THE BIOGEOGRAPHIC PATTERNS OF SEABIRDS IN THE CENTRAL PORTION OF THE CALIFORNIA CURRENT*

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SUMMARY

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We assessed seabird distributions in the central California Current system by compiling and integrating data from all major seabird distributional studies conducted in the region since 1980. Studies in the compilation included the Minerals Management Service Aerial Surveys, the Seabird Ecology Study, the National Marine Fisheries Service (NMFS) Rockfish Assessment cruises, the National Oceanic and Atmospheric Administration Eastern Pacific Ocean Climate Study cruises, the California Department of Fish and Game Office of Spill Prevention and Response overflights, the San Francisco Deep Ocean Disposal Site cruises and the NMFS Oregon, California and Washington Marine Mammal Survey cruises. Those surveys were used to examine, by oceanographic season, the spatial and temporal distribution of the five most abundant seabird species, and the community biomass and species diversity for the entire seabird community. Noteworthy was the high species diversity along the shelf break (200-m isobath) and a marked high-density "halo" of individuals of breeding species around major nesting colonies during the breeding season.

Key words: California Current, seabird biogeography, seabird ecology, seabird surveys, diversity indices, seabird database

INTRODUCTION

The central portion of the California Current system contains a rich avifauna (e.g. Briggs *et al.* 1987). It is also the site of three U.S. national marine sanctuaries. Since the 1970s, a number of studies have been conducted to characterize the distribution and abundance of seabirds in the region. Although the studies were conducted for diverse reasons (and often using different methodologies), most shared the same goal.

In support of the biogeographic assessment conducted by the National Oceanic and Atmospheric Administration (NOAA) National Marine Sanctuary Program (NMSP) and by the National Centers for Coastal Ocean Science (NCCOS), we assembled a composite database of seabird observations and associated survey effort, characterizing the avifauna from Point Arena to Point Sal (39°N–35°N) and from the shoreline to 250 km offshore (Fig. 1). The effort encompassed eight shipboard and aerial survey programs conducted between 1980 and 2001 (Table 1).

The composite data set contains numerous gaps because not all portions of the study area were sampled within each season of every year. Nonetheless, spatial and seasonal patterns became clearly evident when the available data were analyzed. The extensive nature of the data set also allowed calculation of total biomass and species diversity for various areas.

Presented here are highlights of the analysis completed for seabirds as part of the biogeographic assessment by NOAA–NCCOS. Although we completed that analysis considering 76 species of seabirds, we present here some of the details for the five most abundant species, which together comprised 64% of all individuals and more than 85% of the total avian biomass in the study area. Details for the remaining species can be found in the more extensive NCCOS (2003) report.

METHODS

Data sources and database creation

Sources for aerial data included the Minerals Management Service (MMS) Computer Database Analysis System (MMS–CDAS: Bonnell & Ford 2001) and unpublished data from the California Department of Fish and Game (CDFG) Office of Spill Prevention and Response (OSPR). Early data were collected using methods described by Briggs *et al.* (1983); more recent data were collected using updated technology but using the same general methodology. Ship-based survey data came from DGA, CK and LTB (see Oedekoven *et al.* 2001, Clarke *et al.* 2003; Table 1).

Observation and effort data were converted to a common format, a procedure that required a significant amount of processing, correcting and merging. Because wind speed affects detection of marine birds, data collected when wind speed exceeded 25 knots

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(46.5 km h^{-1}) were excluded from the analysis. Observations and effort were allocated into cells of 5′ latitude by 5′ longitude. All aerial data were continuous. Each ship-based data set was converted separately into a continuous transect format to the extent possible.

The continuous aerial data were binned into the appropriate 5′ grid by clipping the trackline at the boundaries between adjacent cells.

For the San Francisco Deep Ocean Disposal Site (SF–DODS), the NOAA Eastern Pacific Ocean Climate Study (EPOCS) efforts and the NMFS Rockfish Assessment cruises before 1997, we used the beginning position, ship heading and speed to compute the end position of each 2–4 km continuous transect. That information was then used to determine the midpoint of each transect.
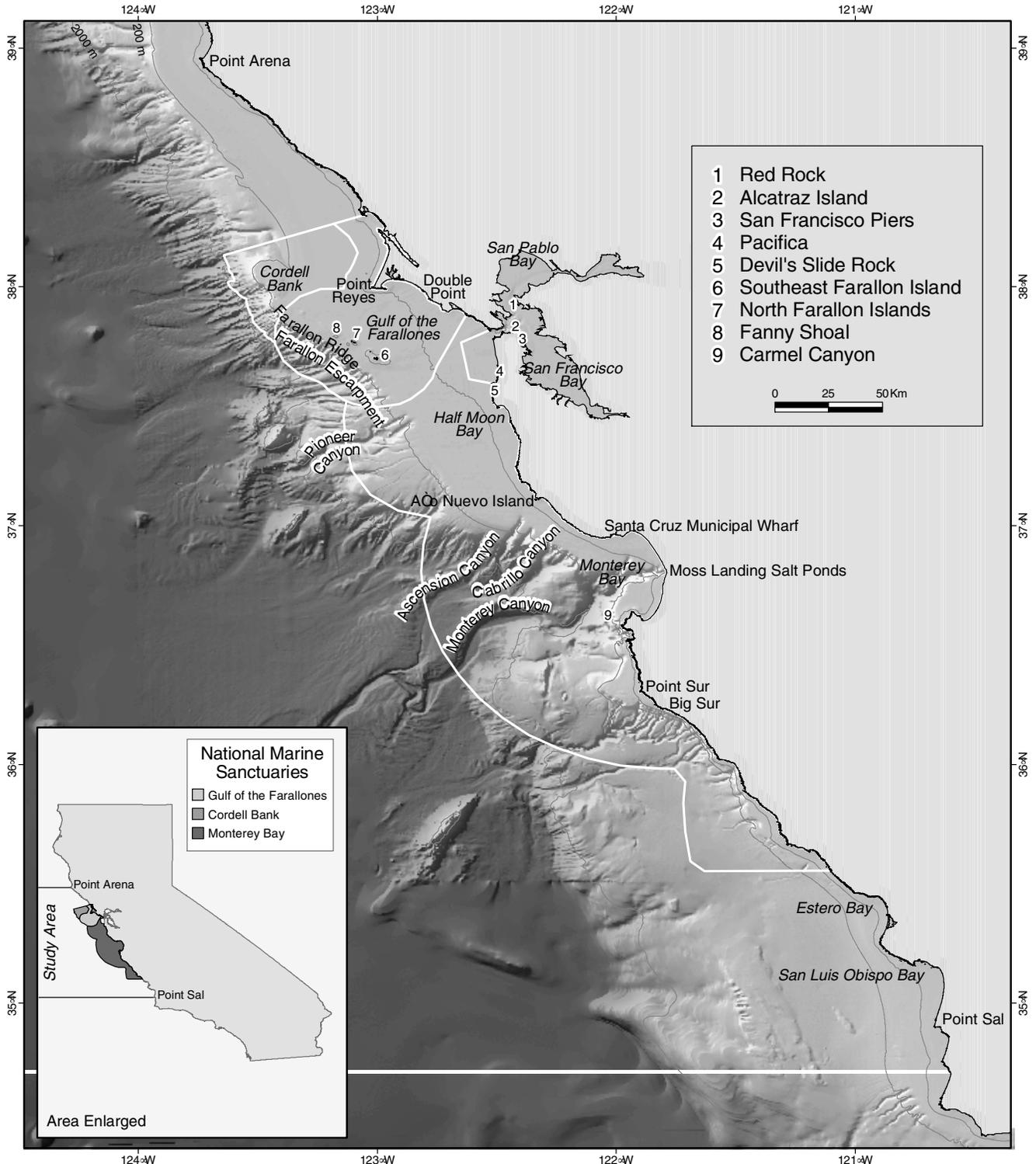

Fig. 1. Overall study area, showing locations of interest and features discussed in the text.

Because the actual times of bird observations were not available, the position of the midpoint was used to select the cell to which each survey effort was assigned. If the midpoint fell exactly on a cell boundary, it was assigned to the cell to the north or to the west (or to the cell to the north and west, if applicable). To maintain correspondence between the survey effort and the bird data, observations were also assigned to the same transect midpoints.

For the Rockfish Assessment cruises from 1997 onward, effort was assigned to the cells through which the vessel passed, based on the proportion of trackline that fell within each cell. Sightings were interpolated along the cruise track according to the time of each observation. (That method assumes that the ship was moving at nearly constant speed.)

The marine bird survey data from the Oregon, California and Washington Marine Mammal Survey (ORCAWALE) cruises were recorded continuously using automatic recording software and were processed in the same manner as the aerial survey data.

Two composite databases resulted from this treatment. The observation database contains information on each individual sighting of a bird or group of birds, including the species, number of individuals in the group, date, time, latitude–longitude position, the source study and the transect width for that species based on the ambient conditions prevailing at the time the observation was made. Other data may have been recorded for some observations, but were not used in the analysis. The effort database is based on cells of 5′ latitude by 5′ longitude, with each data-containing record describing the effort expended in one visit to one cell by researchers from one study on a given day. The information includes the latitude–longitude coordinates of the cell, the date of the visit, the source study and the number of kilometers of trackline in that cell for that visit.

Effort and species data were organized and mapped into three distinct ocean seasons (Bolin & Abott 1963, Fargion *et al.* 1993, Hayward & Venrick 1998, Pelaez & McGowan 1986)—Upwelling, Oceanic and Davidson Current—because ocean conditions differ between those seasons and because the biota of the California Current is strongly affected by seasonality (e.g. Ainley 1976, Briggs *et al.* 1987). Significant interannual variation can occur in the initiation and termination of the seasons; but, for purposes of the present analysis, we used the following fixed dates to define the approximate average dates for each season: Upwelling season, 15 March–14 August; Oceanic season, 15 August–14 November; and Davidson Current season, 15 November–14 March.

TABLE 1
Summary of at-sea survey data sets used to assess spatial patterns, by season, in the distribution of seabirds of the central California Current system, 1980–2001

Data set	Principal investigator	Platform and height	Habitat covered	Years	Oceanographic seasons covered	Transect width
MMS aerial surveys	Briggs	Pembroke, 62 m	Shelf, slope	1980–1983	Year-round	50 m
EPOCS	Ainley, Ribic, Spear	RV *Surveyor,* 12 m RV *Discoverer,* 15 m RV *Oceanographer,* 15 m	Deep ocean	1984–1994	Year-round	300–600 m
Seabird Ecology aerial surveys	Briggs	Partenavia, 62 m	Shelf, slope	1985	Mainly Upwelling	50 m
NMFS Rockfish Assessment	Ainley, Keiper	RV *David Starr Jordan,* 10 m	Coast to 3000 m depth	1985–2001	Mainly Upwelling	300 m
OSPR	Bonnell, Tyler	Partenavia, 62 m	Shelf, slope	1994–1998, 2001	Year-round	50 m
MMS Santa Barbara Channel	Bonnell	Partenavia, 62 m	Shelf, slope	1995–1997	Year-round	50 m
SF–DODS	Ainley	RV *Point Sur*, 8 m	Coast to 3000 m depth	1996–2000	Year-round	300 m
NMFS ORCAWALE cruises	Ballance	RV *MacArthur,* 11 m	Shelf, slope, deep ocean	2001	Mainly Oceanic	200–300 m (depends on species)

MMS = Minerals Management Service; EPOCS = Eastern Pacific Ocean Climate Study; NMFS = National Marine Fisheries Service; OSPR = Office of Spill Prevention and Response; SF–DODS = San Francisco Deep Ocean Disposal Site; ORCAWALE = Oregon, California and Washington Marine Mammal Survey.

