Studies in Avian Biology No. 14:139–148, 1990.

PHYSICAL AND BIOLOGICAL DETERMINANTS OF THE ABUNDANCE, DISTRIBUTION, AND DIET OF THE COMMON MURRE IN MONTEREY BAY, CALIFORNIA

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Abstract. Physical and biological factors affecting the diet, distribution, and abundance of the Common Murre (*Uria aalge*) in Monterey Bay, California were investigated from September 1981 through September 1983. Murre diet shifted both seasonally and annually, indicating an opportunistic feeding strategy. Highest abundance of murres was found during the summer period of late upwelling when murres exploit a dependable peak in prey availability (juvenile rockfish, *Sebastes* spp.) resulting from earlier upwelling episodes. Murres probably use this peak in food availability to feed dependent chicks at sea, replenish fat stores, and molt. During fall and winter productivity in Monterey Bay is low, and its importance to murres is reduced.

Distribution during summer when murre abundance is high is probably determined by local upwelling and current patterns. Densities were highest in the northern region of Monterey Bay, probably due to higher food availability. Water is advected from the southern to the northern portions of the Bay, carried by an eddy of the California Current. Upwelling is centered off of Point Pinos to the South. As recently upwelled, nutrient rich water is transported from south to north, it promotes increased phytoplankton production, which works its way to higher trophic levels as it is carried north. This results in higher prey availability in the north, and thus higher Common Murre density.

The primary effect of the 1982/1983 El Niño-Southern Oscillation phenomenon was a decrease in primary productivity that lead to a reduced availability of the normally dependable summer prey resources. As a consequence, murres which came into the Bay in June 1983 in large numbers quickly dispersed, resulting in low densities in July and August. Murres that were found in Monterey Bay at this time were thin and fed on a different array of prey items.

This study supports the hypothesis that concentrations of higher trophic level marine predators are concentrated "downstream" from upwelling centers. Peak abundance of murres in Monterey Bay occurred shortly after the seasonal peak in upwelling. During this peak abundance, murres were concentrated in the northern portion of the Bay (Soquel Cove) which is downstream of the upwelling center off of Point Pinos to the south.

Key Words: Seabird; murre; distribution; diet; Monterey Bay; El Niño.

The importance of food availability in the determination of seabird numbers has long been suggested but rarely documented quantitatively (e.g., Ashmole 1971, Shuntov 1972). The interrelation of breeding success, timing of breeding, and food availability has received considerable attention (e.g., Lack 1954, 1966, 1968), leading Ashmole (1971) to conclude that the location of breeding colonies may be determined in large part by the productivity of surrounding waters. For example, Anderson et al. (1982) found that Brown Pelican (*Pelecanus occidentalis*) reproductive output is closely related to local prey availability and abundance.

The role that food availability and productivity play in governing seabird distributions during nonbreeding seasons has not been determined clearly. Briggs et al. (1984) found that the distribution of phalaropes during the winter in the California Current was correlated with oceanographic "fronts." Haney (1987) found the nonbreeding seabirds he studied in the South Atlantic Bight off the southeastern United States were concentrated on the "crests" of internal waves, whereas Woodby (1984) found that the spring distribution of murres (*Uria* spp.) was only loosely correlated with prey patches in the southeastern Bering Sea. Brown (1980) suggested the characterization of nonbreeding seabird distribution on the basis of water types, while recognizing the importance of locally concentrated food. I used Brown's approach in analyzing the results of the present study.

The Common Murre (*Uria aalge*) is the most abundant breeding seabird along the coast of California (Briggs et al. 1983), typically arriving on central California colonies in February or March. Monterey Bay (Fig. 1) is approximately 32 km north of a small breeding colony of 2000–5000 birds at Hurricane Point, and approximately 160 km south of colonies on the Farallon Islands that number 60,000–100,000 birds (Sowls et al. 1980, Briggs et al. 1983). The first murres with dependent chicks normally appear in Monterey Bay in July (Alan Baldridge, Hopkins Marine Station, pers. comm.), but post breeding females, nonbreeders, and failed breeders may arrive earlier (pers. obs.). Although present in Monterey Bay throughout the year, murre abundance varies seasonally, apparently in concert with seasonal

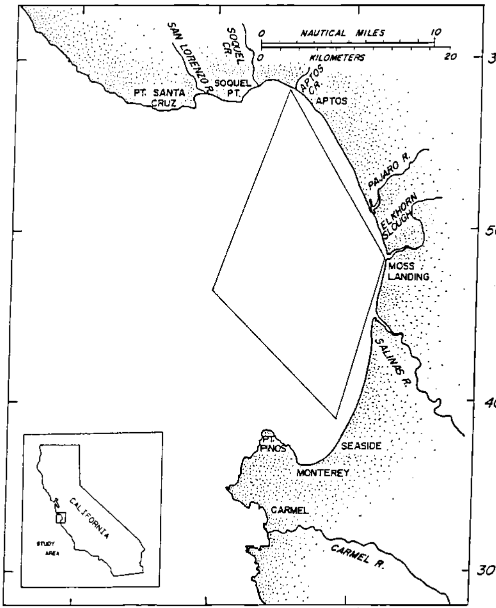

FIGURE 1. Monterey Bay, California study site. Transect route is indicated.

