FOOD HABITS AND NICHE OVERLAP OF SEABIRDS WINTERING ON MONTEREY BAY, CALIFORNIA

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Abstract.—A study of nonbreeding populations of seabirds was undertaken in Monterey Bay, California, to determine degree of predation on prey species such as fish and cephalopods. Seabirds were found to exploit many of the same prey species. Many seabird species relied heavily on the abundance of the northern anchovy (*Engraulis mordax*) and the market squid (*Loligo opalescens*). Both of these prey species were available to and exploited by their avian predators during all months of the study (September through April).

The high measures of food niche overlap between some avian predator species could lead to severe competition were it not for temporal and spatial segregation of some of the avian predator populations reducing chances for competition. Varying feeding techniques allowed many predator species to exploit different segments of the same prey population. Multispecific feeding assemblages of birds form for mutual benefit in exploiting schools of prey species.

Two alcids, the Common Murre and the Rhinoceros Auklet, occupied similar habitats and exploited their food resources in the same way, utilizing five of the same prey species. Niche overlap is reduced between these predator species by extensive predation on the market squid by the Rhinoceros Auklet.—*Moss Landing Marine Laboratories, Box 223, Moss Landing, California 95039.* Accepted 25 November 1976. This paper was subsidized by the authors.

Most feeding studies of seabirds have been made on breeding populations when the acquisition of food was of primary importance. In nontropical species, one of the factors governing the timing and location of breeding activities appears to be regulated by availability of abundant food resources (Payne 1962, Moyle 1966, Ashmole 1971, Maher 1974, Wiens and Scott 1975). Many individuals of a population do not breed each year and those that do still spend most of the year in migration and on wintering grounds (Recher 1966). The present study was thus undertaken on the feeding habits of nonbreeding populations under what may be less favorable feeding conditions in waters distant from breeding grounds.

A deep submarine canyon divides Monterey Bay (Fig. 1). North and south of the canyon lie two large neritic areas, and over the canyon deep water of more oceanic nature occurs. Seasonal hydrographic conditions and plankton abundances in the bay are representative of the western coast of the United States north of Point Conception (Bolin and Abbott 1962). The general yearly hydrographic cycle for Monterey Bay can be divided into three overlapping seasons that are governed largely by prevailing winds (see Table 1). The dominant season is the upwelling season from February through September when northeasterly winds prevail. During this season strong upwelling occurs at the upper reaches of the Monterey Submarine Canyon within a few hundred yards from shore at Moss Landing.

In neritic waters and oceanic regions of upwelling seabirds usually fish by plunging or pursuit diving. They exploit populations of small fishes typical of upwelling regions (e.g. *Engraulis* spp. and *Sardinops* spp.) that feed mainly on phytoplankton and small zooplankton (Ashmole 1971). Monterey Bay includes most of these features.

More than 40 species of seabirds have been identified in the area. Species that feed by plunging or pursuit diving that we studied include shearwaters, loons, alcids, gulls, and cormorants. Only two species are residents, the Western Gull (*Larus occidentalis*) and Brandt's Cormorant (*Phalacrocorax penicillatus*). The remaining

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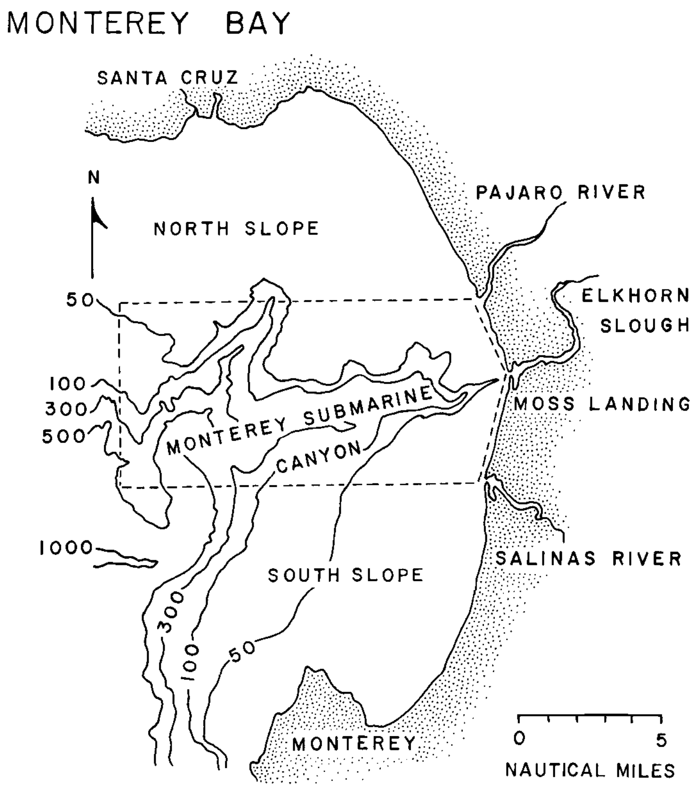

Fig. 1. Monterey Bay, California, with depth contours in fathoms. The 100-fathom contour divides Monterey Bay into 3 areas of almost equal size: (1) north slope; (2) Monterey Submarine Canyon, and (3) south slope. The dashed line indicates the course of transect.

species are transients whose stay on Monterey Bay varies from a few weeks to 10 months.

Whenever assemblages of birds have been studied, the individual species have been found to overlap in some aspects of the environment they utilize (Fisher and Lockley 1954, Recher 1966, Ashmole 1968, Sealey 1973, Wiens and Scott 1975). As food is one of the most important aspects of the niche, the degree of specialization in selecting prey by a predator species and the degree of prey overlap between predator species are important elements of community structure.

Materials and Methods

Stomach contents of 17 species in 7 families were examined to identify prey species eaten. These stomachs were obtained from birds collected on Monterey Bay or found dead on beaches near Moss Landing Marine Laboratories. Cruises on R/V 'Orca' and R/V 'Artemia' for the purposes of collection and observation were made weekly, weather permitting, from September 1974 to April 1975. Birds were collected on the bay along the transect lines or within the waters enclosed by the transects shown in Fig. 1. The contents of the proventriculus and ventriculus were sorted into their taxonomic categories and identified to family, genus, and species. Cephalopod beaks were stored in 40% isopropyl alcohol, and fish otoliths were washed in water and stored dry as recommended by Fitch and Brownell (1968). All other contents (partially digested items) were fixed in 10% formaldehyde and then transferred to 40% isopropyl alcohol.

