

SEASONAL ABUNDANCE OF MARINE BIRDS IN NEARSHORE WATERS OF MONTEREY BAY, CALIFORNIA

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ABSTRACT: Monterey Bay, California, is a site of regional significance for marine birds. I studied the seasonal abundance of marine birds within 1 km of shore in Monterey Bay during 1999 and 2000. Total bird abundance was greatest during spring and fall migration, whereas diversity was greatest during winter. Species assemblages were fairly consistent by season in both years, but three species were more abundant during summer and fall 2000 than during those seasons in 1999. This increased abundance may have been a response to reduced prey availability outside the study area, related to sea-surface temperature in spring 2000 being higher than in spring 1999. The mean density of all species (363 birds/km²) was considerably greater than the density reported for Monterey Bay as a whole, indicating that the nearshore environment should receive unique consideration in studies of the abundance and distribution of marine birds.

Waters over the continental shelf of central California sustain the greatest biomass and density of seabirds within the California Current system (Briggs et al. 1987). Within this area, Monterey Bay is an area of regional significance, with an abundant and diverse assemblage of seabirds throughout the year. The majority of seabirds occurring in Monterey come here to feed on abundant prey when not breeding. Although seabirds in Monterey Bay have been fairly well studied (Stallcup 1976, Baltz and Morejohn 1977, Mason 1997, Benson 2002), there have been no published studies focusing on the seasonal abundance or distribution of marine birds very near shore (<1 km from shore). Opportunistic observations and aerial survey data from Monterey Bay (Bonnell and Ford 2001) indicate that the density of marine birds within 1 km of shore is greater than the density farther offshore.

The seasonal abundance of marine birds in Monterey Bay is related to marine productivity, climatic conditions, and the breeding and migratory behavior of individual species (Ainley 1976, Benson 2002). Marine productivity is greatest in summer, after northwest winds induce coastal upwelling

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north of the bay. Cool, upwelled waters are advected into the bay, where the surface circulation is cyclonic, flowing from south to north along the shore (Breaker and Broenkow 1994, Paduan and Rosenfeld 1996). Temperature and chlorophyll concentration in summer usually are greatest in the northeast corner of Monterey Bay, where an "upwelling shadow" results in water remaining longer (Graham and Largier 1997, Pennington and Chavez 2000). Chlorophyll concentration and carbon uptake within Monterey Bay are generally greatest near shore in the fall (Pennington and Chavez 2000). Although primary productivity in winter is lower, some upwelling occurs within Monterey Bay year round as a result of the orographic effects of the steep Monterey Submarine Canyon (Breaker and Broenkow 1994). Very near shore (at depths generally less than 10 m), these oceanographic factors may have less effect on marine productivity than wave action and nutrient input from two rivers, the Pajaro and the Salinas.

Three oceanographic seasons have been recognized for Monterey Bay: upwelling (approximately March to August), oceanic (October to December), in which warm surface water is advected into the bay, and Davidson Current (December to March), in which the warm north-flowing Davidson Current enters the bay (Bolin and Abbott 1963). These seasons can be indistinct and vary considerably in timing and intensity from year to year (Pennington and Chavez 2000). The occurrence of different seabird assemblages in Monterey Bay appears to be related to both oceanographic and climatic seasons and is affected by variation from year to year in marine productivity (Ainley 1976, Mason 1997, Roberson 2002).

From February 1999 to March 2001, I studied the seasonal abundance of marine birds near shore in Monterey Bay. This study provides baseline data on the abundance of seabirds in this highly productive but little-studied portion of Monterey Bay.

METHODS

I conducted 34 at-sea surveys for marine birds between 11 February 1999 and 19 March 2001. Transects paralleled the shore, between 400 m and 800 m off shore (the distance to shore varied as a result of surf conditions), between Capitola (Santa Cruz County) and Monterey Harbor (Monterey County). I covered the northern and southern sections of Monterey Bay, separated at Moss Landing, over two consecutive days. The combined length of the transects was approximately 47 km. The habitat surveyed was off of a sandy shoreline, in water <10 m deep. The study area receives freshwater input seasonally from the Pajaro and Salinas rivers, and a tidal plume formed daily at the mouth of Elkhorn Slough, a large tidal embayment at Moss Landing. Also at Moss Landing, the deep Monterey Canyon provides topographic relief to the otherwise gently sloping continental shelf offshore of the survey area. To avoid temporal autocorrelation, bay-wide transects were conducted at least two weeks apart.

Surveys were conducted from a 17-foot (5.2-m) open motorboat traveling consistently at 15 km/hr (8 knots). Two observers recorded birds within 50 m of the vessel, for a 100-m strip transect. All birds on the surface of the water were identified to the lowest level possible and recorded. Birds of

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several categories were difficult to identify to species. Western and Clark's Grebes (*Aechmophorus occidentalis* and *A. clarkii*) frequently dove in response to the survey vessel and were difficult to distinguish; they were pooled as "Western/Clark's Grebe." On the basis of surveys when the two species could be distinguished, Clark's Grebes probably composed 5–10% of the total number of *Aechmophorus* grebes. Subadult gulls were often unidentified, and contributed the majority of the "unidentified gulls." Thayer's Gulls (*Larus thayeri*) were not distinguished from Herring Gulls (*Larus argentatus*); these two species were pooled. Finally, the Eared and Horned Grebes (*Podiceps nigricollis* and *P. auritus*) were pooled. Flying birds were recorded only if they were plunge-divers (i.e., terns and pelicans) because other birds in flight were presumed to be passing through and not associated with the habitat surveyed. Surveys were conducted only in sea conditions of Beaufort 3 or less. Sea-surface temperature (SST) was measured every 5 seconds approximately 0.5 m below the surface by means of an Onset Tidbit XT temperature logger. I calculated mean SST for each survey, and mean monthly SST as the mean of all survey means during that month. I calculated a mean monthly upwelling index from daily upwelling index values measured at 36° N, 122° W, southwest of Monterey (Pacific Fisheries Environmental Lab 2001; www.pfeg.noaa.gov/).

I computed the mean density of each seabird species or pooled category by survey, by month, and by season. I chose four seasons that corresponded to approximate oceanographic seasons: spring or early upwelling (March, April, and May), summer or late upwelling (June, July, and August), fall (September, October, and November), and winter (December, January, and February). These seasons also corresponded to the life cycles of many seabirds, which breed in spring and summer and migrate to and from wintering sites in fall and spring. I compared seasonal seabird abundance data graphically and by means of the percentage-similarity index, in which percentage similarity is the sum of all the minimums of either the percentage of a given species (out of the total) in sample 1, or the percentage of that species in sample 2 (Krebs 1999). Using Student's *t* tests (Zar 1996), I tested for differences by season between 1999 and 2000 in overall bird density, richness (species count), SST, upwelling, and density of 17 species with mean densities >1.0 birds/km.

RESULTS

Oceanographic Factors

The mean SST recorded during all transects was 13.2° C [standard deviation (SD) 1.7]; it was highest in August and lowest in February (Figure 1). A reduction in temperature in April of both years probably indicated the onset of spring upwelling. With readings throughout each year combined, there was no significant difference in mean temperatures between 1999 and 2000 (*t* test, $P = 0.32$). In spring 1999, however, mean SST was significantly greater than in spring 2000 than (*t* test, $P = 0.002$); between other pairs of seasons the mean SST did not differ significantly (*t* test, $P > 0.88$).

