklet may be linked to its habit of feeding on jellyfish.

Key Words: Crested Auklet; Least Auklet; jellyfish; ctenophore; diet; Bering Sea.

Bédard (1969a) studied the feeding habits of the Parakeet Auklet (*Cyclorhynchus psittacula*), the Least Auklet (*Aethia pusilla*), and the Crested Auklet (*A. cristatella*) on St. Lawrence Island in the Northern Bering Sea. He found very little dietary overlap among the three species. The Least and Crested Auklets were dependent on seasonally abundant zooplankton, copepods and euphausiids, respectively. Parakeet Auklets had a varied diet which included hyperiid amphipods, fish larvae and other large zooplankton; there was less temporal variation in their diet than in the diets of the *Aethia* species. All three species fed in the same areas at sea, and the low dietary overlap suggested there were fundamental differences in their foraging behavior.

Colony attendance patterns indicate that the Parakeet Auklets spend more time at sea than the *Aethia* auklets (Bédard 1969a, Manuwal and Manuwal 1979). Least and Crested auklets have activity patterns on the colony that suggest they feed after dawn and in the late afternoon (Sealy and Bédard 1973). The largest numbers of Parakeet Auklets occur on the colony at midday; they spend 60% more time at sea than the *Aethia* auklets (Bédard 1969a) and potentially feed at night as well as during the day (Bédard 1967, pers. obs.).

The auklets are in effect partitioning resources. The Least Auklet is smaller than the Crested and Parakeet auklets, and it consistently feeds on smaller prey. The Crested and Parakeet auklets,

however, are of similar size and bill proportions, yet have completely different diets. Bédard (1969a) concluded that the differences in prey selection by these two species must result from differences in daily activity patterns, subtle differences in bill morphology and innate preferences for different zooplankton. It is difficult to infer how the auklets maintain their dietary specialities without an understanding of their foraging habitat, and the patterns in which they encounter their prey.

Birds living in terrestrial environments are often seen to feed in different microhabitats, the vegetation providing habitat structure that determines where they search for prey. In marine environments jellyfish potentially provide similar habitat structure (Hamner et al. 1975), offering surfaces for other creatures to sit upon and forests of tentacles to hide among, and they are ubiquitous and abundant.

I first noted Parakeet Auklets feeding on jellyfish at sea in the area of St. Matthew Island in 1983 (Harrison 1984); there are two reasons for suspecting that jellyfish are a frequent prey. First, Parakeet Auklets often have material in their stomachs that is amorphous, well digested, and difficult to identify (Bédard 1969a, pers. obs.). Second, many of the prey documented for the species (Bédard 1969a, Hunt et al. 1981) are jellyfish symbionts or parasites. Hyperiid amphipods are typically jellyfish associates (Harbison et al. 1977, Laval 1980) as are gadid fish larvae

(Mansueti 1963, Van Hyning and Cooney 1974). My observations were the first sign of the jellyfish host in their diet.

In this paper I assess the relative importance of jellyfish in the diet of the Parakeet Auklet. I address the following questions. To what extent do Parakeet Auklets eat jellyfish? Do crustaceans and fish associated with jellyfish constitute an important part of their diet? Do food habits vary geographically? Do jellyfish occur less in the diet of Parakeet Auklets from a site where more nutritious prey are abundant? How do the diets of Parakeet, Crested and Least Auklets differ? How are the distributions of Least and Parakeet Auklets affected by spatial patterns of prey availability?

METHODS

Collections

Foraging auklets were collected at sea during the breeding season (late June–August) from 1983 to 1986 in the waters surrounding St. Matthew Island and in the Chirikov Basin (Fig. 1). Small numbers of birds were collected from a number of sites, usually only one or two species represented in any single collection. Least Auklets were collected in the Chirikov Basin just north of Gambell, St. Lawrence Island, near the location of Bédard's study. Both *Aethia* species were collected north of Savoonga, St. Lawrence Island. Least and Parakeet auklets were collected in 1984 and 1985 at many positions along the "King Island transect" from east of King Island to a point 64 km due west (Fig. 1). Auklets were frequently collected from mixed-species feeding flocks in the St. Matthew area; in 1984 all St. Matthew collections were made on the east side of the island, where large aggregations of murrets (*Uria* spp.) and auklets fed on euphausiids (Hunt et al. 1988). In 1985 and 1986 all collections were made in the Sarichef Strait area.

The proventriculus and gizzard were removed promptly after a bird was shot and the gular pouch was searched for prey. I found no difference between the contents of the proventriculus and the gular pouch (Harrison 1987) and combined the data for analysis.

Food samples were examined while fresh for the presence of fragile prey, such as jellyfish and ctenophores. The presence of ctenophores was confirmed by the identification of comb rows; nematocysts helped confirm the presence of jellyfish. Gut contents were preserved in 80% ethanol for later study.

