The Condor 98:691–705

TEMPORAL AND SPATIAL PATTERNS IN THE DIET OF THE COMMON MURRE IN CALIFORNIA WATERS[1]

DAVID G. AINLEY[2]
Point Reyes Bird Observatory, Stinson Beach, CA 94970

LARRY B. SPEAR[2]
Point Reyes Bird Observatory, Stinson Beach, CA 94970

SARAH G. ALLEN
Pt. Reyes National Seashore, Pt. Reyes Station, CA 94907

CHRISTINE A. RIBIC
National Biological Service, Wisconsin Cooperative Wildlife Research Unit, University of Wisconsin, Madison WI 53706

Abstract. We investigated temporal and spatial variation in the diet of the Common Murre *Uria aalge,* the most abundant, locally breeding seabird of the central California continental shelf. We collected murres in coastal, mid-shelf, and outer-shelf waters of the Gulf of the Farallones during the murres' pre-breeding (March–April), breeding (May–August), and wintering (September–February) periods, 1985–1988. Diet samples formed persistent groups as a function of these six spatio-temporal combinations of murre foraging habitat and life-history periods. Temporally, diets varied on a seasonal and interannual basis, with diets during winter and El Niño periods being the most disparate. Spatially, diets differed among the three habitats, independent of time. During the pre-breeding season after the onset of upwelling, euphausiids and juvenile rockfish (*Sebastes* spp.) became prevalent in the diet. Diets were least diverse during the breeding season because of the dominance of rockfish, especially among murres foraging in mid- and outer-shelf habitats. Other important prey were also significant for commercial or sport fishing: *Engraulis mordax* and *Clupea harengus* in coastal waters, *Merluccius productus* and *Loligo opalescens* in mid- and outer-shelf waters, and surfperch *Cymatogaster aggregata* and *Brachyistius frenatus* in coastal and outer-shelf waters (near reefs), respectively. Results support a hypothesis that diet varies as a function of where murres forage. Hence, if the most characteristic prey of one habitat disappears, murres switch foraging areas, bringing a switch in diet. Owing to environmental changes in the region, murres may be losing the option of prey switching as a strategy to maintain an adequate intake of food.

Key words: annual and seasonal variation; Common Murre; diet; foraging area; foraging habitat; prey selection; Uria aalge.

INTRODUCTION

The Common Murre *Uria aalge* is the most abundant seabird breeding at sites in coastal waters of the California Current region, from central California north through Oregon (Briggs et al. 1987, Carter et al. 1992). In fact, it is one of the characteristic species of boreal waters throughout the North Pacific and North Atlantic (AOU 1983). In the California Current region, where this species' diet has been well investigated compared to most seabird species, at least five spring and summer studies have characterized this species as a consumer of fish and squid, caught in shallow waters close to shore (Table 1). Commonly eaten fishes have included rockfish *Sebastes* spp., anchovies *Engraulis mordax,* sanddabs *Citharichthys sordidus* and herring *Clupea harengus,* although some other species, such as tomcod *Microgadus proximus,* salmon *Onchorhyncus* spp. and sandlance *Ammodytes hexapterus* were also commonly eaten in Oregon (hereafter, see Table 2 for common and scientific names of prey). The most comprehensive study of murre diet, anywhere in this species' range (Matthews 1983), covered three different localities along the coast of Oregon. Sampling was done from spring to autumn at one site (Coos Bay) and spring to summer at others. Mathews

[1] Received 5 January 1996. Accepted 1 August 1996.
[2] Present address: H. T. Harvey & Associates, P.O. Box 1180, Alviso, CA 95002. Send correspondence to senior author. e-mail: htharvey@ix.netcom.com

TABLE 1. A summary of results from studies of the Common Murre's diet in the California Current region.

Area	Habitat	Season	Sample[a]	Dominant prey[b]	Study
Central California	Inner shelf	Winter	24	Anchovy, rockfish, market squid, whiting, sanddab.	Baltz and Morejohn (1977)
Central California	Inner shelf	Spring, Summer	238	Rockfish, lingcod, anchovy, market squid.	Croll (1990)
Central California	Entire shelf	Summer	>1,000	Rockfish, anchovy, market squid, sanddab.	Ainley et al. (1990)
Oregon	Inner shelf	Spring, Summer	638	Tomcod, rockfish, smelt, sandlance, salmon, anchovy, market squid, herring.	Matthews (1983)
Central Oregon	Inner shelf	Summer	27	Rockfish, anchovy, herring.	Scott (1990)

[a] All samples are number of murres collected, except for Ainley et al. (1990) where sample size is the number of identified feeds brought by parents to waiting chicks in the colony at the Farallon Islands.
[b] See Table 2 or text for scientific names of prey, except for the two smelt species *Hypomesus pretiosus* and *Allomerus elongatus*.

noted that murre diet during winter was distinct from that of spring/summer. Most intriguing, however, was the dominance of euphausiids, a crustacean, during one summer off Coos Bay. As noted above, the Common Murre is considered to be a piscivore (Spring 1971, Bradstreet and Brown 1985, Hobson et al. 1994), but perhaps this conclusion has been reached because most studies have sampled inshore.

Matthews (1983) and Ainley et al. (1990) proposed that murre diet in the California Current region varied with prey availability and foraging habitat, which were functions of where murres could find ample food. Indeed, Sydeman et al. (1991) and Ainley et al. (1993) recently confirmed that the interannual prevalence of rockfish in the diet of murres correlated closely with their availability, as determined by trawls conducted annually by National Marine Fisheries Service (NMFS) in the Gulf of the Farallones. These authors also found that the intensity of upwelling or downwelling explained much of the variation in the availability of these prey to the murres (also see Briggs et al. 1988).

We sought to make a more comprehensive study of the various seasonal, geographic, and habitat differences indicated in the above short-term and single-season studies. To do this, we conducted a four-year, year-round investigation of diet of the Common Murre in all this species' foraging habitats within one, mesoscale-sized region—the Gulf of the Farallones, California—which undergoes marked seasonal changes in oceanographic climate. A major impetus that led us to conduct this study were proposals to develop a commercial fishery in the California Current on a species of fish (shortbelly rockfish *Sebastes jordani*; e.g., PCFFA 1986, Dept. Commerce 1989) that we knew was critical to the Common Murre during summer (e.g., Ainley et al. 1990). However, we had no year-round perspective of how representative was the summer diet. At the same time, we were aware of data indicating that heavy fishing pressure on seabird forage fish can drastically affect population size in seabirds (summarized in Furness and Monaghan 1987, Montevecchi 1993). We also attempted to provide a basis on which to evaluate the hypothesis proposed by Ainley et al. (1994) that a changing marine climate, in conjunction with increased fishery pressure, has affected the availability of critical prey and, in turn, has prevented growth in the murre population of central

California since the early 1980s. Besides comparing diet composition by location, habitat, season, and year, we also describe within-year changes in the size of prey taken because most of the fish prey eaten by Common Murres in central California grow to become too large for consumption by this predator. Thus, fish growth affects availability to murres. Finally, we present results of our at-sea censuses of foraging murres to provide a spatial context to our diet studies.