The monthly upwelling index was greatest from March to August (Figure 2). Although upwelling in the California Current was unusually strong in

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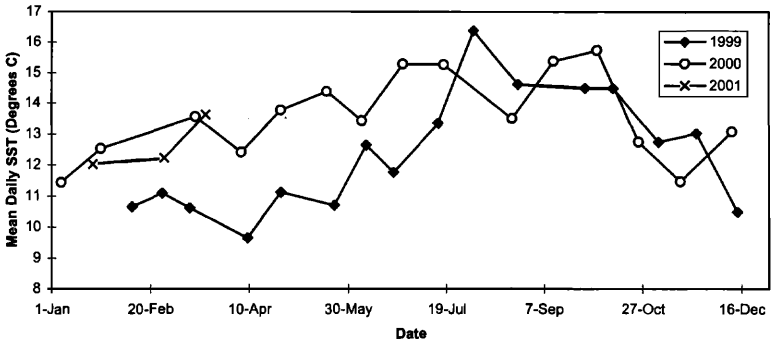


Figure 1. Mean daily sea-surface temperature recorded during 34 transects in nearshore Monterey Bay from 1999 to 2001.

summer 1999 (Schwing et al. 2000), there was no significant difference between 1999 and 2000 in mean upwelling indices at 36° N, 122° W (t test, $P = 0.41$). Neither was there any difference in mean upwelling between 1999 and 2000 in any pair of seasons (t test, $P > 0.11$).

Bird Abundance and Diversity

I recorded 43 species of seabirds (Table 1). Within the categories of pooled species, I identified all species except Thayer's Gull, and each species contributed to the figures for overall diversity. The mean density of all species combined was 362.6 birds/km² (SD 264.7). Overall seabird density was greatest in winter 1999–2000, least in summer 1999. Peaks in seabird abundance in September and April (Figure 3) resulted from increased numbers of Sooty Shearwaters and, in April 1999 and 2000, from increased numbers of Western/Clark's Grebes. The mean number of species per survey was

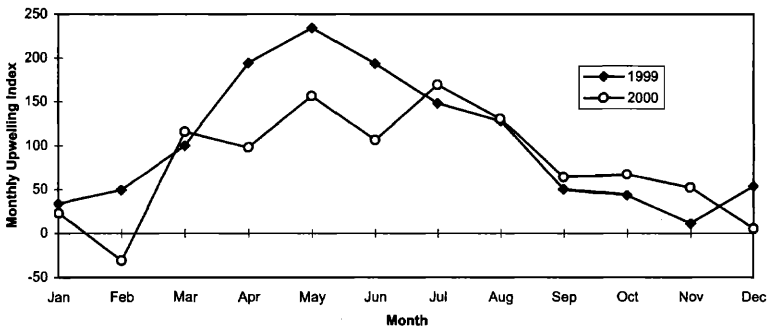


Figure 2. Mean monthly upwelling index reported by the Pacific Fisheries Environmental Lab (www.pfeg.noaa.gov/) west of Monterey Bay in 1999 and 2000. Means are calculated from daily upwelling values.

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Table 1 Mean Density of Seabirds in Nearshore Monterey Bay, 1999–2001^a

Species ^b	Mean density ^c	Spring 1999	Summer 1999	Fall 1999
Western/Clark's Grebe (<i>Aechmophorus</i> spp.)	202.42 (0.89) ^e	325.25 (1.01)	35.51 (0.25)	225.86 (0.93)
Sooty Shearwater (<i>Puffinus griseus</i>)	46.14 (4.09)	0.00 (0.00)	0.08 (2.24)	0.05 (2.00)
California Gull (<i>Larus californicus</i>)	22.62 (1.17)	7.68 (0.84)	5.16 (1.34)	29.42 (0.66)
Surf Scoter (<i>Melanitta perspicillata</i>)	20.09 (1.03)	26.96 (0.38)	12.15 (1.02)	11.26 (1.26)
Brandt's Cormorant (<i>Phalacrocorax penicillatus</i>)	14.35 (1.55)	1.79 (1.08)	8.14 (1.02)	11.90 (1.03)
Western Gull (<i>Larus occidentalis</i>)	13.83 (0.83)	3.90 (0.73)	8.71 (0.56)	32.58 (0.33)
Brown Pelican (<i>Pelecanus occidentalis</i>)	6.87 (1.40)	1.83 (1.19)	6.95 (0.59)	8.21 (0.97)
Heermann's Gull (<i>Larus heermanni</i>)	5.57 (1.90)	0.11 (2.00)	2.86 (1.44)	13.43 (1.05)
Elegant Tern (<i>Sterna elegans</i>)	5.48 (2.08)	0.00 (0.00)	15.82 (1.00)	6.63 (1.14)
Unidentified gull	5.41 (1.52)	2.05 (1.73)	4.67 (1.57)	11.24 (1.35)
Common Murre (<i>Uria aalge</i>)	3.52 (1.87)	0.00 (0.00)	2.40 (1.99)	6.69 (1.18)
Marbled Murrelet (<i>Brachyramphus marmoratus</i>)	2.74 (1.99)	1.78 (1.84)	0.17 (1.05)	3.94 (1.82)
Mew Gull (<i>Larus canus</i>)	1.34 (3.21)	0.05 (2.00)	0.04 (2.24)	1.00 (1.49)
Forster's Tern (<i>Sterna forsteri</i>)	1.33 (1.38)	1.68 (1.01)	0.13 (1.49)	2.16 (1.11)
Pacific Loon (<i>Gavia pacifica</i>)	1.29 (1.63)	2.48 (1.78)	0.00 (0.00)	0.73 (1.06)
White-winged Scoter (<i>Melanitta fusca</i>)	1.29 (1.50)	1.26 (1.41)	0.04 (2.24)	0.79 (2.00)
Caspian Tern (<i>Sterna caspia</i>)	1.15 (1.73)	3.98 (0.75)	2.76 (0.79)	0.05 (2.00)
Common Loon (<i>Gavia immer</i>)	0.99 (1.35)	3.46 (0.74)	0.21 (1.23)	1.15 (0.94)
Eared/Horned Grebe (<i>Podiceps</i> spp.)	0.83 (1.33)	0.84 (0.94)	0.08 (2.24)	0.79 (1.38)
Glaucous-winged Gull (<i>Larus glaucescens</i>)	0.73 (1.55)	0.37 (1.35)	0.13 (2.24)	0.53 (2.00)
Pigeon Guillemot (<i>Cephus columba</i>)	0.72 (1.55)	0.42 (0.82)	1.42 (0.92)	0.63 (1.18)
Bonaparte's Gull (<i>Larus philadelphia</i>)	0.56 (3.49)	0.21 (1.41)	0.00 (0.00)	0.16 (2.00)
Pelagic Cormorant (<i>Phalacrocorax pelagicus</i>)	0.54 (1.22)	1.42 (0.61)	0.71 (1.50)	0.52 (1.48)
Herring/Thayer's Gull (<i>Larus</i> spp.)	0.53 (2.32)	0.11 (2.00)	0.29 (0.96)	1.79 (1.85)
Unidentified loon	0.46 (2.28)	1.47 (1.91)	0.04 (2.24)	0.32 (1.15)
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	0.44 (3.48)	0.00 (0.00)	0.29 (2.24)	2.94 (1.33)
Unidentified cormorant	0.17 (3.55)	0.79 (1.83)	0.04 (2.24)	0.58 (1.55)
Red-necked Phalarope (<i>Phalaropus lobatus</i>)	0.15 (4.61)	0.00 (0.00)	0.80 (2.24)	0.00 (0.00)
Unidentified scoter	0.14 (3.06)	0.05 (2.00)	0.00 (0.00)	0.00 (0.00)
Other waterfowl ^d	0.14 (2.69)	0.21 (1.41)	0.00 (0.00)	0.05 (2.00)
Rhinoceros Auklet (<i>Cerorhinca moncerata</i>)	0.13 (2.50)	0.00 (0.00)	0.00 (0.00)	0.48 (1.72)