All intact crustaceans and fish were tallied. When possible I measured the volume of each prey species or species group (e.g., Scyphomedusae). I calculated the frequency occurrence of prey among the samples (frequency occurrence = number of stomachs containing a given prey/number of stomachs examined \times 100). Estimates of jellyfish are conservative because many samples had remnants of possible jellyfish tissue that could not be confirmed. The number of prey items is usually ambiguous in these samples because many prey are represented by fragments. I did not compare number, volumes or weights of prey, as these are likely to be biased by relative digestibility, especially for gelat-

inous zooplankton. However, to obtain some measure of the relative importance of prey, I used prey number and volume (for gelatinous zooplankton) to assess the importance of each prey in a given sample. I then made separate tallies of all prey in the stomachs, and assigned these to one, two or all three of the categories based on the following criteria:

1. Any identifiable prey type was tallied in the "all prey" frequency analysis.

2. Prey occupying at least one third of a sample's volume, or constituting at least one third of the number of prey items, was considered "significant prey."

3. Prey dominating a sample in volume or number by 10 fold was considered "dominant."

In comparing the diets of the auklets I used an overlap index (Horn 1966, Diamond 1983), "C," with values ranging from "0" for no overlap to "1" indicating complete overlap

$$C = \frac{2 \sum_{i=1}^s x_i y_i}{\sum_{i=1}^s x_i^2 + \sum_{i=1}^s y_i^2}$$

where s is the number of prey categories in the two bird species being compared, and category i is represented x times in species x and y times in species y . Although "1" indicates total overlap, the actual value calculated for a pair of samples depends on the number of prey categories (Diamond 1983). I did not include squid beaks, nereid beaks or fish bones when calculating overlap indices because they are retained an unknown time in the guts.

Using overlap indices is a problematical procedure because there is no theoretical statistical distribution that can be used to compare overlap measures. However, by taking random combinations of the data, a "random expectation" can be established. For example, to compare the diets of birds collected from a single feeding flock, I entered the prey of all individuals of each species pair (i.e., 6 Parakeet Auklets and 4 Least Auklets) into a Turbo Pascal program. The program shuffled the data into all possible permutations (a total of 10 birds redistributed into 210 possible combinations of 4 and 6), calculated overlap indices for each new set of 4 and 6 in turn (210 overlap values) and then determined the mean overlap and the standard deviation. The actual overlap between the two samples can then be compared to the calculated random expectation.

Overlap indices were also used to compare species using the full set of data. I did not run all possible combinations because of the very large numbers of permutations. After the program calculated 1000 overlap values for a species pair, the mean changed relatively little, and the standard deviation was nearly constant. Mean overlaps are presented based on 1000 permutations.

Plankton sampling

Acoustic data were collected by T. Cooney using a Biosonics high-frequency echosounder (200 kHz). Acoustic records showing plankton biomass, integrated with depth, are presented for the full water column

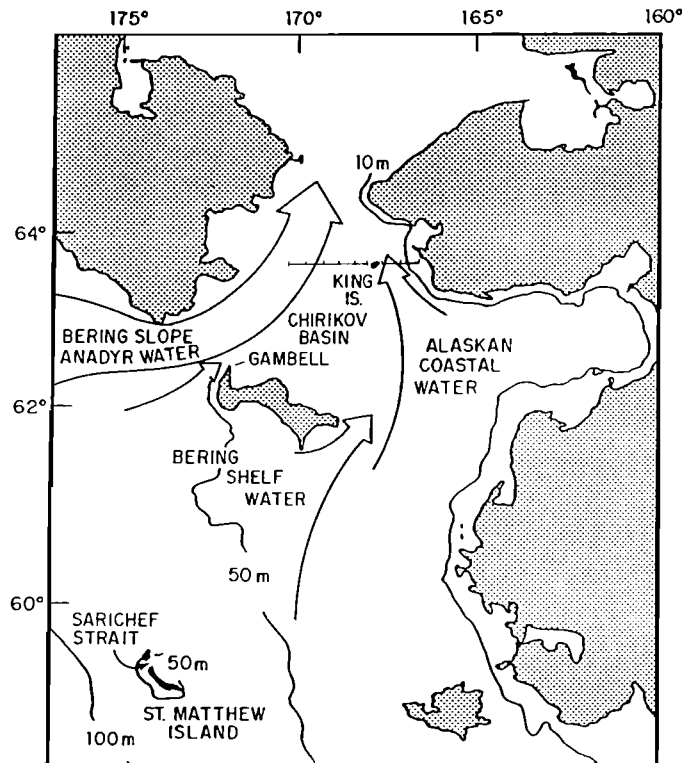


FIGURE 1. Location of the Chirikov Basin and St. Matthew Island in the northern Bering Sea, with transect shown extending east and west of King Island.

along two transects, one in the St. Matthew Island area, through the Sarichef Strait, and the second across the Chirikov Basin, west of King Island.

Plankton tows were made as part of a concurrent study (Hunt et al. 1990). A one-meter 505-micron mesh net was lowered to within 5 m of the bottom, then hauled vertically to the surface. Plankton were preserved in formalin, split into subsamples and counted in the laboratory. Gelatinous animals tend to be damaged or destroyed by nets, and no quantitative data are provided on their abundance.