changes in oceanographic conditions. In their large scale study of seabird distribution off Central California, Briggs et al. (1983) found significant seasonal changes in Common Murre distribution. However, the large scope of that study precluded the description of small scale distribution patterns in populations responding to local changes in currents and productivity.

Since nonbreeding seabirds are not tied to a colony site, their distribution should, to a large degree, be a reflection of prey distribution. The diet of the Common Murre in the northeastern Pacific has received considerable attention (see Ainley and Sanger 1979 for a review). Unfortunately, studies of the winter diet of the Common Murre suffer from low sample size, making both seasonal and interspecific comparisons difficult (e.g., Baltz and Morejohn 1977).

By coupling bimonthly shipboard transects with feeding data from Common Murres incidentally entangled in commercial gill nets, I sought answers to the following questions for Monterey Bay Common Murres: 1) are there major seasonal or yearly changes in the diet? 2) are there major seasonal or yearly changes in distribution and abundance? 3) how do observed changes reflect spatial and temporal differences in oceanographic conditions and biological productivity?

Normal oceanographic seasonal transitions within Monterey Bay have been described by several authors (Bolin and Abbott 1963, Abbott and Albee 1967, Broenkow and Smethie 1978, Shea and Broenkow 1982). Generally, the hydrographic cycle may be divided into three variable, overlapping seasons: 1) upwelling from February through August, which encompasses both the Common Murre breeding period in the spring (February through May) and postbreeding period in the summer (June through August); 2) the fall, when offshore California Current waters enter the coastal region from September through October; and 3) the winter, when the California Counter Current (Davidson Current) surfaces from November through January. For the present study I considered the oceanographic seasons of Monterey Bay as follows: February–May (early upwelling period), spring; June–August (late upwelling period), summer; September–October (oceanic period), fall; November–January (Davidson period), winter.

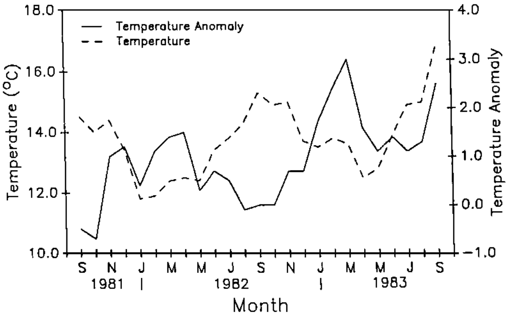

FIGURE 2. Monthly mean temperature and temperature anomaly for Monterey Bay, California. Temperature anomaly is the difference between the mean monthly temperature and the 30 year mean monthly temperature (Avers 1981, 1982, 1983).

Beginning in fall, 1982 there was an increase in water temperature in Central California caused by a strong "El Niño," persisting through the end of this study (Fig. 2). This provided an opportunity to compare the feeding and distribution of Common Murres under different circumstances: a normal year (1981–1982) and an "El Niño" year (1982–1983).

METHODS

FEEDING

I examined the stomach contents of 238 murres incidentally entangled in commercial gill nets in Monterey Bay. One hundred ninety-nine samples were taken from June 1981 through August 1982, excluding November through January. In addition, 39 samples were taken June through August 1983. All individuals were caught within the Bay at depths ranging from 3 to 70 m. As the gill nets were set over a 24 hour period, exact time of capture could not be determined. Birds taken from the fishermen who were hauling in their nets were placed immediately on ice to retard digestive processes during transport to the laboratory. In the laboratory, the peritoneal cavity was opened and sex, length and width of gonads, and diameter of largest follicle in females were determined. The proventriculus and gizzard were removed and frozen for later analysis of their contents.

Fat analysis

As an objective index of the fat condition of each bird, I measured the thickness of the dermis at an incision made in the skin over the left part of the upper breast (over the furculum) to the nearest 0.5 mm. Chu (1984) found that this measurement is a reliable predictor of fat condition in shearwaters. Individuals collected in summer were separated by sex and breeding status. Nonbreeders were defined as those lacking a brood patch. In the fall (September–October), individuals were simply separated by sex.

All comparisons of fat thickness were made by analysis of variance or Student's t-test (Zar 1974). Multiple comparisons were made using the Student Newman Keuls (SNK) multiple comparisons test (Zar 1974).