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Winter 2000	Spring 2000	Summer 2000	Fall 2000	Winter 2001
405.70 (0.07)	197.80 (0.47)	230.71 (0.57)	115.68 (0.73)	221.57 (1.19)
0.00 (0.00)	171.64 (2.00)	0.00 (0.00)	220.42 (2.00)	0.00 (0.00)
70.91 (0.43)	0.31 (1.59)	10.57 (0.89)	42.03 (0.65)	36.61 (0.96)
25.81 (0.59)	22.22 (1.08)	0.95 (1.16)	8.57 (1.81)	54.93 (0.63)
2.03 (0.76)	2.20 (0.69)	55.79 (0.61)	35.06 (0.47)	2.86 (0.33)
12.34 (0.48)	3.62 (1.27)	15.90 (0.73)	27.70 (0.14)	10.80 (0.43)
0.14 (0.87)	1.63 (0.72)	11.70 (1.01)	24.96 (0.45)	1.60 (1.00)
0.07 (1.73)	0.00 (0.00)	8.59 (1.01)	21.39 (0.85)	0.28 (1.73)
0.00 (0.00)	0.11 (2.00)	10.20 (1.83)	9.89 (1.71)	0.00 (0.00)
5.89 (0.93)	1.63 (1.02)	8.71 (1.26)	10.38 (1.07)	1.18 (1.06)
0.14 (0.87)	0.05 (2.00)	6.35 (0.71)	13.69 (0.83)	0.00 (0.00)
4.91 (0.86)	1.05 (1.51)	0.05 (2.00)	1.06 (1.75)	8.70 (1.73)
0.14 (1.73)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	7.25 (1.51)
1.40 (0.48)	4.20 (0.64)	0.37 (1.18)	1.00 (1.61)	0.28 (1.15)
0.84 (0.50)	0.89 (1.12)	0.63 (1.19)	3.31 (1.06)	2.16 (0.62)
3.43 (0.71)	1.26 (0.98)	0.00 (0.00)	0.11 (2.00)	2.37 (0.50)
0.00 (0.00)	0.53 (1.06)	1.63 (1.35)	0.11 (1.15)	0.00 (0.00)
0.42 (0.86)	0.95 (0.73)	0.26 (1.20)	0.84 (0.74)	1.11 (0.47)
0.98 (0.33)	0.63 (1.58)	0.00 (0.00)	1.27 (1.50)	2.58 (0.49)
3.09 (0.58)	0.10 (1.15)	0.11 (2.00)	0.58 (2.00)	1.74 (0.07)
0.07 (1.73)	0.21 (1.41)	1.94 (1.00)	1.05 (1.37)	0.00 (0.00)
3.57 (1.63)	0.21 (1.41)	0.00 (0.00)	1.32 (2.00)	0.07 (1.73)
0.49 (0.25)	0.53 (0.76)	0.26 (0.77)	0.05 (2.00)	0.07 (1.73)
1.47 (0.14)	0.05 (2.00)	0.05 (2.00)	0.42 (1.69)	0.70 (1.25)
0.21 (1.00)	0.84 (1.06)	0.05 (2.00)	0.10 (2.00)	0.63 (1.20)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.42 (0.91)	0.00 (0.00)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
0.00 (0.00)	0.00 (0.00)	0.31 (2.00)	0.00 (0.00)	0.00 (0.00)
0.84 (1.52)	0.16 (2.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
0.14 (0.87)	0.16 (2.00)	0.00 (0.00)	0.11 (1.15)	0.77 (1.50)
0.35 (1.25)	0.00 (0.00)	0.05 (2.00)	0.05 (2.00)	0.14 (0.87)

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Table 1 (continued)

Species ^b	Mean density ^c	Spring 1999	Summer 1999	Fall 1999
Long-tailed Duck (<i>Clangula hyemalis</i>)	0.11 (2.85)	0.42 (2.00)	0.00 (0.00)	0.00 (0.00)
Red-throated Loon (<i>Gavia stellata</i>)	0.11 (2.52)	0.42 (1.69)	0.04 (2.24)	0.11 (2.00)
Parasitic Jaeger (<i>Stercorarius parasiticus</i>)	0.10 (3.06)	0.00 (0.00)	0.04 (2.24)	0.37 (1.64)
Unidentified bird	0.10 (2.42)	0.16 (1.27)	0.00 (0.00)	0.53 (0.95)
Ring-billed Gull (<i>Larus delawarensis</i>)	0.08 (2.88)	0.11 (1.15)	0.00 (0.00)	0.05 (2.00)
Brant (<i>Branta bernicla</i>)	0.04 (2.96)	0.11 (2.00)	0.00 (0.00)	0.00 (0.00)
Red-necked Grebe (<i>Podiceps grisegena</i>)	0.04 (2.95)	0.16 (1.27)	0.00 (0.00)	0.00 (0.00)
Red Phalarope (<i>Phalaropus fulicarius</i>)	0.03 (5.83)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Unidentified alcid	0.01 (4.06)	0.00 (0.00)	0.04 (2.24)	0.05 (2.00)
Northern Fulmar (<i>Fulmarus glacialis</i>)	0.01 (5.83)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Ancient Murrelet ^e (<i>Synthliboramphus antiquus</i>)	0.01 (5.83)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Total	362.61	391.53	109.75	376.98

^aFigures in parentheses are coefficients of variation.

^bIn order of abundance.

^cIn birds per square kilometer.

^dIncludes Ross' Goose (*Chen rossii*), Cinnamon Teal (*Anas cyanoptera*), unidentified scaup (*Aythya* sp.), Bufflehead (*Bucephala albeola*), Red-breasted Merganser (*Mergus serrator*), and Ruddy Duck (*Oxyura jamaicensis*).

^eAncient Murrelets occurred during February 1999, outside of seasonal categories.

16.8 (SD 3.2). Species richness (maximum number of species recorded) by season was greatest in December and November and least in June and May (Figure 4). Six species or pooled categories had mean densities >10.0 birds/km²: Western/Clark's Grebe, Sooty Shearwater, California Gull, Surf Scoter, Brandt's Cormorant, and Western Gull.

The Western Grebe was the most abundant species. The mean density for the genus *Aechmophorus* was 204.4 birds/km (SD 180.2), composing 56% of all birds recorded (Table 1). Western/Clark's Grebes were recorded on all surveys but were most abundant in winter and spring. Counts regularly exceeded 1000 birds per survey. The highest count, in April 1999, was of more than 3800 birds. High counts in late spring coincided with a shift in distribution to the north end of Monterey Bay, where courting behavior was occasionally observed. Western Grebes were usually found in large dense flocks. Single grebes identified outside of flocks were more likely to be Clark's than the Western.

Large flocks of Sooty Shearwaters were encountered twice, in April and September 2000. Although shearwater flocks were recorded on only two surveys, Sooty Shearwaters were the second most abundant species, with

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Winter 2000	Spring 2000	Summer 2000	Fall 2000	Winter 2001
0.07 (1.73)	0.05 (2.00)	0.00 (0.00)	0.05 (2.00)	0.14 (1.73)
0.00 (0.00)	0.16 (2.00)	0.00 (0.00)	0.11 (1.15)	0.07 (1.73)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.42 (1.35)	0.00 (0.00)
0.00 (0.00)	0.05 (2.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
0.07 (1.73)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.28 (1.73)
0.00 (0.00)	0.11 (2.00)	0.00 (0.00)	0.00 (0.00)	0.07 (1.73)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.21 (1.00)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.35 (1.73)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.14 (1.73)
0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
545.55	413.33	365.20	542.17	359.65

a mean density of 46.1 birds/km² (SD 188.8). On the surveys when they were encountered, density exceeded 680 birds/km², and the shearwaters were in dense flocks (all 3268 birds recorded in April 2000 were within 1 km of transect near Capitola). One to two birds were recorded on surveys in July and September 1999.