Bird distributions

Numbers of Least Auklets and Parakeet Auklets were censused along a transect near King Island (Fig. 1), which extended 32 km due east of King Island to 64 km west. At 16 km intervals we made vertical plankton tows and measured physical properties of the water column (temperature, salinity and density with depth) using a CTD (Conductivity-Temperature-Depth probe). The transect was run 15 times during the four year study.

Continuous counts were made from the ship, the *R/V Alpha Helix*, while steaming between hydrographic stations. All birds were counted within a 90 degree arc from bow to beam to a distance of 300 m; only those auklets sitting on the water were used in the analysis of foraging dispersions.

I compared the distribution of Least and Parakeet auklets using Kolmogorov and Smirnov methods (Sokal and Rohlf 1981). I divided each continuous transect into 10 minute intervals, then established a frequency distribution based on the number of 10 minute observation blocks with 0 birds, 1 bird, 2 birds, etc. I compared each species to the expected cumulative frequency distribution for the Poisson distribution. If the frequency distribution was significantly different from the Poisson ($P < 0.05$) then I determined by inspection whether the birds were more clumped or more dispersed than random.

STUDY AREAS

The Chirikov Basin is the shallow (50 m) northern extreme of the Bering Sea. The western half has an oceanic fauna because of the influence of the Anadyr Current; the current passes from the deeper Bering Sea north through the Bering Strait (Coachman et al. 1975) (Fig. 1), carrying in large calanoid copepods and other oceanic zooplankton (Cooney and Coyle 1982). The plankton community changes across the basin, with a zooplankton community characteristic of coastal Alaskan waters in the east. The coastal community has a relatively low plankton biomass, and a high diversity of jellyfish, small fish and crab larvae (Cooney 1981). The highest biomass of plankton is in the central Chirikov Basin where the oceanic water and coastal water

TABLE 1. FREQUENCY OF OCCURRENCE OF PREY FROM PARAKEET AUKLETS¹

	St. Matthew Island				Chirikov Basin	
	1983	1984	1985	1986	1984	1985
No. samples	8	14	7	10	9	4
Gelatinous zooplankton						
Ctenophora					66	75
Scyphomedusae	75	43	43	60	56	50
Medusa associates						
Amphipoda						
<i>Hyperia</i>	38			10		
<i>Hyperoche</i>			43			
Unid. hyperiid					11	25
Gadid fish						
<i>Theragra chalcogramma</i>	25		100	40		
Unid. gadid larvae					33	
Free-swimming prey						
Pteropoda						
<i>Limacina</i>	25			20	33	50
Polychaeta						
Nereid beaks	25		57	80		
Copepoda						
<i>Neocalanus plumchrus</i>						25
<i>N. cristatus</i>					11	
<i>Calanus marshallae</i>			14			
<i>Pseudocalanus elongatus</i>			43			
Unid. copepod	13					
Amphipoda						
<i>Parathemisto libellula</i>	25		43	80	11	
Euphausiacea						
<i>Thysanoessa raschii</i>		64		60		

¹ For example, 75% of the 8 Parakeet Auklets collected in 1983 had Scyphomedusae in their stomachs, the remaining 25% without Scyphomedusae.

meet (Hunt et al. 1990); in these hydrographically structured areas there are high densities of large calanoid copepods (*Neocalanus plumchrus* and *N. cristatus*) and large numbers of larval shrimp and lithode crabs. Two species, frequently important prey for seabirds, also occur in these areas: the hyperiid *Parathemisto libellula*, a voracious predator on copepods, and euphausiid *Thysanoessa raschii* (Motoda and Minoda 1974).

St. Matthew Island is centrally located on the Bering Shelf in an area where there is a variety of zooplankton species from both northern and southern Bering Sea communities. Substituting for the large copepods of the Chirikov Basin is *Calanus marshallae*, which is the prey of carnivorous plankton such as walleye pollock larvae (*Theragra chalcogramma*) (Motoda and Minoda 1974).

The abundance of jellyfish and other gelatinous animals such as ctenophores is not discussed in the literature on the zooplankton of the region, most sampling based on net tows. However, their abundance is readily apparent. Divers suggest they are one of the dominant groups of the Bering Shelf community (Hamner 1982). Fishermen trawling for walleye pollock routinely complain about how jellyfish foul fishing nets.

The large medusae, *Chrysaora* (4–50 cm diameter bell) and the other common jellyfish of the Bering shelf

community, *Cuspidella*, *Cyanea* and *Aequorea*, have benthic polyp stages that produce medusae asexually in the spring (Hamner 1982). The medusae are abundant in the midwater environment from spring through fall, when they develop gonads and become sexually mature. They produce planulae, which descend to spend the winter on the bottom.

RESULTS

Parakeet Auklets persistently fed on gelatinous animals such as jellyfish and ctenophores (Table 1). Comparisons of food samples with reference specimens confirm that the Scyphomedusae *Chrysaora* and *Cyanea* were among the auklet's prey; these are very large jellyfish (up to 50 cm diameter), which were abundant throughout the study area. The high occurrence of ctenophores (probably *Beroe*) in birds from the Chirikov Basin illustrates how generalized the Parakeet Auklet is in this behavior.