Molt analysis

I evaluated the stage of molt for each individual. Body molt was scored as present when new pinfeathers were found over approximately 10% or more of the breast area. Wing molt was recorded if one primary was missing with a pinfeather coming in to replace it, or if two or more primaries were missing on both wings.

Stomach analysis

The contents of the proventriculus and gizzard were sorted to the lowest determinable taxonomic category. The volume of each category was then measured by displacement of water in a graduated cylinder. Cephalopod beaks and fish otoliths were washed, and then identified by comparison with reference collections at Moss Landing Marine Laboratories, and pictorial guides (Fitch 1964, 1966; Iverson and Pinkas 1971; Morrow 1977). The minimum number of fish represented by otoliths was taken to be the greatest number of left or right sagittae; the minimum number of individual cephalopods was taken to be the greatest number of upper or lower beak halves (Baltz and Morejohn 1977).

Data analysis

To describe the seasonal importance of each prey species, I calculated percent composition of prey by number (%N), volume (%V), and frequency of occurrence (%FO). Using these values, I then calculated an Index of relative importance (IRI) developed by Pinkas et al. (1971) to avoid biases in assessing prey importance indicated by the above categories. This index is calculated for each prey category as:

$$(\%N_i + \%V_i)(\%FO_i) = IRI_i$$

Diversity indices

Green (1979) and Hurlbert (1971) suggest that simple indices such as the number of prey species (S) is a biologically meaningful measure that is a less ambiguous and better measure of biological change with respect to its relationship to environmental change than the more complex diversity indices. Accordingly, I calculated the simpler values: number of species (which is the number of species found in each stomach averaged over the sampling period), and percent dominance for each season. The percent dominance of prey species in the diet was calculated as follows:

$$D = \sum_{i=1}^{s} (n_i/N)^2$$

where Σ = total number of prey species eaten, n_i = number of individuals of prey species, i, present in sample, and N = total number of individuals in sample.

This value was then averaged over all stomachs for the sampling period. Dominance values range from 0 to 1. A dominance value of 1 indicates a sample with only one prey species.

Overlap indices

I used the percent similarity index (PSI) (Saunders 1960) to measure dietary overlap by season and year. It is calculated by summing the smallest percent by number of each prey species within the seasons or years under comparison:

$$PSI = \sum_{i=1}^{s} \min \%N_i$$

There are no statistical tests for computing significant overlap; I follow Silver (1975) in using 80%. I used chi-square analysis of the raw numerical prey data to compare yearly and seasonal murre diets. Prey observed in less than 10 stomachs were lumped as "other fish." I computed the G-statistic for significance testing (Sokal and Rohlf 1981).

TRANSECT

Thirty-five strip transects were surveyed within Monterey Bay from September 1981 through September 1983, using methods similar to those described by Briggs and Hunt (1981), except that the zone distances were modified to 200 m. These transects occurred approximately bimonthly, conditions permitting. To facilitate seasonal comparisons of relative densities, the ship ran an identical rectangular course for each census (Fig. 1) at a constant speed of 18.5 km/hr. Course was selected to sample adequately both the inshore region of the Bay, and the offshore canyon slope.

Two observers sat 3 m above the water line and recorded murres observed between 0 and 90 degrees to port and starboard of the bow. To minimize variation due to observer bias, the same observers made almost all surveys. In addition to number of individuals, the following data were taken: 1) distance from the ship, visually estimated and coded as Zone 1, 0–50 m from the ship or Zone 2, 51–200 m from the ship; 2) time of observation; 3) behavior of bird (flying, sitting on water surface, or following the ship); 4) sea condition (Beaufort scale), glare, percent cloud cover, precipitation, and a subjective evaluation of sighting conditions were recorded each hour or as conditions changed; the transect was terminated if sea state was greater than Beaufort 3, or subjective sighting conditions were poor; 5) boat speed, location, and time were logged every 15 min and at course changes to ensure that the ship followed the designated track for placement of sightings along the track line; 6) during the late upwelling period, Common Murre chick/adult pairs were noted.

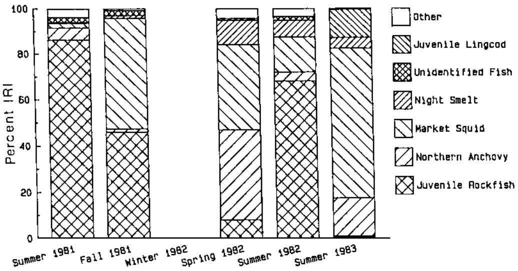

FIGURE 3. Seasonal diet of Monterey Bay Common Murres. Importance of prey species represented by percent index of relative importance (see text for explanation). ND = data not available for this season.