The California Gull was the third most abundant species, with a mean density of 22.6 birds/km² (SD 26.6). California Gulls were recorded in all months but were most abundant from September to January. The Surf Scoter was the fourth most abundant species, with a mean density of 20.9

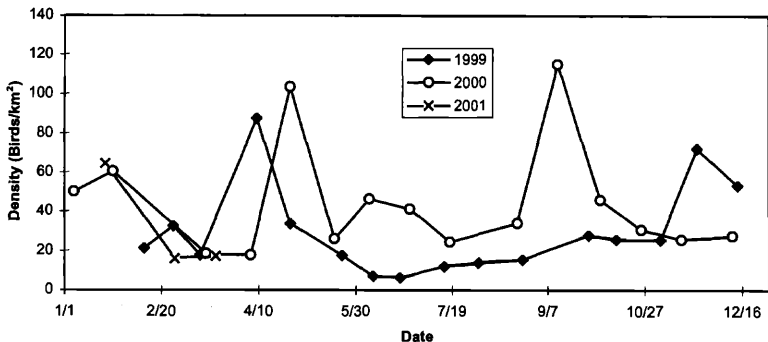


Figure 3. Daily density of all seabirds in nearshore Monterey Bay, 1999–2001.

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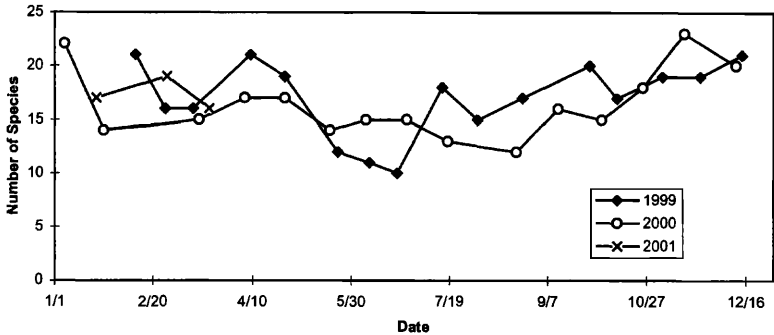


Figure 4. Daily species richness (species count) of seabirds in nearshore Monterey Bay, 1999–2001.

birds/km² (SD 20.7). Surf Scoters were most abundant in winter (December to March) but were recorded in all months except September. Surf Scoters were usually in fairly dense flocks, sometimes associated with White-winged Scoters.

Brandt's Cormorants were mostly absent from the study area from January through May, during prebreeding colony attendance and the early part of their breeding season. This species was common on Monterey Bay from June to November, with an overall mean density of 14.4 birds/km² (SD 22.3). Brandt's Cormorant was the fifth most abundant species, with >50 birds/km² on several days. The Western Gull was the sixth most abundant species, with a mean density of 13.8 birds/km² (SD 11.5). Western Gulls were present year round but were most abundant during fall.

The 26 most abundant species or pooled categories whose seasonal abundance I analyzed comprised four general categories: migrants (occurring primarily March–May and September–November), winter birds (November–March), summer birds (April–September), and fall birds (July–November). Nine species occurred primarily during winter (Figure 5), nine occurred during fall (Figure 6), six occurred primarily during migration, in spring and fall (Figure 7), and two occurred primarily during summer (Figure 8).

The percent similarity index (PSI) for each season ranged from 0.46 to 0.95 (Table 2). I excluded the Sooty Shearwater from the PSI calculations because this species was so patchy, temporally and spatially, extremely abundant when present, and not effectively sampled in this nearshore study. Although the Sooty Shearwater is usually the most abundant bird in Monterey Bay during spring and summer (Ainley 1976, Briggs et al. 1987, Mason 1997), it was rarely recorded during this study. In comparisons between seasons, the PSI implied greatest similarities between spring 1999 and spring 2000, spring 1999 and winter 2000, winter 2000 and spring 2000, and winter 2000 and winter 2001. These values were affected positively by density values for Western/Clark's Grebes, which usually composed more than 50% of all birds recorded. Separate PSI values calculated with the Sooty Shearwater and Western/Clark's Grebes excluded never exceeded

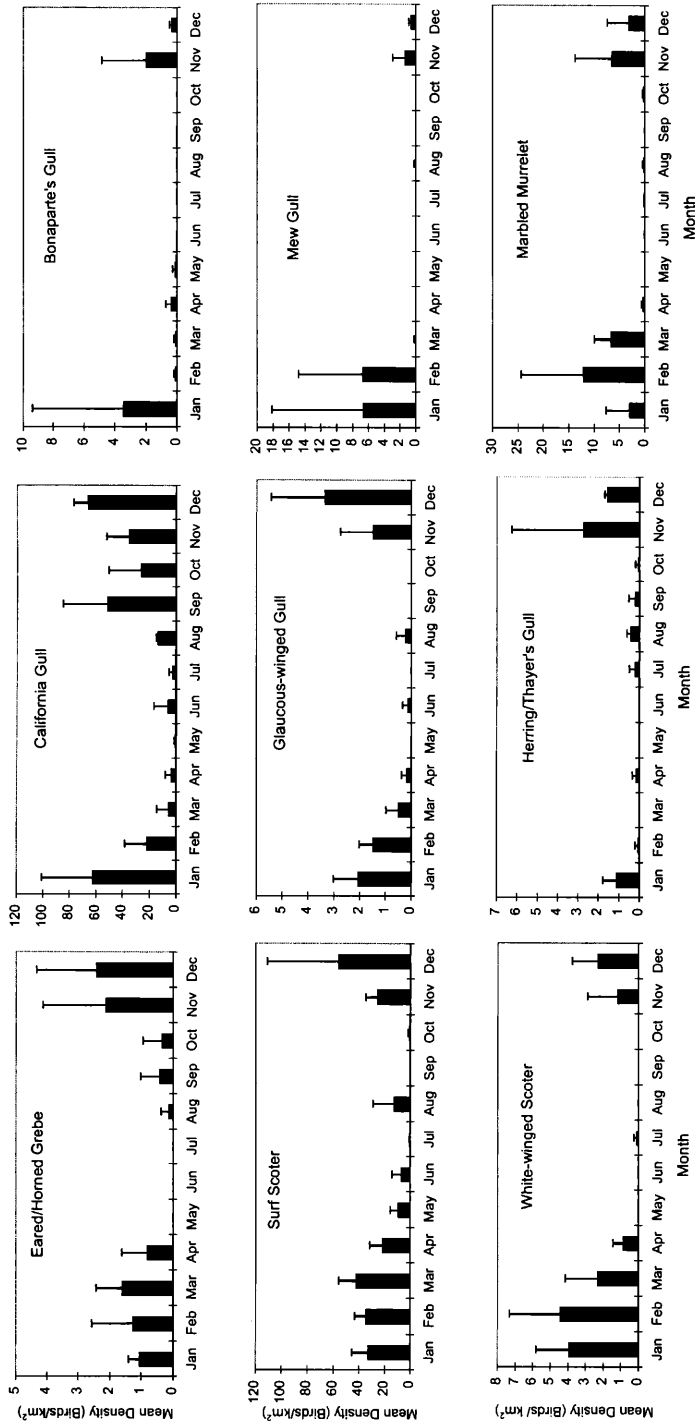


Figure 5. Mean monthly density of nine species or pooled categories of seabirds occurring in nearshore Monterey Bay primarily during winter, based on 34 surveys from 1999 to 2001. Error bars show one standard deviation. Note differences in y-axis scales.