Many of the prey (Table 1) may have been ingested as a unit with medusae. The amphipods *Hyperia* and *Hyperoche* as well as gadid fish live in association with jellyfish (Van Hyning and Cooney 1974, Laval 1980). The pteropod *Li-*

TABLE 2. FREQUENCY OF OCCURRENCE OF PREY FROM THREE AUKLET SPECIES FROM ST. MATTHEW ISLAND, FOR ALL PREY OCCURRING IN SAMPLES ("ALL"), PREY OCCURRING IN SIGNIFICANT NUMBERS OR VOLUMES ("SIG"), AND PREY DOMINATING SAMPLES ("DOM")¹

Taxon	<i>C. psittacula</i> (N = 39)			<i>A. pusilla</i> (N = 58)			<i>A. cristatella</i> (N = 6)		
	All	Sig	Dom	All	Sig	Dom	All	Sig	Dom
Gelatinous zooplankton									
Scyphomedusae	54	38	13	5	0	0	17	0	0
Medusa associates									
Amphipoda									
<i>Hyperia</i>	10	5	0						
<i>Hyperoche</i>	8	3	0	5	0	0			
Unid. Hyperiidae				2	0	0			
Gadid fish									
<i>Theragra chalcogramma</i>	33	18	13	16	3	0	67	17	0
<i>Theragra otolith</i>	33			22			83		
Free-swimming prey									
Chaetognatha									
<i>Sagitta</i>				3	2	0			
Pteropoda									
<i>Limacina</i>	10	0	0	5	0	0			
Polychaeta									
Nereid beaks	36								
Copepoda									
<i>Calanus marshallae</i>	5	0	0	64	53	26			
<i>Pseudocalanus elongatus</i>	8	0	0						
Amphipoda-Hyperiidae									
<i>Parathemisto libellula</i>	33	18	3	36	7	2	67	0	0
Amphipoda-Gammaridae									
<i>Protomeia</i>				5	0	0			
<i>Monoculodes</i>				7	0	0			
<i>Anonyx</i>				2	0	0			
Pleustidae				3	0	0			
Unid. Gammaridae				5	0	0			
Unid. Amphipoda				9	5	2			
Euphausiacea									
<i>Thysanoessa raschii</i>	39	26	23	29	14	7	100	83	67
Decapoda									
Pandalidae larvae				3	0	0			
Hippolytidae larvae				16	5	2			
Crangodidae larvae				2	0	0			
Lithode crab larvae				22	2	0			
Brachyuran crab larvae				5	0	0			
Fish									
<i>Ammodytes</i>				3	0	0			

¹ For example, 54% of the 39 Parakeet Auklets collected near St. Matthew Island contained Scyphomedusae, the remaining 46% without Scyphomedusae. Of the same 39 birds, 38% had "significant" volumes of Scyphomedusae, the remaining 62% either had not eaten Scyphomedusae or only eaten a small amount. 13% of the 39 birds had Scyphomedusae dominating their stomach contents.

macina is the primary prey of the jellyfish *Chrysaora*, and it may have been ingested by the birds incidentally (Hamner 1982). Note the much lower occurrence of jellyfish associates among the prey of Parakeet Auklets from the Chirikov Basin, where they ate more ctenophores than jellyfish. *Beroe* does not typically have numerous associated fish and crustaceans as do jellyfish, and the birds with ctenophores in their crops tended to have little else.

All three auklet species fed both on jellyfish and jellyfish associates (Tables 2, 3). Parakeet Auklets more often had jellyfish associates in the "significant prey" category and the "dominant prey" category than did the other auklets. Very few symbiotic hyperiid amphipods were eaten by the *Aethia* auklets, although gadid fish larvae were frequently eaten. The contribution of jellyfish to the diet of the *Aethia* species was minor. On the other hand, jellyfish occurred more often

TABLE 3. FREQUENCY OF OCCURRENCE OF PREY FROM THREE AUKLET SPECIES FROM THE CHIRIKOV BASIN, FOR ALL PREY OCCURRING IN SAMPLES ("ALL"), PREY OCCURRING IN SIGNIFICANT NUMBERS OR VOLUMES ("SIG"), AND PREY DOMINATING SAMPLES ("DOM")¹