Many stomachs were found to be nearly empty but retained cephalopod beaks and/or fish otoliths or

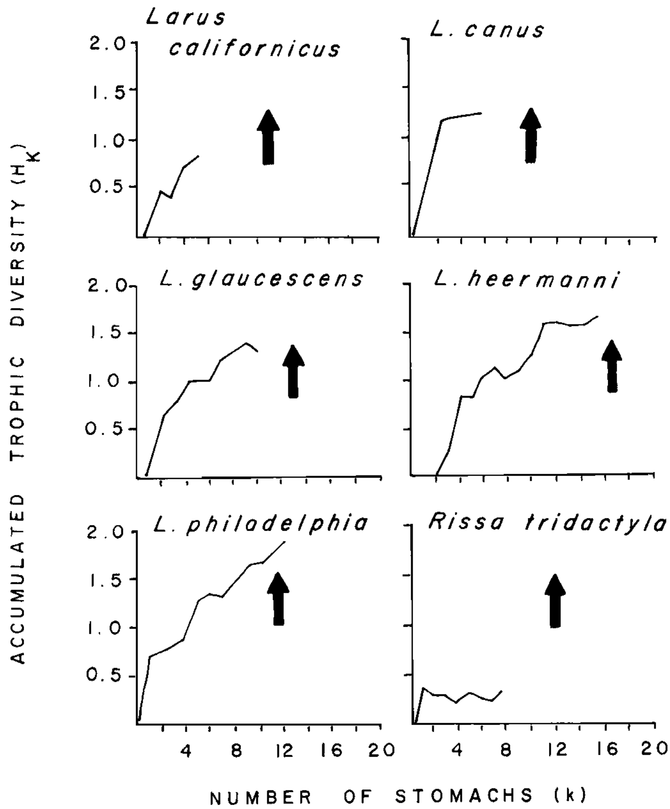

Fig. 2A. Plots of accumulated trophic diversity (H_k) versus counts of individual stomachs (k). Arrows indicate stability of collected samples (→) or that samples collected are not good estimates of the total accumulated trophic diversity (↑) of prey items eaten by the particular species.

crustacean parts. Accurate means to assess volume based on these structures within the intact prey species have not been developed. Data are therefore presented in numerical fashion even though this method probably overemphasizes the importance of otoliths and cephalopod beaks and de-emphasizes the amount of crustaceans and other invertebrates. This is justified because invertebrates other than cephalopods were relatively insignificant prey items of the birds examined in this study. Many stomachs also contained plastic particles (Baltz and Morejohn 1977).

Identifications of cephalopods were accomplished by comparisons with beaks in our reference collection and the pictorial guide provided by Iverson and Pinkas (1971). Fish otoliths were identified by John E. Fitch. The minimum number of fish represented in a stomach sample by otoliths was taken to be the greatest number of right or left sagittae. When the sagittae were too badly deteriorated to determine right or left, the total number was divided by two to estimate the minimum number of fish represented. The minimum number of individuals of species represented by cephalopod beaks was taken to be the greatest number of upper or lower beak halves.

The degree of prey diversity or specialization as measured by information theory is an expression of niche breadth (Levins 1968). Hurtubia (1973) applied Pielou's (1966a, b) method to the study of trophic (prey) diversity of sympatric predators. Diversity indices were computed according to the Brillouin formula:

$$H = (1/N)(\ln N! - \sum_{i=1}^{s} \ln N_i!) \quad (1)$$

where N_i is the number of individuals of the i^{th} species (Pielou 1966b). Following Hurtubia, the accumulated trophic diversity (H_k) approaches stability at some point t for a predator population (Fig. 2) as the contents of individual stomachs (k) are pooled. Values of H_k for $k \geq t$ can be used to estimate the average trophic diversity (H'_{pop}) of a predator population with its variance and standard error. Where plots of

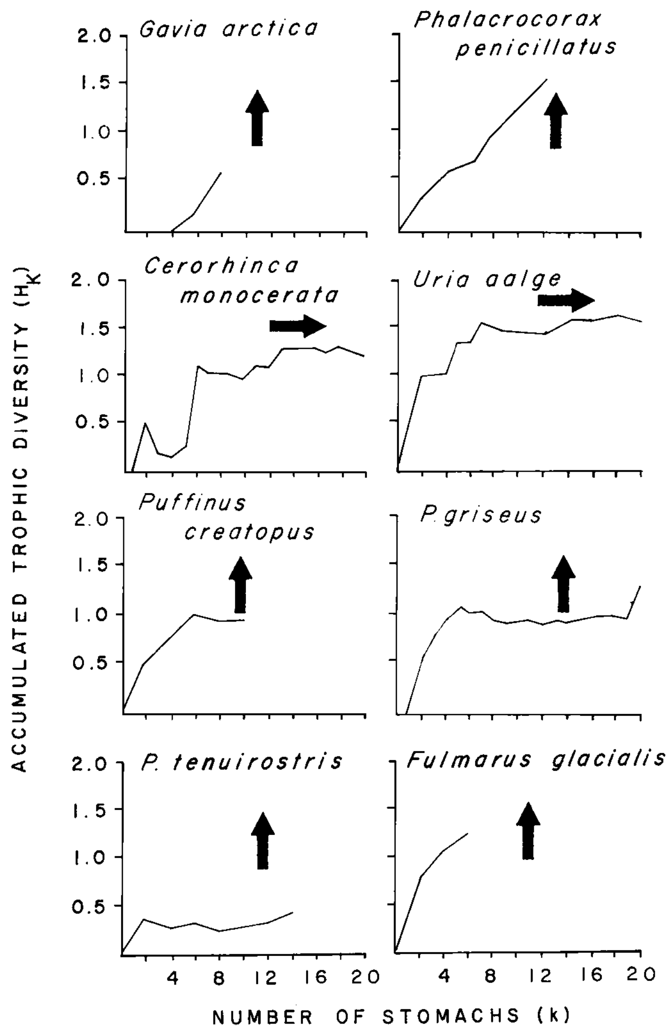

Fig. 2B. See legend for Fig. 2A on facing page.

accumulated trophic diversity (H_k) do not reach a stable level, the total accumulated trophic diversity (H_z) of all available samples is a first estimate for the predator population.

Morisita's (1959) index of overlap between the food niches of sympatric predators is a measure of the similarity between their diets. Morisita's index can be simplified to:

$$\hat{C}_\lambda = \frac{2 \sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2} \qquad (2)$$

where the data are expressed as the numerical proportions x_i and y_i of prey individuals in the respective samples composed of i prey species in predators x and y (Horn 1966). Values vary from 0 when the samples are completely distinct to 1 when they are identical.

