

Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years

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Abstract

We used a 17-year time series of shipboard observations to address the hypothesis that marine birds associate with persistent hydrographic features in the southern California Current System (CCS). Overall, approximately 27,000 km of ocean habitat were surveyed, averaging 1600 km per cruise. We identified mesoscale features (eddy centers and the core of the California Current), based on dynamic height anomalies, and considered habitat associations for seven migratory seabird species: black-footed albatross (*Phoebastria nigripes*), Cook's petrel (*Pterodroma cookii*), Leach's storm-petrel (*Oceanodroma leucorhoa*), dark shearwaters (mainly sooty shearwater *Puffinus griseus*, with a few short-tailed shearwaters *Puffinus tenuirostris*), northern fulmar (*Fulmarus glacialis*), red phalarope (*Phalaropus fulicaria*), and red-necked phalarope (*Phalaropus lobatus*). We explored associations (presence/absence and density relationships) of marine birds with mesoscale features (eddies, current jet) and metrics of primary productivity (chlorophyll *a* and nitrate concentrations). Mesoscale eddies were consistently identified in the study region, but were spatially and temporally variable. The resolved eddies were large-scale features associated with meanders of the equatorward-flowing California Current. Cook's petrel was found offshore with no specific habitat affinities. Black-footed albatross, red phalarope, and Leach's storm petrel were found in association with offshore eddies and/or the core of the California Current, but the functional relationship for these species varied, possibly reflecting differences in flight capabilities. The more coastal species, including the shearwaters, fulmar, and red-necked phalarope, were positively associated with proxies of primary productivity. Of the hydrographic habitats considered, the upwelling region of Point Conception appears to be an important "hotspot" of sustained primary production and marine bird concentrations. Point Conception and other similar coastal locations (upwelling cells) may warrant protection as key foraging grounds for seabirds.

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Keywords: California Current; Top predators; Marine birds; Chlorophyll *a*; Anticyclonic/cyclonic eddy; Protected areas

Bounding box: 125°W; 36°N; 29°N; 117°W

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1. Introduction

Identifying locations of tight coupling between physical and biological processes is critical to understanding energy transfer from lower to upper trophic levels in marine food webs. It is increasingly apparent that certain areas of the oceans are characterized by enhanced primary and secondary productivity and/or aggregation of plankton and other weakly swimming organisms. In turn, upper trophic-level predators (sea turtles, marine birds, and mammals) track this spatial variability and concentrate where prey is abundant near the surface (Hunt et al., 1996; Polovina et al., 2001, 2004; Davis et al., 2002; Hyrenbach et al., 2002; Croll et al., 2005). Foraging “hotspots” of diverse types and spatial/temporal scales (this volume) may be ecologically and demographically significant by concentrating energy transfer, thereby affecting growth and survival of fish (e.g., Logerwell et al., 2001) and the foraging success of top predators (e.g., Nel et al., 2001). Therefore, documenting the persistence and use of regions of tight bio-physical coupling is essential for fisheries and protected species management. It is also critical to the design of effective protected areas for the conservation of ecosystem functions in general (Hyrenbach et al., 2000; Bograd et al., 2004; Drapeau et al., 2004).

The California Current System (CCS) is a dynamic and productive North Pacific large marine ecosystem, stretching over 3000 km from British Columbia, Canada to Baja California, Mexico (PICES 2004: www.edc.uri.edu/lme). In this system, top predators are known to aggregate at both bathymetric (e.g., seamounts, shelf-breaks, canyons) and hydrographic (e.g., temperature and color fronts, upwelling plumes) features (Smith et al., 1986; Laurs and Lynn, 1991; Etnoyer et al., 2004; Yen et al., 2004, 2005; Ainley et al., 2005; Tynan et al., 2005). Due to the economic value (e.g., rockfishes, tunas, swordfish) and conservation status (e.g., cetaceans, albatrosses, sea turtles) of many top predators in the CCS, the study of ocean habitat associations is key for implementing ecosystem-level management approaches. Additionally, because some top predators are quite conspicuous (e.g., seabirds), they may be useful bio-indicators of foraging “hotspots”, and the structure and variability of marine ecosystems generally (Montevecchi, 1993; Sydeman et al., 2001; Block et al., 2003).

In the southern CCS, the California Cooperative Oceanic Fisheries Investigation (CalCOFI) has monitored ecosystem dynamics since 1949 (Bograd et al., 2003; Ohman and Venrick, 2003). CalCOFI research has established the importance of both coastal and oceanic habitats to a variety of plankton and fish species (Checkley et al., 2000; Logerwell et al., 2001). Starting in the spring of 1987, a long-term observational program for marine birds was added to seasonal CalCOFI cruises. This program has provided novel understanding of seabird responses to temporal environmental variability in the CCS (Veit et al., 1997; Hyrenbach and Veit, 2003), but spatial habitat associations have yet to be investigated.

Herein, we investigate spring-time habitat associations of a select group of migratory marine birds in the study region, with an emphasis on their affinities to eddies and the core of the California Current. We use a 17-year time series (1987–2004, missing 1997) of shipboard observations to address the hypothesis that marine birds associate with *persistent* hydrographic features in the southern CCS. More specifically, we (1) describe and characterize the spatial and temporal persistence of eddy features and the core of the California Current; (2) relate the observed hydrographic variability to the distribution of marine birds; and (3) evaluate potential mechanisms underlying sea-bird-habitat associations. We consider the significance of these features in relation to the migratory behavior and feeding ecology of the birds, and discuss potential conservation and management implications.

2. Materials and methods

2.1. Study area

In its current form, the CalCOFI survey grid consists of six parallel transects, ranging in length from 470 km (northernmost) to 700 km (southernmost). This study area, encompassing over 300,000 km² of the Pacific Ocean, from 30° to 35°N and from the southern California coast to 124°W (Fig. 1), includes a variety of bathymetric domains (e.g., shelf-slope regions and deep water) and hydrographic habitats (e.g., water masses, mesoscale features). Four hydrographic and floral domains have been documented within this region in spring-time: a southern coastal domain influenced by northward incursions of warm and salty