Although the present study spans the years 1980–2001, data were not available for all seasons in all years. Data were available as follows (Table 2):

- upwelling season, 1980–1982 and 1985–2001
- oceanic season, 1980–1982, 1991 and 1994–2001
- Davidson Current season, 1980–1986 and 1991–2001

Analyses
We calculated four different metrics to characterize the spatial and temporal variability in the observation and effort databases: density, seasonal high use, biomass density and diversity. These data were summarized into 5′ latitude by 5′ longitude cells. Depth and distance to land were also calculated for the cells based on the values at the midpoints of the cells.

We present seasonal density distributions for the five numerically most-dominant species found during the entire study: Sooty Shearwater *Puffinus griseus,* Western Gull *Larus occidentalis,* Common Murre *Uria aalge,* Cassin's Auklet *Ptychoramphus aleuticus* and phalaropes (both Red and Red-necked: *Phalaropus fulicarius* and *P. lobatus*).

Seasonal high use is a spatial index that shows the extent to which a particular region is important to a particular species over the course of the year (independent of season). We also calculated biomass density and diversity for all 76 observed species combined, and we analyzed potentially complicating factors in combining disparate data sets.

Density
Densities were calculated for each 5′ latitude by 5′ longitude cell. The length and width of the survey trackline in a given cell were used to estimate the area sampled for a particular species. (Estimated survey strip width varied for different seabird species and by platform—depending on cruising speed, height above water and observation conditions.) The number of birds of each species seen in a cell was divided by the area sampled in the cell, taking into account the various species-specific strip widths. For construction of density plots, if a cell underwent a census in other years or during the same year during another survey, densities in cells were averaged and weighted according to effort.

Maps of individual species density show their abundance (birds km^{-2}) displayed in 5′ latitude by 5′ longitude cells during the Upwelling, Oceanic and Davidson Current seasons. The colors and

TABLE 2
Survey effort[a] by season and year

Year	Davidson Current season 15 November–14 March			Upwelling season 15 March–14 August			Oceanic season 15 August–14 November		
	Total cells	Total visits	Trackline (km)	Total cells	Total visits visits	Trackline (km)	Total cells	Total visits visits	Trackline (km)
1980	381	381	2 858.4	369	1 272	9 170.0	418	765	5 576.2
1981	550	1 149	8 271.6	405	1 325	9 819.1	332	784	5 768.4
1982	452	1 053	7 618.8	535	1 376	9 892.5	380	798	5 730.4
1983	279	736	5 438.8	—	—	—	—	—	—
1984	5	5	50.4	—	—	—	—	—	—
1985	181	181	1 414.3	313	613	3 523.6	—	—	—
1986	35	64	292.3	173	626	2 970.4	—	—	—
1987	—	—	—	180	618	2 548.0	—	—	—
1988	—	—	—	136	346	1 469.9	—	—	—
1989	—	—	—	123	266	1 057.1	—	—	—
1990	—	—	—	140	337	1 296.4	—	—	—
1991	9	9	135.5	192	508	2 137.0	22	22	320.5
1992	212	380	1 786.0	222	490	2 140.3	—	—	—
1993	220	365	1 646.7	148	300	1 194.5	—	—	—
1994	122	193	832.6	169	300	1 639.8	65	65	1 565.1
1995	105	155	3 699.7	35	35	906.8	39	39	832.4
1996	67	224	1 586.2	110	287	2 338.4	121	421	3 087.7
1997	34	100	442.0	166	555	2 345.7	67	414	1 500.4
1998	39	305	1 541.8	156	637	2 632.1	43	94	381.3
1999	51	142	497.9	194	379	1 983.2	69	164	680.8
2000	39	121	425.4	153	292	1 334.7	49	121	474.8
2001	129	189	939.8	269	488	3 777.2	301	484	3 345.1
2002	125	126	787.3	—	—	—	—	—	—
TOTAL	1 583	5 878	40 265.4	1 335	11 050	64 176.7	1 130	4 171	29 263.1

[a]Three measures of effort are given: number of 5′ latitude by 5′ longitude cells visited, total number of cell visits and linear kilometers of trackline. Cell totals are not additive.

mapping intervals were customized to show the most structure and to highlight high-density areas, while allowing comparisons between species.

Seasonal high use

To integrate the patterns of spatial and temporal occurrence in the study area for each species into one map, the seasonal density data were binned into 10′ latitude by 10′ longitude cells for each species or species group. Non-zero cells were then ranked. Those in the top 20% were selected and defined as seasonal high-use areas. Cells were then mapped with intensity of color corresponding to the number of seasons of high use. Cells in which an effort was undertaken, but in which birds were not observed, and cells in which sightings occurred, but that never appeared in the top 20% of cells, were also mapped using two additional colors. Where applicable, best-available breeding colony data (number of

breeding birds from Carter *et al.* 1992, with some updates) were also mapped for each species.

Biomass density

Biomass density was calculated using all 76 species identified in the study area during each of the three oceanographic seasons. The calculation provided a measure of the total avian biomass per unit area (kg km^{-2}) within each 5′ cell. Unidentified birds (e.g. gulls, phalaropes) were included as well, their mass having been estimated using the body weights of the most numerous species of the same taxonomic groups.

The overall biomass density for each 5′ cell was estimated as the sum of the cell density estimates for each species, multiplied by the body mass of each species present in the cell, as reported in the literature (Dunning 1993, Spear & Ainley unpubl. data; Table 3).

TABLE 3
List of marine bird species used for analysis, together with body mass used in estimation of biomass

Common name	Scientific name	Body mass (kg)	Common name	Scientific name	Body mass (kg)
Common Loon	*Gavia immer*	4.134	Pelagic Cormorant	*Phalacrocorax pelagicus*	1.915
Pacific Loon	*Gavia pacifica*	1.659	Red-necked Phalarope	*Phalaropus lobatus*	0.034
Red-throated Loon	*Gavia stellata*	1.551	Red Phalarope	*Phalaropus fulicarius*	0.056
Western Grebe	*Aechmophorus occidentalis*	1.477	South Polar Skua	*Stercorarius maccormicki*	1.156
Clark's Grebe	*Aechmophorus clarkii*	1.477	Pomarine Jaeger	*Stercorarius pomarinus*	0.694
Horned Grebe	*Podiceps auritus*	0.453	Parasitic Jaeger	*Stercorarius parasiticus*	0.465
Red-necked Grebe	*Podiceps grisegena*	1.023	Long-tailed Jaeger	*Stercorarius longicaudus*	0.297
Eared Grebe	*Podiceps nigricollis*	0.297	Glaucous Gull	*Larus hyperboreus*	1.413
Black Scoter	*Melanitta nigra*	0.950	Western Gull	*Larus occidentalis*	1.011
Surf Scoter	*Melanitta perspicillata*	0.950	Glaucous-winged Gull	*Larus glaucescens*	1.010
White-winged Scoter	*Melanitta fusca*	1.350	Herring Gull	*Larus argentinus*	1.000
Laysan Albatross	*Phoebastria immutabilis*	3.041	Thayer's Gull	*Larus thayeri*	0.996
Black-footed Albatross	*Phoebastria nigripes*	3.015	Heermann's Gull	*Larus heermanni*	0.500
Northern Fulmar	*Fulmarus glacialis*	0.544	Bonaparte's Gull	*Larus philadelphia*	0.212
Murphy's Petrel	*Pterodroma ultima*	*0.428*	Mew Gull	*Larus canus*	0.404
Cook's Petrel	*Pterodroma cookii*	*0.190*	Ring-billed Gull	*Larus delawarensis*	0.519
Parkinson's Petrel	*Procellaria parkinsoni*	*1.062*	California Gull	*Larus californicus*	0.609
Pink-footed Shearwater	*Puffinus creatopus*	*0.721*	Sabine's Gull	*Xema sabini*	0.191
Sooty Shearwater	*Puffinus griseus*	0.787	Black-legged Kittiwake	*Rissa tridactyla*	0.407
Black-vented Shearwater	*Puffinus opisthomelas*	0.276	Red-legged Kittiwake	*Rissa brevirostris*	0.391
Buller's Shearwater	*Puffinus bulleri*	0.380	Arctic Tern	*Sterna paradisaea*	0.110
Flesh-footed Shearwater	*Puffinus carneipes*	1.560	Common Tern	*Sterna hirundo*	0.120
Short-tailed Shearwater	*Puffinus tenuirostris*	0.543	Forster's Tern	*Sterna forsteri*	0.158
Manx Shearwater	*Puffinus puffinus*	0.453	Caspian Tern	*Sterna caspia*	0.661
Townsend's Shearwater	*Puffinus auricularis*	0.276	Elegant Tern	*Sterna elegans*	0.257
Fork-tailed Storm-Petrel	*Oceanodroma furcata*	0.055	Royal Tern	*Sterna maxima*	0.470
Leach's Storm-Petrel	*Oceanodroma leucorhoa*	0.040	Common Murre	*Uria aalge*	0.993
Ashy Storm-Petrel	*Oceanodroma homochroa*	0.037	Thick-billed Murre	*Uria lomvia*	0.964
Black Storm-Petrel	*Oceanodroma melania*	0.059	Pigeon Guillemot	*Cepphus columba*	0.487
Wedge-rumped Storm-Petrel	*Oceanodroma tethys*	0.024	Marbled Murrelet	*Brachyramphus marmoratus*	0.222
Markham's Storm-Petrel	*Oceanodroma markhami*	0.059	Ancient Murrelet	*Synthliboramphus antiquus*	0.206
Least Storm-Petrel	*Oceanodroma microsoma*	0.021	Xantus's Murrelet	*Synthliboramphus hypoleucus*	0.159
Wilson's Storm-Petrel	*Oceanites oceanicus*	0.034	Craveri's Murrelet	*Synthliboramphus craveri*	0.159
Red-billed Tropicbird	*Phaethon aethereus*	0.750	Parakeet Auklet	*Aethia psittacula*	0.318
Brown Booby	*Sula leucogaster*	1.248	Cassin's Auklet	*Ptychoramphus aleuticus*	0.188
Brown Pelican	*Pelecanus occidentalis*	3.392	Rhinoceros Auklet	*Cerorhinca monocerata*	0.520
White Pelican	*Pelecanus erythrorynchos*	7.500	Tufted Puffin	*Fratercula cirrhata*	0.779
Brandt's Cormorant	*Phalacrocorax penicillatus*	2.113	Horned Puffin	*Fratercula corniculata*	0.619
Double-crested Cormorant	*Phalacrocorax auritus*	1.679			

Species diversity

Because different diversity indices have somewhat different properties, we compared three separate indices to estimate overall species diversity:

- Shannon-Wiener index (Shannon & Weaver 1949)

- Simpson's index of diversity (Simpson 1949)

- Hill's N_2 (Hill 1973)

These indices measure the degree to which the overall density of birds within a cell is dominated by a small number of species (low diversity) or by an even mix of many species (high diversity). Diversity was calculated over all seasons using all 76 species recorded during the study. Diversity was also calculated for each season separately, using the Shannon-Wiener index.