METHODS

STUDY AREA AND PERIOD

We conducted this study in the Gulf of the Farallones, California, during the years 1985 to 1988 (Fig. 1). Common Murres are known to forage at least to 180 m depth (Piatt and Nettleship 1985). Thus, they are capable of exploiting virtually all waters overlying the continental shelf in the study area. Whether or not samples were obtained in a given habitat during a collecting trip depended on whether murres were present. Collections were made in coastal waters (i.e., those < 40 m depth) off Pedro Point, Duxbury Reef, and Double Point (Fig. 1), in waters of the mid-shelf (40–70 m deep) approximately in the middle of the Gulf of the Farallones, and in outer-shelf waters (70–120 m deep) along the Farallon Ridge.

Besides the spatial dimension, there was also a temporal dimension to our study. Upwelling, or its absence, is the dominant process that drives development of the California Current food web (e.g., Glanz and Thompson 1982). Therefore, to better understand how upwelling affected prey availability and, thus, murre diet composition, we sampled in three seasons: (1) March–April, the prebreeding period, when murres are acquiring reserves to produce eggs, and the period immediately after the onset of seasonal upwelling, (2) May–August, the breeding period, when murres are incubating eggs and feeding chicks, and the period of peak upwelling intensity, and (3) September–February, the wintering period, when juveniles become independent and adults recover from the breeding season, and the period of minimal upwelling. Fortuitously, our study period included one weak El Niño (ENSO), 1986–1987 (Ainley et al. 1995), which by its inclusion, besides attention to seasonal upwelling, increases the validity of any attempt to describe temporal biotic variation in the California Current.

DATA COLLECTION

We collected murres during each of the seasonal periods (245, 219, and 90 birds, respectively) over the course of the four-year study. We usually collected 6 murres at each locality per trip and, in total, collected 554 individuals during 41 collections. Upon collection of birds, stomachs were removed immediately and injected with ethanol and/or frozen to stop digestive processes. Birds were saved as specimens or were used for contaminant analysis (U.S. Fish and Wildlife Service, unpubl. data).

Prey fed by parents to chicks at the breeding site were identified visually during temporally standardized watches from the blind at Shubrick Point, Southeast Farallon Island, each year during June and early July (see Ainley and Boekelheide 1990, for more details). We also assessed the prey fed to chicks once they had left the breeding ledges. During late July 1985 and 1987, we collected six adult murres (all males) with the chicks they were accompanying at sea, four pairs in coastal and two in outer-shelf waters.

Murre densities (birds/km^2) at sea were determined by shipboard censuses during the first two weeks of June each year (the period when most adults are feeding chicks). Two or more observers censused simultaneously. Only birds sitting on the water or diving were included in analyses, and only if they occurred within 300 m of one forequarter of the ship (the side having the least glare). Continuous censuses were divided into 15-min segments; the area of ocean surveyed (km^2) equaled the distance traveled during each segment (usually 3–6 km) times 0.3 km.

DATA ANALYSIS

Whole prey items were measured (standard lengths for euphausiids and fish, mantle lengths for cephalopods). Otherwise, prey length and mass were estimated by regression against length of the lower rostrum for squid or longest otolith diameter for fish. Cephalopod beaks were included in analyses only if not abraded; otoliths were included if they showed no or little sign of erosion. We deleted items if we thought they were in the murre stomach due to secondary ingestion from the murres' prey. This problem occurred mainly with euphausiids eaten by Pacific whiting, whose stomachs were full of these organisms. Regression equations for estimating sizes of prey were taken from the literature or

TABLE 2. The composition of the diet of Common Murres captured in the Gulf of the Farallones, 1985–1988, partitioned by season and location/habitat and described in four ways: by percent frequency of occurrence, percent composition by number and by mass, and the index of relative importance (IRI/100) of prey in the stomachs. Sample size, *n*, indicates the number of murre stomachs inspected.

	Coast				Mid-shelf				Outer shelf			
	Freq.	No.	Mass	IRI	Freq.	No.	Mass	IRI	Freq.	No.	Mass	IRI
A. PRE-EGG-LAYING PERIOD (MARCH-APRIL)												
	$n = 62$				$n = 40$				$n = 143$			
Invertebrates												
Euphausiid												
Euphausia pacifica	3	7	< 1	0.2					48	50	5	26.4
Euphausiid												
Thysanoessa spinifera	10	3	< 1	0.3	5	56	< 1	2.8	36	41	13	21.2
Market squid												
Loligo opalescens	7	1	6	0.5					30	< 1	15	4.5
Octopus												
Octopus rufescens									4	< 1	< 1	
Fish												
Northern anchovy												
Engraulis mordax	13	49	44	12.2	30	4	< 1	1.2	2	< 1	< 1	
Shiner surfperch												
Cymatogaster aggregata	3	< 1	4	0.1								
Kelp surfperch												
Brachyistius frenatus									7	< 1	30	2.2
Pacific whiting												
Merluccius productus	3	< 1	5	0.2	12	32	99	15.7	9	< 1	18	1.6
Medusafish												
Icichthys lockingtoni					5	< 1	< 1					
Lingcod												
Ophiodon elongatus	17	31	12	0.7								
Pacific sanddab												
Citharichthys sordidus									18	1	2	0.5
Midshipman												
Porichthys notatus									2	< 1	< 1	
Spotted cusk-eel												
Chilara taylori	3	< 1	1	0.6								
Pacific herring												
Clupea harengus	28	6	28	1.0								
Night smelt												
Spirinchus starksi	3	< 1	< 1		5	1	< 1		4	< 1	2	

TABLE 2. Continued.

	Coast				Mid-shelf				Outer shelf			
	Freq.	No.	Mass	IRI	Freq.	No.	Mass	IRI	Freq.	No.	Mass	IRI
Rockfish												
Sebastes spp.	3	< 1	< 1	20	6	1	1.4		54	2	15	9.2
Unidentified spp.									< 1	6	2	0.1
Diet diversity[a]		1.36	1.46			1.03	0.06			1.00	1.89	
B. BREEDING PERIOD (MAY-AUGUST)												
		n = 118				n = 34				n = 67		
Invertebrates												
Euphausia pacifica									5	< 1	< 1	
Thysanoessa spinifera					80	77	2	63.2				
Loligo opalescens	25	7	20	6.8					10	3	< 1	0.3
Octopus rufescens	7	4	1	0.4					< 1	< 1	< 1	
Fish												
Jacksmelt												
Atherinops affinis	< 1	1	4	0.1								
Engraulis mordax	61	28	31	39.5	20	< 1	< 1	0.2				
Cymatogaster aggregata	14	3	11	2.1								
Brachyistius frenatus									5	< 1	4	0.2
Merluccius productus					50	16	95	55.5				
Ophiodon elongatus	14	3	4	1.0					5	< 1	1	0.1
Citharichthys sordidus	23	6	16	5.1	< 1	3	1		43	4	3	3.0
Clupea harengus	4	1	4	0.2								
Spirinchus starksi	14	5	1	0.8								
Sebastes spp.	66	42	7	32.3	20	3	2	10.0	51	93	91	93.8
Diet diversity[a]		1.66	1.88			0.70	0.25			0.30	0.37	
C. WINTER PERIOD (SEPTEMBER-FEBRUARY)												
		n = 28				n = 13				n = 49		
Invertebrates												
Thysanoessa spinifera									10	68	2	7.0
Loligo opalescens	14	2	10	1.7	100	47	61	108.0	17	9	47	9.5
Octopus rufescens					40	22	< 1	8.8				
Fish												
Engraulis mordax	23	73	29	23.5	20	3	1	0.8				
Cymatogaster aggregata	14	2	44	6.4								
Citharichthys sordidus									< 1	< 1	< 1	

TABLE 2. Continued.