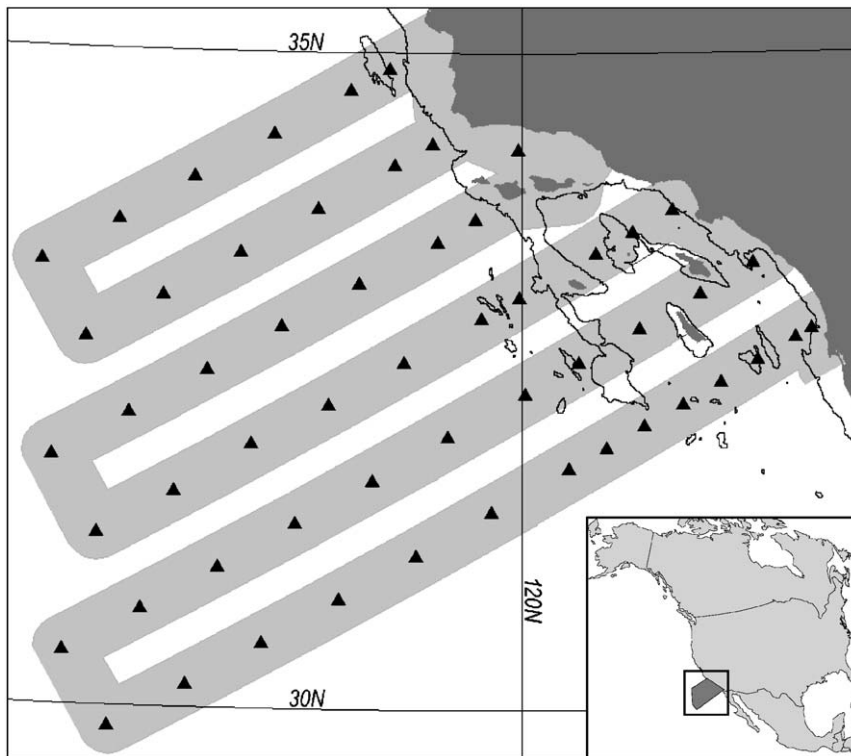


Fig. 1. The study area in the southern California Current System (CCS), showing the CTD stations, transects, and the 25-km buffer around each transect use to standardize marine bird observations between years.

water, a northern coastal domain influenced by coastal upwelling at Point Conception, a transition domain delineated by the location of the California Current, and an oceanic domain offshore (Hayward and Venrick, 1998).

We focus our study on spring cruises for three reasons: (1) the onset of coastal upwelling and the regeneration of the California Current make this a very dynamic, variable, and important oceanographic period (Lynn et al., 2003); (2) the highest annual integrated chlorophyll *a* concentrations occur at this time (Hayward and Venrick, 1998); and (3) this is a sensitive phase in the seasonal cycle for seabirds in the region in terms of migration (Hyrenbach and Veit, 2003). This study was conducted during a period of substantial interannual variability in physical and biological properties of the southern CCS (Schwing et al., 2000; Bograd and Lynn, 2003; Hyrenbach and Veit, 2003; McGowan et al., 2003), including major El Niño—Southern Oscillation events in 1992–93 and 1997–98, and a possible “regime shift” in 1999 (Peterson and Schwing, 2003).

2.2. Hydrographic surveys and contouring

Water-column density can be used to characterize vertical (e.g., pycnocline depth and strength) and horizontal (e.g., the location and extent of meso-scale oceanographic features, such as eddies and fronts) gradients, which are known to influence primary and secondary productivity in the CCS (Haury et al., 1993; Hayward and Venrick, 1998; Lynn et al., 2003; McGowan et al., 2003). We used the data from conductivity–temperature–depth (CTD) casts at 66 standardized CalCOFI stations, with a spatial resolution of 20 nm (36 km) onshore and 40 nm (72 km) offshore, to characterize horizontal gradients in physical, chemical, and biological properties within the study area (Fig. 1). From published CalCOFI reports (<http://www.calcofi.org/data>), we used the dynamic height (hereafter DyHt) of the surface relative to a reference depth of 500 m at each CTD station, to generate sea-surface height contours for each cruise. We used ArcGIS 8.3 and ArcView 3.2a Geographical Information System (GIS) software (ESRI, 2004) to contour the CTD

point data into surfaces using the “spline tension algorithm” (Webster and Oliver, 2001). We used the resulting DyHt surfaces to identify eddy centers and the position of the dominant geostrophic current in the region, i.e. the core of the California Current itself.

2.3. Proxies for primary productivity

We used near-surface (10 m) nitrate concentrations ($\mu\text{M L}^{-1}$) and chlorophyll *a* concentrations ($\mu\text{g L}^{-1}$) as proxies for primary productivity at each CTD station. These properties have previously been used to characterize spatial and temporal changes in spring-time physical–biological coupling in the southern CCS (Hayward and Venrick, 1998; Haurv et al., 1986, 1993; Lynn et al., 2003) and the Gulf of Alaska (Yen et al., 2005). After contouring these properties, we sampled the productivity data for those locations where we had made concurrent seabird observations.

2.4. Seabird surveys

We used standard techniques for vessel-based censusing of birds at sea (Tasker et al., 1984). For all surveys, one observer identified and counted birds from the flying bridge or the pilot house of one of three vessels (R.V. *David Starr Jordan*, R.V. *New*

Horizon, and R.V. *Roger Revelle*), from approximately 10 m above the sea surface, during all daylight hours. A hand-held range finder was used to ground-truth the width of the survey strip (Heinemann, 1981). Seabirds that entered a 90° arc from the bow to the beam and out to 300 m on the one side with best visibility (e.g., lowest sun glare) were enumerated, assigned to one of five behavioral codes (flying, sitting on the water, feeding, ship-following, milling), and logged into a field computer with a temporal resolution of 0.1 min. Ship-following individuals were recorded when first sighted and ignored thereafter. The positions of the boat were time-coded into the survey log every 10 min and at the beginning and end of each transect, or on-effort session, using the ship’s GPS. Surveys were conducted while the vessel was underway at a speed of 10–12 knots ($18.6\text{--}22.3 \text{ km h}^{-1}$). Seabird relative abundance was expressed as the number of individuals sighted per unit area surveyed (birds km^{-2}). Overall, a total of $\sim 27,000 \text{ km}$ of track-line were surveyed during 17 years (Table 1).