Classification of climate anomalies

In addition to seasonal variation in ocean climate, the study area is strongly affected by conditions propagated from the tropical Pacific by the El Niño Southern Oscillation (ENSO) and from variations in the Aleutian low-pressure system (Ainley *et al.* 1995). Interannual variation can be divided into three periods:

- El Niño (warm-water conditions)

- La Niña (cold-water conditions)

- neutral (intermediate conditions)

Official periods when these conditions are in effect can be determined by various ENSO Index models (Table 4). However, because of time lags, an El Niño or La Niña is felt later in central California and lasts longer than suggested by the "official" NOAA announcement for the tropical Pacific Ocean (based on the analysis of Trenberth 1997).

As noted earlier, waters in the study area also are strongly affected by the atmospheric circulation generated by the Aleutian low-pressure system (relative to the continental pressure systems; Ainley *et al.* 1995 and references therein). Thus, during periods of strong onshore or northward wind flow, warm-water events off central California may not be related to the Southern Oscillation. In such periods, the onshore winds move the oceanic water closer to shore and generate, in a sense, an extended Oceanic season.

Our approach to reconcile the remote and the local atmospheric and oceanographic conditions was to use the ocean temperature data collected at the Farallon Islands from 1974 to 1998 (P. Pyle, Point Reyes Bird Observatory, pers. comm.), in conjunction with remote sensing CoastWatch sea surface temperature data for central California from 1992 to 2002. Using a standardized criterion (mean deviance by 0.5°C from the seasonal average over all years in the time series), we assigned, by year, ENSO periods to each oceanographic season included in these data sets and compared those periods with known ENSO periods (Trenberth 1997 and http://www.cdc.noaa.gov/ENSO/enso.different.html). We note that, after the 1998–1999 La Niña, the cold phase of the Pacific Decadal Oscillation (PDO) may have been responsible for the cold ocean temperatures observed thereafter (Mantua & Hare 2002, Schwing *et al.* 2002).

Regression analysis for bird density

To determine the factors affecting the abundance of marine birds in the study area, a regression model was developed (Seber 1977, Kleinbaum *et al.* 1988), with marine bird density as the dependent variable and the following independent variables:

- oceanic season

- year

- ocean depth

- distance to the nearest breeding colony

- distance to shelf break (the 200-m isobath)

- distance to the continental slope (the 2000-m isobath)

- latitude

- extent of short-term ocean climate anomalies (e.g. El Niño and La Niña events; Table 4)

Potential biases in combining studies with differing methodologies

In all of the studies analyzed here, observers did not record data when visibility was compromised by fog, glare or darkness. Protocols for the studies—and our own experience with seabird observers—indicate that surveys are usually halted under poor

TABLE 4
Warm (El Niño and Aleutian Low), cold (La Niña) and neutral periods used in the analysis [a]

Year	Davidson Current season	Upwelling season	Oceanic season
1975	Cold	Cold	Cold
1976	Cold	Cold	Warm
1977	Warm	Cold	Neutral
1978	Warm	Warm	Cold
1979	Cold	Neutral	Neutral
1980	Warm	Neutral	Cold
1981	Warm	Cold	Cold
1982	Neutral	Neutral	Neutral
1983	Warm	Warm	Warm
1984	Warm	Neutral	Neutral
1985	Cold	Warm	Cold
1986	Neutral	Neutral	Neutral
1987	Warm	Warm	Warm
1988	Neutral	Neutral	Cold
1989	Cold	Neutral	Neutral
1990	Cold	Cold	Neutral
1991	Cold	Cold	Neutral
1992	Warm	Warm	Warm
1993	Warm	Warm	Warm
1994	Warm	Neutral	Cold
1995	Neutral	Warm	Neutral
1996	Warm	Neutral	Cold
1997	Neutral	Neutral	Warm
1998	Warm	Warm	Cold
1999	Cold	Cold	Cold
2000	Cold	Cold	Cold
2001	Cold	Cold	—

[a] Data from Scripps Institution of Oceanography (sea-surface temperature from Southeast Farallon Island) and the National Oceanic and Atmospheric Administration CoastWatch.

viewing conditions and that the thresholds for ceasing observer activity in various studies are similar. To the extent that data may have been collected when visibility was compromised by fog, glare or low light levels, we assumed that such variability does not represent a source of systematic bias because the conditions are spread across a range of times and locations.

High wind speed also has the potential to limit observer effectiveness. At wind speeds greater than 25 knots (46.5 km h^{-1}), spray and trailing whitecaps form a complex visual backdrop that fatigues observers and makes observation difficult. We used a 25-knot cutoff for wind speed on all ship-based data. Wind speed is not easily measured from aircraft, but observers generally record a Beaufort state. We used the corresponding Beaufort state of 5 as a cutoff for the aerial survey data.

Effects of wind speed
Wind speed has the potential to be a source of systematic bias. Because wind speeds may be consistently stronger in some parts of the study area (north of Point Reyes as compared with south of Point Reyes, for example), the possibility exists that observer efficiency varied systematically.

We examined this issue by regressing bird density on wind speed for Sooty Shearwater, Ashy Storm-Petrel, Red Phalarope, Common Murre, Cassin's Auklet and Rhinoceros Auklet. The results of the analyses were mixed. Ashy Storm-Petrel density showed a positive and significant relationship with wind speed ($P < 0.001$); densities were higher where wind speeds were greater. Cassin's Auklet, Red Phalarope and Sooty Shearwater densities were not significantly related to wind speed ($P = 0.18$, $P = 0.40$ and $P = 0.19$ respectively). Common Murre and Rhinoceros Auklet densities showed a significant negative response to wind speed ($P < 0.001$ and $P < 0.001$ respectively); densities were lower where wind speed was greater.

If higher wind speeds inhibit the ability of observers to detect seabirds, then we would expect a consistent negative relationship between those two variables. This was not the case. The three smallest and most inconspicuous species (Ashy Storm-Petrel, Red Phalarope and Cassin's Auklet) were either more likely to be observed in high wind or to show no relationship with wind. Two of the larger and most conspicuous species (Common Murre and Rhinoceros Auklet) were the only ones that were less likely to be observed in high wind conditions.

Lower densities when the wind speed is higher may arise because the birds are more likely to occur during times and within areas where the wind speed is lower, or because the birds are harder to see during high wind conditions. Our data do not allow us to separate those possibilities.

Comparison of ship and aircraft surveys
To assess potential survey biases, we also compared the mean densities of the same species as determined from aircraft and vessels. The comparison was restricted to the Common Murre and the two phalarope species combined, in 10' cells that were surveyed from both sea and air during comparable seasons and ENSO conditions. The mean Common Murre density was very similar regardless of survey method, as was the frequency distribution of cell densities (Fig. 2). Mean cell density for Common Murre in the region of overlap was 0.519 birds km^{-2} ($n = 302$) based on aerial

surveys and 0.493 birds km^{-2} ($n = 302$) based on shipboard surveys. The mean density of the phalarope species was higher from aerial surveys than from shipboard surveys: 0.338 birds km^{-2} ($n = 306$) and 0.220 birds km^{-2} ($n = 306$) respectively.

For both species, the distribution of cell densities differed markedly from a normal distribution, even after the densities were log transformed (see Fig. 2). We therefore used the nonparametric Kolmogorov–Smirnov test to compare the distributions. For both species, the distribution of aerial and shipboard 10' cell densities were significantly different ($P < 0.01$ for both species). For murres, the two platforms appeared to differ primarily in terms of the frequency of the zero-density class, with fewer zero densities being recorded by aircraft-based observers.

Inspection of the cell density distributions for phalaropes from air and sea surveys suggested that the differences between sea and air are more complex. Although observations of zero or small numbers of phalaropes were more common from ships, larger numbers of phalaropes were more frequently sighted from aircraft. It does not seem likely that the difference is based on detectability alone, because shipboard observers actually recorded more observations of small numbers of birds than did aerial observers. It is possible, however, that an avoidance response by flocks of phalaropes causes them to move away from approaching ships, or that shipboard
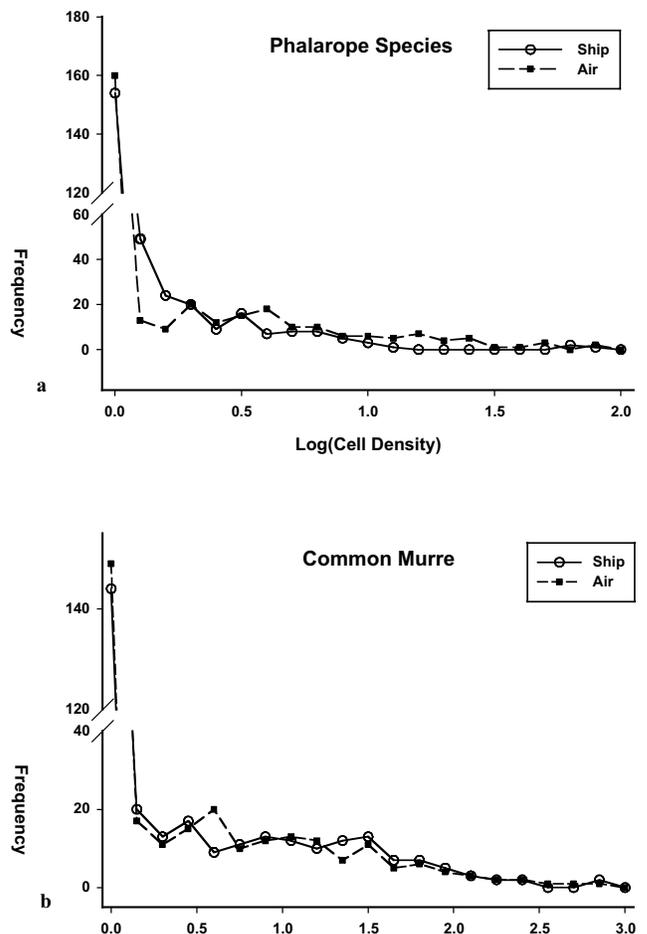

Fig. 2. The frequency of log density for 10' cells sampled by both shipboard and aerial surveys during the same season and climate status for (a) Phalaropes and (b) Common Murre.

observers are underestimating flock size because the larger survey swath (300 m versus 50 m) allows a higher proportion of a large flock to be contained by the survey strip.

Comparison of shipboard and aerial survey results is a complex issue and cannot be fully resolved here. We cannot derive general patterns from our analyses; but, on the basis of our results for the Common Murre and the phalaropes, the differences in densities appear small compared with other sources of variation (e.g. seasons, ENSO periods, locations). Nonetheless, for species that exhibit avoidance or attraction toward ships, potential biases between the two survey platforms should be considered when interpreting at-sea distribution and abundance patterns.

RESULTS AND DISCUSSION

The data analyzed in the present study comprise more than 133 705 km of trackline and 128 886 observations of 973 318 birds (Table 2). To achieve the highest possible level of spatial and temporal coverage, we combined data from eight different studies (Table 1). Those studies include observations made under a variety of ambient conditions from both aircraft and ships.