Taxon	<i>C. psittacula</i> (N = 13)			<i>A. pusilla</i> (N = 83)			<i>A. cristatella</i> (N = 22)		
	All	Sig	Dom	All	Sig	Dom	All	Sig	Dom
Gelatinous zooplankton									
Ctenophora	69	54	38						
Scyphomedusae	54	38	15	5	2	2	23	10	5
Medusa associates									
Amphipoda									
Unid. Hyperiidae	23	0	0	2	0	0	5	0	0
Gadid fish									
Unid. Gadidae larvae	23	23	0	4	1	0	36	0	0
<i>Theragra otolith</i>				1					
Free-swimming prey									
Pteropoda									
<i>Limacina</i>	38	0	0						
Cephalopoda									
Squid beaks							5		
Polychaeta									
Nereid beaks				1					
Copepoda									
<i>Neocalanus plumchrus</i>	8	0	0	53	29	23	10	10	0
<i>N. cristatus</i>	3	8	8	64	29	7	14	5	0
<i>Calanus marshallae</i>				1	0	0			
<i>Pseudocalanus elongatus</i>				1	0	0			
<i>Eucalanus bungii</i>				11	1	0	5	0	0
Unid. Copepoda				11	2	2			
Amphipoda-Hyperiidae									
<i>Parathemisto libellula</i>	8	0	0	19	5	1	23	18	9
Amphipoda-Gammaridae									
<i>Byblis</i>				1	0	0			
Pleustidae				4	0	0			
Unid. Amphipoda				7	0	0			
Euphausiacea									
Euphausiid larvae				1	0	0			
<i>Thysanoessa raschii</i>				16	4	4	36	27	14
Decapoda									
Pandalidae larvae				39	22	7	23	14	5
Hippolytidae larvae				5	2	0			
Lithode crab larvae				8	1	0	5	0	0
Crab megalops				4	1	0			

¹ Explanation same as for Table 2.

in Parakeet Auklets than hyperiids or fish, suggesting the jellyfish frequently were ingested on their own.

Parakeet Auklets also fed on zooplankton that do not associate with jellyfish. Parakeet Auklets from the St. Matthew collections in 1984 were full of euphausiids (Table 1), as were all seabird species feeding in the area (Hunt et al. 1988). Most of the Parakeet Auklets collected in 1986 were part of mixed-species feeding flocks, and these birds had free-swimming prey such as euphausiids and the hyperiid amphipod *Parathemisto*.

Figure 2 compares auklet diets at St. Matthew Island, the Chirikov Basin and St. Lawrence Is-

land; the information on the latter site is from Bédard (1969a). Bédard evaluated the relative importance of various prey by combining all samples from a given species and comparing the volume occupied by each prey. He calculated the volume using numerical data and estimated the volume that fresh, intact prey would occupy. Bédard's volumetric measure of prey importance is only roughly comparable to my measure based on the frequency occurrence of prey. Our data nonetheless permit comparison.

Bédard (1969a) did not identify jellyfish as a food of the Parakeet Auklet, although he observed ctenophores in their diet. While he did not separate free-swimming *Parathemisto* from

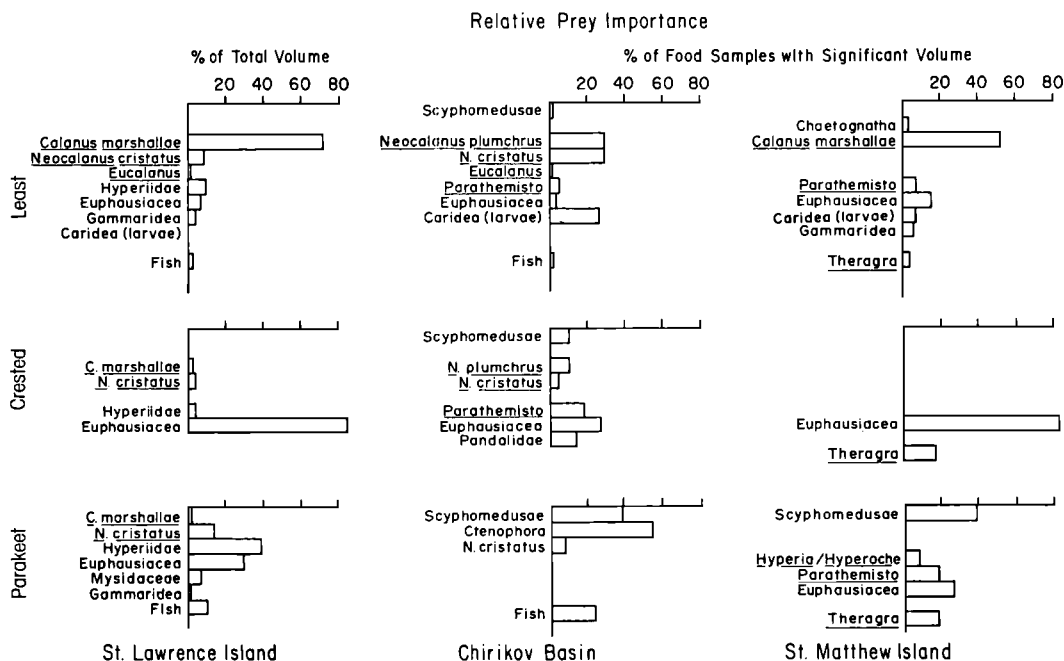


FIGURE 2. Diets of Parakeet, Crested and Least Auklets at three sites in the northern Bering Sea.

the parasitic hyperiid amphipods, combining them in the category Hyperiididae, he stated that *Parathemisto* was the most important constituent of the Parakeet Auklet's diet.