2.5. Species selection

This study considers seven seabird species: black-footed albatross (*Phoebastria nigripes*), Cook’s petrel (*Pterodroma cookii*), Leach’s storm-petrel

Table 1

Survey effort, including area, bounding box, the start and end dates, and duration of each spring CalCOFI cruise

Year	Survey length (km)	Observers	Bounding box				Start (mm/dd/yy)	End (mm/dd/yy)	Days
			North	South	East	West			
1987	1589.3	R. Veit	35.077	29.870	–117.922	–124.322	05/02/87	05/13/87	11
1988	1323.7	R. Veit	35.085	30.564	–117.258	–122.808	04/28/88	05/11/88	13
1989	1621.5	R. Russell	35.146	29.851	–117.726	–124.175	04/17/89	04/30/89	13
1990	1482.4	P. Pyle	34.306	29.864	–117.327	–124.020	04/17/90	04/30/90	13
1991	1177.4	P. Pyle	34.272	30.024	–117.335	–124.165	02/26/91	03/10/91	12
1992	2132.9	C. Alexander	35.083	29.949	–117.816	–124.213	04/14/92	04/29/92	15
1993	1667.3	R. Veit	35.085	29.849	–117.329	–124.171	03/30/93	04/14/93	15
1994	1484.7	R. Forstser	35.077	30.188	–117.834	–124.320	03/23/94	04/07/94	15
1995	1625.8	A. Reitsch	35.078	29.852	–117.770	–124.148	04/07/95	04/20/95	13
1996	1168.6	D. Hyrenbach	34.886	31.474	–117.812	–124.316	04/22/96	04/30/96	8
1998	1591.8	D. Hyrenbach	34.880	29.837	–117.284	–124.316	04/02/98	04/17/98	15
1999	1651.9	D. Hyrenbach	35.078	29.851	–117.300	–124.286	04/01/99	04/15/99	14
2000	1661.1	D. Hyrenbach	35.083	29.835	–117.259	–124.126	04/06/00	04/22/00	16
2001	1477.2	C. Oedokoven	35.255	29.849	–117.433	–124.324	04/06/01	04/23/01	17
2002	1248.7	S. Webb	35.083	29.886	–117.456	–124.441	03/28/02	04/12/02	15
2003	2350.7	C. Oedokoven	35.013	29.854	–117.352	–124.322	04/06/03	04/24/03	18
2004	1786.7	C. Oedokoven	35.086	29.848	–117.314	–124.316	03/23/04	04/09/04	17

(*Oceanodroma leucorhoa*), dark shearwaters (mainly sooty shearwater *Puffinus griseus*, with a few short-tailed shearwaters *Puffinus tenuirostris*), northern fulmar (*Fulmarus glacialis*), red phalarope (*Phalaropus fulicaria*), and red-necked phalarope (*Phalaropus lobatus*). These taxa were selected because they were consistently recorded in the study region during spring (Hyrenbach and Veit, 2003). Together, they accounted for 51% of all the birds sighted during this study.

2.6. Spatial autocorrelation analysis

Because this study tests for spatial associations between seabirds and the marine environment, we began by assessing the degree of spatial autocorrelation within our sampling structure. A lack of sample independence, if found, would enhance the likelihood of falsely rejecting the null hypothesis (type I error), thus finding spurious habitat relationships (Hurlbert, 1984). We evaluated spatial autocorrelation patterns using the Moran's I index (Fig. 2); for details see Yen et al. (2004, 2005). Based on the results of the spatial autocorrelation analysis (see Fig. 2; indicative of little spatial autocorrelation), we used the minimum survey bin (3 km) to generate indices of seabird distribution and abundance. We analyzed species presence/absence (0 vs. 1) and apparent density (birds km⁻²) against habitat covariates.

2.7. Oceanographic features

Prominent hydrographic features in the study region were identified from the surface DyHt fields. Mesoscale eddies were identified as regions of closed or nearly closed DyHt contours encompassing a local maximum (anticyclonic, symbolized as 'H') or minimum (cyclonic, symbolized as 'L'). The position of the strongest equator-ward flow, which is generally associated with the main core of the California Current jet, was identified visually as the local maximum cross-shore DyHt gradient. We note that the spatial resolution of the standard CalCOFI grid and CTD cast locations can only resolve large eddies (diameters > 100 km) and may not capture their full extent. Thus, their boundaries must be viewed as approximate. Consequently, we were unable to estimate the size of eddies and provide other statistics. Moreover, in some cases, these centers may represent large-scale cyclonic or

anticyclonic meanders, rather than closed rotational features.

2.8. Analytical methods

We related marine bird distributions to eight habitat covariates, including the minimum distance from each 3-km survey bin centroid to the following: (1) core of the California Current, (2) all eddies, (3) cyclonic eddies, and (4) anticyclonic eddies. Additionally, we characterized hydrographic conditions within each survey bin using the following metrics: (5) the mean DyHt, (6) the DyHt gradient ($[\max - \min] / \max \cdot 100\%$), (7) the mean chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), and (8) the mean nitrate concentration ($\mu\text{M L}^{-1}$).

Because seabird presence/absence and densities were not normally distributed, and we could not adequately transform these data for parametric analyses, we used a nonparametric approach to investigate habitat associations (Sokal and Rohlf, 1981). This was done in two steps. First, we tested for significant associations between the binomial variable "occurrence" (presence/absence) for each species using logistic regression (Hosmer and Lemeshow, 2000). Next, we investigated the response of seabird densities using 'presence only' data in an ordered logistic regression (Yen et al., 2004, 2005). The data used in the ordered logistic regressions were combined for a given species and re-coded by categorizing "density" in each bin into three classes, '1' = low (< 33 percentile), '2' = intermediate (34–66 percentile), '3' = high densities (> 66 percentile).

Surveys were not conducted at exactly the same time period each year (Table 1). To account for latitudinal (north–south), and temporal (within-season and interannual) variability, we assessed the effect of each hydrographic variable after including latitude ($df = 1$), date ($df = 1$), and year ($df \leq 17$) in each regression model. Year was entered as a categorical variable, whereas latitude and date were continuous treatment effects. We also evaluated several transformations for each habitat variable instead of selecting one arbitrary transformation for all variables (Table 2). We selected the 'best' transformation by selecting the model with the largest likelihood ratio statistic (LRS) (Hosmer and Lemeshow, 2000). Three transformations and the original (untransformed) values were considered: (i) logarithmic, (ii) squared, and (iii) square root (Table 2).