Sooty Shearwater
The Sooty Shearwater (Fig. 3) nests in the sub-Antarctic, on offshore islands of Tierra del Fuego and New Zealand, and winters in the Peru and California Current regions (Harrison 1983). It is the most abundant seabird off California (e.g. Ainley 1976, Briggs *et al.* 1987), especially within the central California National Marine Sanctuaries.

The species is present within the study area mainly during the Upwelling and early Oceanic seasons. Surveys tallied 20 750 sightings of 323 176 individuals (33.2% of all seabirds), indicating that the species usually occurs in large concentrations (mean: 15.6 shearwaters per sighting). The species was most common in continental shelf waters (less than 200 m deep) and upper slope waters (from 200 m to approximately 500 m). The mean ocean depth among the 5' cells where Sooty Shearwaters occurred was 380±10 m.

A multiple regression analysis of seven independent variables explained 43.3% of the variation in cell density. Season, year (inverse relationship) and ENSO period (periods of unusually warm or cold sea temperatures) were the most important variables. Those results emphasize the fact that this species occurs off California largely in the Upwelling season and is more abundant when ocean climate is unaffected by short-term climate perturbations. In other words, Sooty Shearwaters were less abundant in the study area during both El Niño and La Niña. Numbers increased slightly between 1985 and 1991, declined sharply to 1998 and have subsequently shown a moderate increase. Whether the latter increase is a response to the shift to a cold PDO regime in 1999 remains to be seen.

The species appears to have declined severely in abundance throughout the California Current during the recent warm PDO regime from 1976 to 1999 (Veit *et al.* 1997), although data suggest that the population may have increased in recent years (Hyrenbach & Viet 2003). Nevertheless, the species remains very abundant in Monterey Bay and in the vicinity of Heceta Bank/Cape Blanco, Oregon (Ainley *et al.* in press) with densities comparable to those

documented by Briggs *et al.* (1987) for central and northern California during the early 1980s. Both of those areas contain a recirculating eddy lying south of a large, shallow bank, and those features may account for continued high availability of prey.

Other important areas for shearwaters within the boundaries of this study (although densities are not comparable to those in Monterey Bay) include Pioneer and Ascension canyons, Farallon Escarpment and Fanny Shoal, as well as the area off Pacifica and the Estero/San Luis Obispo bays (Fig. 1). The national marine sanctuary waters become even more important to this species during the Oceanic season, just before their long southward migration, because remnants of the population fatten on the oil-rich anchovies at that time (e.g. Briggs & Chu 1987).

Western Gull
The largest Western Gull breeding colony in the world occurs on the Farallon Islands (Ainley & Boekelheide 1990). Smaller numbers breed on coastal rocks, Año Nuevo Island, the Santa Cruz Wharf and Moss Landing salt ponds, Alcatraz Island, Red Rocks and the roofs of wharf warehouses within San Francisco Bay (Fig. 1; Carter *et al.* 1992). The species begins to occupy its nesting colonies during the Davidson Current season and breeds through the Upwelling season (Ainley & Boekelheide 1990). This breeding phenology is reflected by the high at-sea densities evident throughout the year within the study area (Fig. 4). Surveys recorded 14 726 sightings of 34 504 individuals (3.5% of total seabirds), with solitary individuals and small groups being most prevalent (mean: 2.3 gulls per sighting).

A multiple regression model of eight independent variables explained 44.2% of the variation in density. Distance to colony (inverse relationship), distance to land (inverse) and climate period were the most influential variables. Those results reflect the widespread distribution of the species within the study area— primarily over the continental shelf, except in the vicinity of the Gulf of the Farallones and southeast along the slope to Monterey Canyon.

Off the Farallones during the Upwelling (nesting) season, this species spreads over the continental slope and beyond, like the murre (see "Common Murre,*"* next), in a "halo" of high density. That feature is perhaps a response to intraspecific competition among the large number of breeding individuals on the Farallon Islands. Owing to nesting duties (feeding chicks), breeders have to feed as close as possible to the nesting area to maximize food-load delivery frequency. That necessity means that they apparently will forage in suboptimal habitat (deep ocean west of the islands) instead of commuting to their typical habitat during the non-breeding season (near shore waters much farther away to the east).

The species was most abundant in the Gulf of the Farallones south to Año Nuevo, an area that includes the Farallon Escarpment and Ridge. Pioneer and Ascension canyons appeared also to be important "hot spots." The species was also prevalent in Estero and San Luis Obispo bays.

Common Murre
The Common Murre (Fig. 5) is the second most numerous marine bird in central California (e.g. Briggs *et al.* 1987). There were 21 893 sightings of 141 964 individuals (14.6% of the total seabirds counted), with most observations involving small flocks (mean:

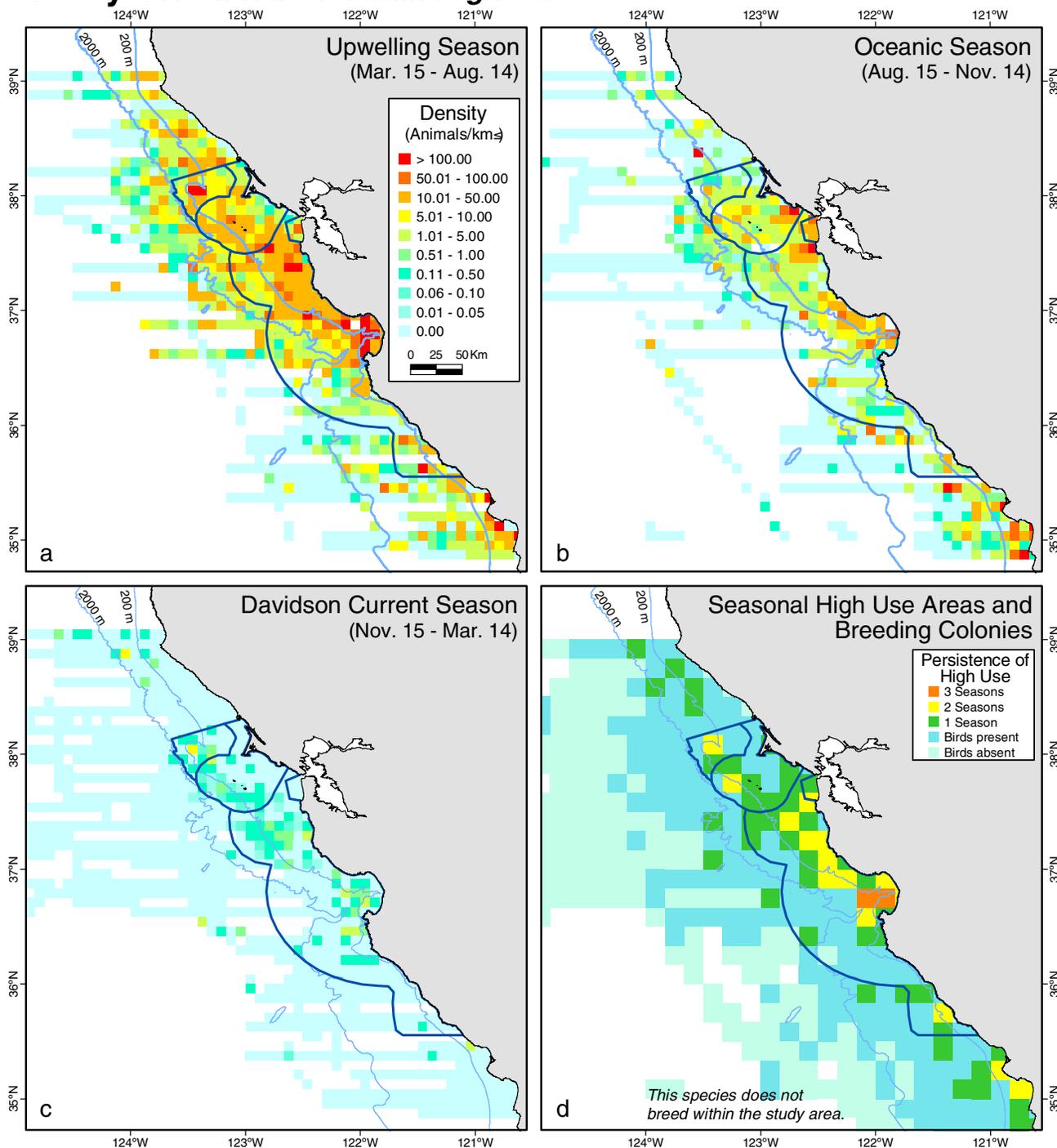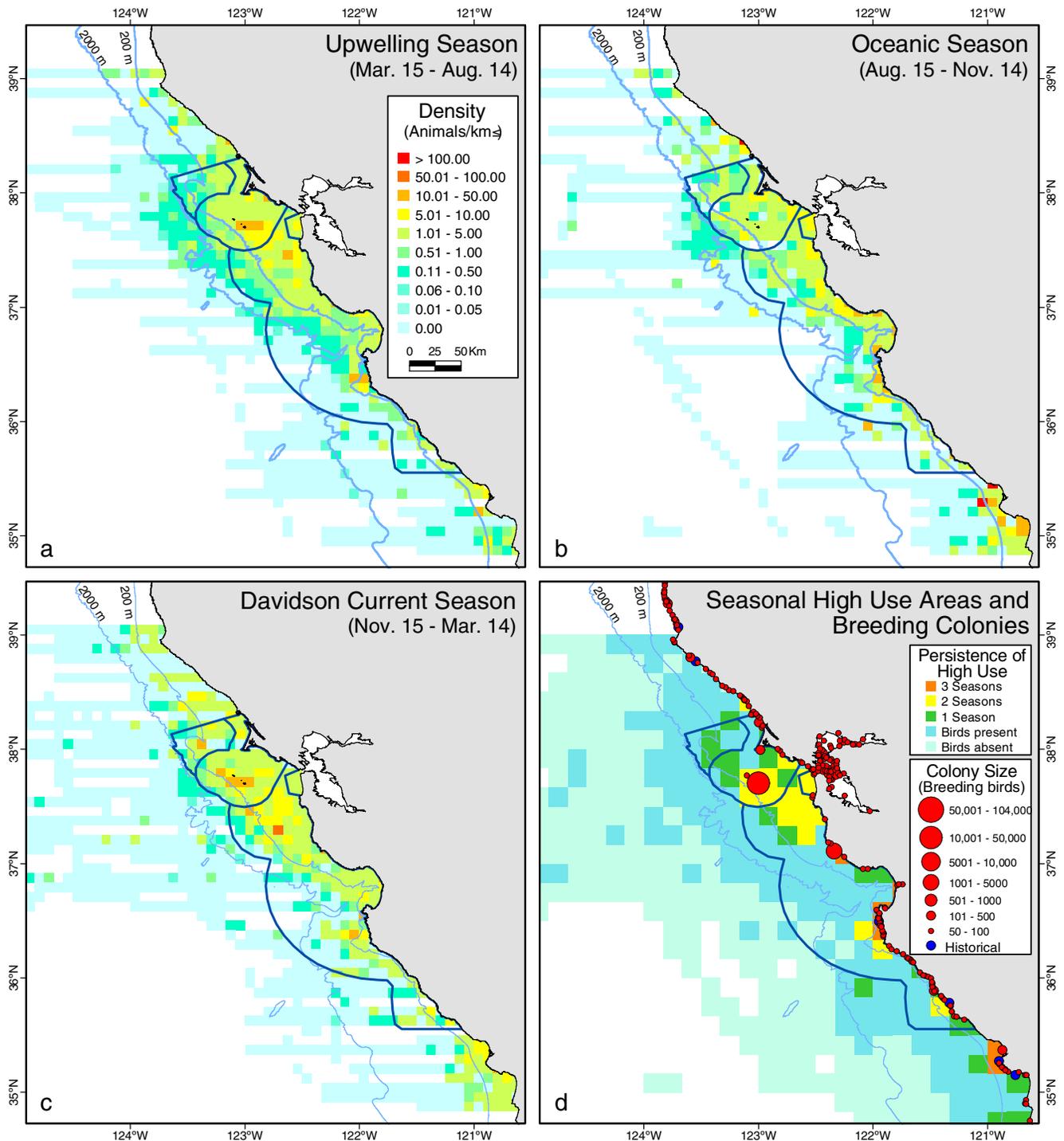# Sooty Shearwater *Puffinus griseus*