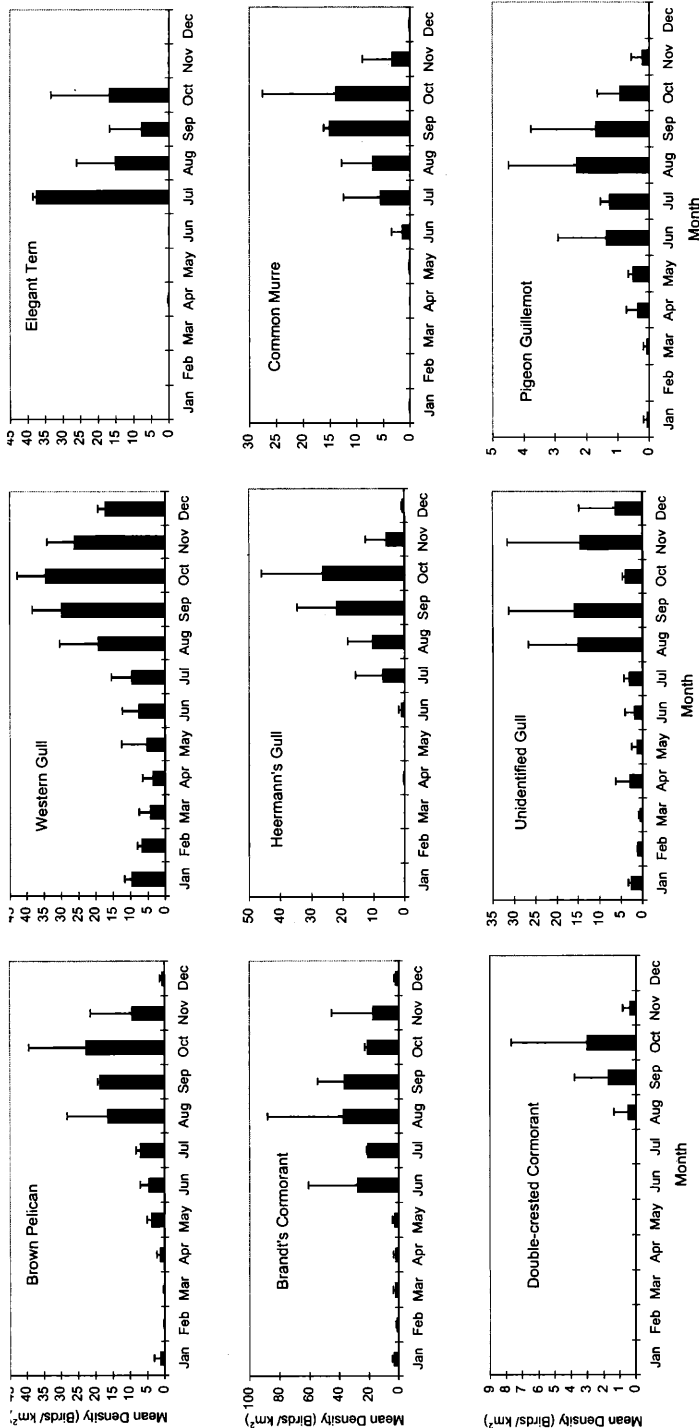


Figure 6. Mean monthly density of nine species or pooled categories of seabirds occurring in nearshore Monterey Bay primarily during fall, based on 34 surveys from 1999 to 2001. Error bars show one standard deviation. Note differences in y-axis scales.

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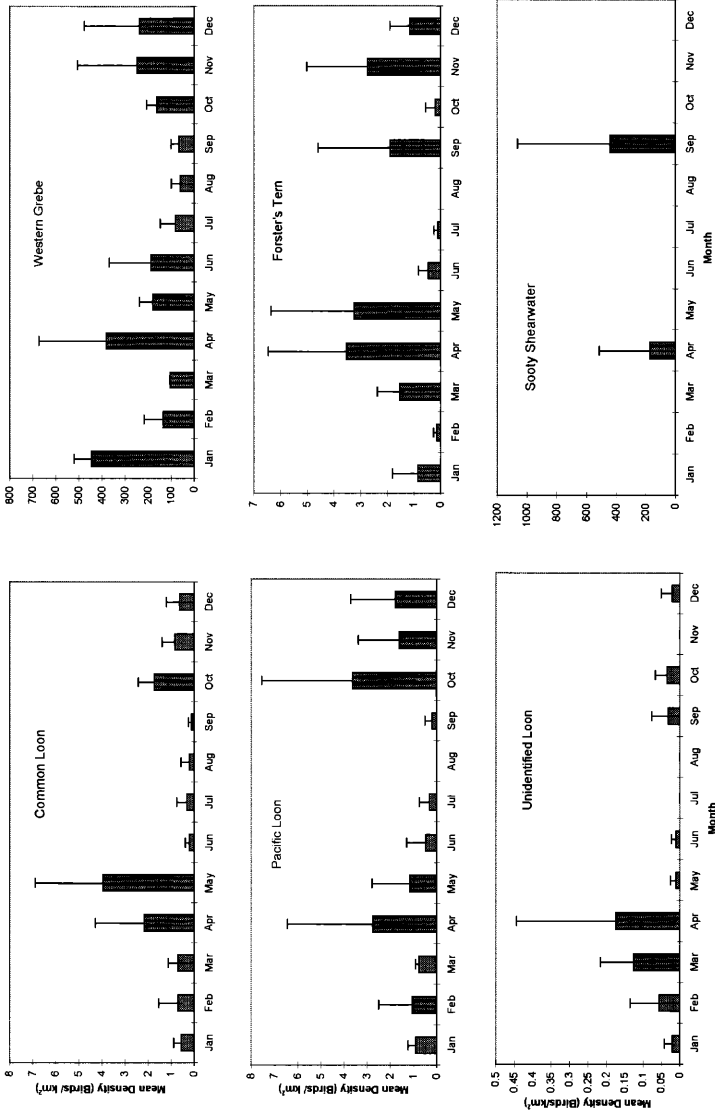


Figure 7. Mean monthly density of six species or categories of seabirds occurring in nearshore Monterey Bay primarily during migration, based on 34 surveys from 1999 to 2001. Error bars show one standard deviation. Note differences in y-axis scales.

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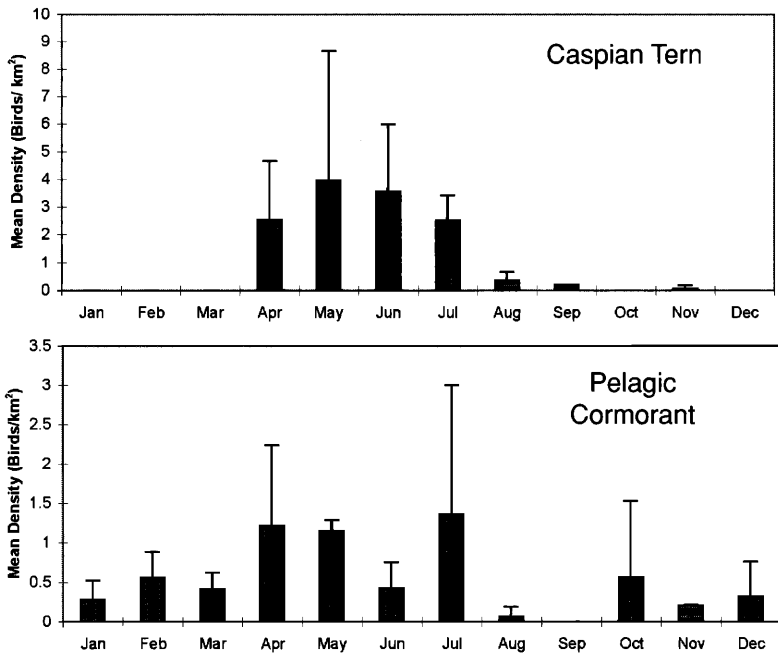


Figure 8. Mean monthly density of two species of seabirds occurring in nearshore Monterey Bay primarily during summer, based on 34 surveys from 1999 to 2001. Error bars show one standard deviation. Note differences in y-axis scales.

0.8 (range 0.25 to 0.77; Table 3), indicating that consistent high counts of Western/Clark's Grebes affected PSI values greatly. PSI values for the remaining species exceeded 0.7 three times, two of which were for the same season (spring 1999/spring 2000 and fall 1999/fall 2000), with the remaining value between spring 1999 and winter 2001.