Bédard's (1969a) data for Least and Crested auklets were more similar to my data for these species at St. Matthew Island than in Chirikov Basin (Fig. 2). The Least and Crested auklets that I collected near Bédard's site both fed on *Neocalanus* copepods, whereas Bedard found Least Auklets feeding on *Calanus* and Crested Auklets feeding on euphausiids. Searing (1977) studied the *Aethia* on another St. Lawrence colony and his results were similar to mine. Given that *Calanus* is indicative of coastal influence and *Neocalanus* of the influence of the oceanic Anadyr Current, the changes in diet probably reflect a changing community and are linked to oceanographic variation.

There were marked differences in prey distributions at my two study sites. Figure 3 shows acoustic records for a transect across the Chirikov Basin, and another through the Sarichef Strait at St. Matthew Island. The mean biomass in the Chirikov Basin was 5.8 g/m²; near St. Matthew Island it was 10.2 g/m². The variance to mean ratio for plankton biomass for the Chirikov Basin transect was 2.6, whereas the ratio along the St. Matthew transect was 21.2, indicating a much patchier biomass along the St. Matthew transect. Plankton tows indicated the patches of prey near St. Matthew were made up of euphausiids and hyperiid amphipods (*Parathemisto*).

There were differences between the two sites in the extent of dietary overlap among the auklets (Tables 4, 5). Only a few overlap values deviated significantly from the random expectation. There was relatively low overlap between the Parakeet

TABLE 4. DIETARY OVERLAP BETWEEN THREE AUKLET SPECIES IN THE CHIRIKOV BASIN

	"Sig. prey" category		"All prey" category	
	Actual overlap	Mean overlap (sd) ¹	Actual overlap	Mean overlap (sd)
Parakeet vs. Crested	0.13	0.50 (0.12)	0.36	0.51 (0.10)
Parakeet vs. Least	0.09	0.20 (0.07)	0.16	0.29 (0.06)
Crested vs. Least	0.52	0.50 (0.09)	0.53	0.65 (0.05)

¹ Mean overlap and standard deviation calculated from random permutations of data; see text.

Auklet and the *Aethia* auklets in the Chirikov Basin, and greater overlap at St. Matthew Island. The use of gelatinous prey by the Parakeet Auklet was most pronounced in the Chirikov Basin, where I calculated the lowest overlap values (Parakeet vs. Least 0.09, Parakeet vs. Crested 0.13). The Parakeet Auklets often captured locally abundant euphausiids and *Parathemisto* at St. Matthew Island, as did the Least and Crested auklets, and their diets were more similar. Least and Crested auklets differed more in their prey selection around St. Matthew Island where there were large patches of the preferred prey of each species, and less so in the Chirikov Basin. While some Crested Auklets fed on euphausiids, both *Aethia* species were eating mostly copepods in the Chirikov Basin; it is not clear whether this was due to a shortage of euphausiids or the abundance of large copepods.

The small scale distribution of prey is likely to affect the extent of dietary overlap between the three species. Table 6 describes the diet of auklets collected from a single feeding flock. The three species tended to have many of the same prey types in their stomachs. However, the various prey were represented in different proportions, resulting in distinct differences between auklet species in their prey selection; the differences are evident in the "significant prey" category. I found no overlap between the Crested Auklet and the other species in the "significant prey" category (Table 7). Least and Parakeet auklets had only slightly lower dietary overlap than would have occurred by chance. The Parakeet Auklets mostly ate *Parathemisto* and jellyfish (Table 6); the Least Auklets ate *Parathemisto* and copepods.

Least and Parakeet Auklets, while frequenting the same ocean habitat, behave differently. Parakeet Auklets were distributed randomly along the transect (Fig. 4) in a pattern that could not be differentiated from the Poisson distribution, while the Least Auklets were non-random, and clumped (K-S comparison to Poisson, $P = 0.05$). Least Auklets occurred in several patches between stations 5 and 7, an area with high densities of *Neocalanus copepods*. The eastern end of the transect (salinity 30–32‰) has lower

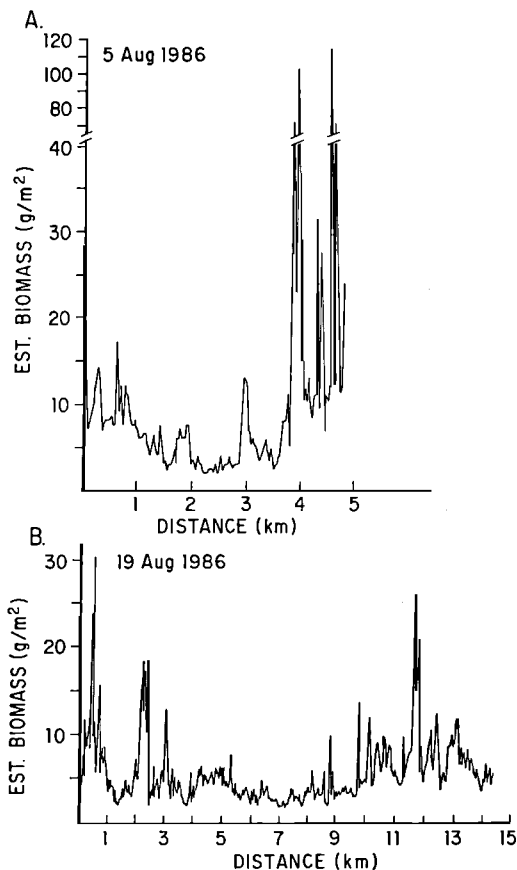


FIGURE 3. Acoustic records showing planktonic biomass along a transect through the Sarichef Strait, St. Matthew Island (A) and a transect west of King Island in the Chirikov Basin (B).