The treatment of unidentified species of fishes and cephalopods presents a problem when calculating measures of food niche overlap. The unidentified species may be: (1) excluded from the calculations, (2) considered to be species that are common, or (3) considered to be species uncommon in the diets of the predators being compared. Overlap values for all three alternative situations were calculated. The maximum differences between values of Morisita's index calculated with unidentified species excluded

TABLE 1

OCCURRENCE BY SEASON AND HABITAT OF SELECTED SEABIRDS ON MONTEREY BAY

	Zone[1]	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Divers													
Gavia arctica	iO	—	—	?	—							—	—
Cerorhinca monocerata	iO	—	—	—	—						—	—	—
Uria aalge	iO	—	—	—	—	—			—	—	—	—	—
Ptychoramphus aleutica	oP	—					—	—				—	—
Synthliboramphus antiquum	oP											—	—
Procellariiforms													
Puffinus creatopus	OP	—						—	—	—	—	—	?
Puffinus griseus	Op	—			—		—	—	—	—	—	—	—
Puffinus tenuirostris	Op	—	—		—					—	—	—	—
Fulmarus glacialis	OP		—	—	—	—				—	—	—	—
Diomedea nigripes	oP			—	—	—	—	—	—				
Gulls													
Larus californicus	IO	—	—	—	—					—	—	—	—
Larus canus	IO	?	—					—			—	—	?
Larus glaucescens	iO	—	—	—	?	—		—				—	—
Larus heermanni	IO	—	—				—	—	—	—	—	—	—
Larus philadelphia	Io	—	—	—	—						—	—	—
Rissa tridactyla	OP	—	—	—	—								
Sterocorarius pomarinus	IO				—	—		—		—	—	—	
Hydrographic cycle[2]													
Oceanic season										—	(CALM)	—	
Davidson season		—	(SE) —									— (SE)	—
Upwelling season			—	—	—	—	(NW)	—	—	—			

[1] Habitat indicated by zone: inshore (I), offshore (O), and pelagic (P). Lower case indicates secondary zone of occurrence.
[2] For comparison with avian occurrence, the generalized hydrographic cycle proposed by Bolin and Abbott (1962) is included with direction of prevailing wind.

and the two alternative values, ranged from 0 to 0.05 with a mean difference of 0.0140 and a standard deviation of 0.01. Differences between alternative values of Morisita's index were not great; therefore only overlap values with unidentified fishes and cephalopods excluded were used.

RESULTS

As compiled from field observations, collections and records of beach-cast specimens (Table 1), migratory species are absent from the Monterey Bay area during their breeding seasons, except for a few juvenile and vagrant individuals. Species that breed nearby are generally present in the bay for a greater portion of the year than are species that breed farther away.

The usual area of occurrence of each species on Monterey Bay is indicated by zone (Table 1), following classification of marine zones proposed by Wynne-Edwards (1930). The inshore zone is that area within sight of shore. Cormorants, gulls, and terns are usually considered to be inshore species. The offshore zone is those waters over the continental shelf out of sight of shore. The Rhinoceros Auklet (*Cerorhinca monocerata*) and Common Murre (*Uria aalge*) are the most common members of the offshore contingent in Monterey Bay during winter months. The pelagic zone is those waters beyond the continental shelf, which is arbitrarily delimited from the offshore zone by the 100-fathom contour. Inhabitants of the pelagic zone include the Black Footed Albatross (*Diomedea nigripes*), shearwaters of several species, and the Black-legged Kittiwake (*Rissa tridactyla*).

This classification of zones is simple, and many species occur in more than one zone. Marine birds are distributed over the surface in a two-dimensional plane, but their prey are distributed in three dimensions. Most seabirds descend below the

TABLE 2

SUMMARY OF STOMACH CONTENTS OF *GAVIA ARCTICA* AND *PHALACROCORAX PENICILLATUS*

	G. arctica (N = 4)			*P. penicillatus* (N = 6)		
Prey items	A[1]	B[2]	C[3]	A[1]	B[2]	C[3]
Fishes						
Engraulis mordax	1	4.6	25.0	15	23.4	16.7
Icichthys lockingtoni	3	13.6	25.0			
Citharichthys sordidus				8	12.5	33.3
Citharichthys stigmaeus				1	1.6	16.7
Symphurus atricauda				1	1.6	16.7
Porichthys notatus			2	2	3.1	33.3
Medialuna californiensis				1	1.6	16.7
Sebastes spp.				16	25.0	33.3
Unidentified spp.	2	9.1	25.0			
Cephalopods						
Loligo opalescens	16	72.7	50.0	9	14.1	33.3
Other invertebrates						
Cymothoidae (?*Aegathoa*)				1	1.6	16.7
Lironeca vulgaris				10	15.6	33.3
Prey species		4			10	

[1] Total number of items in each category (A).
[2] Percentage of total individuals by number (B).
[3] Frequency of occurrence of various prey and nonprey items (C).

surface to feed in a third dimension at some depth in the water column, but the potential and normal feeding depths of most species are unknown. Ashmole (1971) described the feeding methods used by marine birds to capture prey at various depths in the water column; his terminology is followed here.

SPECIES ACCOUNTS

Gavia arctica.—Arctic loons were usually encountered in Monterey Bay in the offshore zone between 1 and 5 miles from land. They occasionally come closer to shore, but Common Loons (*Gavia immer*) inhabit the inshore zone which includes Moss Landing Harbor and Elkhorn Slough, and may exclude their smaller relative. Arctic Loons were usually found as solitary individuals or in pairs and occurred only rarely in multispecific feeding assemblages. Common Loons arrived in the study area in October, but Arctic Loons were not positively identified until mid-November when they were the most abundant loon species on Monterey Bay. Arctic Loons remained on Monterey Bay into April 1975 (Table 1).

Of five Arctic Loons examined during this study, four had food in their stomachs (Table 2). The stomach of the fifth specimen contained only 15 pebbles. All the specimens had pebbles in their gizzards, with the mean number of pebbles per individual being 15.2.

Phalacrocorax penicillatus.—Brandt's Cormorants are year-round residents in the Monterey Bay area. They inhabit the inshore zone, especially in association with kelp beds, and the offshore zone to a lesser extent. They occurred as solitary individuals, in dense flocks, and all intermediate groupings. Brandt's Cormorants occasionally join multispecific feeding assemblages, but they were not numerous in these assemblages except near kelp beds.

The six specimens reported here were collected in the offshore zone and were preying primarily on fishes, with juvenile rockfishes (*Sebastes* spp.) and northern

TABLE 3
SUMMARY OF STOMACH CONTENTS OF *PUFFINUS CREATOPUS* AND *PUFFINUS GRISEUS*

	P. creatopus (N = 5)			*P. griseus* (N = 21)		
Prey items	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]
Fishes						
Engraulis mordax	17	8.9	60.0	55	8.6	61.9
Merluccius productus				2	0.3	4.8
Porichthys notatus				1	0.2	4.8
Clupea harengus				2	0.3	9.5
Sebastes spp.				56	8.8	9.5
Unidentified spp.	3	1.6	60.0			
Cephalopods						
Loligo opalescens	136	71.2	60.0	234	36.6	42.9
Onychoteuthis borealijaponicus	24	12.6	40.0			
Unidentified spp. A	11	5.8	80.0	55	8.6	71.4
B				1	0.2	4.8
Other Invertebrates						
Thysanoessa spinifera				232	36.3	4.8
Unidentified Crustaceans				1	0.2	4.8
Prey species		5			10	

[1] For explanation see Table 2.

anchovy comprising 48.4% of their prey numerically (Table 2). All fishes combined comprised 68.8%. The market squid was the third most abundant prey item (14.1%) if gill lice are excluded from the list of prey items (Table 2). The gill lice, *Lironeca vulgaris*, were probably acquired indirectly from parasitized fishes; they are parasitic on rockfishes (*Sebastes* spp.), flounders, and other fish genera, and range from Washington to Baja California (Schultz 1969).