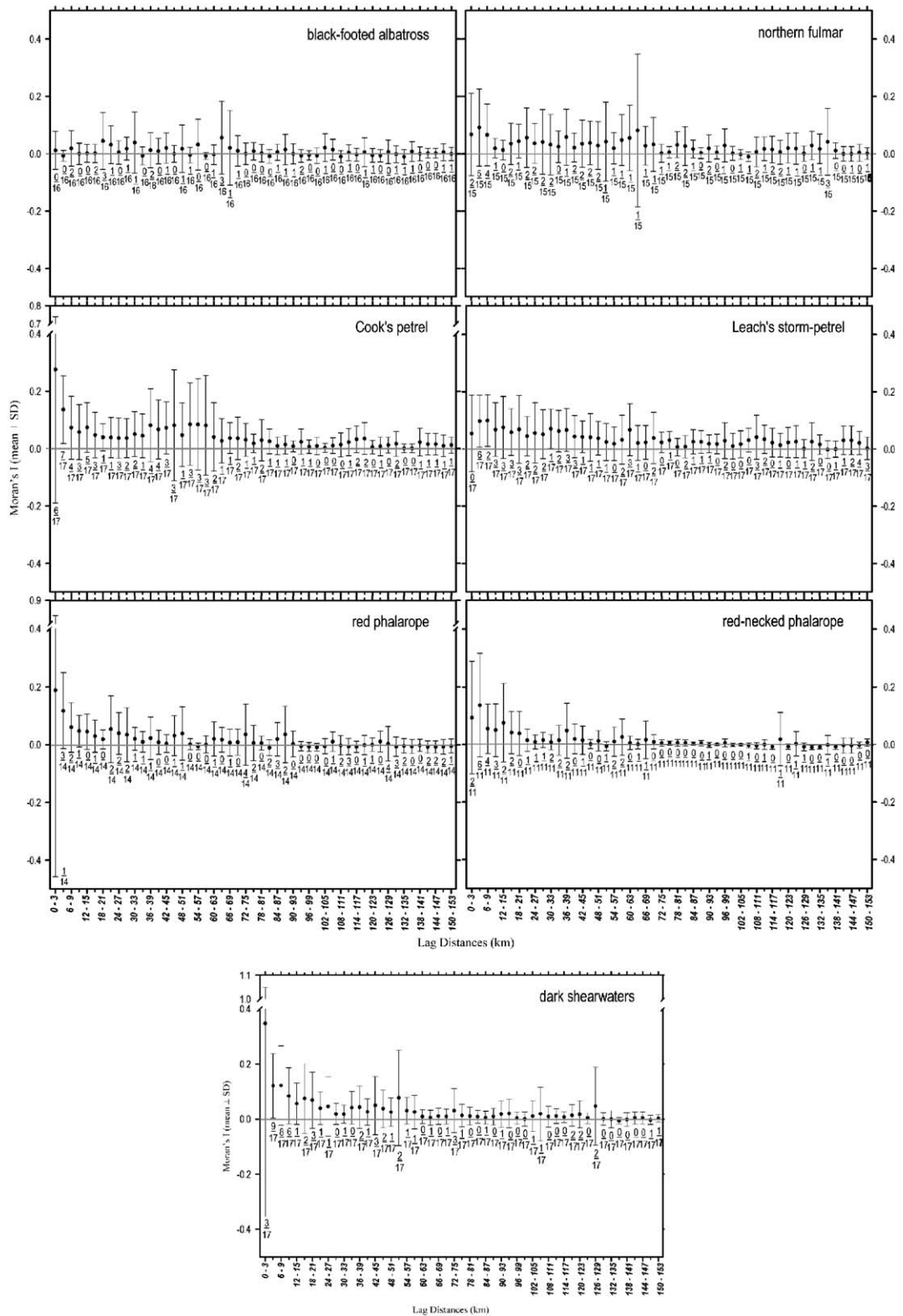


Fig. 2. Moran's I index values (y-axis: mean ± SD), as a function of the spatial separation (x-axis: lag in km) between survey bins for the focal species. Large positive indices are indicative of similar (positive) and dissimilar (negative) predator abundances, while small indices (close to 0) indicate a lack of spatial structure in the data. For each lag, the fractions denote the number of significant ($P < 0.01$) autocorrelation indices (determined by randomization tests) out of the number of years analyzed (maximum $n = 17$).

Table 2

The transformation applied to each habitat covariate for analysis in logistic and ordered logistic regressions

	Black footed albatross	Cook's petrel	Leach's storm-petrel	Dark shearwaters	Northern fulmar	Red phalarope	Red-necked phalarope
<i>(a) Logistic</i>							
CC jet	SQ	SQ	SQ	LN	SQ	LN	L
Dyn ht mean	LN	SQ	SQ	LN	LN	SQ	SQ
Dyn ht CI	SQ	LN	SQ	LN	LN	SQ	LN
Chlo <i>a</i>	LN	SQRT	SQ	LN	SQ	LN	SQRT
NO ₃	LN	SQRT	SQ	LN	LN	SQ	LN
Eddy	SQ	SQRT	SQ	SQ	SQ	LN	LN
L eddy	SQ	LN	SQ	L	SQ	SQ	SQRT
H eddy	SQ	SQRT	SQ	SQ	SQRT	L	LN
<i>(b) Ordered logistic</i>							
CC jet	L	SQRT	SQ	LN	SQRT	SQ	LN
Dyn ht mean	LN	LN	LN	LN	SQ	SQ	SQ
Dyn ht CI	SQRT	SQ	SQRT	SQ	L	SQRT	SQ
Chlo <i>a</i>	LN	LN	LN	LN	LN	SQRT	LN
NO ₃	LN	L	SQRT	LN	LN	SQ	LN
Eddy	SQ	L	SQ	L	SQ	SQ	L
L eddy	SQ	SQ	SQ	SQ	SQ	SQ	LN
H eddy	SQ	SQ	SQ	SQRT	SQ	SQ	SQ

Transformations were logarithmic (LN), square (SQ), square root (SQRT), and non-transformed (L).

3. Results

3.1. Interannual variability in hydrographic features

Mesoscale eddies were consistently identified in the region, but were variable spatially and temporally (Fig. 3). Over 17 years, we identified 26 eddies, with roughly equal numbers of cyclonic and anticyclonic features. We found no persistent pattern in the numbers or locations of eddies. Large-scale anticyclonic eddies (or meanders) were most common (10 of 17 years) in the offshore regions, west of the core of the California Current.

Strong equator-ward flow was a prominent feature each spring, although there was substantial variability in its position and route through the study area (Fig. 3, blue contours). The core was farther inshore in 1987, 1988, 1994, 1995, and 1998, and farther offshore in 1999–2004 and 1991–1993. The initiation of upwelling each spring results in the uplifting of nearshore isopycnals, and hence the development of a strong nearshore equatorward jet. The development of this upwelling jet appears to be independent of the winter-time manifestation of the California Current, which tends to be much further offshore (Lynn et al., 2003). Therefore, the feature we have identified as the core of the California Current may, in some cases, include the local

upwelling jet, and its offshore position may reflect differences in the onset of the spring transition relative to the timing of the spring cruises. Nonetheless, we have used this maximum offshore gradient of DyHt as a physical metric to relate to seabird distributions.

There were persistently high chlorophyll *a* values (with the exception of the El Niño years of 1992–94) associated with the upwelling domain around Point Conception and the northwestern Channel Islands (Fig. 3, red, orange and yellow contours). High chlorophyll *a* concentrations often were found downstream from Point Conception (e.g., 1988), presumably due to the entrainment of “green” waters in the southern California Bight.