The transect was broken into 3 km segments for analysis. For each segment a density was calculated (number of murres per 3 km × 0.2 km segment) to be used as a discrete sample for statistical comparisons. Because variances were proportional to the means, samples were transformed by a square-root transformation for statistical testing. Comparisons between density values for each season were made by analysis of variance (Zar 1974). The data were subdivided into two depth categories: offshore (waters deeper than 40 m), and inshore (waters ≤40 m deep). The Monterey submarine canyon axis was chosen as the north–south dividing line. Therefore, comparisons within each season were made with respect to: north bay, inshore; north bay, offshore; south bay, inshore; and south bay, offshore. Comparisons between locations were made with one-way ANOVA or Student's t-test (Zar 1974).

Sea-surface temperature was measured by aircraft within four days of transect date using a radiation thermometer (Barnes PRT-5) mounted through the aircraft floor (see Briggs et al. 1981 for system description). Isotherms were plotted from aircraft data and then superimposed on transect data. Chlorophyll-a was measured by the Coastal Zone Color Scanning satellite (CZCS-Nimbus 7; see Gordon et al. 1980 for system description) within two days of transect date. Relative chlorophyll values are derived for each km^2. The satellite-derived chlorophyll values for the center of each discrete transect segment were used for data analysis. Depth was taken as the depth at the center of each discrete transect segment. Distance from nearest point of land was taken from the center of each discrete transect segment.

RESULTS

FEEDING

Percent IRI values show that the diet of Common Murres in Monterey Bay is dominated by juvenile rockfish (*Sebastes* spp.), market squid (*Loligo opalescens*), northern anchovy (*Engraulis mordax*), and night smelt (*Spirinchus starksi*) (Fig. 3). The importance of each of these species changed seasonally (Fig. 3). Juvenile rockfish (primarily *Sebastes jordani*) dominated during summer 1981 (% IRI = 83.5), then became less important during the 1981 fall period (% IRI = 45.5), when market squid became much more important (% IRI = 48.0). By winter, 1982 juvenile rockfish % IRI had dropped to a low of 8.0 and market squid to 36.9, while northern anchovy dominated (% IRI = 38.5), and night smelt increased to 10.7%. The diet of the Common Murre was different each season (G = 198.465, $P < .001$), and subdivision of the chi-square showed that each season was different from both the previous and subsequent season.

Diets in the summers of 1981, 1982, and 1983 were significantly different (G = 198.7, $P < .001$) (Fig. 3). As in 1981, the diet in 1982 was dominated by juvenile rockfish (% IRI = 66.8); however, in 1982 market squid and night smelt were much more important. There was also a significant difference (G = 67.26, $P < .001$) in summer diets in 1981 and 1982.

In the summer of 1983 the murres' diet changed dramatically, and differed significantly from 1981 (G = 444.08, $P < .001$) and 1982 (G = 274.8, $P < .001$). Juvenile rockfish were not important in 1983 and were replaced by market squid as the important food item, followed by northern anchovy. Also, a new species became important, juvenile ling cod (*Ophiodon elongatus*). Table 1 reveals that there was no seasonal difference either in the number of prey species per stomach (Kruskall Wallis; H = 9.452, $P > .05$) or in dominance values (Arcsine transform ANOVA; F = 1.289, $P > .05$). Therefore, individuals at any one time only fed upon one or two prey types. Within year overlap comparisons from June 1981 through May 1982 (Table 2) revealed that there were notable seasonal shifts in diet.

Results of between-year overlap comparisons from the summers of 1981, 1982, and 1983 (Table 2) show that overlap was high (PSI = 77.6) for 1981 vs. 1982, whereas it was low between 1981 vs. 1983 (PSI = 25.6) and 1982 vs. 1983 (PSI = 9.5). Thus in 1983 murres preyed upon a much different array of prey than in the previous two years.

FAT ANALYSIS

Summer fat indices did not differ between 1981 and 1982 for each breeding or sex category (Student's t-test, $P < .05$). Therefore, the indices for each category were combined for analysis. Mean (±SD) summer indices for each category were: nonbreeding female 3.3 mm (±1.0), N = 37; postbreeding female 2.1 mm (±0.9), N = 48; nonbreeding male 3.5 mm (±0.9), N = 69; postbreeding male 3.0 mm (±1.0), N = 50. Mean values for the four categories were significantly different (one way ANOVA; F = 22.04, $P < .001$), and female postbreeders were significantly leaner than all other categories (SNK; q = 11.14;

TABLE 1. NUMBER OF SPECIES PER STOMACH AND SPECIES DOMINANCE VALUES FOR MONTEREY BAY COMMON MURRES

Season	Number species/ stomach	Dominance
Summer 1981	1.63	0.72
Fall 1981	1.13	0.75
Spring 1982	1.80	0.53
Summer 1982	1.47	0.68
Summer 1983	1.59	0.67

TABLE 2. COMPARISONS OF MONTEREY BAY COMMON MURRE DIET BY SEASON AND YEAR (AS MEASURED BY PERCENT SIMILARITY INDEX)

Comparison	PSI
Summer 1981 vs. Fall 1981	53.18
Fall 1981 vs. Spring 1982	49.74
Spring 1982 vs. Summer 1982	37.50
Summer 1981 vs. Summer 1982	77.61
Summer 1981 vs. Summer 1983	9.46
Summer 1982 vs. Summer 1983	25.60

$P < .001$). No difference was found between the remaining three categories (SNK; $P > .05$). Therefore, summer postbreeding females were leaner than all other birds, which in turn exhibited no important differences in fat indices.