Fig. 3. Maps showing the density (birds km⁻²) of the Sooty Shearwater in the (a) Upwelling, (b) Oceanic and (c) Davidson Current seasons, displayed in 5′ latitude by 5′ longitude cells. Cells that were surveyed but that yielded no Sooty Shearwater sightings show a density of zero and are colored light blue. Areas not surveyed appear white. Cells range in color from blue to red, the warmer end of the spectrum denoting higher densities. Dark blue lines indicate the boundaries of the national marine sanctuaries (NMSs) in the study area (from north to south: Cordell Bank NMS, Gulf of the Farallones NMS and Monterey Bay NMS). Lighter blue lines show the bathymetric contours defining the edges of the continental slope, 200 m and 2000 m. A fourth map shows (d) seasonal high-use areas, displayed in 10′ latitude by 10′ longitude cells. Cells in the 20th percentile of density in one season are colored green. If a cell was in the 20th percentile for two seasons, it is colored yellow; in three seasons, it is colored orange. Cells are shown in light blue-green where the cell was sampled but the species was not recorded, and in light blue where the species was present but did not reach the 20th percentile of density in any season.

6.5 individuals per sighting). This species nests at a complex of densely occupied colonies that include the Farallon Islands, Point Reyes, and rocks near Double Point. A small colony occurs at Devils Slide (Carter *et al.* 1992). Two small, disjunct breeding colonies, the southernmost for this species, occur off the Big Sur coast in the southern part of the study area (cf. Carter *et al.* 1992).

Murres were present in high densities year-round and were particularly abundant in waters overlying the shelf (mean depth: 110±5 m), with little seasonal change. However, murre densities were generally higher during the Upwelling season, perhaps because the entire population, including both breeders and non-breeders, was present within the study area at that time. Lower
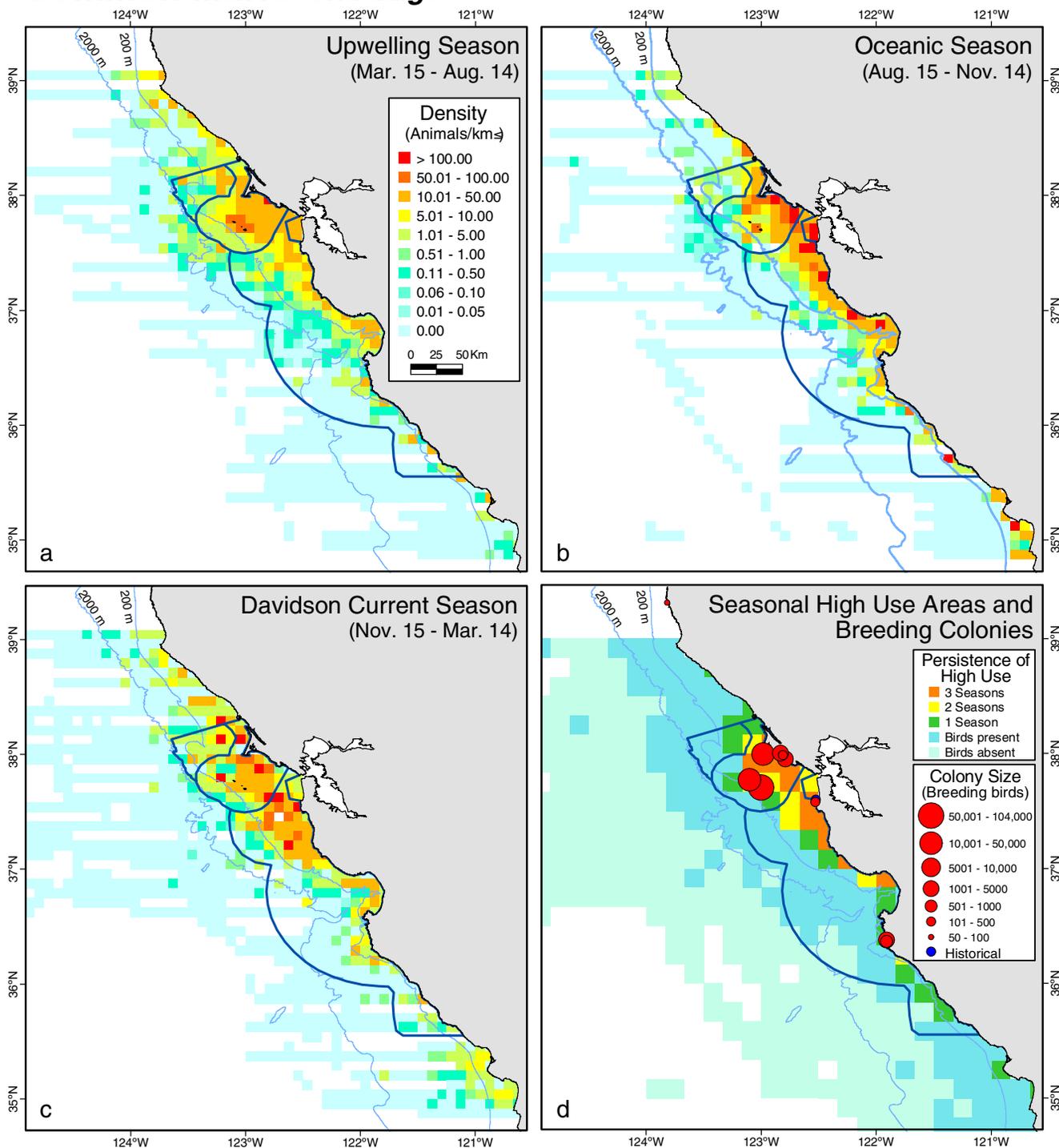

Fig. 4. Maps showing the density (birds km^{-2}) of the Western Gull in the (a) Upwelling, (b) Oceanic and (c) Davidson Current seasons, displayed in 5′ latitude by 5′ longitude cells. See Fig. 3 for the legend. Colony locations and sizes are from Carter *et al.* (1992), with updates from Warzybok (2002).

densities during the other seasons suggest that some individuals likely dispersed outside of the study area. As a part of that dispersal, many birds apparently moved to the inshore waters of Monterey Bay during the Oceanic season.

During years of unusually warm water and prey depletion, murres occurred more frequently inshore, where a more varied foraging habitat was present. That habitat selection was, in turn, reflected in the higher diet diversity of the birds (Ainley & Boekelheide 1990).
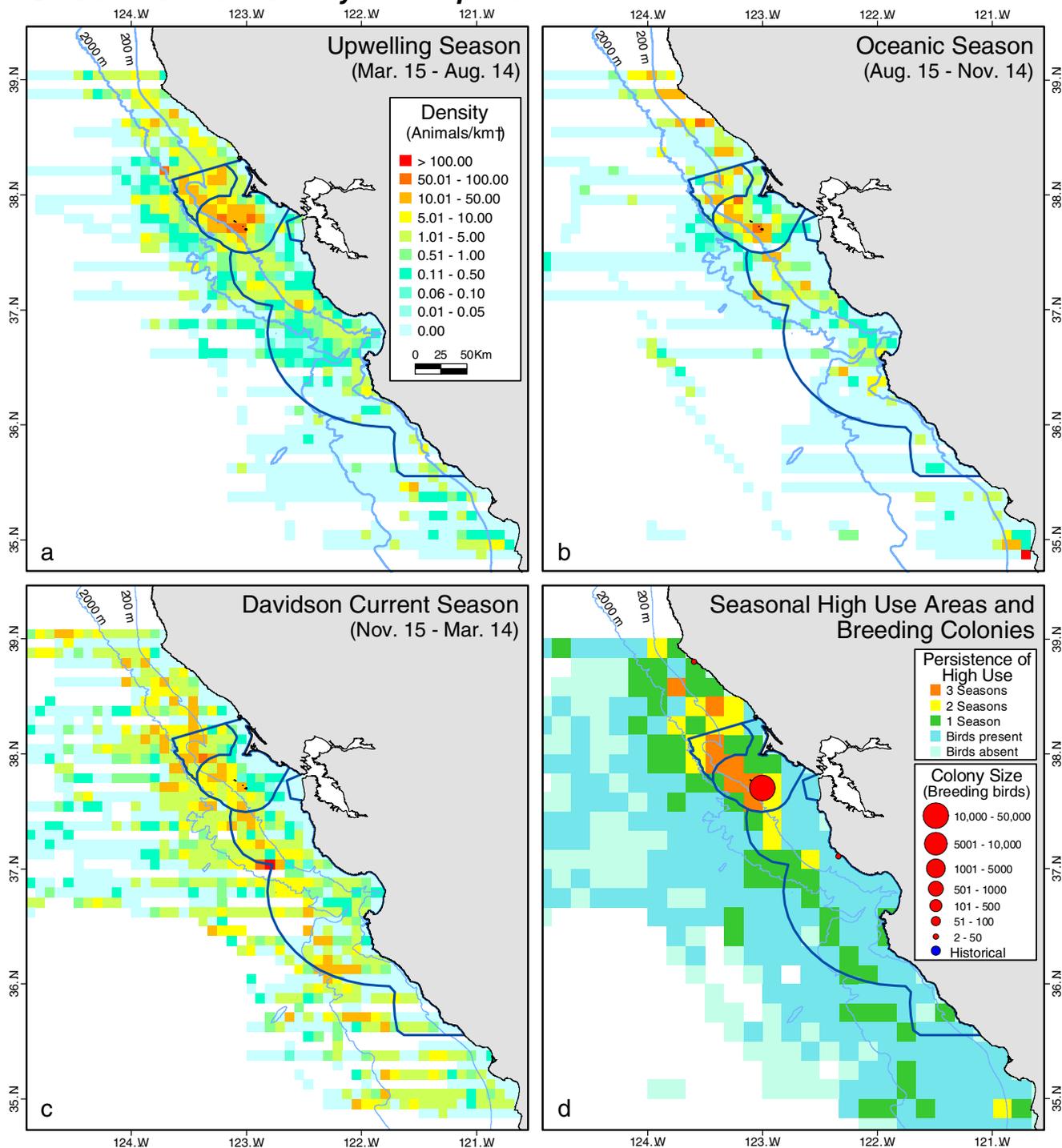

Fig. 5. Maps showing the density (birds km^{-2}) of the Common Murre in the (a) Upwelling, (b) Oceanic and (c) Davidson Current seasons, displayed in 5′ latitude by 5′ longitude cells. See Fig. 3 for details of National Marine Sanctuaries. Colony locations and sizes, shown as red circles, are from Carter *et al.* (1992), with updates from Warzybok (2002) and McChesney (pers. comm.).