Shearwaters, *Puffinus* spp.—Several *Puffinus* species occur in the Monterey Bay area at various times of the year (Table 1). Only three are common: the Sooty Shearwater (*P. griseus*), the Short-tailed (*P. tenuirostris*), and the Pink-footed (*P. creatopus*). Other seasonal visitors are the New Zealand Shearwater (*P. bulleri*), the Manx (*P. puffinus*), and the Flesh-footed (*P. carneipes*).

Shearwaters are gregarious. During periods of slack wind, usually in the mornings, dense flocks settled in long windrows and were frequently encountered between 3 and 5 km from shore. Typically in Monterey Bay, northwest winds begin to blow daily in the afternoons during most of the year (Table 1). As the wind picked up, the flocks dispersed into long lines of loosely associated individuals that meandered over the surface in a northerly direction in the course of the spring migration. In August and September Sooty Shearwaters migrate south along the California coast (Palmer 1962). Shearwater flocks were composed primarily of Sooty Shearwaters most of the year but other species occurred with them during other months. The Short-tailed Shearwater was the most abundant species during January and February.

Shearwaters feed primarily by pursuit plunging and to a lesser extent by surface seizing and pursuit diving (Ashmole 1971).

Puffinus creatopus.—Pink-footed Shearwaters were less commonly encountered on Monterey Bay than either Sooty or Short-tailed Shearwaters. Analysis of a small sample (N = 5) indicates that squid constituted 83.8% of the Pink-footed Shearwater's diet (Table 3). The market squid (*Loligo opalescens*) was the single most important prey species. The occurrence of *Onychoteuthis borealijaponicus*, an oceanic

TABLE 4
SUMMARY OF STOMACH CONTENTS OF *PUFFINUS TENUIROSTRIS* AND *FULMARUS GLACIALIS*

	P. tenuirostris (N = 6)			*F. glacialis* (N = 3)		
Prey items	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]
Fishes						
Engraulis mordax	3	3.6	50.0			
Sebastes spp.				1	3.7	33.3
Unidentified spp.	1	1.2	16.7	1	3.7	33.3
Cephalopods						
Loligo opalescens	77	91.7	66.7	8	29.6	66.7
Onychoteuthis borealijaponicus	1	1.2	16.7	4	14.8	33.3
Gonatus spp.				6	22.2	33.3
Octopus spp.				1	3.7	33.3
Octopoteuthidae				5	18.5	33.3
Unidentified spp.	2	2.4	33.3	1	3.7	33.3
Prey species		5			8	
Pebbles	24		28.6	16		66.7

[1] For explanation see Table 2.

squid, supports the observation that Pink-footed Shearwaters tend to be distributed farther offshore than Sooty Shearwaters, as *O. borealijaponicus* was lacking in the Sooty Shearwater stomachs analyzed.

Puffinus griseus.—Sooty Shearwaters are the most common shearwaters in the Monterey Bay area. Some immature birds remain in the northern hemisphere for several years before returning to the southern hemisphere to breed (Serventy et al. 1971). Sooty Shearwaters generally inhabit the pelagic zone, but they are common in the offshore zone, and on occasion they are seen inshore. Their prey consisted of cephalopods, fishes, and crustaceans (Table 3).

Puffinus tenuirostris.—During monthly shipboard observations over the past 7 years the Short-tailed Shearwater was found to be the second most abundant shearwater on Monterey Bay. In the field Sooty and Short-tailed Shearwaters are very difficult to distinguish. Both species share the same general distribution, but differ in the times of peak abundance on Monterey Bay. Short-tailed Shearwaters reach their peak abundance on Monterey Bay in January and February on the southward move or segment of their clockwise North Pacific migration (Serventy et al. 1971). Sooty Shearwaters reach their first peak in late April or May as the population moves northward, and the second peak occurs in late August or September as the birds move southward (Palmer 1962), but in Monterey Bay the southward movement was difficult to discern. Immature Short-tailed Shearwaters may spend more than 2 years in the northern hemisphere before returning to the southern hemisphere to breed (Serventy et al. 1971). A small sample (N = 6) indicates that Short-tailed Shearwaters rely heavily on the market squid (Table 4).

Fulmarus glacialis.—The Northern Fulmar occurred sporadically in small numbers on Monterey Bay during this study but every 3 to 4 years they are common off coastal California. They were most frequently encountered in the pelagic zone but were occasionally found offshore and inshore. The three specimens examined contained 92.6% cephalopods and 7.4% fishes. All other food items were cephalopods belonging to a minimum of five genera (Table 4). Fulmars were not seen feeding during this study but Ashmole (1971) indicated that fulmars feed by surface seizing, surface filtering, and scavenging.

TABLE 5

SUMMARY OF STOMACH CONTENTS OF *LARUS CALIFORNICUS*, *LARUS CANUS*, AND *LARUS GLAUCESCENS*

Prey items	*L. californicus* (N = 5)			*L. canus* (N = 3)			*L. glaucescens* (N = 8)		
	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]
Fishes									
Engraulis mordax	3	16.7	40.0	4	26.7	100.0	3	15.0	12.5
Phanerodon furcatus				1	6.7	33.0			
Zalembius rosaceus							1	5.0	12.5
Unidentified sp.							1	5.0	12.5
Cephalopods									
Loligo opalescens	9	50.0	60.0	4	26.7	33.3	11	55.0	37.5
Onychoteuthis borealijaponicus	5	27.8	20.0	4	26.7	33.3	1	5.0	12.5
Unidentified sp.				1	6.7	33.3	1	5.0	12.5
Other invertebrates									
Orchomere obtusa	1	5.6	20.0						
Blepharipoda occidentalis							1	5.0	12.5
Unidentified crustacean				1	6.7	33.3	1	5.0	12.5
Prey species		4			6			8	
Pebbles	137		100.0				10		50.0

[1] For explanation see Table 2.