Fall fat indices of males did not differ from females ($t = 1.54$, $P > .05$), and the combined mean fat value was 3.9 mm (±1.0), $N = 42$.

Summer 1983 fat values did not differ significantly among the breeding/sex categories, in contrast to the situation in 1981 and 1982 (one way ANOVA; $F = 2.592$, $P > .05$). Therefore, the 1983 fat values were combined (combined mean 2.6 [±0.9], $N = 34$) and compared with 1981–1982 values. The 1983 summer birds were significantly fatter than 1981–1982 summer postbreeding females (Student's t-test; $P > .05$), but significantly leaner than all other 1981–1982 summer categories (one way ANOVA; $P > .05$).

MOLT

Body molt began in early July and finished by early November. Body molt occurred gradually over an extended period, while wing molt was rapid; all primaries were lost simultaneously.

Comparison of the number of postbreeding (as indicated by brood patches) vs. nonbreeding Common Murres molting in July shows that nonbreeding birds begin their molt sooner than postbreeding birds (G test; $G = 7.38$, $P < .01$).

TRANSECT

Seasonal abundance: September 1981–August 1982

In Monterey Bay, Common Murres were most abundant during the summer and fall (Fig. 4). Beginning in September 1981, population densities declined and remained low through the winter (Fig. 4). Density increased abruptly in March 1982, suggesting a strong northward migratory pulse, since 12.6% ($N = 144$) of all murres sighted were actively flying to the north, whereas 85.0% ($N = 1057$) were sitting on the water, and the remainder (2.4%, $N = 39$) flew in directions other than north. Moreover, numbers rapidly dropped again in April and remained low until July. Murre numbers then increased and peaked in late August. Thirty-two percent of all murres observed during summer 1982 were adult/chick pairs. The remarkably high mean density (169.2 birds/km^2) for late August was due primarily to a feeding flock comprised of over 3000 individuals in the northern, inshore region.

Areal utilization: September 1981–August 1982

Not all areas of Monterey Bay were equally important to Common Murres. In fall 1981 and summer 1982, the greatest concentrations were found in the northern inshore regions of the bay (Fig. 5) (Table 3). During other seasons the four areas were used equally (Table 3). However, numbers increased sharply during March in the offshore regions of the bay due to the migration pulse mentioned above.

Environmental correlates: September 1981–August 1982

A correlation matrix from environmental measurements along the transect line on 22 September 1981 and 30 August 1982, when murre densities were high, showed that densities were positively correlated with temperature, but not with distance from land or depth of water (Table 4; critical $r_{(.05,21)} = 0.413$). While chlorophyll was negatively correlated with both depth and distance from land, temperature was not correlated with either parameter. Although positively correlated in 1981, chlorophyll and temperature were not correlated in 1982. Murre density was highly correlated with chlorophyll in 1981 but not in 1982 (Table 4).

Seasonal abundance: September 1982–September 1983

From September 1982 through May 1983 (fall–spring) murre abundance was similar to that of the previous year (Fig. 4). However, the influx observed during the spring 1982 was not duplicated in 1983. In 1983 there were marked differences in murre abundances during the summer months. There was a rapid, large buildup in June, followed by an exodus in July. Numbers

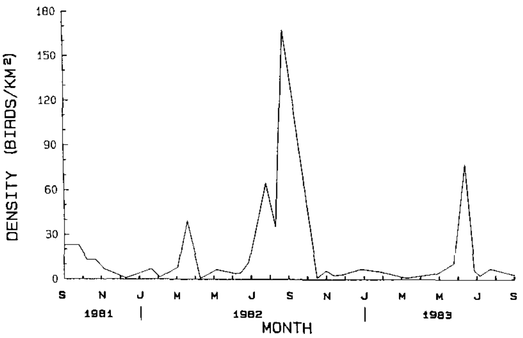

FIGURE 4. Common Murre densities in Monterey Bay from bimonthly transects.