	Coast				Mid-shelf				Outer shelf			
	Freq.	No.	Mass	IRI	Freq.	No.	Mass	IRI	Freq.	No.	Mass	IRI
Porichthys notatus	14	2	2	0.6	20	3	28	6.2				
Chilara taylori					20	3	4	1.4				
Clupea harengus	10	9	12	2.1								
Spirinchus starksi	57	9	1	6.3	20	16	4	4.0	< 1	< 1	1	
Sebastes spp.					40	6	1	2.8	37	17	49	24.4
Pacific butterfish												
Peprilus simillimus	< 1	2	2									
Unidentified spp.									< 1	6	1	0.1
Diet diversity[a]		1.21	1.41			1.47	1.01			0.95	0.88	

[a] Diet diversity is determined using both numerical and mass percentage of diet.

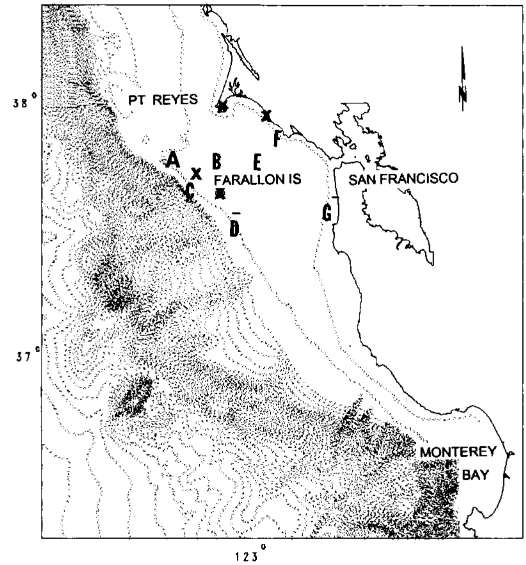

FIGURE 1. The Gulf of the Farallones showing areas where Common Murres were collected within coastal (G & F), mid-shelf (B & E) and outer-shelf habitats (A, C, D); the actual extent of each collecting locality is, to scale, the area covered by each letter. Xs mark locations of major breeding colonies of Common Murres at Point Reyes and the Farallon Islands. Contour interval of isobaths is 20 fathoms; scale 1:32,000.

were determined by us on the basis of measurements of whole prey items (Ainley and Spear, unpubl. data). For a few species, regression equations were not available. Mass and length of these prey items were estimated by comparison to complete specimens of known size and mass.

Each sample was composed of all the murres collected at a specific time and place. We summarized diet composition in four ways: (1) frequency of occurrence (percent of samples in which prey species were present); (2) and (3) percent composition by number and by mass, respectively; and (4) the Index of Relative Importance (IRI; see Day and Byrd 1989 for the formula). We employed various statistical procedures to describe and compare the diet, seasonally and spatially. Diet similarity (or overlap) among samples was determined by using percent composition by mass and Morisita's Index Of Diet Similarity, which expressed similarity as a percent (see Baltz and Morejohn 1977 for the formula). In order to group samples (identified by season and collecting locality), we then used average-linkage-between-groups of Morisita's indices in a cluster analysis (SPSS PC+, Norusis

1986). We used the formula reported in Balz and Morejohn (1977) to estimate diet diversity on the basis of both numerical and mass composition in samples combined for different seasons and habitats. Finally, we calculated IRI to aid in comparisons of our data with those of Croll (1990). Except for the clustering, statistical analyses were completed using the computer program STATA (Computing Resource Center 1989).

Maps showing densities of foraging murres were constructed using the Geographic Information System package, ARC/INFO (Version 6.1, ESRI, Inc., Redlands, California). Density estimates (birds/km^2) of birds on the water were plotted on a 5 × 5 km grid of the Gulf of the Farallones. If more than one census segment appeared in a grid, densities were averaged; if one segment crossed the boundary of more than one grid cell, those densities were assigned to each cell. We present data only for 1986–1988; the data for 1985 were insufficient for spatial analysis comparable to the other years.

RESULTS

DISTRIBUTION OF FORAGING ADULT MURRES

In many studies of seabird diet, the degree to which samples represent the entire foraging distribution of the species in the study region is rarely apparent. Therefore, we include here our data on the distribution of foraging murres gathered throughout central California waters during June, the breeding/peak-upwelling period (Fig. 2). The murres were concentrated throughout the Gulf of the Farallones and became much less abundant peripherally. As our diet collections were also confined to the Gulf, we feel that the results of our diet analysis are representative of the major habitats occupied by this species in the region. We did not sample any of the peripherally located murres (cf. Figs. 1 and 2).

The patterns shown in Figure 2 were representative also of the murres' foraging distribution during the pre-breeding period (see charts in Allen 1994). During winter, the species generally feeds inshore from Pt. Reyes to Monterey Bay (see Fig. 1; Briggs et al. 1987, Ainley, unpubl. data). Thus, we had to use our diet sampling during winter, which was confined to the northern Gulf of the Farallones, to reflect diet in areas not sampled by us in the region of central California. As noted in the Introduction, though, the inshore habitat of murres in Monterey Bay during winter was sampled by Baltz and Morejohn (1977).

Many more murres fed near the mainland and between the Farallones and Point Reyes in June 1986 than they did in June of the other two years (Fig. 2). In addition, mean at-sea densities were lower in 1986 than in other years (Allen 1994), indicating that the murres were more dispersed in 1986 and fed in all available habitats about equally. In 1987 and especially 1988, the murres fed close to the breeding colonies at the Farallones and Point Reyes. More coastal feeding during ENSO 1986 (with the event extending into the winter 1987), was also pointed out by Ainley and Boekelheide (1990).

DIET OF ADULTS AT SEA

Prey items that contributed ≥10% of the diet included mostly the fish species discussed in the Introduction, two species of euphausiids, *Euphausia pacifica* and especially *Thysanoessa spinifera,* and two species of surfperch, *Cymatogaster aggregata* and *Brachyistius frenatus* (Table 2). Within the component classified as "juvenile rockfish", shortbelly rockfish was the overwhelmingly dominant species. Particularly common during prebreeding and breeding periods were euphausiids, whiting, and rockfish in mid-shelf and outer-shelf waters, and anchovies and herring in coastal waters. The deep-water surfperch (*B. frenatus*), on occasion was eaten with these prey. During the wintering period, anchovies and the other, shallow-water surfperch (*C. aggregata*) dominated diets of murres feeding in coastal waters, while euphausiids, squid, and rockfish dominated in mid- and outer-shelf waters (Table 2). These groupings were confirmed by cluster analysis.