3.2. Spatial autocorrelation

Autocorrelation analysis revealed no significant spatial dependencies (Fig. 2). None of the Moran's *I* values surpassed 0.37 (dark shearwaters), and even for species showing some degree of autocorrelation, none showed significant patterns for more than 50% of the years (see fractions in Fig. 2). For example, consider the Cook's petrel. For this species, only ~35% (7/17) years showed a correlation of slightly >0.2 at a spatial scale of 3-km. Overall, Cook's petrel, red phalarope, red-necked

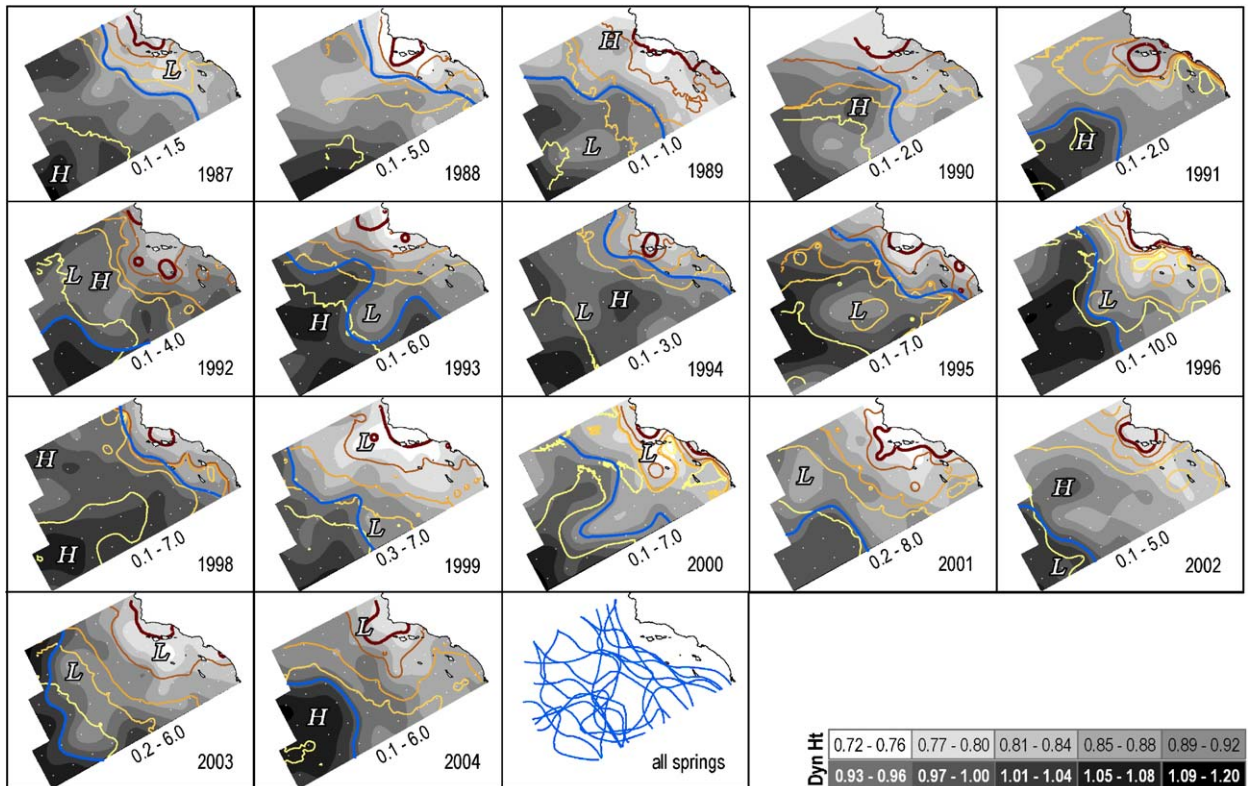


Fig. 3. Year-to-year variability, 1987–2004 and all years combined (“all springs”) of productivity and mesoscale features off southern California. Chlorophyll *a* concentrations ($\mu\text{g L}^{-1}$) at 10-m depth (red, orange and yellow contours) are overlaid over dynamic heights (gray shading). The core of the California Current (blue line) varies spatially, whereas chlorophyll concentrations were persistently high around and downstream from Point Conception.

phalarope, and dark shearwaters displayed some positive autocorrelation at small spatial scales (3–9 km), but none of these were consistently significant between years.

3.3. Seabird distribution and abundance

The black-footed albatross was most numerous in the pelagic zone (> 3000 m; Fig. 4), and occurred in high abundances in some years, but was essentially absent from the region in 1998–2000. Both the Cook’s petrel (Fig. 5) and the Leach’s storm-petrel (Fig. 6) were generally found beyond the 3000 m isobath. Cook’s petrel exhibited a latitudinal gradient, with greater abundance in the south. Leach’s storm-petrel, while found well off the continental shelf, showed an area of concentration just to the north of the San Juan Seamount (see Briggs et al., 1987, p. 2). Dark shearwaters were most abundant on the shelf, with concentrations near Point Conception (Fig. 7). These birds also

exhibited a latitudinal gradient, with higher abundances along northern transects. The northern fulmar occurred mainly shoreward of the 3000 m isobath, but extended further offshore along the northern lines (Fig. 8). Fulmars were not observed in 1992 or 2000, and were rare in many years (1987–88, 1993, 1999, and 2002). Conversely, they were relatively abundant in 4 years (1996, 2001, 2003, and 2004). The red phalarope had a broad cross-shelf to pelagic distribution (Fig. 9); in 1996, 1999, and 2000 this species was not recorded, but this was due to difficulties in species identification, not a lack of presence in the study area (KDH personal observation). The red-necked phalarope was found in great abundances along the coast, especially around Point Conception (Fig. 10).

3.4. Seabird associations with eddies

Table 2 shows which transformation was used for each covariate in species-specific habitat modeling.