Between 1999 and 2000 overall mean density did not differ significantly, but in comparisons between paired seasons, density was greater in summer 2000 than in summer 1999 ($P < 0.001$). There was no difference in density between other paired seasons ($P > 0.28$). Mean species richness (number of species per survey) did not vary significantly from 1999 to 2000 or in comparisons of any pair of seasons ($P > 0.57$). Of the 17 most abundant species whose abundance I compared by paired seasons in 1999 and 2000, only three varied significantly in abundance. The mean density of Western/Clark's Grebes and Brandt's Cormorants was significantly greater in summer 2000 than in summer 1999 (Table 1; t test, $P = 0.01$ and $P = 0.02$, respectively). The mean density of Brown Pelicans was significantly greater in fall 2000 than in fall 1999 (t test, $P = 0.05$). The other 14 species did not differ by year at any season ($P > 0.05$).

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Table 2 Percentage Similarity Indexes of the Species Composition of the Nearshore Avifauna of Monterey Bay by Season, All Species Except the Sooty Shearwater Included^a

	Spring 1999	Summer 1999	Fall 1999	Winter 2000	Spring 2000	Summer 2000	Fall 2000	Winter 2001
Spring 1999	1.0	0.46	0.70	0.85	0.95	0.69	0.45	0.75
Summer 1999		1.0	0.64	0.47	0.47	0.61	0.74	0.54
Fall 1999			1.0	0.77	0.69	0.82	0.73	0.78
Winter 2000				1.0	0.84	0.71	0.57	0.82
Spring 2000					1.0	0.68	0.45	0.76
Summer 2000						1.0	0.68	0.70
Fall 2000							1.0	0.56

^aValues greater than 0.8 are in bold.

DISCUSSION

Bird Abundance and Diversity

As expected, the density of seabirds near shore in Monterey Bay was considerably greater than mean densities reported from studies conducted at larger spatial scales farther offshore. The mean density of 362.6 birds/km² in this study was more than double the 173 birds/km² reported primarily offshore in Monterey Bay from 1992 to 1994 (Mason 1997). Briggs et al. (1987) reported a density of 110 birds/km² over the continental shelf in California from 1975 to 1983, and Gould et al. (1982) reported a density of 158 birds/km² in the Gulf of Alaska. Seabird densities reported by other studies elsewhere in the North Pacific are typically <100 birds/km² (Gould and Piatt 1993). Because most of these other researchers recorded all birds in flight (not plunge-divers only), if I had followed the same protocol the densities I report would be even higher, especially for gulls. Mason (1997), for example, estimated that 44% of gulls recorded were flying. The only re-

Table 3 Percentage Similarity Indexes of the Species Composition of the Nearshore Avifauna of Monterey Bay by Season, All Species Except the Sooty Shearwater and Western/Clark's Grebes Included^a

	Spring 1999	Summer 1999	Fall 1999	Winter 2000	Spring 2000	Summer 2000	Fall 2000	Winter 2001
Spring 1999	1.0	0.46	0.42	0.50	0.75	0.26	0.36	0.72
Summer 1999		1.0	0.60	0.40	0.42	0.64	0.62	0.37
Fall 1999			1.0	0.50	0.37	0.57	0.77	0.46
Winter 2000				1.0	0.42	0.25	0.43	0.65
Spring 2000					1.0	0.25	0.31	0.62
Summer 2000						1.0	0.69	0.22
Fall 2000							1.0	0.41

^aValues greater than 0.7 are in bold.

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gional studies indicating greater densities of birds in the marine environment include wintering waterfowl. Kelly and Tappen (1998), for example, reported densities of >500 birds/km² on Tomales Bay, Marin County, California, but the majority of these birds were waterfowl. The high density of marine birds in my study largely was due to Western/Clark's Grebes. I recorded a mean of 202.4 grebes/km², whereas Mason (1997), studying a larger area, reported a mean of 33.2 grebes/km². I also recorded greater densities of gulls, although Mason recorded greater densities of Sooty Shearwaters and Common Murres.

The species richness I recorded was less than that reported by Mason (1997). Mason recorded 57 species, whereas I recorded 43; Mason recorded a mean of 20.5 species per survey, whereas I recorded 16.8. Greater overall bird abundance and differences in dominant species in my study were likely a result of the distance from shore at which surveys were conducted ($<20\%$ of Mason's surveys were within 1 km of shore). Greater diversity in Mason's study was likely a result of a greater diversity of habitats sampled, including the Monterey Canyon. I did not encounter many large flocks of Sooty Shearwaters in summer months probably because I usually conducted my surveys between 0800 and 1200 hours, when Sooty Shearwaters seem less common near shore (pers. obs).

Several species were remarkably abundant near shore in Monterey Bay. Western/Clark's Grebes occurred year round, but they were most abundant during migration. If Western/Clark's Grebes are found in similar densities from shore to about 1 km offshore (and additional birds can be found considerably farther offshore), the total number of Western/Clark's Grebes on Monterey Bay in winter during my study was probably in excess of 10,000 individuals and may have occasionally exceeded 30,000. Briggs et al. (1987) estimated that the population of Western/Clark's Grebes spending the winter in California is less than 60,000, so up to half of the state's wintering population may congregate in Monterey Bay. Winter counts of California Gulls of more than 75 birds/km² can be extrapolated to a local population in winter of 5000 or more birds. Numbers of California Gulls breeding in south San Francisco Bay have increased dramatically in the last 20 years (Shuford and Ryan 2000), and this colony may contribute to the large population of California Gulls wintering on Monterey Bay. The local (southernmost) population of the Marbled Murrelet, breeding in the Santa Cruz Mountains just north of the study area, consists of approximately 600 birds (Z. Peery pers. comm.). Extrapolating observed densities of Marbled Murrelets to the nearshore zone from about 300 to 1300 m offshore, it appears that about half of this population may move into Monterey Bay for the winter. During winter 2000–2001, this extrapolation suggested a population of >400 birds in Monterey Bay.

Because of the high abundance of birds in nearshore waters of Monterey Bay this area is of conservation importance, particularly for some species that occur only near shore. The Surf and White-winged Scoters, Marbled Murrelet, and Pigeon Guillemot are among several species that are limited in their local distribution to within a few kilometers of the coast. Many other species, including Western/Clark's Grebes and all three cormorant species, occur in greater densities near shore than farther off shore. Nearshore

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waters of Monterey Bay may be particularly important for species that molt their flight feathers here, especially those that are flightless while molting their remiges simultaneously. Common Murres, Marbled Murrelets, Pigeon Guillemots, and Western/Clark's Grebes are flightless during remex molt in late summer and early fall, and loons are flightless during midwinter molt, confining them to prey available locally during this time. Summering Surf Scoters may also be flightless. In addition, during late summer, the study area is likely an important nursery area for young Common Murres.

The abundance of birds in nearshore Monterey Bay presumably is linked to prey abundance and availability. Most seabirds recorded in this study feed primarily on small fish, especially the northern anchovy (*Engraulis mordax*; Morejohn et al. 1978). Although no studies comparing the abundance of small fish in nearshore and offshore waters of Monterey Bay have been conducted, in Kachemak Bay, Alaska, Abookire et al. (2000) found small schooling fish more abundant in stratified nearshore waters than in deeper water. Chlorophyll concentrations off California are often greatest in Monterey Bay (Breaker and Broenkow 1994, Croll 1990), and within Monterey Bay, chlorophyll values are greatest near shore (Pennington and Chavez 2000). The increased phytoplankton abundance indicated by these high chlorophyll concentrations presumably leads to a greater abundance of zooplankton and small fishes near shore. Greater primary production near shore in Monterey Bay may result from relatively greater input of nutrients from rivers (Skov and Prins 2001) and wave action on beaches (Ross et al. 1987) or from nutrient-rich upwelled water advected into southern Monterey Bay and circulated along shore to the north (Croll 1990, Graham and Langier 1997). In addition, the nearshore environment provides a greater range of foraging opportunities for marine birds. Not only are small schooling fishes available here, benthic and epibenthic fishes and invertebrates more accessible to birds in shallower water.