The correspondence between diets when grouped by season and habitat is shown also in Table 3, where especially strong overlap is apparent within coastal collections, those of the mid-shelf, and those of the outer-shelf regardless of season. Among the particularly strong overlaps (> 50%), 5 of 6 were of the same habitat but of a different season; the sixth compared mid-shelf with outer-shelf during the same season, winter. Conversely, among the 17 comparisons showing particularly weak overlaps (< 10%), 13 differed in both habitat and season, 3 differed in habitat only, and one differed in season only. These trends confirm that diet differences were

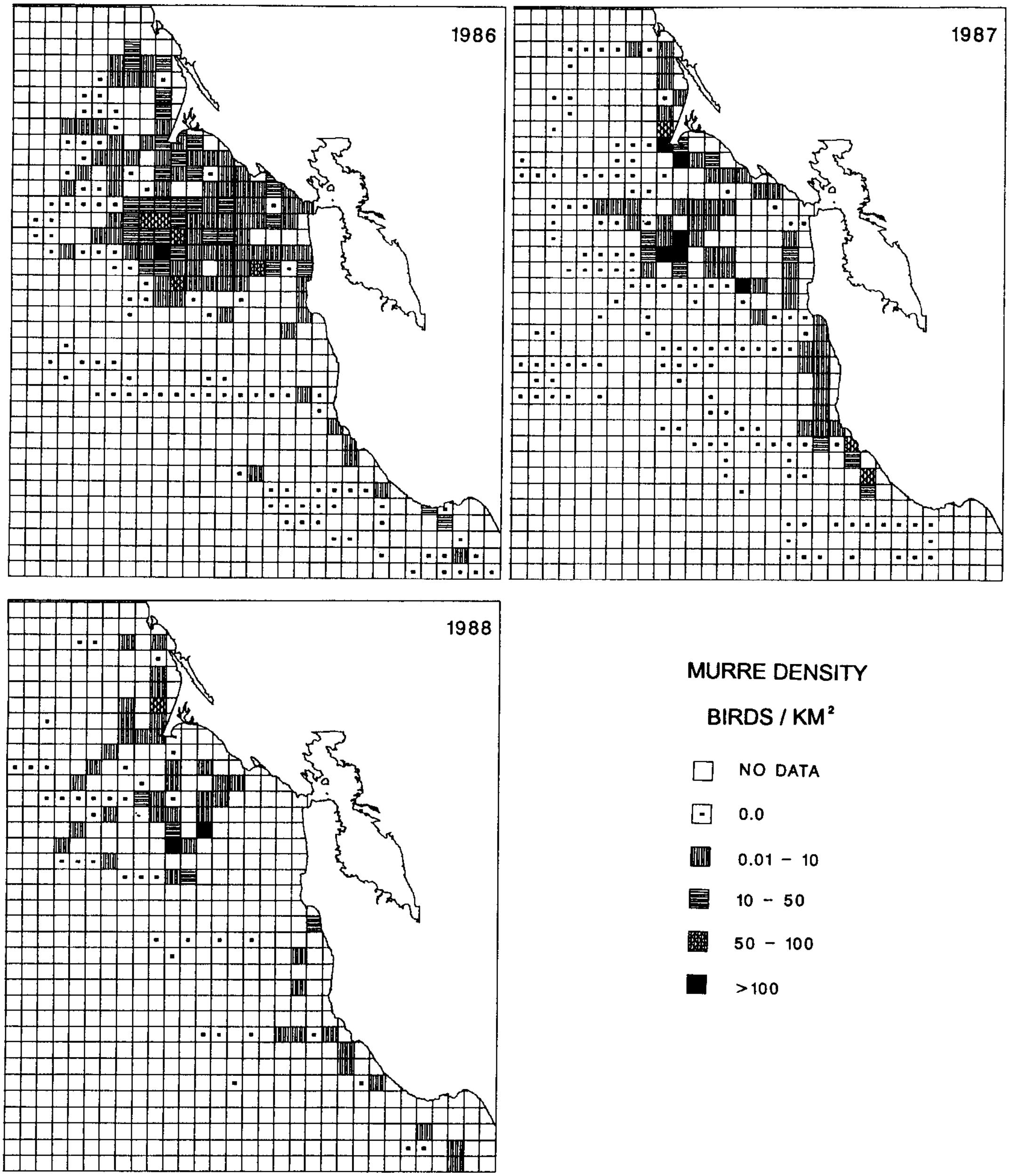

FIGURE 2. Foraging distribution of Common Murres in the Gulf of the Farallones during June, 1986–1988; as shading of 5 × 5 km blocks become darker murre density (birds/km^2) becomes greater.

due mainly to habitat and not season. Differences in diet diversity were also related to habitat, with diversity decreasing with increasing distance from shore (Table 2). Overall, diversity was the lowest during the breeding season, primarily because of the preponderance of juvenile rockfish in the diet.

Sufficient data were available to express temporal variation graphically only for coastal and outer-shelf habitats (Fig. 3). Anchovies dominated the diet of murres feeding in coastal waters (regardless of season), especially during 1986 and early 1987, when a mild El Niño occurred. Rock-

TABLE 3. Morisita's Index showing similarity of diet, on the basis of percent composition by mass, among the season/location samples of Common Murres in the Gulf of the Farallones. Overlap > 0.50 in bold type; multiply numbers by 100 to obtain percent overlap.

	Prelaying		Breeding			Wintering		
	Mid	Outer	Coast	Mid	Outer	Coast	Mid	Outer
Prelaying/coast	0.08	0.13	**0.71**	0.08	0.00	**0.60**	0.00	0.08
Prelaying/mid-shelf		0.31	0.00	**1.00**	0.05	0.00	0.00	0.00
Prelaying/outer-shelf			0.24	0.32	0.29	0.06	0.29	0.45
Breeding/coast				0.00	0.14	**0.67**	0.40	0.40
Breeding/mid-shelf					0.00	0.00	0.00	0.14
Breeding/outer-shelf						0.00	0.00	**0.69**
Wintering/coast							0.18	0.12
Wintering/mid-shelf								**0.64**

fish always dominated the diet when murres frequented outer-shelf waters, which they did during the breeding season. Surfperch were important during 1985, 1986, and 1988, but were largely absent in the diet during 1987. Except in 1987, herring and smelt were important to murres foraging inshore in the wintering period.

In outer-shelf waters, two markedly different diets were evident, depending on the year: 1985–1986 vs. 1987–1988. Rockfish and surfperch dominated during the early years, whereas—after ENSO—euphausiids and Pacific whiting dominated during the later years. Market squid showed the least temporal variation in dietary importance among the more important prey of those murres feeding in outer-shelf waters.