plankton biomass than the oceanic western end (salinity 32–32.5‰). The Least Auklets were more restricted to the oceanic areas with high plankton biomass, whereas Parakeet Auklets were found in both habitats.

When all distributional data from the King Island area (15 transects) were compared to a Poisson distribution, Least Auklets were more aggregated than the random distribution on 14

TABLE 5. DIETARY OVERLAP BETWEEN THREE AUKLET SPECIES AT ST. MATTHEW ISLAND

	"Sig. prey" category		"All prey" category	
	Actual overlap	Mean overlap (SD) ¹	Actual overlap	Mean overlap (SD)
Parakeet vs. Crested	0.49	0.73 (0.11)	0.70	0.74 (0.09)
Parakeet vs. Least	0.18	0.24 (0.02)	0.49	0.47 (0.02)
Crested vs. Least	0.24	0.89 (0.13)	0.48	0.76 (0.07)

¹ Mean overlap and standard deviation calculated from random permutations of data; see text.

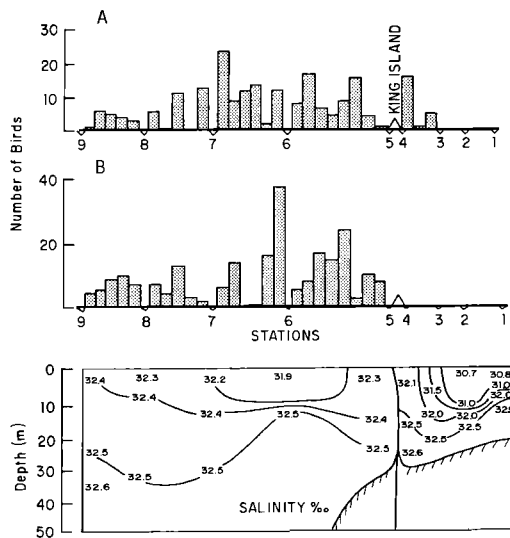


FIGURE 4. Distribution of Parakeet Auklets (A) and Least Auklets (B) relative to a salinity profile for the King Island transect.

of the 15 transects, and random on 1 of the 15 transects (K-S comparison to Poisson, $P = 0.05$). The Parakeet Auklets were aggregated on 6 of the 15 transects and random for the other 9.

DISCUSSION

Gelatinous zooplankton are an important part of the Parakeet Auklet's diet, and probably are a preferred food. The primary reason for feeding on jellyfish may be the high nutritive value of associated crustaceans and fish larvae; hyperiid amphipods and fish larvae are easily observed on and around jellyfish in the surface waters. All hyperiid amphipods are tied to jellyfish at some stage of their life cycle; some are specialized for a parasitic existence on jellyfish (Laval 1980). Fish larvae seek out the tentacles for protection

(Dahl 1961), and association with jellyfish may be essential for the larval stages of many gadid species (Walford 1958). Many ctenophores and salps also often have hyperiid associates (Madin and Harbison 1977, Harbison et al. 1977).

Most seabirds in the Bering Sea feed on jellyfish (Harrison 1984). Gadid larvae together with small amounts of jellyfish are found in the guts of many alcids including Thick-billed Murres (*Uria lomvia*) and Common Murres (*U. aalge*). In the Bering Sea only Northern Fulmars (*Fulmarus glacialis*) approach Parakeet Auklets in the frequency of jellyfish in their diet. Most of these species have eaten very little gelatinous tissue and probably are in pursuit of associated zooplankton. The quantities of gelatinous tissue in Parakeet Auklets, however, suggest that they are taking more than would be ingested incidentally while capturing associates. They also fed on a variety of ctenophore, which apparently had few associates, if any.

The Parakeet Auklet's bill is highly specialized and unusual in that the lower mandible is a narrow hook that curves up and around the blunt upper mandible. How Parakeet Auklets use this tool in capturing prey has long been disputed (Bent 1946). It has been suggested that the beak is a tool for picking crustaceans out of crevices, or prying open bivalves; given the pelagic distribution of Parakeet Auklets at sea, these explanations are unlikely.