Diomedea nigripes.—One Black-footed Albatross collected on Monterey Bay contained cephalopod beak fragments, otoliths, and crustacean parts. The beak fragments represented a minimum of one oceanic squid, *O. borealijaponicus*, the otoliths represented a minimum of five Pacific hake, and the crustacean parts were unidentifiable. Albatrosses feed primarily by surface seizing and scavenging, and pursuit diving is of minor importance (Ashmole 1971). Black-footed Albatrosses have been recorded in both the offshore and pelagic zones on Monterey Bay. They are normally seen singly, but they are gregarious and often enter into multispecific feeding assemblages.

Larus occidentalis.—The Western Gull is the only resident gull on Monterey Bay. Together with other large and medium-sized gulls, Western Gulls have learned to follow fishing vessels to pick up items thrown overboard or lost from nets. As they feed largely by scavenging in Monterey Bay they were not sampled.

Larus californicus.—California Gulls occur on Monterey Bay from September through April (Table 1). They are opportunistic feeders and are found in all three zones. The northern anchovy (*E. mordax*) and the market squid (*L. opalescens*) were found in 2 and 3 stomachs respectively, while 2 of 7 specimens contained no food (Table 5). Pebbles were found in the gizzards of all 5 of the California gulls examined and the mean number per bird was 27.4.

Larus canus.—Mew Gulls are transient visitors on Monterey Bay. They probably occur from October through February, but conclusive observations are lacking for December and January (Table 1). Three of four specimens examined contained fish and cephalopods (Table 5). One specimen contained no food.

Larus glaucescens.—Immature Glaucous-winged Gulls were common but not abundant on Monterey Bay, and adults were seldom seen. They probably occur from November through May, but conclusive observations are lacking for April (Table 1). They were distributed over all three zones and frequently were seen in feeding assemblages. One of 11 specimens examined contained no food, and 2 contained only unidentifiable flesh. The market squid and the northern anchovy appeared to be

TABLE 6

SUMMARY OF STOMACH CONTENTS OF *LARUS HEERMANNI*, *LARUS PHILADELPHIA*, AND *RISSA TRIDACTYLA*

	L. heermanni (N = 15)			*L. philadelphia* (N = 12)			*R. tridactyla* (N = 8)		
Prey items	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]
Fishes									
Engraulis mordax	12	27.9	46.7	7	1.7	16.7	2	11.8	25.0
Citharichthys sordidus	7	16.3	26.7						
Porichthys notatus	1	2.3	6.7	1	0.2	8.3			
Brosmophycis marginata				1	0.2	8.3			
Chilara taylori				1	0.2	8.3			
Lampanyctus ritteri							1	5.9	12.5
Sebastes spp.	5	11.6	20.0	16	3.8	33.3			
Unidentified spp.	2	4.7	13.3	3	0.7	25.0			
Cephalopods									
Loligo opalescens	11	25.6	13.3				14	82.4	87.5
Gonatus sp.	1	2.3	6.7						
Unidentified spp.	2	4.7	13.3						
Other Invertebrates									
Perineries monterea or *Neanthes brandti*	2	4.7	6.7						
Nereid spp.				40	9.5	8.3			
Hyale sp.				5	1.2	8.3			
Unidentified amphipods				5	1.2	8.3			
Crab megalops				62	16.9	50.0			
Idothea resecata				3	0.7	8.3			
Idothea fewkesi				1	0.2	8.3			
Euphausia sp.				11	3.1	16.7			
Unidentified euphausiids				2	0.5	8.3			
Pasiphaea pacifica				6	1.4	8.3			
Thysanoessa spinifera				30	7.1	8.3			
Unidentified insects				4	1.0	33.3			
Maggots				13	3.1	16.7			
Pupae				200	47.6	8.3			
Prey species		9			18			3	

[1] For explanation see Table 2.

important prey species (Table 5). Ten pebbles were found in the gizzards of four of the specimens.

Larus heermanni.—Heerman's Gulls occur on Monterey Bay from mid-June through February. They are distributed inshore and offshore. Heerman's Gulls feed by dipping, surface seizing, scavenging, plunging, and aerial pursuit (Ashmole 1971). Fishes and squids were the main prey, with the northern anchovy and market squid being the two most important species (Table 6). Polychaete jaws representing two individuals of either *Perinereis monterea* or *Neanthes brandti* were the only evidence of predation on noncephalopod invertebrates. Three of 18 specimens examined contained no food. Gizzards of 13.3% of the birds examined contained 27 pebbles in all.

Larus philadelphia.—Bonaparte's Gulls occur on Monterey Bay from November through April (Table 1). They are distributed offshore, inshore, and in the sloughs and rivers around Monterey Bay. They feed by dipping, surface seizing, and plunging (Ashmole 1971). As they are small, they are not able to take large prey, and this is evident in the summary of stomach contents (Table 6). The 12 specimens examined had preyed largely on invertebrates (93.1%) with fishes making up a small portion (6.9%) of the diet. Six pebbles having a frequency of occurrence of 16.7% were found in the birds examined.

Bonaparte's Gulls were noted feeding in a variety of habitats including brackish

TABLE 7

SUMMARY OF STOMACH CONTENTS OF *CERORHINCA MONOCERATA* AND *URIA AALGE*

	C. monocerata (N = 26)			*U. aalge* (N = 24)		
Prey items	A[1]	B[1]	C[1]	A[1]	B[1]	C[1]
Fishes						
Engraulis mordax	32	9.0	38.5	27	32.5	54.2
Merluccius productus				3	3.6	8.3
Citharichthys spp. larvae	23		11.5			
Citharichthys sordidus				1	1.2	4.2
Sebastes spp. post-larvae	28	7.9	11.5	25	30.1	33.3
Sebastes spp. larvae	3	0.9	3.9			
Medialuna californiensis	1	0.3	3.9			
Peprilus simmillimus	1	0.3	3.9	3	3.6	4.2
Icichthys lockingtoni	3	0.9	11.5			
Clupea harengus	1	0.3	3.9	3	3.6	12.5
Microstomus pacificus				1	1.2	4.2
Trachurus symmetricus				1	1.2	4.2
Unidentified spp.	1	0.3	3.9	2	2.4	4.2
Cephalopods						
Loligo opalescens	250	70.4	84.6	16	19.3	33.3
Unidentified spp. A	10	2.8	7.7	1	1.2	4.2
B	2	0.6	3.9			
Prey species		12			11	

[1] For explanation see Table 2.

water sloughs. Two crustacean genera, *Hyale* and *Idothea,* in the list of prey items are normally found on algae. On several occasions large flocks were seen feeding along lines trailing to seaward from the Moss Landing Harbor jetties. The lines were formed during receding tides by the interface of turbid waters from Moss Landing Harbor and Elkhorn Slough with the relatively clear waters of Monterey Bay. The gulls were probably taking advantage of prey items concentrated along the interface of the dissimilar waters.