That pattern of aggregation inshore was especially apparent along the coast from Point Reyes south to Año Nuevo Island, the usual area of concentration of this population during the relatively warm Oceanic (non-breeding) season.

A multiple regression model of eight independent variables explained 52.3% of the variation in cell density for this species. Most important were inverse relationships between abundance and distance to colony, and between ocean depth and distance to land. No significant trend in murre abundance was apparent between 1985 and 2002, and abundance was not affected by short-term climate fluctuations (e.g. periods of unusually warm or cold sea temperatures).

Murres begin to occupy breeding ledges sporadically during the Davidson Current season, but consistently by the early Upwelling season (Ainley & Boekelheide 1990). During the Upwelling season, many murres ranged well seaward of the shelf break and seaward of sanctuary boundaries (Fig. 5). This "halo" of high density surrounding the Farallon Islands can be attributed to the need to provision prey to the chick as quickly as possible and to the resulting high intraspecific competition for resources close to the breeding colonies. Thus, individuals are forced to forage in suboptimal habitat (deep ocean) to reduce time away from the chick. As a result, the Farallon Escarpment (very deep water) and the shallower waters of the Farallon Ridge and shelf waters inshore of it became areas of high murre concentration.

Cassin's Auklet
Although listed by the State of California as a "species of special concern," Cassin's Auklet is abundant and widely distributed in the study area (Fig. 6). Surveys recorded 11 661 sightings of 69 733 birds (7.2% of the total seabirds, with an average of 6.0 auklets per sighting). Therefore, they occurred in flocks of comparable size to those of murre. The prime nesting area in the region is on the Farallon Islands (Carter *et al.* 1992). Those auklets visit colonies only at night and do so throughout most of the Davidson Current and Upwelling seasons (Ainley & Boekelheide 1990).

This species was recorded mainly in waters of the outer shelf and inner slope, both inside and outside sanctuary boundaries (mean depth of occurrence: 354±13 m), depending on season. Cassin's Auklets were most abundant during the Upwelling (nesting) season (mean density: 4.62 birds km^{-2}) compared to the Oceanic and Davidson Current seasons (188 birds km^{-2} and 132 birds km^{-2}, respectively). During the latter period, the auklets occurred farther offshore (mean depth: 1338 m; mean distance from land: 35 km) than they did during the other two seasons.

A multiple-regression model of eight independent factors explained 25.8% of the variation in cell density. Important variables included negative relationships with distance to land, distance to the colony and year. The decreasing trend with year was very abrupt between 1984 and 1997. The declining trend was also evident off southern California (Hyrenbach & Veit 2003). However, for the entire study period (1985–2002), the relationship was curvilinear, indicating that the population later stabilized and had possibly begun to increase with the switch to the cold-water regime after 1999 (Mantua & Hare 2002). Should the population increase further, we expect its distribution to expand into the waters around the Farallones, mimicking the "halo" effect exhibited by gull and murre.

During the Upwelling season, the primary occupied habitat shrank to the slope and outer shelf (mean depth: 262 m; mean distance from shore: 12.4 km), and the population became more centered around the Farallones. During the Oceanic season, the Cassin's Auklet population moved northward toward Cape Mendocino, although it remained close to the shelf break (mean depth: 385 m). Such a movement complements the reduced densities in the Gulf of the Farallones outside of the Upwelling season. Cordell Bank, Fanny Shoal and the Farallon Escarpment were important areas as well. During the Upwelling season, the Cordell and Gulf of the Farallones National Marine Sanctuaries and the northern part of the Monterey Bay National Marine Sanctuary contained a sizeable proportion of the region's auklets.

Red-necked and Red Phalarope
Red-necked and Red phalaropes occurred commonly in the study area during both their southward and northward migrations between Arctic nesting areas and wintering areas in the ocean off South and Central America (Harrison 1983). These birds are often difficult to separate visually, especially from aircraft. Of the 49 195 sightings of phalaropes, 33 074 were not designated at the species level. Together, the two phalarope species comprised 5.1% of all seabirds recorded.

The combined multiple-regression model for Red and Red-necked phalaropes explained only 9.6% of the variation in the cell density of those species. That relatively low value may have resulted from differences in habitat use by the two species, thus masking the effect of environmental variables in the analysis. Sample sizes were insufficient to analyze each species separately. Important variables were ENSO period (more abundant during La Niña) and ocean depth (negative relationship indicating association with the mid-slope waters; mean depth: 941 m) and distance from land (negative relationship; mean distance: 27.7 km). Within the study area, abundance of these species has exhibited no concerted trend between 1985 and 2002.

On surveys in which the two phalarope species were differentiated, 782 sightings of 7670 Red-necked Phalaropes (Fig. 7) were recorded (9.8 birds per sighting). They were most abundant in the study area during the early and late Upwelling season. Thus, their time in the Arctic was relatively short. The Red-necked Phalarope, which occurred principally over the continental shelf, was concentrated farther inshore than was the Red Phalarope. During the Oceanic season, phalaropes were scattered. Both species were mostly absent during the Davidson Current season.

Among differentiated phalaropes, 1546 sightings of 8451 Red Phalarope were recorded (5.5 birds per sighting). The Red Phalarope (Fig. 8) was more concentrated over the continental slope than was the Red-necked Phalarope, which was found relatively closer to shore. That dichotomy was particularly evident off central California, where the two species were differentiated during vessel-based surveys. On aerial surveys, which spanned the entire coast, the dichotomy was not evident. Occurrence during the other two seasons was much more scattered.

Biomass density
Seabird biomass was computed using all species combined (Fig. 9). Looking first at a summary of all seasons, high biomass densities occurred in the Gulf of the Farallones, especially around the Farallon

Islands, the San Francisco Bay tidal plume, off Half-moon Bay, just south of Point Año Nuevo, and in inner Monterey Bay. During the Upwelling season, high biomass was associated with the shelf and upper slope, with highest density areas occurring at Monterey Bay, Farallon Ridge and Cordell Bank. The distribution of high biomass during the Upwelling season mimicked that described in the map for all seasons combined [Fig. 9(d)]. During the Oceanic season, high biomass was concentrated more over the inner shelf than it was in the Upwelling season. That pattern was particularly evident from Point Reyes to Monterey and off San Luis Obispo Bay. During the Davidson Current season, virtually the entire continental shelf from Point Reyes to Point Sur exhibited high marine bird biomass.
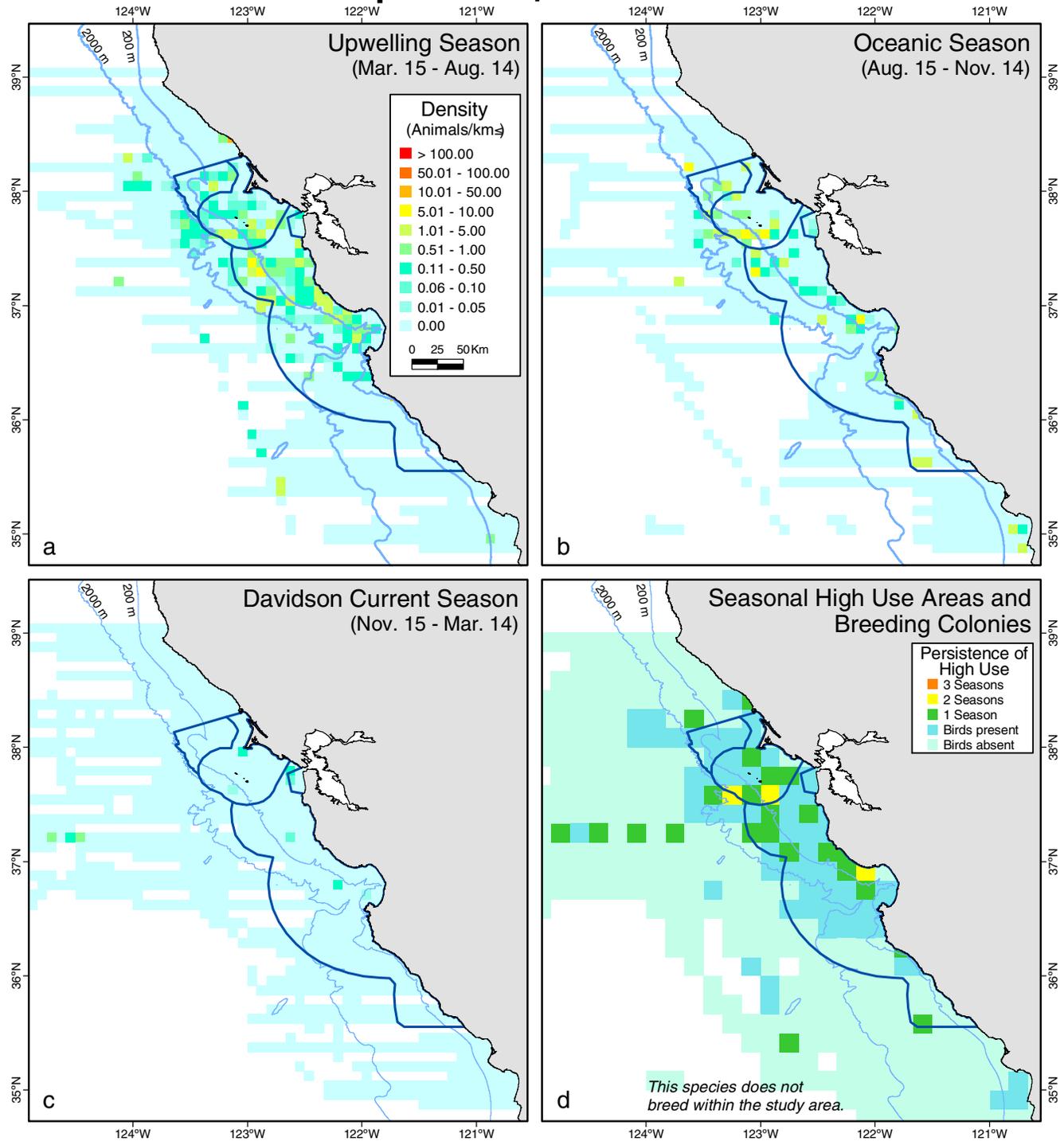

Fig. 6. Maps showing the density (birds km^{-2}) of the Cassin's Auklet in the (a) Upwelling, (b) Oceanic and (c) Davidson Current seasons, displayed in 5′ latitude by 5′ longitude cells. See Fig. 3 for details of National Marine Sanctuaries. Colony locations and sizes are from Carter *et al.* (1992), with updates from Thayer & Sydeman (2002), Warzybok (2002) and McChesney (pers. comm.).