Samples combined from all habitats to increase sample size, revealed seasonal and annual variation in the size of the fish eaten. For example, among the rockfish eaten (Fig. 4), 1985 samples progressed from small, 0-year-class fish during prebreeding (March–April), to larger individuals from that year class plus perhaps 1-year-olds during breeding (May–August), and to only the larger 0-year-class fish during the wintering period ($\chi^2 = 336.85$, df = 6, $P < 0.001$). A somewhat similar progression was evident in 1988 ($\chi^2 = 39.00$, df = 6, $P = 0.001$). During 1986, the ENSO, two very distinct size classes were consumed during the early part of the year, and none later; more of the larger fish were consumed during ENSO, too. A seasonal progression in size class wasn't as obvious among the anchovies eaten (not shown; range 30–140 mm). However, the murres did eat slightly, but statistically smaller fish during spring compared to those eaten during early and late summer ($\chi^2 = 27.89$, df = 4, $P < 0.001$), and the ENSO pattern was similar (two size classes early, none later, and particularly large fish eaten). In terms of the biomass of rockfish and anchovies consumed, the fact that the fish grew larger from spring to summer compensated for the fewer individuals eaten (and fed to chicks) during summer compared to spring (Table 2). The size ranges of other important prey were as follows: market squid, 31–176 mm (especially 71–121 mm); Pacific whiting, two size-classes centered at 56 and 91 mm; Pacific herring, 100–190 mm; and Pacific sanddab, 30–50 mm.

DIET FED BY ADULTS TO CHICKS

Juvenile rockfish dominated diets fed to chicks at the breeding ledges in June 1985, 1987, and 1988, but were much less common in 1986 (ENSO), when anchovy was the most common prey (Tables 4, 5). Except for the ingestion of surfperch and various invertebrates by adults, importance values for the major components of the adult diet during June–July (cf. Table 2) ranked similarly to the prey fed to chicks. We did not undertake any further, more quantitative comparison owing to the disparate methods by which the adult and chick samples were taken.

Among males and the chick accompanying them away from breeding ledges, the same prey species were present in both members of each adult-chick pair; the stomachs of the six adults contained 9 prey items and those of the six chicks contained 12 items (Table 5). Morisita's Index of Diet Similarity between the two samples was 70.8%. What caused the slight dissimilarity was the larger squid in one adult and the few more juvenile rockfish (hence greater mass) in the chicks.

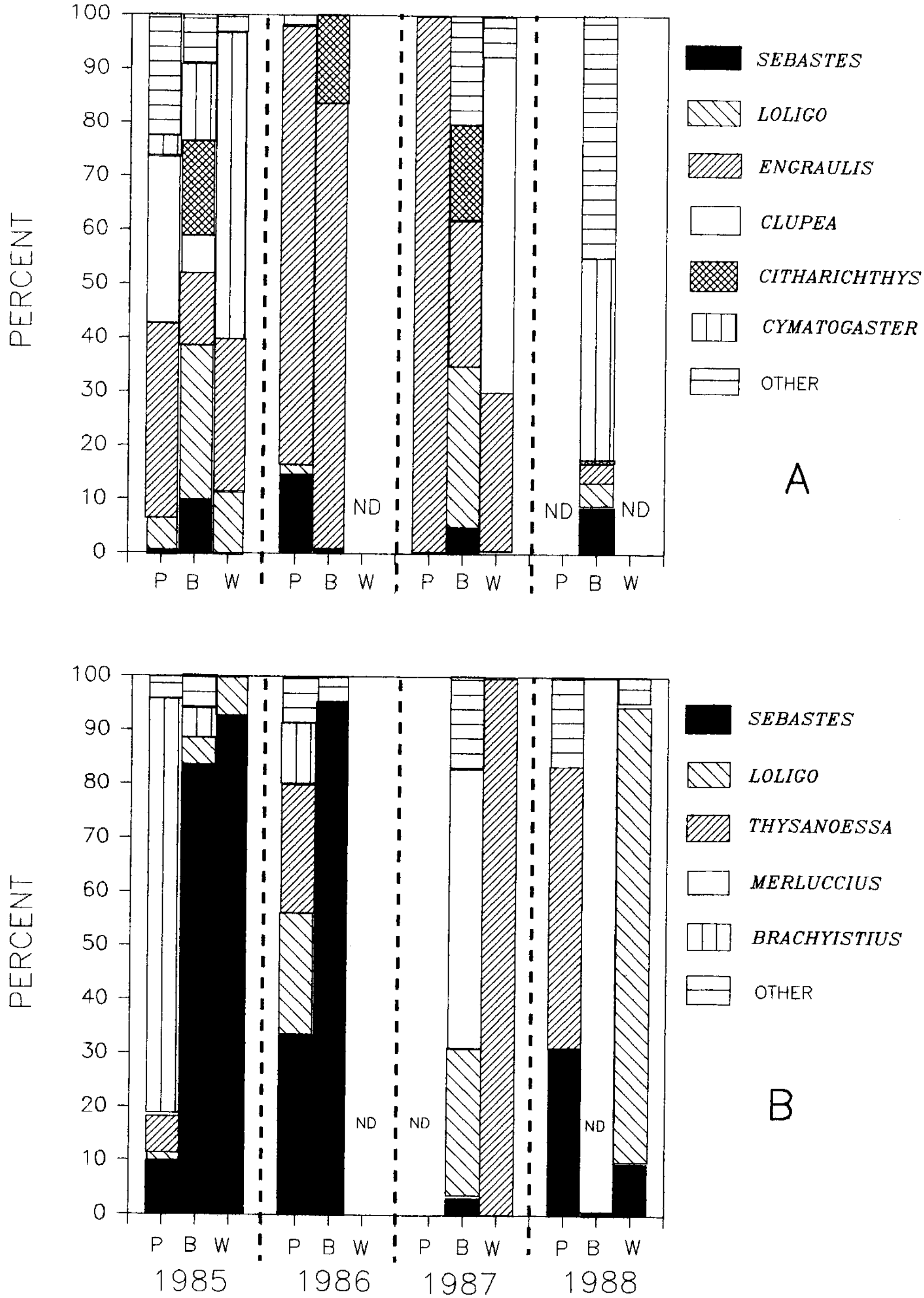

FIGURE 3. Variation in the percent composition by mass of the diet of Common Murres in the Gulf of the Farallones, by year, habitat: (A) coastal and (B) outer-shelf waters, and season (prebreeding, breeding and winter).