Rissa tridactyla.—Black-legged Kittiwakes occurred on Monterey Bay from January through April (Table 1). They were usually observed in the pelagic zone but were seen in the offshore and inshore zones occasionally. They feed by dipping, surface seizing, and plunging (Ashmole 1971). One of nine specimens contained no food (Table 6).

Stercorarius pomarinus.—Three Pomarine Jaegers were collected during September and October 1974. While jaegers were not numerous on Monterey Bay, Pomarine Jaegers were the most common species. They are distributed in all zones. Their pirating behavior is well known (Ashmole 1971); they were not seen to catch their own food during this study. One of the three specimens examined contained otoliths representing one juvenile rockfish (*Sebastes* sp.), another contained two northern anchovies, and the third contained one northern anchovy and one Pacific butterfish (*Peprilus simmillimus*).

Cerorhinca monocerata.—Rhinoceros Auklets occur on Monterey Bay from October through April (Table 1). They are generally distributed offshore but are occasionally observed inshore, and they feed by pursuit diving (Ashmole 1971). All 26 specimens examined contained food items (Table 7). One pebble was found in the gizzard of one bird.

Uria aalge.—The Common Murre occurs on Monterey Bay in all months of the year, but it is abundant only from August through May (Table 1). The nearest murre

TABLE 8

RANGE AND MEAN VALUES OF TROPHIC DIVERSITY (H) IN INDIVIDUAL STOMACHS AND TOTAL ACCUMULATED DIVERSITY[1] (H_z) FOR SELECTED SEABIRDS

	Individual trophic diversity		Total accumulated trophic diversity
	Range	Mean (H)	(H_z)
Gavia arctica	0–0.4605	0.1151	0.6961
Phalacrocorax penicillatus	0–0.7164	0.3762	1.6084
Puffinus creatopus	0.2986–0.5991	0.4550	0.9039
Puffinus griseus	0–1.0079	0.4135	1.4103
Puffinus tenuirostris	0–0.4069	0.1703	0.3849
Fulmarus glacialis	0.2986–0.8525	0.5421	1.3585
Larus californicus	0–0.5991	0.1198	0.9452
Larus canus	0–1.1925	0.3975	1.2243
Larus glaucescens	0–0.3662	0.0765	1.2422
Larus heermanni	0–0.7500	0.1748	1.5965
Larus philadelphia	0–1.1173	0.3404	1.7837
Rissa tridactyla	0–0.3466	0.0867	0.4483
Cerorhinca monocerata	0–1.1103	0.2376	1.0675
Uria aalge	0–0.7059	0.2157	1.5372

[1] As plots of H_k versus k did not reach a stable level except for *C. monocerata* and *U. aalge* in Figure 3, the total accumulated diversity values (H_z) do not adequately represent the food niche breadth of these species on Monterey Bay.

rookery is on the Farallon Islands, less than 160 km from Monterey Bay. They are generally distributed offshore but occasionally are seen inshore. Common Murres feed by pursuit diving (Ashmole 1971). Of 28 specimens examined 4 contained no food (Table 7).

Ptychoramphus aleutica.—Cassin's Auklets were normally encountered only in the pelagic zone and rarely came closer than 13 km west of Moss Landing. They are probably present along the outer edge of Monterey Bay during most of the year, but regular observations in that vicinity were prevented by weather conditions and the limitations of research vessels. One specimen collected in January 1975 contained euphausiid parts. The other specimen collected in November 1974 contained otoliths representing a minimum of three medusafish, four flatfish (possibly *Citharichthys*), and an unidentified crustacean.

NICHE BREADTH AND OVERLAP

Fourteen of the more abundant seabird species that winter on Monterey Bay were found to exploit many of the same prey populations (see Tables 2 through 7). Northern anchovy, market squid, juvenile rockfishes, and flatfishes were common to the diets of most of the seabirds. Measures of niche breadth and niche overlap were used to analyze the degree of avian specialization to prey eaten and prey overlap within the predator community.

The Common Murre and the Rhinoceros Auklet were the only species for which the plots of accumulated diversity (H_k) definitely reached a stable level (Fig. 2). Therefore, any number of stomachs greater than k = t is sufficient to estimate H'_{pop} for either population. The plots of accumulated diversity (H_k) for the Sooty Shearwater and the Glaucous-winged Gull appear to approach a stable point (t) but more samples are required. The H_z values in Table 8 are probably good first estimates for Sooty Shearwaters and Glaucous-winged Gulls on Monterey Bay. For the remaining predator species the plots of accumulated diversity have not leveled off, and the total accumulated diversities (H_z) presented in Table 8 cannot be considered to be good estimates of food niche breadth for these species on Monterey Bay.

The Common Murre and Rhinoceros Auklet were the only predators sampled sufficiently to characterize fully the range and proportions of prey species in their diets as indicated by plots in Fig. 2. Although the auklets sampled had preyed on 12 species compared to 11 for the murres, over 70% of the auklets' prey consisted of one species: the market squid. The total accumulated diversity values (H_z) are 1.07 for the auklets and 1.54 for the murres. These values suggest that the murre is a more generalized predator than the auklet. H'_{pop} values were calculated from values of H_k for $k \geqslant t$ following Hurtubia (1973). H'_{pop} values indicate that the Common Murres fed on a higher diversity of prey items ($H'_{pop} = 1.92 \pm 0.23 = \overline{X} \pm 1.96\sigma/\sqrt{n}$) than the Rhinoceros Auklets ($H'_{pop} = 1.24 \pm 0.39$). The student's *t*-test (df, 20) indicates that these H'_{pop} values are different at the 0.05 level of significance. Total accumulated trophic diversity values (H_z) are within the 95% confidence intervals of H'_{pop}. Morisita's index of overlap indicates a 0.50 similarity between the diets of Common Murres and Rhinoceros Auklets on Monterey Bay; this moderate value is due in part to the high dominance of market squid in the diet of Rhinoceros Auklet and because only 5 of 11 and 12 prey species respectively are common to the diets of both predators.

Food overlap between the Arctic Loon and the Brandt's Cormorant is low ($\hat{C}_\lambda = 0.29$). That the cormorant is a more generalized predator than the loon is suggested by total accumulated trophic diversity values (H_z) of 1.88 and 0.86, respectively. Measures of food niche overlap between diving species in Table 8 suggest that overlap is highest between the Rhinoceros Auklet and the Arctic Loon ($\hat{C}_\lambda = 0.97$) and between the Common Murre and Brandt's Cormorant ($\hat{C}_\lambda = 0.86$). The Rhinoceros Auklet and Arctic Loon prey heavily on the market squid, while the Common Murre and Brandt's Cormorant have a more generalized diet of fishes and squid.