Seasonality

The seasonality of seabird abundance is a function of several factors, including breeding and molting seasons, prey availability, and climate. Forage fish probably are most abundant near shore in Monterey Bay during summer and fall. In trawls conducted to sample potential prey of the harbor porpoise (*Phocoena phocoena*) near shore in northern Monterey Bay from September to December 1996, the white croaker (*Genyonemus lineatus*) and northern anchovy were the most abundant species caught (Byrd 2001). Although the exact seasonal distribution of anchovies in Monterey Bay has not been studied, large shoals of anchovies can often be seen near shore in summer and fall (pers. obs.). In southern California, Allen and DeMartini (1983) found that anchovies are most abundant near shore in late summer, when SST is greatest. In California Common Murres typically move closer to shore in late summer, presumably to feed on abundant northern anchovies (Oedekoven et al. 2001). Castillo et al. (1996) found that off Chile a thermal front predictably moves toward shore during summer, concentrating anchovies between the front and shore. A similar phenomenon may result in high concentrations of anchovies in nearshore Monterey Bay. Market squid (*Loligo opalescens*), which during summer concentrate near shore in

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southern Monterey Bay to spawn, also are an important prey for seabirds (Morejohn et al. 1978, McInnis and Broenkow 1978).

In general, seabird seasonality appears to be more a function of the breeding and migratory behavior of the birds in the study area than of oceanographic seasons. Of the birds whose abundance peaked during fall, most have early breeding seasons, allowing them to take advantage of abundant prey in Monterey Bay during late summer and fall (Briggs et al. 1983). Fall is also the season during which most seabirds molt their flight feathers. Birds undergoing molt are limited in their foraging ranges and thus rely heavily on localized prey during this time.

Seabird species whose abundance peaks during winter breed mostly north of Monterey Bay, and for these species, Monterey Bay likely represents a good trade-off of migration distance, prey availability, and mild climate. Although prey available in Monterey Bay are probably fewer in winter than in summer, winter prey abundance there may be greater than at lower latitudes, where year-round primary production is lower (Hickey 1998). In addition, winter weather generally is more severe north of San Francisco Bay, affecting the ability of marine birds to forage and maintain their body temperature (Schreiber 2002).

Despite the high diversity and abundance of many species during winter, total bird abundance was greatest during migration periods in April and September. Similarly, Mason (1997) recorded the greatest density of seabirds in Monterey Bay during fall, in September 1992. Portions of most populations of migrants also winter in the study area. The peaking of Western/Clark's Grebes during migration was unexpected. This pattern of seasonal abundance differs from that elsewhere in coastal California, where these grebes are most abundant in winter (Briggs et al. 1987, Shuford et al. 1989). In late spring, I observed dense large flocks in northern Monterey Bay. These flocks may have been composed of birds staging for migration to breeding areas, primarily in the Great Basin. Western/Clark's Grebes are typically absent from coastal California during summer (Briggs et al. 1987, Shuford et al. 1989), thus relatively high densities of these grebes in summer (ca. 100 birds/km²) may be unique to Monterey Bay. Most Western/Clark's Grebes apparently leave Monterey Bay during August and September, to undergo flight feather molt elsewhere (Stout and Cooke 2003).

Year-to-Year Variability

Between the two years of the study patterns of seasonal abundance were fairly consistent. Pairwise comparisons of the PSI for all species by seasons corresponded loosely to expected values: all values >0.8 were for the same season or adjacent seasons (i.e., values were not high for opposite seasons, such as winter and summer). The greatest PSI value was between spring 1999 and spring 2000. With Sooty Shearwaters and Western/Clark's Grebes removed from the analyses, the pattern still held. The only exception was a value >0.7 between spring 1999 and winter 2001. This similarity between spring 1999 and winter 2001 may have been related to the mean SST being coldest in spring 1999, resulting in conditions similar to those typical of winter.

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With and without Sooty Shearwaters and Western/Clark's Grebes, PSI values were high in spring (March, April, and May). During spring, marine birds probably use the nearshore waters of Monterey Bay as a predictable site for locating prey. Predictability of prey is important before the breeding season, when birds must be in peak physical condition. In comparisons of the same seasons in different years, summer (June, July, and August) had the lowest PSI values in both analyses and was the period of least overall abundance. Birds were less abundant in nearshore Monterey Bay during summer because most species bred outside the study area. Birds present during summer likely represented wandering nonbreeders. During summer, when upwelling in the California Current is highly variable, the distribution of marine birds in the current may be less predictable than during winter. During late summer and fall, variation in postbreeding dispersal may cause the spatial and temporal distribution of many species to vary greatly from year to year (Briggs et al. 1987).

Between the two years of the study upwelling and SST were similar, and I did not expect significant differences in density or abundance of nearshore birds. Western/Clark's Grebes and Brandt's Cormorants, however, were more abundant in summer 2000 than in 1999, and Brown Pelicans were more abundant in fall 2000 than in 1999. The greater density of birds overall in summer 2000 primarily was a result of the greater abundance of Western/Clark's Grebes, the most abundant species. The greater abundance of these species in 2000 could be the result of greater prey availability in 2000. SST, however, was significantly higher in spring 2000 than in spring 1999, indicating greater water-column stratification, and lower primary productivity in spring 2000, potentially leading to a reduction in prey abundance during summer. Species more abundant in 2000 than in 1999 may have been responding not to an increase in prey availability in the study area but to a decrease in prey availability outside the study area. Given the typically high availability of prey near shore in Monterey Bay, these species may have responded to a decrease in prey abundance on a regional scale (e.g., the central coast of California) by moving to nearshore Monterey Bay. In Monterey Bay, prey may have been similarly reduced, but still may have been more abundant than elsewhere. Greater prey abundance near shore is likely the reason for Common Murres shifting closer to shore in central California during El Niño (Ainley et al. 2002). Similarly, Benson et al. (2002) found that during El Niño of 1998 some cetaceans were more abundant in Monterey Bay than normal; they proposed that this shift was a result of this "oasis" effect when productivity elsewhere was reduced.

This study provided data on the year-round occurrence of seabirds in Monterey Bay over more than one year, but annual variability cannot be explored fully in a two-year study. Annual variability in oceanographic conditions (especially El Niño) can have dramatic effects on the abundance and distribution of marine birds in the California Current (Ainley et al. 1995, Becker and Beissinger 2003). During a pilot study in 1998 (unpubl. data), I recorded >1000 Surf Scoters on two different surveys in March, more than five times the abundance recorded during this study. El Niño prevailed in 1998, so this substantial annual variability likely was related to oceanographic or climatic

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factors. Decadal-scale changes in oceanographic conditions also have been found to affect marine food webs and seabird distribution in the northeast Pacific (Veit et al. 1996, Anderson and Piatt 1999, Chavez et al. 2003). Changes in oceanographic conditions at various temporal scales presumably lead to changes in abundance of marine birds using the nearshore waters of Monterey Bay. Quantifying this variability through long-term monitoring would be useful in determining the effects of oceanographic conditions.