Species diversity

Fig. 10 shows the geographic distribution of seabird diversity based on three alternative metrics: Simpson's index, Hill's N_2 and the Shannon-Wiener index. To visually emphasize areas of high diversity, the Hill's N_2 and the Shannon-Wiener indices are shown as geometrically scaled percentile rankings, in which the five colors from red to blue represent approximately 3%, 6%, 13%, 26% and 52% of the sampled 5' blocks, respectively.

Because Simpson's index resulted in large numbers of cell values that were either 0.00 or 1.00 (minimum and maximum bounds for that index), the geometric percentile scaling that we used for the

Red-necked Phalarope *Phalaropus lobatus*
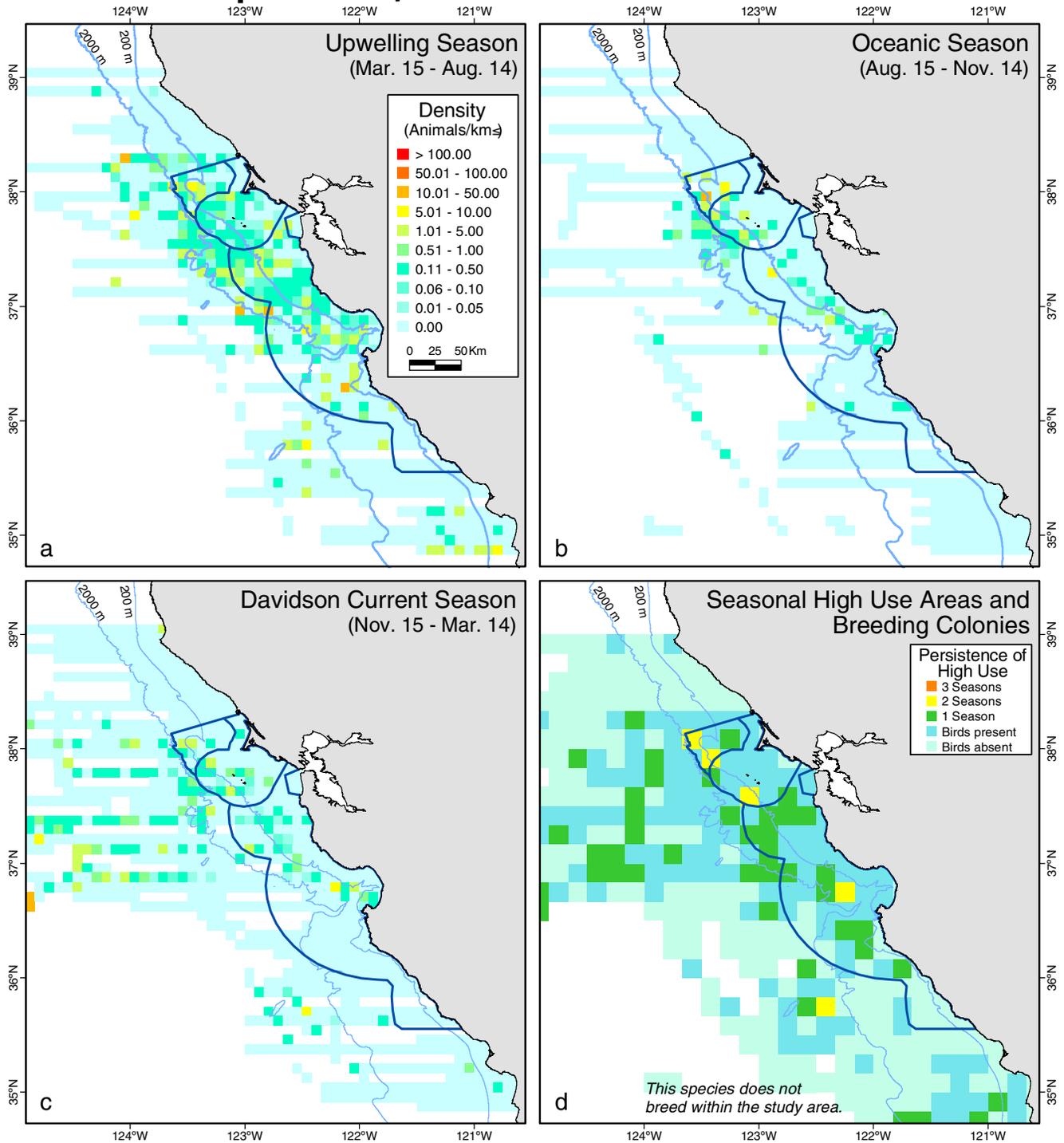

Fig. 7. Maps showing the density (birds km^{-2}) of the Red-necked Phalarope in the (a) Upwelling, (b) Oceanic and (c) Davidson Current seasons, displayed in 5′ latitude by 5′ longitude cells. See Fig. 3 for details of National Marine Sanctuaries.

other indices was inappropriate. Instead, we used a quintile ranking system in which roughly equal numbers of 5' cells were placed in each of five categories. Simpson's index functioned poorly in areas with low numbers of species and effort, such as the pelagic zone, where it tended to oscillate between minimum and maximum values. The discussion that follows is based primarily on Hill's N$_2$

and the Shannon-Wiener index, which yielded very similar patterns and, in this context, appeared to be more spatially consistent than Simpson's index.

Seabird species were most diverse in areas largely outside of national marine sanctuary boundaries, especially on the shelf break (200-m

Fig. 8. Maps showing the density (birds km^{-2}) of the Red Phalarope in the (a) Upwelling, (b) Oceanic and (c) Davidson Current seasons, displayed in 5′ latitude by 5′ longitude cells. See Fig. 3 for details of National Marine Sanctuaries.

isobath) and particularly along the Farallon Escarpment. Nevertheless, some localized areas of high diversity did occur within sanctuary boundaries: Pioneer, Ascension, Cabrillo and Carmel canyons, and along the continental slope off Point Sur (Fig. 11).

During the Upwelling season, the avifauna was the least diverse. Areas of highest diversity included the Farallon Escarpment, several canyons (Pioneer, Ascension and Carmel) and the Gulf of
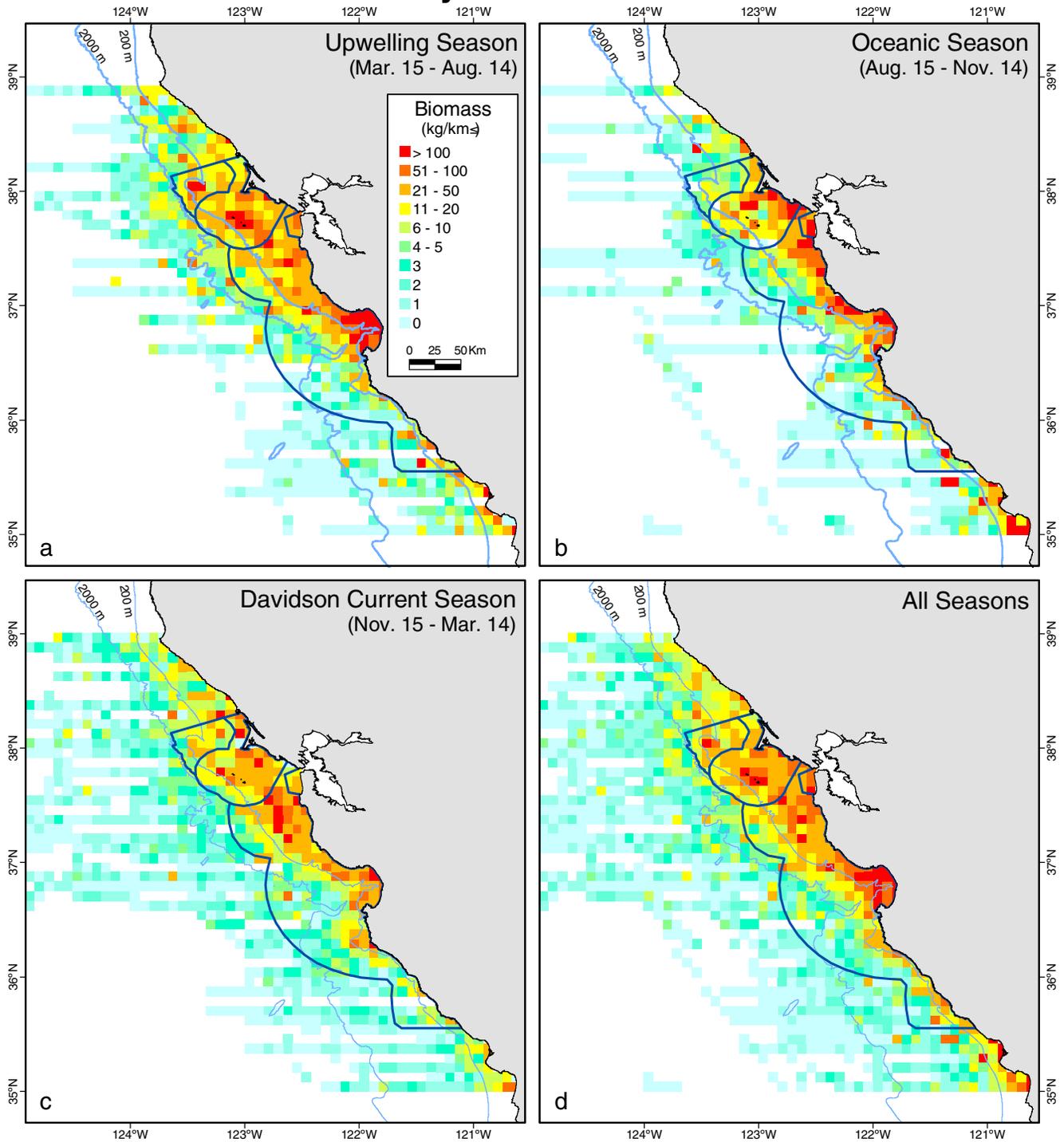
Seabird Biomass Density