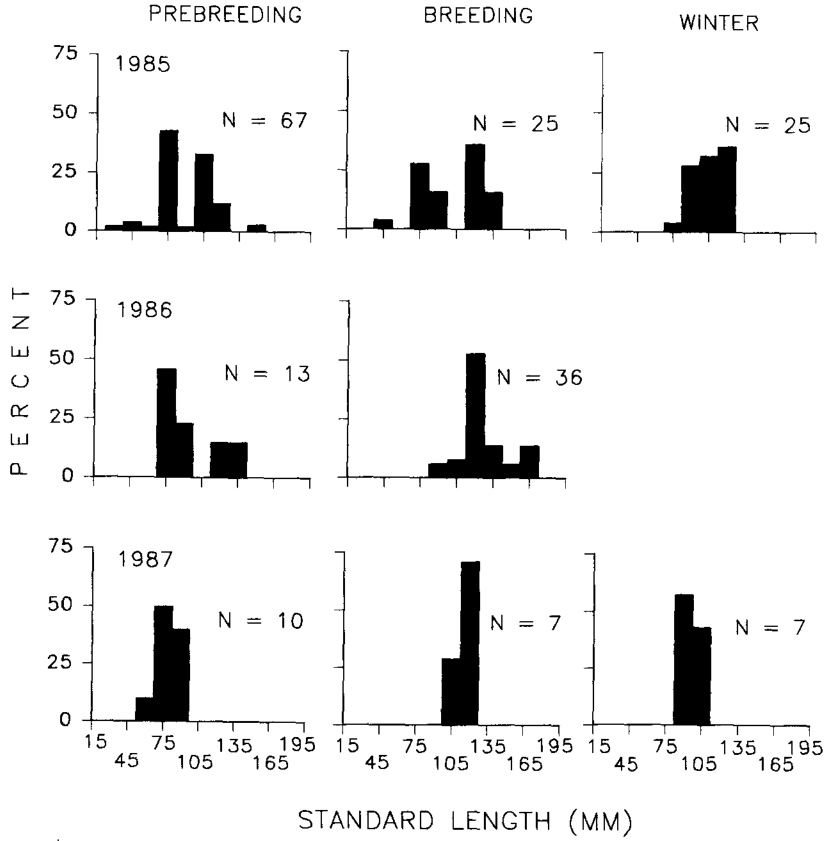

FIGURE 4. Variation in the length of rockfish taken by Common Murres in the Gulf of the Farallones, by season and year. Sample size, *n*, represents the number of fish whose total length was estimated from otolith diameter (Ainley and Spear, unpubl. regression equations).

DISCUSSION

TEMPORAL AND SPATIAL CHANGES IN DIET

Important prey identified in this study were similar to those noted in previous studies of murres in the California Current, but by delimiting prey according to foraging habitat and by providing broader spatial and temporal coverage, our study increases the value of the previous work. Our results showed that what may have appeared from shorter-term studies to be seasonal differences in diet—as a function of prey availability—are likely more a function of seasonal difference in foraging habitat, with some exceptions.

One of the exceptions is the strong reliance of murres on euphausiids during the prebreeding period. Feeding on these prey is likely a response to exceptional availability in an offshore habitat that can also provide fish and cephalopods (see below). On the other hand, on the basis of the similarity of our results in the Gulf of the Farallones during winter, when the murres feed inshore, to those of Baltz and Morejohn (1977) for inshore Monterey Bay during winter, we con-

TABLE 4. Percent composition of prey items (by number) brought by Common Murre parents to chicks on Southeast Farallon Island during June of each year.

Year	1985	1986	1987	1988
Total items	1,185	1,180	2,638	2,526
Invertebrates				
Loligo opalescens	1	2	1	1
Fish				
Engraulis mordax	19	56	8	14
Merluccius productus			< 1	
Citharichthys sordidus	< 1	1	< 1	< 1
Clupea harengus	< 1			
Spirinchus starksi	< 1	1	1	2
Sebastes spp.	74	38	89	82
Other	3	2	< 1	< 1

clude that we have characterized pretty well the diet of murres frequenting the 70 km of inshore habitat between the two areas, and likely without exception.

Euphausiids, in fact, and especially *T. spinifera,* may have been the most abundant prey available to murres during March and April when these crustaceans are preyed on heavily (Smith and Adams 1988, Ainley et al. 1996). This preponderance of euphausiids in the diet of murres has not been reported previously in the California Current region for any season, although Matthews (1983) and Scott (1990) found a few euphausiids in murre diets during the summer off Oregon, 1981–1982 and 1970–1972, respectively. However, euphausiids (mainly *T. inermis)* are consumed in abundance by non-breeding Common Murres residing in pelagic, subarctic waters of the Gulf of Alaska (Ogi and Tsujita 1977, Ogi et al. 1985). Studies of the planktivorous Cassin's Auklet *Ptychoramphus aleuticus* in the Gulf of the Farallones (Ainley and Boekelheide 1990, Ainley et al. 1996), conducted simultaneously to this one, indicate that euphausiids are available to murres in murre feeding areas. There is a close correspondence between the appearance of *T. spinifera* in the auklet diet and onset of upwelling, which normally happens during early March (Bolin and Abbott 1963). With upwelling, and perhaps as a response to enrichment of surface waters, *T. spinifera* begin to swarm for reproductive reasons, rendering them much more vulnerable to predation (Smith and Adams 1988). Auklets and murres take advantage of this situation, and diet composition becomes similar between the two species. Trawls during spring also revealed a preponderance of euphausiids, with small (< 50 mm) pelagic juveniles of *Merluccius, Sebastes, Citharichthys* and *Octopus rufescens* mixed in (Ainey, pers. observ., qualitative assessment of NMFS trawls). The euphausiids continued to dominate the auklet diet through July, indicating that this prey is available to murres, but the murres switch to juvenile rockfish when the latter attain sufficient size, usually in May.

Our results show other strong patterns of switching from one prey to another, presumably in response to differing levels of availability. Ainley et al. (1990, 1993, 1995) showed a switch in the diet of breeding murres from juvenile shortbelly rockfish to anchovies during murre breeding seasons when the rockfish were not available but the anchovies were. This pattern also was seen during the present study, by comparing 1986 (ENSO) with the other three years (NMFS trawls captured few juvenile rockfish in 1986; W. Lenarz, NMFS-Tiburon Lab, pers. comm.). Our study confirms that such a switch results from murres foraging for anchovies in coastal waters, when they can not find rockfish near to the Farallon Islands. Apparently, the large, oily anchovy makes the murres' long commute to coastal waters worthwhile (see caloric analysis in Spear 1993). In the occasional summer when neither rockfish nor anchovy were available, the reproductive performance of murres has been low (Ainley and Boekelheide 1990, Ainley et al. 1995)

Adult murres probably could live on euphausiids, and our results show that they do so during spring, before the 0-year-class rockfish become available and after the previous year class has disappeared from shelf waters. Unlike switching to anchovies, however, it likely is not energetically feasible for them to switch to feeding euphausiids to their chicks; thus, they do not do so (Table 4; i.e., no euphausiids seen fed to chicks). They feed the chicks one prey item at a time, and their strategy is to maximize the size of the fish and the nutrient transfer, within the physical limitations of a chick's throat. In addition to small size, euphausiids are of lower caloric content than fish (Spear 1993). Scott (1990) noted that in one parent-chick pair of Common Murres collected together at sea off the Oregon coast, the adult's stomach was full of euphausiids but that of the chick was empty.