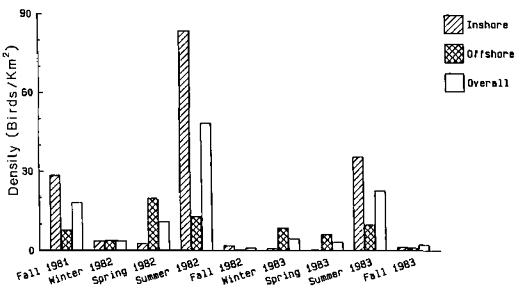

FIGURE 5. Areal distribution of Monterey Bay Common Murres. Depths greater than 40 meters considered offshore.

throughout the rest of the summer remained at low levels, similar to those in winter.

Areal utilization: September 1982–August 1983

Unlike in 1981, murres did not utilize the various regions of Monterey Bay differently during the fall period (Fig. 5). In the winter and spring of 1983, density was significantly higher in the offshore regions. These differences were not observed the previous year. Differences in areal utilization from the previous year were also evident during the summer. Similarly to summer 1982, murres were concentrated in the northern inshore region during summer 1983.

DISCUSSION

Throughout the year murres in Monterey Bay preyed upon groups that form large surface schools as adults (market squid, northern anchovy, night smelt), or have schooling juvenile forms (rockfish). The importance of the various species in the diet changed from season to season and from year to year. The widest variety of important prey species (% IRI values greater than 5) is taken by murres in the spring, whereas in summer murres appear to depend mainly on juvenile rockfish. As a population, the murres fed on a wide range of prey items, but the number of different prey species found in each individual bird was low. Evidently individual murres feed opportunistically, and since most of the prey species form large, monospecific schools (Frey 1971), an individual gut will show high dominance of a few species.

TABLE 3. ANOVA COMPARISONS OF SEASONAL MONTEREY BAY COMMON MURRE DENSITIES (BIRDS/KM²) BY AREA

Season	F	Error df	Significance
Fall 1981[a]	7.02	100	$P < 0.01$
Winter 1982	1.38	106	N.S.
Spring 1982	2.39	126	N.S.
Summer 1982[a]	5.11	152	$P < 0.01$
Fall 1982	1.85	22	N.S.
Winter 1983[b]	15.78	100	$P < 0.01$
Spring 1983[b]	12.52	94	$P < 0.01$
Summer 1983[a]	3.10	126	$P < 0.05$

[a] Student Newman Keuls multiple comparisons found Common Murre density was significantly higher in the northern inshore area; no significant difference between other areas.

[b] Student Newman Keuls multiple comparisons found Common Murre density was significantly higher in the offshore area; no significant difference between north-south densities.

Because wintering seabirds are not tied to breeding colonies, they are able to exploit ephemeral prey patches. Accordingly, one may expect winter seabird distribution and abundance to be adjusted rapidly as prey availability changes. The primary reason for an overwintering seabird to be found at sea is to exploit food resources dependably available there. Thus, differential seasonal abundance of wintering seabirds should be a reflection of differential seasonal availability of prey within a particular area.

The seasonal abundance of murres in Monterey Bay was greatest in the summer. Abundance then dropped rapidly during the fall, and remained low during the winter and spring (breeding) seasons. Their absence during the breeding season indicates that Monterey Bay is not an important area to breeders. However, it is used by adults with dependent chicks, molting nonbreeders, and lean, molting postbreeding females as a feeding area beginning in July. Braune and Gaskin (1982) speculated that the build-up of postbreeding larids off Deer Island, New Brunswick, indicated the importance of the area as a reliable food source for the replenishment of energy reserves lost during breeding, and as a feeding area to meet the energetic demands of molting. Monterey Bay probably serves a similar function for Common Murres.

TABLE 4. CORRELATION MATRICES OF COMMON MURRE DENSITIES AND ENVIRONMENTAL PARAMETERS DURING SUMMER 1981 AND 1982 IN MONTEREY BAY

	Depth	Distance	Temperature	Chlorophyll
Murre density	−0.291[a]	−0.378	0.442	0.622
	−0.303[b]	−0.348	0.594	0.202
Depth		0.832	−0.381	−0.515
		0.832	−0.281	−0.544
Distance			−0.270	−0.736
			−0.264	−0.783
Temperature				0.565
				0.361

[a] Transect date: 22 September 1981.

[b] Transect date: 30 August 1982.

The productivity of the waters of Monterey Bay has been studied intensively, mostly through the efforts of the California Cooperative Oceanic Fisheries Investigations program (e.g., Bolin and Abbott 1963, Broenkow and Smethie 1978, Garrison 1979, Shea and Broenkow 1982). Garrison (1979) found that phytoplankton standing stocks peaked during the spring and summer upwelling period between February and June and dropped to their lowest levels during winter. One would expect to first see an increase in grazers, followed by an increase in higher-level zooplankton feeders resulting from this increase in phytoplankton standing stocks. Anchovy, which feed directly on phytoplankton as well as on zooplankton, form large surface schools between April and June off California (Frey 1971). Cailliet et al. (1979) found that northern anchovy had the highest relative abundance of all shoaling prey groups collected in midwater trawls in February in Monterey Bay. It appears they are available to murres between February and June, when the anchovy possibly take advantage of the increase in phytoplankton standing stocks. Indeed, the northern anchovy was the most important prey of murres at this time.