Fig. 9. Total marine bird biomass density (kgs km^{-2}) in each 5′ latitude by 5′ longitude cell is shown for each oceanographic season and for all seasons combined. Density for each of 76 species was multiplied by the average body mass for that species and summed for all species. Unsurveyed areas are shown in white. Cells range in color from blue to red, the warmer end of the spectrum denoting higher densities. Dark blue lines indicate the boundaries of national marine sanctuaries (NMSs) in the study area (from north to south: Cordell Bank NMS, Gulf of the Farallones NMS and Monterey Bay NMS). Bathymetric contours defining the shelf break, 200 m and 2000 m, are shown in lighter blue.
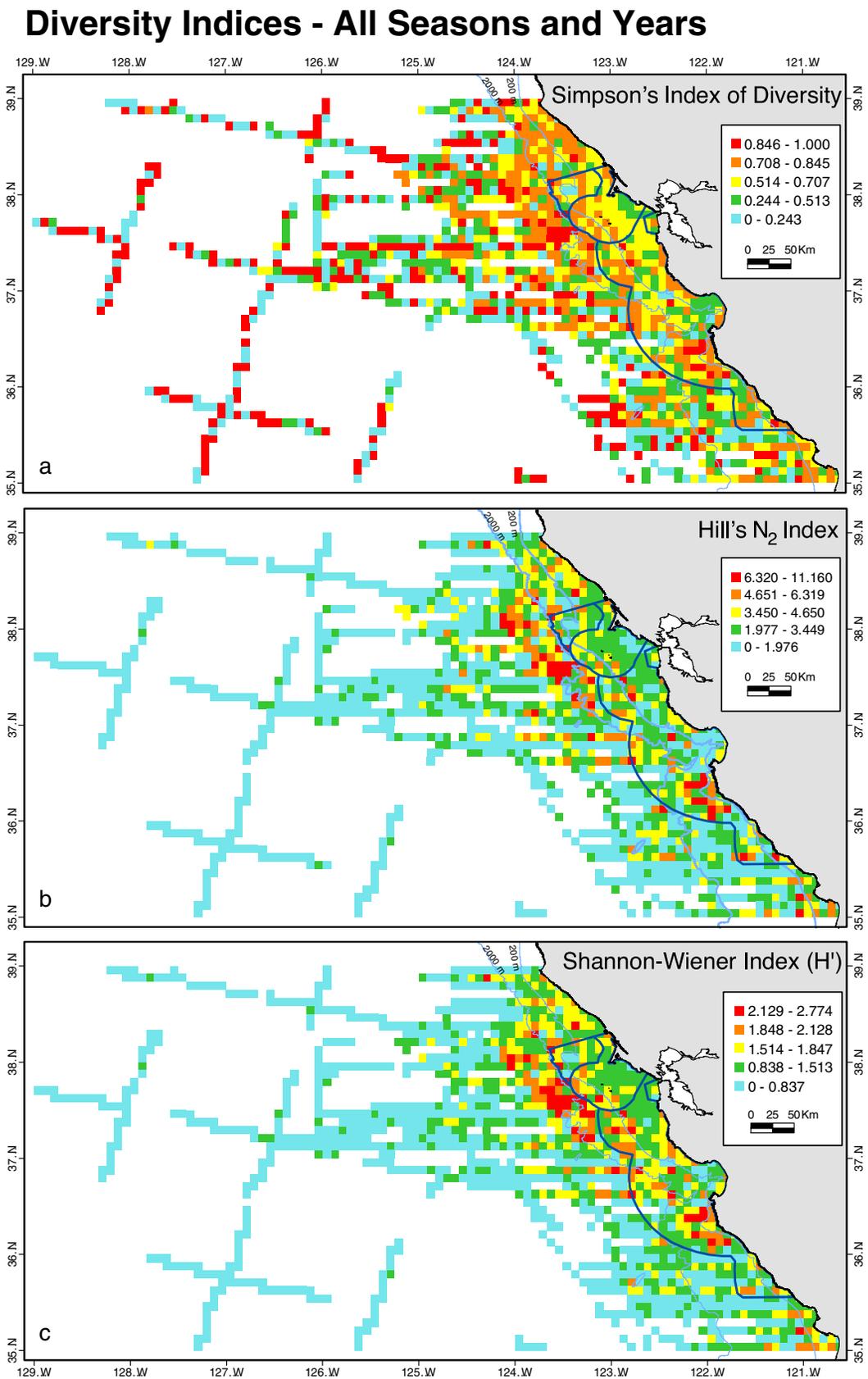
Diversity Indices - All Seasons and Years

Fig. 10. Distribution of diversity index values for three diversity metrics. Hill's N2 index and the Shannon-Wiener index are scaled so that the highest (most diverse) category contains about 3% of the 5' cell values and the remainder contain 6%, 13%, 26% and 52% respectively. Simpson's index of diversity yields values of 0 or 1 under many circumstances and could not be scaled in the same way. It is scaled so that approximately 20% of the observations fall into each color category.

the Farallones and Monterey Bay. During the Oceanic season, diversity was broadly comparable to that of the Upwelling season. Areas of high diversity included the Farallon Escarpment, Pioneer Canyon and inner Monterey Bay Canyon. During the Davidson Current season, marine bird diversity was the highest of the year. Areas of high diversity were all localized and occurred mostly over the continental slope (e.g. Farallon Escarpment and Pioneer, Ascension, Monterey Bay and Carmel canyons), but some also

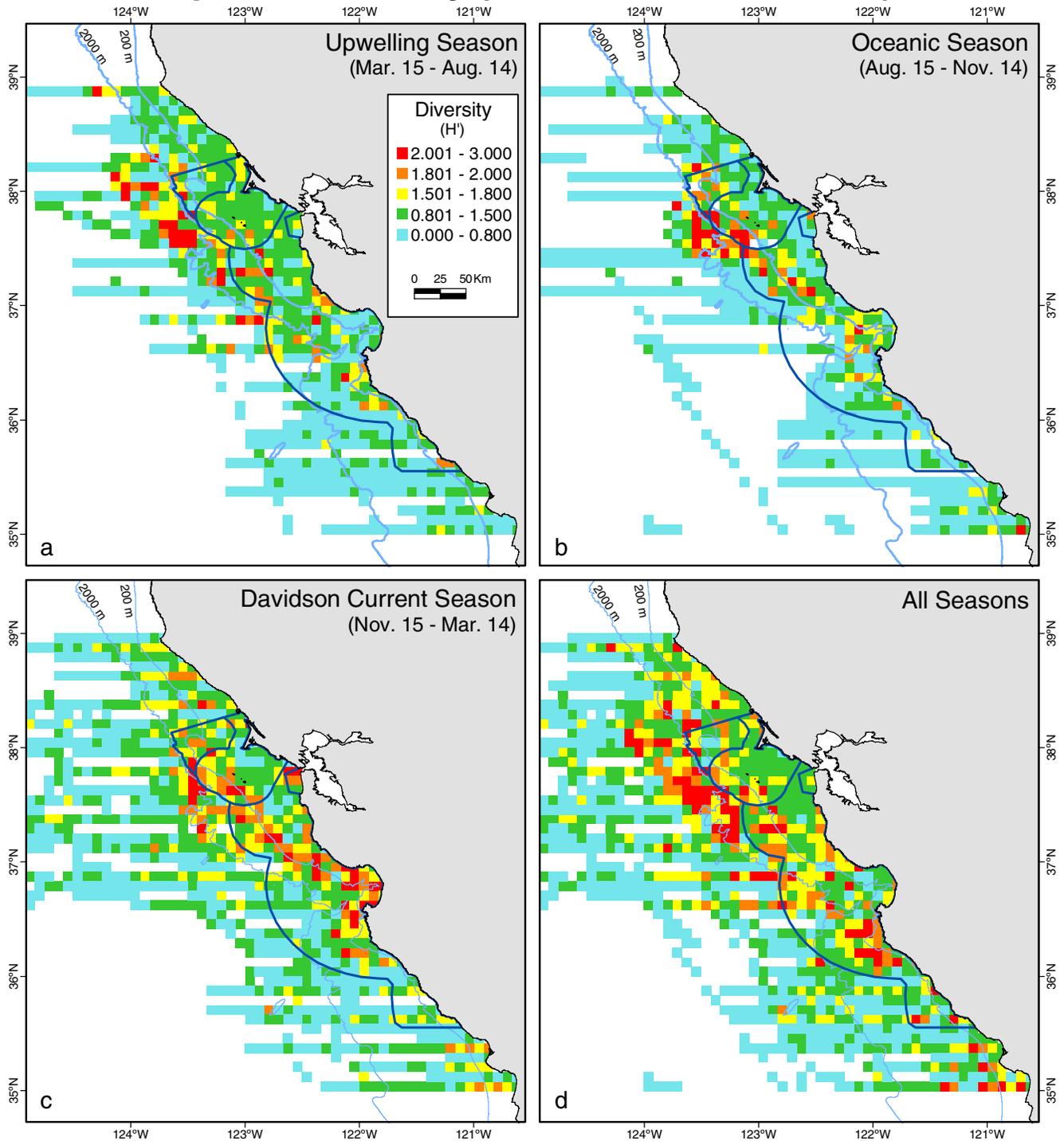# Seabird Species Diversity (Shannon-Wiener Index)

Fig. 11. Species diversity calculated for each 5' by 5' cell, using density as the variable in the Shannon-Wiener diversity index (Shannon & Weaver 1949). If a cell contains high densities of a few species and low densities of all others, the value of H' will be low, indicating low diversity. Alternatively, if many species are present at similar densities, the value will be high, indicating high diversity. Maps (a), (b) and (c) show the diversity index H' in three oceanographic seasons; map (d) shows H' for all seasons and years combined. Cells are colored based on the value of H'; warmer colors indicate higher diversity. See Fig. 9 for details of National Marine Sanctuaries.

occurred over the shelf (e.g. the inner San Francisco Bay tidal plume and inner portions of Monterey Bay).

The largest and most consistent area of high diversity occurred along the continental shelf, west-southwest of the Farallon Islands. High diversity in this area probably resulted in part from the overlap of species associated with the outer continental shelf, continental shelf break and pelagic waters. The shelf break was generally high in diversity because of the overlap between species from the continental shelf, the shelf break and the deeper pelagic habitats. If conditions off central California are analogous to those documented off Oregon, a dynamic upwelling front or jet may often be present along the shelf break, leading to the high heterogeneity of this area (see Ainley *et al.* in press). However, the area west of the Farallon Islands was especially diverse because it also included species such as cormorants that would not normally be found that far to sea except for the presence of the Farallon Islands.

Not surprisingly, high diversity tended to be inversely related to high biomass. One reason for the tendency is that high density often results from an influx of large numbers of a single species— for example, Sooty Shearwaters moving into Monterey Bay. The negative relationship between biomass and diversity holds in time as well as in space: the highest regional diversity occurred during the Davidson Current season, a period when density and biomass were lower than during the remainder of the year.

CONCLUSIONS

A huge amount of effort has been expended over the last four decades on studies to describe seabird distributions and habitat use in the central California Current system (CCS). The effort has been divided among numerous studies, so that no single study presents the entire picture regarding geographic distribution, seasonal use and population trends. Combining the studies into a single, internally consistent database—as we have done here—provides a perspective in time and space that is not otherwise possible.

Such a perspective has pitfalls related to systematic gaps in coverage and variations in methodology between investigators. Little can probably be done about gaps in coverage without funding for a directed study, as was the case with the MMS-funded work in the early 1980s (Briggs *et al.* 1987). However, the CCS and its avifauna have changed profoundly since that time (e.g. Viet *et al.* 1997, Ainley & Divoky 2001). The patterns revealed in earlier studies are now "snapshots" in time.

Most investigators are opportunistic: they carry out surveys when and where support is available. Ideally, federal and state agencies should try to maintain some degree of consistent coverage in the long term and over a wide spatial scale, as with the CalCofi and Rockfish Assessment cruises. But government programs are funded episodically, and it is difficult to instigate long-term monitoring programs. Ultimately, the desire of seabird biologists to go to sea and to count seabirds is what will maintain the flow of these data.

Some degree of standardization among survey methodologies would make it much easier to combine data sets. Although investigators have widely varying interests, everyone cares about certain things—notably, where the survey occurred, which birds were seen, where the birds were seen, and how many birds there were and what they were doing. These are data that might not be the primary focus of a study, but that are a valuable byproduct, useable for years to come. Some form of mutually agreed protocols for both aircraft and shipboard surveys could help considerably in combining data sets for future analyses. Some effort has been made toward that end, but further work is needed (e.g. Clarke *et al.* 2003, Spear *et al.* in press).

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