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LITERATURE CITED

- Abookire, A. A., Piatt, J. F., and Robards, M.D. 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuarine, Coastal and Shelf Sci.* 51:45–59.
- Ainley, D. G. 1976. The occurrence of seabirds in the coastal region of California. *W. Birds* 7:33–68.
- Ainley, D. G., and Boekelheide, R. J., eds. 1990. *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community*. Stanford Univ. Press, Stanford, CA.
- Ainley, D. G., Nettleship, D. N., Carter, H. R., and Storey, A. E. 2002. Common Murre (*Uria aalge*), in *The Birds of North America* (A. Poole and F. Gill, eds.), no. 666. *Birds N. Am.*, Philadelphia.
- Ainley, D.G., Sydeman, W. J., and Norton, J. 1995. Upper-trophic-level predators indicate interannual negative and positive anomalies in the California Current food web. *Mar. Ecol. Prog. Ser.* 118:69–79.
- Allen, L. G., and DeMartini, E. E.. 1983. Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre–Oceanside, California. *Fish. Bull.* 81:569–586.
- Anderson, P. J., and Piatt, J. F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* 189:117–123.
- Baltz, D. M., and Morejohn, V. 1977. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. *Auk* 94:526–543.
- Becker, B. H., and Beissinger, S.R. 2003. Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system. *Mar. Ecol. Prog. Ser.* 256:243–255.
- Benson, S. R. 2002. *Ecosystem studies of marine mammals and seabirds in Monterey Bay, CA, 1996–99*. M.S. Thesis, Moss Landing Marine Labs, Moss Landing, CA.
- Benson, S. R., Croll, D. A., Marinovic, B., Chavez, F. P., and Harvey, J. T. 2002. Changes in the cetacean assemblage of a coastal upwelling ecosystem during El Niño 1997–98 and La Niña 1999. *Prog. Oceanogr.* 54:279–291.

SEASONAL ABUNDANCE OF MARINE BIRDS IN MONTEREY BAY

- Bolin, R. L., and Abbott, D. P. 1963. Studies of the marine climate and phytoplankton of the central coastal area of California, 1955–1960. CalCOFI Rep. 9:23–45
- Bonnell, M. L., and Ford, R. G. 2001. Marine mammal and seabird computer database analysis system (CDAS). Prepared by Ecological Consulting, Inc., Portland, Oregon, for the Pacific OCS Region, Minerals Management Service.
- Breaker, L. C., and Broenkow, W. W. 1994. The circulation of Monterey Bay and related processes. *Oceanogr. Mar. Biol. Annu. Rev.* 32:1–64.
- Briggs, K. T., and Chu, E. W. 1986. Sooty Shearwaters off California: Distribution, abundance, and habitat use. *Condor* 88:355–364.
- Briggs, K. T., Tyler, W. B., Lewis, D. B., and Carlson, D. R. 1987. Bird communities at sea off California: 1975 to 1983. *Studies Avian Biol.* 11.
- Briggs, K. T., Tyler, W. B., Lewis, D. B., Kelly, P. R., and Croll, D. A. 1983. Brown Pelicans in central and northern California. *J. Field Ornithol.* 54:353–466.
- Byrd, B.L. 2001. Abundance, distribution, food habits, and prey availability of the harbor porpoise (*Phocoena phocoena*) in northern Monterey Bay, California. M.S. Thesis, Calif. State Univ., Stanislaus.
- Castillo, J., Barbieri, M. A., and Gonzalez, A. 1996. Relationships between sea surface temperature, salinity, and pelagic fish distribution off northern Chile. *ICES J. Mar. Sci.* 53:139–146.
- Chavez, F. P., Ryan, J., Lluch-Cota, S. E., and Ñiquen, M. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* 299:217–221.
- Croll, D. A. 1990. Physical and biological determinants of the abundance, distribution, and diet of the Common Murre in Monterey Bay, California. *Studies Avian Biol.* 14:139–148.
- Graham, W. M., and Largier, J. L. 1997. Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. *Continental Shelf Res.* 17:509–532.
- Gould, P. J., Forsell, D. J., and Lensink, C. J. 1982. Pelagic distribution of seabirds in the Gulf of Alaska and Bering Sea. U.S. Fish and Wildlife Serv., Biol. Serv. Prog. FWS/OBS 82/84, Anchorage, Alaska.
- Gould, P. J., and Piatt, J. F. 1993. Seabirds of the central North Pacific, in *The Status, Ecology, and Conservation of Marine Birds of the North Pacific* (K. Vermeer, K. T. Briggs, K. H. Morgan, and D. Siegel-Causey, eds.), pp. 27–38. Can. Wildlife Service, Ottawa.
- Hickey, B. M. 1998. Coastal oceanography of western North America from the tip of Baja California to Vancouver Island, in *The Sea* (A. R. Robinson and K. H. Brink, eds.), vol. 11, pp. 345–393. Wiley, New York.
- Kelley, J. P., and Tappen, S. L. 1998. Distribution, abundance, and implications for conservation of winter waterbirds on Tomales Bay, California. *W. Birds* 29:103–120.
- Krebs, C. J. 1999. *Ecological Methodology*, 2nd ed. Benjamin Cummings, Menlo Park, CA.
- McGinnis, R. R., and Broenkow, W. W. 1978. Correlations between squid catches and oceanographic conditions in Monterey Bay. *Calif. Dept. Fish and Game Bull.* 169:7–9.
- Mason, J. 1997. Distribution and abundance of seabirds in Monterey Bay, California. M.S. Thesis, Calif. State Univ., Fresno.

SEASONAL ABUNDANCE OF MARINE BIRDS IN MONTEREY BAY

- Morejohn, G. V., Harvey, J. T., and Krasnow, L. T. 1978. The importance of *Loligo opalescens* in the food web of marine vertebrates in Monterey Bay, California. Calif. Dept. Fish and Game Bull. 169:67-97.
- Oedekoven, C. S., Ainley, D. G., and Spear, L. B. 2001. Variable responses of seabirds to change in marine climate: California Current, 1985-1994. Mar. Ecol. Prog. Ser. 212:265-281.
- Paduan, J. D., and Rosenfeld, L. K. 1996. Remotely sensed surface currents in Monterey Bay from shore-based HF radar (Coastal Ocean Dynamics Application Radar). J. Geophys. Res. 101(C9):20,669-20,686.
- Pennington, J. T., and Chavez, F. P. 2000. Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll, and primary production at station H3/M1 over 1989-1996 in Monterey Bay California. Deep-Sea Res. II 47:947-973.
- Roberson, D. 2002. Monterey Birds, 2nd ed. Monterey Peninsula Audubon Soc., Carmel, CA.
- Roberson, D., and C. Tenney (eds.). 1997. Atlas of the Breeding Birds of Monterey County, California. Monterey Peninsula Audubon Soc., Carmel, CA.
- Ross, S. T., McMichael, R. H., Jr., and Ruple, D. L. 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Estuarine, Coastal and Shelf Sci. 25:391-412.
- Schreiber, E. A. 2002. Climate and weather effects on seabirds, in Biology of Marine Birds (E. A. Schreiber and J. Burger, eds.), pp. 179-215. CRC Press, Boca Raton, FL.
- Schwing, F. B., Moore, C. S., Ralston, S., and Sakuma, K. M. 2000. Record upwelling in the California Current in 1999. CalCOFI Rep. 41:148-160.
- Shuford, W. D., Page, G. W., Evens, J. G., and Stenzel, L. E. 1989. Seasonal abundance of waterbirds at Point Reyes: A coastal California perspective. W. Birds 20:137-265.
- Shuford, D. W., and Ryan, T. P. 2000. Nesting populations of California and Ring-billed Gulls in California: Recent surveys and historical status. W. Birds 31:133-164.
- Skov, H., and Prins, E. 2001. Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. Mar. Ecol. Prog. Ser. 214:279-287.
- Spear, L. B. 1988. Dispersal patterns of Western Gulls from Southeast Farallon Island. Auk 105:128-141.
- Stallcup, R. W. 1976. Pelagic birds of Monterey Bay, California. W. Birds 7:113-135.
- Stout, B. E., and Cooke, F. 2003. Timing and location of wing molt in Horned, Red-necked, and Western Grebes in North America. Waterbirds 26:88-93.
- Veit, R. R., Pyle, P., and McGowan, J. A. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current system. Mar. Ecol. Prog. Ser. 139:11-18.
- Zar, J. H. 1996. Biostatistical Analysis, 3rd ed. Prentice Hall, Upper Saddle River, NJ.

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