The murre diet was dominated by juvenile rockfish during the summer, which Cailliet et al. (1979) found to be the most abundant prey taxa in shallow water in Monterey Bay during this period. Juvenile rockfish feed primarily on small crustaceans (Todd Anderson, Moss Landing Marine Laboratories, pers. comm.) and probably come into the bay during the summer to take advantage of high zooplankton numbers which result from the earlier phytoplankton increases. These observations best support the hypothesis that Common Murres in Monterey Bay exploited a seasonal peak in prey availability produced by earlier upwelling episodes.

Juvenile rockfish abundance probably drops off beginning some time in the fall, as juvenile rockfish begin to switch to rock substrate habitats offshore (Anderson 1984). This coincides with a reduction of primary productivity in the bay (Bolin and Abbott 1963). At this time murre abundance also drops and those that remain begin to feed upon market squid. However, squid availability is reduced at this time as well (Cailliet et al. 1979). Thus, Common Murres disperse out of Monterey Bay some time during the fall, when primary productivity has dropped considerably (Bolin and Abbott 1963), and prey availability has presumably decreased as well. Evidence suggests that at this time murres may be concentrating in the offshore shelf waters (Briggs et al. 1983).

Differential utilization of various habitats by seabirds has been discussed on both large and small scales (see Hunt and Schneider 1987 for a review). During the summer, murres concentrate in the shallow, northern portions of the bay. Correlation analysis from this time period revealed that murres concentrated in the warmer regions of the bay that were shallow and close to shore; chlorophyll was relatively unimportant in explaining variability in murre density. Thus, within the small-scale area of Monterey Bay during the summer period, murres appeared to select a particular set of environmental parameters.

How do these observations reflect the small scale processes occurring in Monterey Bay? Broenkow and Smethie (1978) found that upwelling occurs predominantly south of Monterey Bay. Nutrient-rich upwelled waters are advected into the Bay from the south by an eddy of the California Current and penetrate northward. Lasley (1977) found a net northerly inshore flow of water from Point Pinos towards Point Santa Cruz. Lasley (1977) also found that as water flowed to the north, chlorophyll levels decreased from a maximum off Point Pinos to a minimum in the northern bay, nutrient levels decreased, while temperature and oxygen levels increased. He believed low chlorophyll-to-phaeophyton ratios in the central and northern bay indicated substantial zooplankton grazing, whereas high ratios in the southern bay suggested little grazing. As water moves to the north, the biomass of higher trophic levels increases. As a result, a relatively higher abundance of species feeding upon zooplankters (i.e., juvenile rockfish) in the northern regions of the bay is expected. It appears that murres are concentrated in the warmer, low chlorophyll waters some distance away from the source of upwelling. This distance allows time for the effects of increased primary production to work its way up the food chain as the water is transported from the upwelling center.

Briggs et al. (1984) concluded similarly from a study of phalarope feeding in the California Current. They found that phalaropes fed upon zooplankton that was concentrated in convergences offshore. Phalarope distribution was correlated negatively with chlorophyll concentration. In their view, the best possible feeding conditions for phalaropes probably occurred "downstream" from an active upwelling center, where productivity resulting from upwelling has had time to work its way up the food chain. In their study of the relationship of seabird distribution to the hydrography of California, Briggs and Chu (1987:295) stated that "for fish and squid and their predators as well, optimal combinations of substrate, circulation, and feeding conditions are met downstream from major upwellings in less turbulent waters." Indeed, zooplankton and phytoplankton stocks were inversely related at smaller scales (Hunt and Schneider 1987). This may explain the relatively poor correlations of higher-trophic-level seabirds with oceanographic indicators of primary productivity such as low water temperature, high nutrient levels, and high chlorophyll concentration.

In winter 1982/1983, the effects of an El Niño-Southern Oscillation (ENSO) were first measured in the California Current off California (Reed 1983). These included anomalously high sea surface temperatures, high sea levels, and a deepening of the thermocline from about 30 m to 60–70 m in 1983 (McClain 1983). McGowan (1985) found zooplankton levels were down to record lows from previous 30 year median values. The 1982/1983 ENSO probably had two possible effects in the Central California region: 1) the onshore transport of warm, low-salinity water from the California Current (Simpson 1984) resulted in a downward tilt of the coastal thermocline; and 2) the poleward propagation of a baroclinic wave created at the equator resulted in an anomalous isotherm deepening off California and enhancement of the Davidson Current during winter 1982/1983, creating record high sea levels (McClain 1983). Whatever the cause, warm oceanic waters intruded into Monterey Bay (Fig. 2), effectively capping the usual nutrient upwelling. Anomalous observations of warm water species from the south (e.g., pelagic red crabs, *Pleuroncodes planipes*; California barracudas, *Sphyraena argentea*; and common dolphins, *Delphinus delphis*) increased (Alan Baldridge, Hopkins Marine Station, pers. comm.), while productivity decreased.