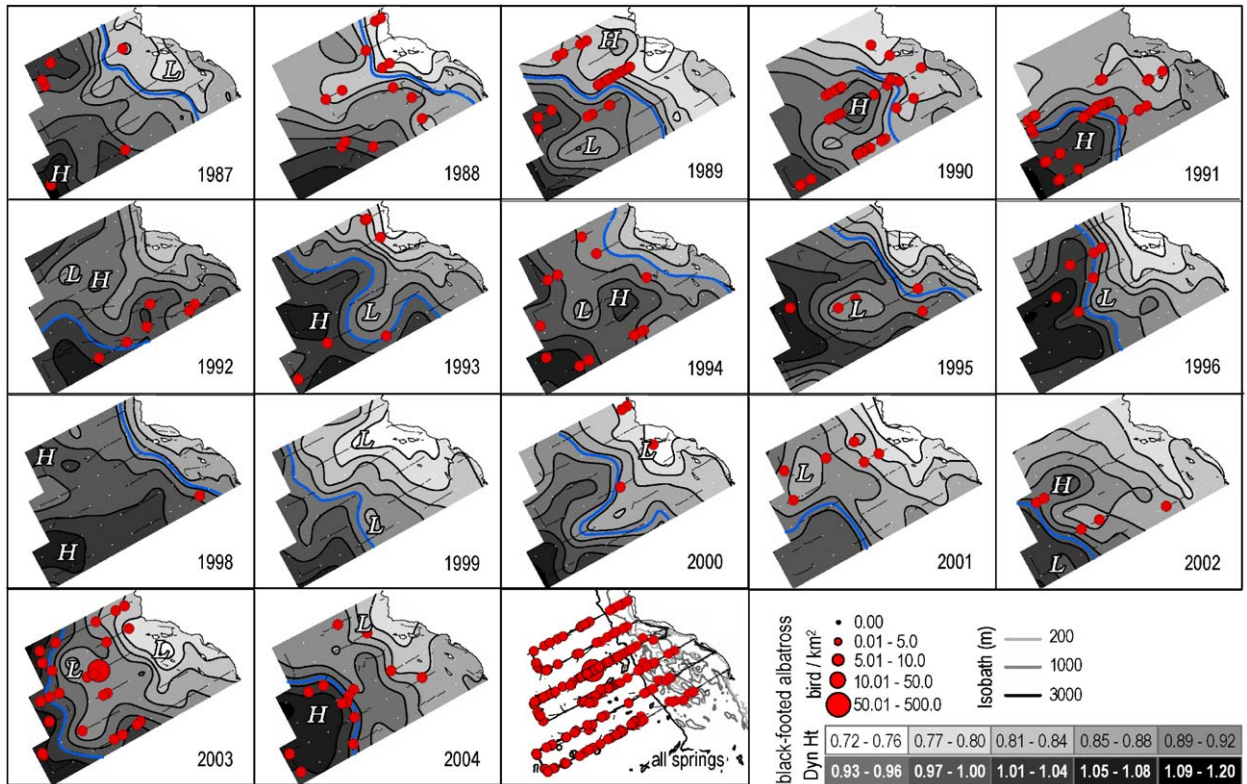


Fig. 4. Black-footed albatross distribution and abundance overlaid on dynamic height contours with the core of the California Current (blue line) over 17 years, 1987–2004. Note that the last panel shows distribution and abundance combined for all years.

For brevity, we have not reported the LRSs or *P*-values for each transformation, but this information is available upon request. Table 3 reports (a) presence/absence and (b) density relationships (using presence only data) for each of the focal species against the eight habitat variables described above, as well as date and latitude. “Year” was included in all models and was significant for each species (all $P < 0.001$); this indicates interannual variability in occurrence (presence/absence) and density of the focal species. Results are summarized showing the LRS and sign (+/–) of the coefficient for each covariate. For metrics involving distance to a feature (i.e., eddies and the core of the California Current), negative coefficients indicate a higher probability of occurrence or higher density closer to the feature. For productivity indices (chlorophyll *a* and nitrate), positive coefficients describe increasing probability of occurrence and/or density with increasing concentrations. Given the large number of univariate tests performed (7 species × 10 variables × 2 tests) and evidence of weak spatial autocorrelation, we consider significance at

$P \leq 0.001$; with $df = 1$, this is equivalent to a critical LRS value ≥ 10.8 .

There was a significant effect of date for all species except the black-footed albatross and the Leach’s storm petrel (Table 3a). After controlling for year, the Cook’s petrel, dark shearwaters, and red phalarope were found in greater abundance during later surveys. For dark shearwaters, this relationship was established using density, not presence/absence. For the northern fulmar and the red-necked phalarope, the relationship with date was negative, indicating a higher probability of encounter during early surveys. These relationships match what is known about the migratory behavior of these species, with shearwaters arriving to feed in the CCS during spring-time, and fulmars and phalaropes leaving the system to breed in the North Pacific during the same period.

There was a significant effect of latitude for all species except black-footed albatross (Table 3a). After controlling for year and date, Cook’s petrel and the Leach’s storm petrel occurrence was greater along southern CalCOFI lines, whereas dark shearwaters,