Values of Morisita's index ($\hat{C}_\lambda$) among procellariiform species range from a low of 0.48 to a high of 0.97 (Table 8). Values of overlap ($\hat{C}_\lambda$) between the fulmar and the three shearwater species are generally lower ($\overline{X} = 0.55$) than values between the shearwaters ($\overline{X} = 0.75$). The apparent high overlap ($\hat{C}_\lambda = 0.97$) between the Pink-footed and Short-tailed Shearwaters is based on small samples (N = 5 and N = 6, respectively), but it is probably closer to the actual value than are the much lower values given in Table 8 for overlap of these species with the Sooty Shearwater. Stomach contents of 21 Sooty Shearwaters were used in these calculations, one of which contained 232 euphausids, *Thysanoessa spinifera*. Numerically these euphausids accounted for 36.3% of the prey taken by the Sooty Shearwater and resulted in a lowered index of overlap. When the Sooty Shearwater containing the *T. spinifera* is excluded from the sample, the recalculated overlap values ($\hat{C}_\lambda$) with the Pink-footed (0.95) and Short-tailed Shearwaters (0.91) are considerably higher. Euphausids are probably common to the diets of all three shearwater species in the Monterey Bay area, but have a very low frequency of occurrence (F.O. = 4.8% in the Sooty Shearwater).

The six species of gulls studied range in size from large to small. Food overlap ($\hat{C}_\lambda$) between the large and medium sized species is moderate to high and ranges from 0.57 to 0.94 (Table 8). Measures of food overlap ($\hat{C}_\lambda$) between the small Bonaparte's Gull and the other gulls is very low and ranges from 0.004 to 0.041.

DISCUSSION

Three ecological groups of seabirds exploit many of the same prey species. Each group exploits its prey by different feeding methods (Ashmole 1971). The divers on

Monterey Bay include species from three orders: loons (Gaviiformes), cormorants (Pelecaniformes), and alcids (Charadriiformes). They pursue their prey by diving from the surface and swimming underwater with their feet or wings. Procellariiform species common on Monterey Bay include the Black-footed Albatross, the Northern Fulmar, three shearwaters, and two species of storm petrels. Albatrosses feed primarily by surface seizing and scavenging. Fulmars feed primarily by surface seizing, and shearwaters feed primarily by pursuit plunging. The many species of gulls form the most diverse group on Monterey Bay; most feed by dipping, surface seizing, and plunging. Species of all three groups frequently fed in multispecific assemblages.

Sealey (1973) described the formation of multispecific feeding assemblages of seabirds (gulls and alcids) off British Columbia and discussed the ecological significance of such assemblages. Other avian species formed multispecific feeding assemblages around birds that served to find the prey items, called "nuclear species," usually Black-legged Kittiwakes. On Monterey Bay, all of the predator species discussed, except Arctic Loons and Fulmars, have been noted in multispecific feeding assemblages. Black-legged Kittiwakes were not abundant during the study and were not observed in the role of "nuclear species." On several occasions, feeding assemblages were formed over schools of prey that were probably driven to the surface by fish predators. On other occasions, feeding assemblages were formed over pods of feeding California sea lions (*Zalophus californianus*) or Pacific striped dolphins (*Lagenorhynchus obliquidens*).

The Arctic Loon preys on pelagic fishes and squid. Unlike the Brandt's Cormorant, it does not exploit bottom fishes. The fishes preyed upon by Brandt's Cormorant are both pelagic and benthic, indicating that it feeds throughout the water column (Table 2). Hubbs et al. (1970) summarized the published accounts of the food of Brandt's Cormorants and presented new data from the San Diego area, listing 35 species of fishes belonging to 31 genera and 18 families. Only two additional fishes, the half-moon and the California tonguefish, were found in the present study. Market squid are also an addition to the list of known prey. No invertebrates were found in the specimens from the San Diego area but Hubbs et al. (1970) cited Schorger's report (*in* Palmer 1962) of one crab and some shrimp in a specimen he examined.

Procellariiforms on Monterey Bay prey on pelagic fishes and squids. Crustaceans are of minor importance. Food niche overlap is very high between shearwaters. It is interesting that the oceanic squid, *O. borealijaponicus,* was exploited by the Black-footed Albatross, the Northern Fulmar, the Pink-Footed and Short-tailed Shearwaters, but not by the Sooty Shearwater. Young (1972) considers *O. borealijaponicus* an epipelagic oceanic species. Sooty Shearwaters are certainly large enough to prey on *O. borealijaponicus,* but their distributions may not overlap.

The recalculated values of food niche overlap between the Sooty, Pink-footed, and Short-tailed Shearwaters are probably closer to the actual values for shearwaters on Monterey Bay as at least Short-tailed Shearwaters are known to feed on euphasids elsewhere. Ogi and Tsujita (1973) examined 29 stomachs of Short-tailed Shearwaters taken in the eastern Bering Sea; they were densely packed with the euphausid *Thysanoessa raschii* and a few specimens of the Pacific sandlance (*Ammodytes hexapterus*). Many workers consider the Pink-footed Shearwater a subspecies of the Flesh-footed Shearwater, which is known to feed on small crustaceans (Palmer 1962).

Gulls are opportunistic feeders, preying on pelagic and benthic fishes and various

TABLE 9

INDICES OF FOOD NICHE OVERLAP: MORISITA'S INDEX BETWEEN SPECIES OF GULLS, PROCELLARIIFORMS, AND DIVERS[1]

	Gulls					
	L. californicus	*L. canus*	*L. glaucescens*	*L. heermanni*	*L. philadelphia*	*R. tridactyla*
L. californicus	1.000	—	—	—	—	—
L. canus	0.8802	1.000	—	—	—	—
L. glaucescens	0.9040	0.7326	1.000	—	—	—
L. heermanni	0.6576	0.6993	0.6985	1.000	—	—
L. philadelphia	0.0089	0.0287	0.0081	0.0407	1.000	—
R. tridactyla	0.8189	0.5658	0.9429	0.5822	0.0041	1.000

	Procellariiforms			
	P. creatopus	*P. griseus*	*P. tenuirostris*	*F. glacialis*
P. creatopus	1.000	—	—	—
P. griseus	0.6644	1.000	—	—
P. tenuirostris	0.9659	0.6196	1.000	—
F. glacialis	0.6320	0.4671	0.5400	1.000

	Divers			
	C. monocerata	*U. aalge*	*P. penicillatus*	*G. arctica*
C. monocerata	1.000	—	—	—
U. aalge	0.5022	1.000	—	—
P. penicillatus	0.3959	0.8569	1.000	—
G. arctica	0.9689	0.3840	0.2943	1.000

[1] Indices vary from near 0, indicative of little overlap, to 1, indicative of complete overlap.