Our results also demonstrate the futility of attempting to characterize the diet of the Common Murre, or other seabirds, with a temporally and spatially limited sample (also see Duffy et al. 1987). Although diet showed some consistency during a given season in more than one year, temporal variability was extensive as murres visited various habitats in search of prey. Alternatively, there was substantial consistency in diet composition among murres feeding in the same habitat, regardless of year or region in central California (compare the results of this study with those of Baltz and Morejohn 1977 and Croll 1990). In the context of all these studies of murre diet in central California and Oregon, the diet of this species is among the best known of any seabird. The availability of this information may be fortunate, given the potential of this species as one that could be used to indicate the status of the food-web in waters overlying the continental shelf of central California and elsewhere (also see Cairns 1987, 1992).

MURRE DIET AND COMMERCIAL FISHERIES

Fish species important to commercial and sport fisheries in central California proved to be important to the murre also. Euphausiids and shortbelly rockfish are not yet fished commercially, although proposals to do so have been made (see Introduction). Except for anchovies and herring, the murres fed on the juveniles of these fishes, whereas the fisheries take the older age classes. A large enough fishery, however, could limit the number of younger fish available. Conversely, predation by murres (and other top-trophic predators) could affect the strength of subsequent year classes of shortbelly rockfish available to a fishery. It is interesting that murres continue to consume, even into the following winter, larger 0-year-class shortbelly rockfish (which have settled to the bottom) well beyond the pelagic juvenile stage that is so important to murres during the breeding season. Juvenile shortbelly rockfish are extremely common in spring everywhere over the shelf, whereas adults occur only in waters of the continental slope, deeper than 100 m (Lenarz 1980). The adults of this species are small (ca. 20 cm) compared to most other rockfish species and, therefore, are vulnerable to many shallow-water predators of all sizes (including other birds, mammals, fish, and cephalopods), as summarized by Lenarz (1980) and others. For example, Ainley et al. (1990) found cormorants *Phalacrocorax* spp. feeding on shortbelly rockfish that were greater than a year old and much larger than those eaten by the murres of this study. Perhaps the migration of this fish species to deeper depths is an escape from the heavy predation apparent in shelf waters, or perhaps what appears as migration is actually the result of the larger, deeper dwelling fish being those that survived, having settled out deeper than the reach of the many shelf-based predators.

The degree to which fisheries affect prey availability for the murre in the California Current awaits further investigation. Studies in the Barents Sea have described serious effects on murres after fisheries depleted capelin *Mallotus villosus* (Erikstad 1990); in the North Sea, seabirds (including murres) were affected after depletion of capelin and sandlance *Ammodytes hexapterus* (Furness and Barrett 1991). For example, would Pacific herring be even more common in the murres' diet if the herring stock was not in such a depleted state in California (Calif. Dept. Fish and Game 1991)?

TABLE 5. Percent composition by mass of the stomach contents of six adult male Common Murres and the chicks accompanying them in coastal (1985, $n = 4$ pairs) and outer-shelf (1987, $n = 2$ pairs) habitats.

Prey species	Adults 9 items 520 g	Chicks 12 items 470 g
Invertebrates		
Loligo opalescens	32.1	3.8
Fish		
Brachyistius frenatus	16.2	13.3
Citharichthys sordidus	14.4	33.1
Ophiodon elongatus	32.5	25.9
Sebastes spp.	2.2	15.3
Spirinchus starksi	2.6	8.6

We argue that, since most fish stocks important to these murres are heavily exploited in central California (Leet et al. 1992, Ainley et al. 1994), the options of prey switching have been reduced. The inclusion of significant amounts of surfperch in the murre diet noted in this study was surprising to us and was unknown in the earlier studies in the California Current region (Baltz and Morejohn 1977, Matthews 1983, Croll 1990, Scott 1990). As they do with the relatively common butterfish *Peprilus simillimus,* murres avoid feeding on surfperch and other fish (e.g. medusafish *Icichthys lockingtoni*) that have a body depth > 40 mm, preferring instead (on the basis of an experimental study) those fish species having a fusiliform shape (Swennen and Duiven 1991)—anchovies, herring, sandlance, capelin, and juvenile rockfish. Adults especially avoid feeding deep-bodied fish to their chicks, who have mouths too small to swallow them. Thus, we question whether the ingestion of surfperch, butterfish, and medusafish by murres is an indication of a food web in stress? Even if not, clearly, commercial exploitation and depletion of the shortbelly rockfish would be a disaster for the common murre of central California, especially since their alternative prey also are fished extensively. The information gathered in this study, and those of other predators, was critical in the decision to forgo development of a fishery for shortbelly rockfish in the California Current (Dept. Commerce 1989).

ACKNOWLEDGMENTS

We thank personnel of the NMFS-Tiburon Laboratory, particularly W. Lenarz, S. Ralston, D. Woodbury, P. Adams, and S. Smith, for making room for us on their rockfish assessment cruises aboard *NOAA Ship David Starr Jordan,* for designing cruises inadvertently to suit our purposes, and for much discussion on the biology of the bird-prey caught in their trawls. They also provided many of the fish specimens we used to develop size-mass regression equations. Indispensable as well were the many ocean trips provided to us by H. Corning and T. Beeson. Financial support for our work was provided by the Gulf of the Farallones National Marine Sanctuary, Minerals Management Service, U.S. Fish and Wildlife Service (Farallon Refuge), and the U.S. Environmental Protection Agency. R. Ferris assisted greatly in the collection and sorting of samples. R. Barrett and I. Timossi kindly provided computer time for GIS spatial analysis. R. H. Day and W. J. Sydeman provided helpful comments on the manuscript and Farallon Biologists R. J. Boekelheide, H. R. Carter, S. D. Emslie, R. P. Henderson, T. and J. Penniman, P. Pyle, C. Strong, and W. J. Sydeman aided in acquiring data on food brought to murre chicks. Murres were collected under permits from the U.S. Fish and Wildlife Service and the California Department of Fish and Game.

LITERATURE CITED

AINLEY, D. G., AND R. J. BOEKELHEIDE [EDS.]. 1990. Seabirds of the Farallon Islands: structure and dynamics of an upwelling-system community. Stanford Univ. Press, Stanford, CA.

AINLEY, D. G., C. S. STRONG, T. M. PENNIMAN, AND R. J. BOEKELHEIDE. 1990. The feeding ecology of Farallon seabirds, p. 51–127. *In* D. G. Ainley and R. J. Boekelheide [eds.], Seabirds of the Farallon Islands: structure and dynamics of an upwelling-system community. Stanford Univ. Press, Stanford, CA.

AINLEY, D. G., L. B. SPEAR, AND S. G. ALLEN. 1996. Seasonal and spatial variation in the diet of Cassin's Auklet reveals occurrence patterns of coastal euphausiids off California. Mar. Ecol. Progr. Ser. 137:1–10.

AINLEY, D. G., W. J. SYDEMAN, S. A. HATCH, AND U. R. WILSON. 1994. Seabird population trends along the west coast of North America: causes and the extent of regional concordance. Stud. Avian Biol. 15:119–133.