Concurrently, on the Farallon Islands off San Francisco, reproduction of seabird species dependent on seasonal upwelling was severely depressed (Boekelheide 1984). Common Murre egg production fell to 49% of the previous year, and the fledging rate of murres dropped from a normal mean of 0.7 to 0.9 chicks per pair to less than 0.05 per pair (Boekelheide 1984). Juvenile rockfish, which are normally the dominant prey delivered to chicks, were delivered in only 17.8% of the feeds in 1983 compared to 64.7% in 1982 (Boekelheide 1984).

There were also changes in murre distribution in Monterey Bay. Significantly more murres were found in the offshore regions in spring 1983. Maximum mean abundance in June increased well above the maximum mean density seen the previous year (from 4 birds/km^2 in 1982 to 88 birds/km^2 in 1983). This increase probably included failed breeders (out of 16 females examined, ova with yolk were found in 3 females, and eggs with complete shells were found in 2 females, pers. obs.). Evidence of widespread breeding failure was indicated by the absence of dependent chicks. Murre numbers then declined rapidly so that by late July the mean density was only 3 birds/km^2 (compared to 65 birds/km^2 in 1982).

Fat indices and diet of Common Murres in Monterey Bay also differed markedly during summer 1983. Murres examined were significantly leaner than those examined in 1981 and 1982, with the exception of the postbreeding females. Juvenile rockfish were the most important prey item to murres during the summer in 1981 and 1982, but in 1983 few juvenile rockfish were taken. Instead, market squid dominated the diet, followed by northern anchovy. Lea and Van Tresca (1984) found reduced rockfish reproductive output in both 1982 and 1983, and McClain (1983) observed lower market squid abundance in Monterey Bay in 1983. A prey species never seen in previous years, juvenile ling cod (*Ophiodon elongatus*), became the third most important prey item in 1983. Juvenile ling cod are widely dispersed on the sandy bottom (Frey 1971). This change in Common Murre diet to include a non-shoaling prey species in significant numbers is especially interesting, since it would require a coincidental change in the normal foraging behavior.

Therefore, as a result of the 1982/1983 ENSO, a large number of lean Common Murres entered Monterey Bay in June 1983. No chicks were found in the bay in 1983. The normally reliable juvenile rockfish resource probably was not available, resulting in a change in diet from that observed in the previous years. With low food availability, the murres quickly moved out of the bay, creating densities in July that are normally observed during the fall and winter seasons of low productivity.

During normal hydrographic years in Monterey Bay, Common Murres exploit a dependable seasonal peak in prey availability resulting from an earlier upwelling episode. Murres use this peak in food availability during the summer to feed dependent chicks, replenish fat stores, and molt. Murre diet and abundance change seasonally in response to changing local productivity. During the summer, when murre densities are highest, murres concentrate in the northern part of Monterey Bay. As advected water is transported from the southern to northern portions of the bay in an eddy of the California Current, the effects of increased production due to offshore upwelling results in a concomitant increase in higher trophic level productivity. This results in higher prey availability in the northern areas, leading to higher Common Murre abundance. The 1982/1983 ENSO resulted in depressed productivity, and ultimately decreased murre abundance in Monterey Bay.

This study indicates the importance of recognizing the temporal lag in productivity that results from increased nutrient availability after a physical event such as coastal upwelling. Biological benefits from increased nutrient availability are separated in time from the physical events that initiated them. Ocean currents translate this temporal separation into a spatial separation. Thus, distributions of higher trophic level organisms such as seabirds will be spatially separated from the physical indicators of primary productivity and nutrient availability.

ACKNOWLEDGMENTS

This work was supported by the Monterey Audubon Society, and the Asociacion de Biologos Ambulantes. Moss Landing Marine Laboratories provided logistical support. Tom Keating, Larry Spear, Jo Guerrero, Michael Newcomer, James Anderson, Bernadette Allen, Margo Jameson, and Lisa Ballance helped in surveys, laboratory analyses, and net observations. Dr. Kenneth Briggs provided invaluable advice in all aspects of the study. Dr. Bernd Wursig, Dr. Michael Foster, Dr. James Nybakken, Dr. Terrie Williams, and Dr. Joseph Jehl gave useful comments of the manuscript. Sheila and Alan Baldridge provided much appreciated encouragement and advice throughout the study.

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