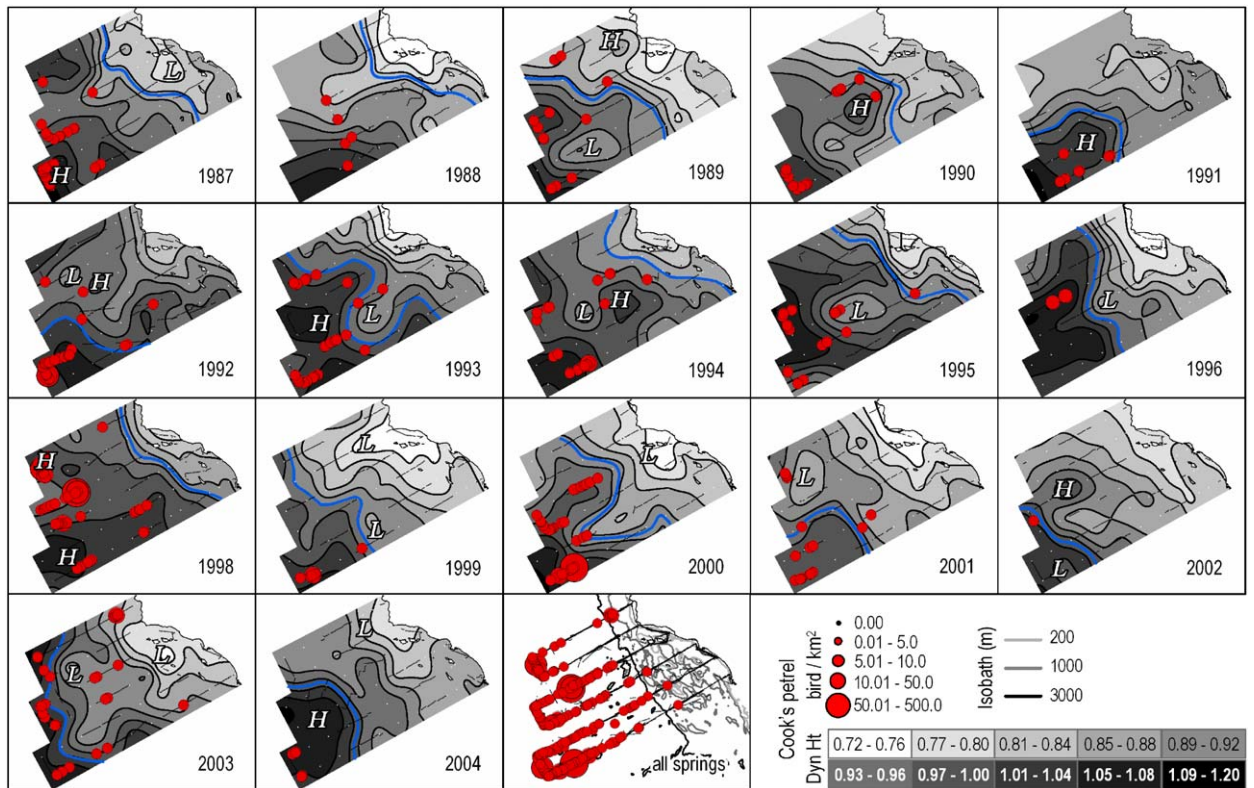


Fig. 5. Cook's petrel distribution and abundance over 17 years.

northern fulmars, and red and red-necked phalaropes were found more often on northerly lines. Moreover, dark shearwater and red-necked phalarope densities were higher in the north. These results reflect the importance of coastal upwelling near Point Conception to phalaropes, fulmars, and shearwaters.

Black-footed albatross occurrence was associated with the core of the California Current, eddies (anticyclonic eddies in particular), and steep gradients in DyHt (Table 3a). We found no significant density relationships for this species (Table 3b). The Cook's petrel occupied unproductive waters (low chlorophyll *a* and nitrate concentrations) generally seaward of the core of the California Current, characterized by high and homogeneous DyHt. We found no significant density relationships for this species (Table 3b). Leach's storm-petrels were associated with the core of the California Current, eddies (both cyclonic and anticyclonic) and high-steep gradients in DyHt. The occurrence this species was negatively correlated with waters of elevated chlorophyll *a* and nitrate. There were no significant

density relationships for the Leach's storm-petrel (Table 3b). Dark shearwaters occurred in productive waters (positive relationships with chlorophyll *a* and nitrate), away from the core of the California Current and anticyclonic eddies, and in areas of low DyHt. These results reflect the affinity of dark shearwaters for the productive coastal domain, especially downstream from Point Conception. The densities of dark shearwaters were higher in nitrate-rich regions and decreased with increasing DyHt. Northern fulmar presence was higher in regions of lower DyHt (nearshore), higher gradients in DyHt, elevated chlorophyll *a* concentrations, and away from anticyclonic (H) eddies. We found no significant density relationships for fulmars. Red phalarope occurrence increased in proximity to the core of the California Current, eddies (particularly anticyclonic eddies), and in regions of steep DyHt; red phalarope occurrence was negatively correlated with nitrate, indicating an offshore distribution. The red-necked phalarope was more prevalent in near-shore waters of high nitrate content, and away from the core of the California Current and eddies.

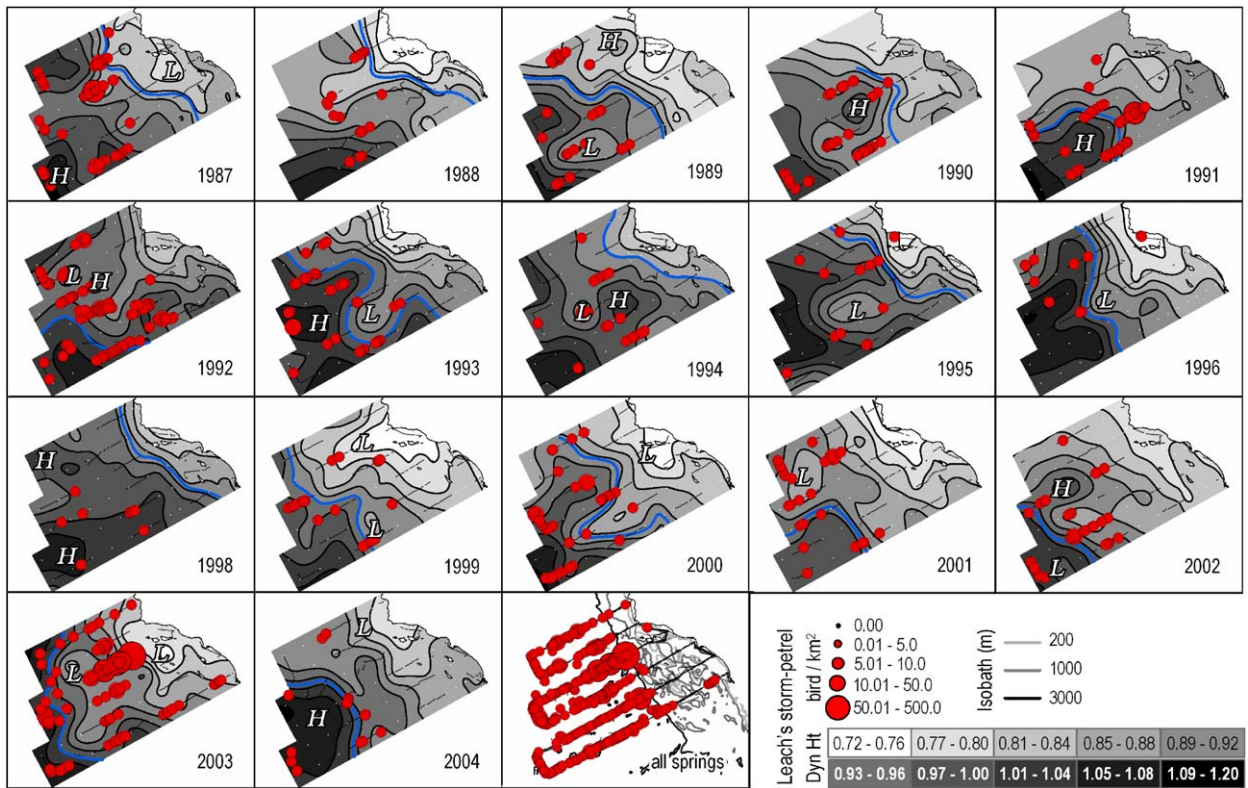


Fig. 6. Leach's storm-petrel distribution and abundance over 17 years.

Red-necked phalarope densities increased with increasing DyHt gradients and chlorophyll *a* concentration.