invertebrates (Tables 5 and 6). Birds have learned to follow fishing vessels and pick up many species of fish routinely discarded by the commercial trawlers. As most gulls follow ships, the question of whether or not some species are natural prey must be asked. One white surfperch was taken by a Mew Gull. White surfperch are common in sheltered bays, including Moss Landing Harbor and Elkhorn Slough, and occur from the surface to 23 fathoms (Miller and Lea 1972, Hart 1973). A Glaucous-winged Gull was found to prey on pink surfperch, which range in depth from 5 to 50 fathoms (Miller and Lea 1972) and an anomuran crustacean, *B. occidentalis*, which occurs in the low intertidal and subtidal zones of sandy beaches (Smith and Carlton 1975); both species are probably natural prey of Glaucous-winged Gulls. A broadfin lampfish was taken by a Black-legged Kittiwake. The broadfin lampfish is a bathypelagic species that occurs off California at depths of 350–599 fathoms (Hart 1973); it probably is not natural prey. Three benthic fishes were represented in the diet of the Bonaparte's Gull by single individuals: the plainfin midshipman (*Porichthys notatus*), the spotted cusk-eel (*Chilara taylori*), and the red brotula (*Brosmophycis marginata*). All three species are possibly natural prey items as they are known to occur within 2 fathoms of the surface (Miller and Lea 1972).

Ashmole (1968) showed a general relationship between predator size and maximum prey size for a group of sympatric terns. His data suggest that the average size of prey taken is also a function of predator size, but discrepancies exist. He also found that the smallest tern in the group fed at a lower trophic level than the larger species. A parallel situation appears to exist among the gulls on Monterey Bay, but detailed analysis of the size distribution of prey taken by the larger species is needed. Bonaparte's Gull, the smallest gull on Monterey Bay, feeds largely on invertebrates other than cephalopods. Inspection of Tables 5 and 6 invites speculation that competi-

TABLE 10

MEAN WEIGHTS AND BODY MEASUREMENTS OF SELECTED SEABIRDS[1]

	Weight[2]	Wing length flat (mm)	Culmen length (mm)	Tarsus length (mm)	Bill XS[3] (sq mm)
Gavia arctica	1955.7	286.2	51.9	71.5	31.4
Phalacrocorax penicillatus	2103.3	275.0	69.0	72.7	46.8
Puffinus creatopus	825.8 (N = 4)	326.4	41.6	57.2	41.3
Puffinus griseus	812.6	290.2	42.8	62.5	35.0
Puffinus tenuirostris	417.2	271.0	32.2	50.8	22.9
Fulmarus glacialis	469.7 (N = 3)	292.8	35.9	48.6	67.7
Diomedea nigripes (N = 2)	3080.0	501.0	101.8	98.5	276.0
Larus glaucescens	1198.0	434.8	57.0	72.2	127.3
Larus occidentalis (N = 2)	1137.0	389.0	52.6	68.3	144.5
Larus californicus	682.8 (N = 4)	392.5 (N = 4)	46.3	59.6	79.7 (N = 4)
Larus canus (N = 3)	383.3	346.3	33.1	50.0	36.8
Larus heermanni	492.4	349.6	44.5	59.6	63.1
Larus philadelphia	176.8	258.8	29.8	35.9	15.2
Rissa tridactyla	400.4	312.0	38.1 (N = 4)	35.3	38.6
Cerorhinca monocerata	616.2	184.4	35.2	30.5	77.9
Uria aalge	966.0	203.0	48.4	47.5	83.4
Ptychoramphus aleutica (N = 1)	164.0	122.0	29.8	26.5	40.4

[1] All weights and measurements are means of five samples unless otherwise indicated.
[2] Weights are in grams and are not corrected for weight of stomach contents.
[3] Bill XS is the cross-sectional area of the bill measured at the proximal end of the gonys. Following Ashmole (1968) measurements of the width (w) and depth (d) of the bills at this level were used to calculate the cross-sectional area. The closed bill was assumed to be elliptical in cross-section and the formula for the area = $\pi(d/2 \times w/2)$ was used.

tion of the Bonaparte's Gull with its larger relatives is avoided by taking at least some of its prey from a lower trophic level by feeding on many small invertebrates that are lacking from the diets of the larger gulls. The tentative conclusion that the Bonaparte's Gull is locally ecologically segregated from its larger relatives is supported by the measures of niche overlap presented in Table 9. Measures of overlap between gulls other than the Bonaparte's Gull are much higher, with values of Morisita's index ranging from moderate (0.57) to great (0.94).

To obtain an overall measure of niche overlap between species, the degree of overlap for each aspect of the niche must be known. The overall measure is then equal to the sum or product of the separate aspects (Levins 1968, May 1975), such as food, space, and seasonal occurrence. Where food or other limited resources are a factor, migratory species may avoid interspecific competition by maintaining spatial or temporal segregation of their populations. Within species, competition may be reduced by the segregation of juveniles from the more efficient adult members of the population (Recher 1966). Juvenile Glaucous-winged Gulls wintering on Monterey Bay may be avoiding competition with adults, which are more efficient feeders. The Sooty and Short-tailed Shearwaters have one of the highest measures of food niche overlap ($\hat{C}_\lambda$ = 0.91) of any pair of species on Monterey Bay, but the periods of peak abundance of the two species differ greatly. The Sooty Shearwater is most abundant during the summer, and it is virtually absent during January and February when the Short-tailed Shearwater reaches its peak abundance. Thus the negative effects of niche overlap, if any, are reduced by temporal segregation of species.

Morphological and behavioral differences between similar species may result in reduced competition through the exploitation of different elements of a prey population or community (Recher 1966). Pink-footed Shearwaters and Sooty Shearwaters are encountered during the same months, but Pink-footed Shearwaters tend to be distributed farther out to sea than Sooty Shearwaters. Niche overlap may be further reduced by size-selective predation, but detailed analysis of the distribution of prey sizes is needed. Size-selective predation by shearwaters is suggested by the presence of a relatively large oceanic squid, *O. borealijaponicus*, in the diet of the largest shearwater, the Pink-footed (Table 10), and its absence in the diet of the smaller Sooty Shearwaters. The smallest shearwater, the Short-tailed (Table 10), is also known to rely heavily on euphausiids in some areas (Ogi and Tsujita 1973).

The Common Murre and Rhinoceros Auklet are very similar in size (Table 10), both occupy the same habitat, both feed by pursuit diving, and both exploit at least six of the same prey populations (Table 7). Field studies suggest that the Rhinoceros Auklet is distributed farther seaward than the Common Murre but data are inconclusive. It appears that niche overlap is reduced between this pair of species by the selective predation of the Rhinoceros Auklet on the market squid. Spring (1971) found that the Common and Thick-billed Murres preyed on the same pelagic fishes when they were abundant, but that the Thick-billed Murre switched to a diet of zooplankton and benthic organisms as concentrations of pelagic fishes declined. Similar examples of prey switching may be found for predators in Monterey Bay.

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