In a study of bill structure in the Alcidae, Bédard (1969b) used bill width and tongue characteristics to place the Parakeet Auklet in an intermediate position between the plankton eating species and the puffins (which eat both plankton and fish). While this is consistent with the eclectic diet of the species, it does not explain the apparent scooping device for a lower mandible, which I suggest functions in either hooking gelatinous animals or picking zooplankton from medusae. Underwater observations of Parakeet

TABLE 6. FREQUENCY OF OCCURRENCE OF PREY FROM THREE AUKLET SPECIES IN THE SARICHEF STRAIT

	Parakeet (N = 6)		Least (N = 5)		Crested (N = 4)	
	All ¹	Sig ²	All	Sig	All	Sig
Gelatinous zooplankton	83	50	0	0	25	0
Chaetognatha	0	0	20	0	0	0
<i>Limacina</i> (pteropod)	33	0	0	0	0	0
<i>Calanus</i> (copepod)	0	0	80	40	25	0
<i>Parathemisto</i> (hyperiid)	83	50	60	40	50	0
<i>Thysanoessa</i> (euphausiid)	33	0	20	0	100	100
Decapod larvae	0	0	20	0	0	0
<i>Theragra</i> (gadid fish)	17	0	20	0	25	0
<i>Ammodytes</i> (fish)	0	0	20	0	0	0

¹ "All prey" category.

² "Significant prey" category.

TABLE 7. DIETARY OVERLAP BETWEEN AUKLETS COLLECTED IN SARICHEF STRAIT

	"Sig. prey" category		"All prey" category	
	Actual overlap	Mean overlap (sd) ¹	Actual overlap	Mean overlap (sd)
Parakeet vs. Crested	0	0.67 (0.23)	0.65	0.83 (0.08)
Parakeet vs. Least	0.44	0.68 (0.19)	0.42	0.76 (0.10)
Crested vs. Least	0	0.62 (0.21)	0.57	0.73 (0.11)

¹ Mean overlap and standard deviation calculated from random permutations of data; see text.

Auklets feeding on a variety of prey will be required to establish the merits of this peculiar bill.

A Parakeet Auklet has to eat a large quantity of jellyfish to derive the same net energy as from a meal of crustaceans (Table 8). Water content varies between 95–99% for both jellyfish and ctenophores (Curl 1962). It requires ten times the amount of gelatinous tissue to obtain the same amount of organic material as found in a hyperiid amphipod or euphausiid.

The frequency occurrence of prey in the Parakeet Auklet's diet appears to depend on the local relative abundance of food. In the St. Matthew Island area, where there were patches of euphausiids and other high quality prey, the Parakeet Auklet fed on a wide variety of animals; in the Chirikov Basin my small sample suggests a dependence on gelatinous animals.

The observations of prey taken by the three auklet species feeding together indicate the auklets are sensitive to fine-scale (10s to 100s of meters) patterns in prey distributions. Crested Auklets fed on euphausiids, whereas Parakeet Auklets from the same flock fed on jellyfish and *Parathemisto*. Parakeet Auklets may be feeding in a microhabitat surrounding and including jellyfish; they may not encounter many of the animals that dominate the diets of the *Aethia* species. The divergent diets of the auklets are probably related to their response to small-scale heterogeneity in their habitat.

Bédard (1969a) observed differences between

the Parakeet Auklet and the *Aethia* species that appeared to be consequences of different foraging strategies. The *Aethia* species switched between zooplankton prey as they became sequentially abundant through the season; Parakeet Auklets maintained a constant diet. Least and Crested Auklets lost more weight during breeding (10–12%) than Parakeet Auklets (5.5%). Parakeet Auklets consistently had larger reserves of subcutaneous fat than the *Aethia* species; Crested Auklets, in particular, appear to experience extreme energetic stress during the breeding season. There is also more annual variation in breeding success in the *Aethia* species than in the Parakeet Auklet. Parakeet Auklets would appear to have a dependable supply of food.

The Parakeet Auklet may represent a species adapted for the capture of a widely dispersed prey, whereas the *Aethia* auklets appear to be adapted for tracking spatially and temporally patchy prey.

Parakeet Auklets occupy areas of the eastern Bering Sea where Least and Crested Auklets are absent (Bédard 1969a). The *Aethia* species are restricted to areas with high seasonal productivity. The Parakeet Auklet appears to find adequate conditions in less productive waters.

While the three auklets are seen feeding in the same marine habitats, they appear to be adapted for different prey distributions. The Parakeet Auklet is unusual among the Alcidae in feeding on a dispersed prey; it may be adapted for the use of a midwater microhabitat. The Parakeet Auklet's persistent use of jellyfish and associated animals may be the explanation for the many differences between it and the *Aethia* species.

TABLE 8. PREY CONTENT FOR SELECTED GELATINOUS ANIMALS AND CRUSTACEANS¹

	% water	% organic content	% ash	Energy (cal/ash free dry wt)
<i>Cyanea</i> (jellyfish)	95.4	1.7	2.9	5.5
<i>Beroe</i> (ctenophore)	95.3	1.4	3.3	4.0
<i>Hyperoche</i> (hyperiid)	80.0	16.7	3.3	6.4
<i>Thysanoessa</i> (euphausiid)	73.0	23.3	3.7	6.4

¹ Derived from Percy and Fife (1981) and Curl (1962).

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