AINLEY, D. G., W. J. SYDEMAN, AND J. NORTON. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Mar. Ecol. Progr. Ser. 118:69–79.

AINLEY, D. G., W. J. SYDEMAN, R. H. PARRISH, AND W. H. LENARZ. 1993. Oceanic factors influencing occurrence patterns of young rockfish (*Sebastes*) in central California: a predator's perspective. Calif. Coop. Ocean. Fish. Investig., Rep. 34:133–139.

ALLEN, S. G. 1994. The distribution and abundance of marine birds and mammals in the Gulf of the Farallones and adjacent waters, 1985–1992. Ph.D. diss., Univ. Calif., Berkeley.

AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds. 6th ed. Allen Press, Lawrence, KS.

BALTZ, D. M., AND G. V. MOREJOHN. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. Auk 94:526–543.

BOLIN, R. L., AND D. P. ABBOTT. 1963. Studies on the marine climate and phytoplankton of the coast of California 1954–1960. Calif. Coop. Ocean. Fish. Invest., Rep. 9:23–45.

BRADSTREET, M. S. W., AND R. G. B. BROWN. 1985. Feeding ecology of the Atlantic Alcidae, p. 264–318. *In* D. N. Nettleship and T. R. Birkhead [eds.], The Atlantic Alcidae. Academic Press, Orlando, FL.

BRIGGS, K. T., D. G. AINLEY, L. B. SPEAR, P. B. ADAMS, AND S. SMITH. 1988. Distribution and diet of Cassin's Auklet and Common Murre in relation to central California upwellings. Acta Congr. Int. Ornithol. 19:981–990.

BRIGGS, K. T., W. B. TYLER, D. B. LEWIS, AND D. R. CARLSON. 1987. Bird communities at sea off California: 1975 to 1983. Stud. Avian Biol. 11:1–74.

CAIRNS, D. K. 1987. Seabirds as indicators of marine food supplies. Biol. Conserv. 5:261–271.

CAIRNS, D. K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94:811–824.

CARTER, H. R., G. J. MCCHESNEY, D. L. JACQUES, C. S. STRONG, M. W. PARKER, J. E. TAKEKAWA, D. L. JORY, AND D. L. WHITWORTH. 1992. Breeding populations of seabirds in California, 1989–1991, Vol. I. Final Rep. U.S. Dept. Interior, Minerals Manage. Serv., Pacific Outer Continental Shelf Region, Los Angeles.

COMPUTING RESOURCE CENTER. 1989. STATA: Reference manual, 4th ed. Santa Monica, CA.

CROLL, D. A. 1990. Physical and biological determinants of the abundance, distribution, and diet of the Common Murre in Monterey Bay, California. Stud. Avian Biol. 14:139–148.

DAY, R. H., AND G. V. BYRD. 1989. Food habits of the Whiskered Auklet at Buldir Island, Alaska. Condor 91:65–72.

DEPARTMENT OF COMMERCE. 1989. Pacific coast groundfish fishery. Fed. Reg. 54(196):41855–41858.

DUFFY, D. C., R. P. WILSON, AND M. P. WILSON. 1987. Spatial and temporal patterns of diet in the Cape Cormorant off southern Africa. Condor 89:830–834.

ERIKSTAD, K. E. 1990. Winter diets of four seabird species in the Barents Sea after a crash in the capelin stock. Polar Biol. 10:619–627.

FURNESS, R. W., AND R. T. BARRETT. 1991. Seabirds and fish declines. Natl. Geogr. Res. Explor. 7(1): 82–95.

FURNESS, R. W., AND P. MONAGHAN. 1987. Seabird ecology. Chapman and Hall, New York.

GLANZ, M. H., AND J. D. THOMPSON. 1982. Resource exploitation and environmental uncertainty. Wiley-Interscience, New York.

HOBSON, K. A., J. F. PIATT, AND J. PITOCCHELLI. 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. 63:786–798.

LEET, W. S., C. M. DEWEES, AND C. W. HAUGEN. 1992. California's living marine resources and their utilization. Calif. Sea Grant, Sea Grant Ext. Publ. UCSGEP-92-12, Davis, CA.

LENARZ, W. H. 1980. The shortbelly rockfish *Sebastes jordani*: a large unfished resource in waters off California. Mar. Fish. Rev. 42:34–40.

MATTHEWS, D. R. 1983. Feeding ecology of the Common Murre, *Uria aalge,* off the Oregon coast. M. Sc. thesis, Univ. Oregon, Newport.

MONTEVECCHI, W. A. 1993. Birds as indicators of change in marine prey stocks, p. 215–266. *In* R. W. Furness and J. J. D. Greenwood [eds.], Birds as monitors of environmental change. Chapman and Hall, New York.

NORUSIS, M. J. 1986. SPSS PC+ advanced statistics. SPSS, Inc., Chicago.

OGI, H., AND T. TSUJITA. 1977. Preliminary examination of stomach contents of murres (*Uria* spp.) from the eastern Bering Sea and Bristol Bay, June–August, 1970 and 1971. Jap. J. Ecol. 23:201–209.

OGI, H., H. TANAKA, AND T. TSUJITA. 1985. The distribution and feeding ecology of murres in the northwestern Bering Sea. J. Yamashina Inst. Ornithol. 17:44–56.

PCFFA (PACIFIC COAST FEDERATION OF FISHERMEN'S ASSOCIATIONS). 1986. Accentuate the positive. PCFFA Friday 14(6):1–3.

PIATT, J. F., AND D. N. NETTLESHIP. 1985. Diving depths of four alcids. Auk 102:293–297.

PINKAS, L., M. S. OLIPHANT, AND I. L. K. IVERSEN. 1971. Food habits of albacore, bluefin tuna, and bonita in California waters. Calif. Dept. Fish and Game, Fish. Bull. 152.

ROEMMICH, D., AND J. MCGOWAN. 1995. Climatic warming and the decline of zooplankton in the California Current. Science 267:1324–1326.

SCOTT, J. M. 1990. Offshore distributional patterns, feeding habits, and adult-chick interactions of the Common Murre in Oregon. Stud. Avian Biol. 14: 103–108.

SMITH, S. E., AND P. B. ADAMS. 1988. Daytime surface swarms of *Thysanoessa spinifera* (Euphausiacea) in the Gulf of the Farallones, California. Bull. Mar. Sci. 42:76–84.

SPEAR, L. B. 1993. Dynamics and effect of Western Gulls feeding in a colony of Guillemots and Brandt's Cormorants. J. Anim. Ecol. 62:399–414.

SPRING, L. 1971. A comparison of functional and morphological adaptations in the Common Murre (*Uria aalge*) and the Thick-billed Murre (*Uria lomvia*). Condor 73:1–27.

SWENNEN, C., AND P. DUIVEN. 1991. Diving speed and food-size selection in Common Guillemots, *Uria aalge.* Netherlands J. Sea Res. 27:191–196.

SYDEMAN, W. J., J. F. PENNIMAN, T. M. PENNIMAN, P. PYLE, AND D. G. AINLEY. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. J. Anim. Ecol. 60:135–149.