4. Discussion

4.1. Temporal variation in eddies

It is widely recognized that mesoscale features (e.g., fronts and eddies) are ubiquitous and important sites of enhanced biological activity in marine ecosystems. Mesoscale features have been related to the distribution of many marine organisms, ranging from primary producers to predators (e.g., Haney, 1986; Haury et al., 1993; Hayward and Venrick, 1998; Nel et al., 2001; Lynn, 2003; Bograd et al., 2004; Etnoyer et al., 2004; Etnoyer et al., 2006, this issue). Research on the ecological significance of mesoscale structures highlights their importance as nursery and foraging habitats (Hunt et al., 1996; Logerwell et al., 2001; Polovina et al., 2001, 2004), and as well as their mechanistic role in coupling coastal and oceanic systems (Mackas and

Coyle, 2005; Whitney et al., 2005). However, no other study has examined the responses of top marine predators to mesoscale features over a long time period, our emphasis herein for migratory marine birds in the southern CCS.

In this study, we demonstrated, as have others (Owen, 1980; Haury et al., 1986; Lynn, 2003), that mesoscale eddies are variable in time and space, but constitute a prevalent hydrographic habitat feature. The southern CCS is characterized by complex and energetic circulation (Hickey, 1979; Lynn et al., 2003). Eddies can be formed through instabilities in flow of the California Current, and this is a likely source for many of the features we identified beyond the continental shelf (Fig. 2). A common feature of this region is the Southern California Eddy (SCE; Lynn and Simpson, 1987), but we did not identify this structure in our analysis.

4.2. Temporal variability in seabird abundance

There was significant variability in the spring-time abundance of each focal species (Figs. 3–10).

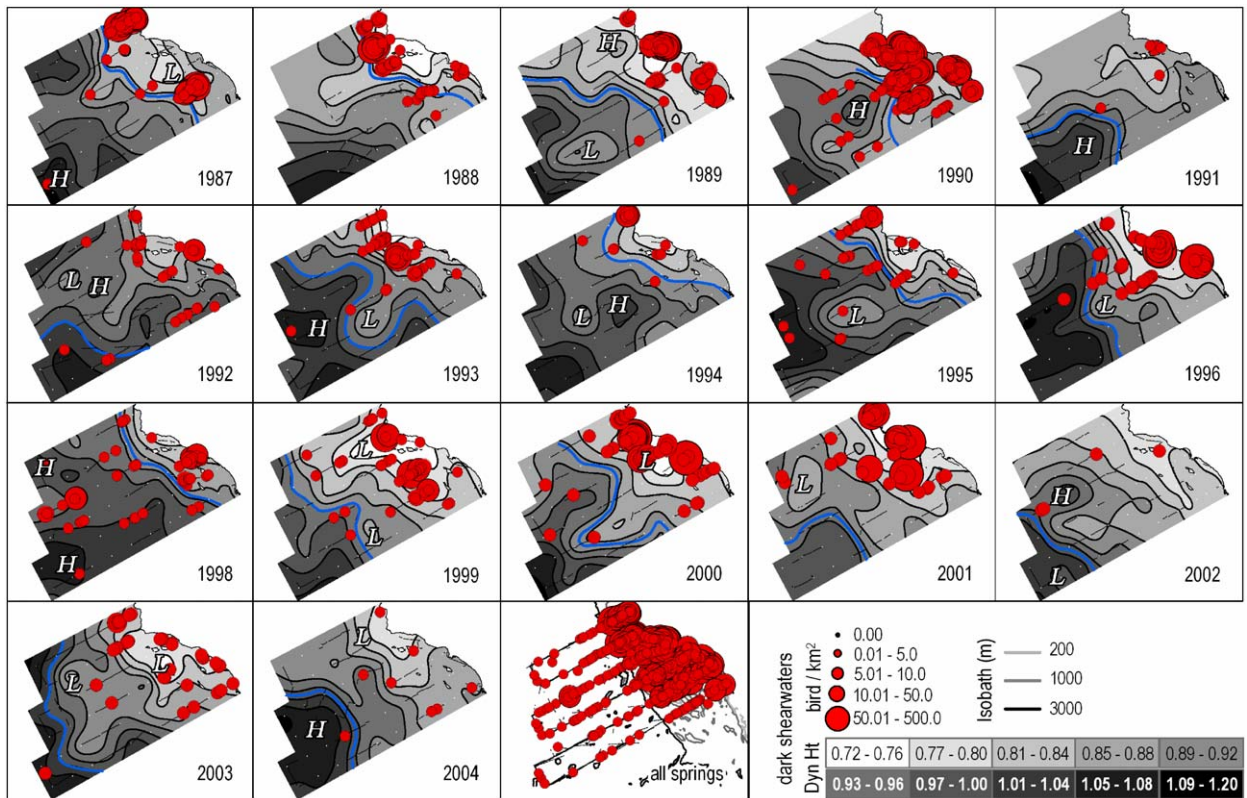


Fig. 7. Dark shearwater distribution and abundance over 17 years.

While considered in detail in previous publications (e.g., Veit et al., 1997; Hyrenbach and Veit, 2003), we mention a few points here to help place habitat analyses in an ecological context. First, the timing of our spring-time cruises varied considerably, from 26 February to 2 May, and clearly influenced the occurrence and density of these migratory species (Table 3, see also Yen et al., 2005). Moreover, from a physical oceanographic perspective, the dominant process in the California Current during spring is the transition from less energetic winter-time conditions to highly energetic (windy) spring-time conditions which facilitates coastal upwelling. The spring transition is associated with an increase in primary productivity (Lynn et al., 2003). In some cases (e.g., 1991), the spring transition had not occurred by the time of the spring-time cruises, whereas in other years (e.g., 1995, 1998), the shoreward location of the core of the California Current implies that the spring transition had already occurred. The relative abundance of the focal species, particularly those of the coastal realm (shearwaters and fulmars), may have reflected

timing of the spring transition and resultant changes in ecosystem productivity.

Second, it is important to consider bio-geographic affinities and reproductive cycles of the focal species. The Cook's petrel is a subtropical species that enters the study area in years of warm spring-time surface sea temperatures (Hyrenbach and Veit, 2003). In 1994, when surface temperatures were anomalously warm and DyHt was generally high, the Cook's petrel distribution was closest to the coast, probably reflecting a water mass redistribution (Fig. 5). Alternately, in 1999–2001, this species was found in the southwest corner of the study area, an area under influence of the subtropical gyre during this “cold-water” period (Peterson and Schwing, 2003; Venrick et al., 2003). Black-footed albatrosses forage close to their Hawaiian breeding colonies in January–February, but commute to the California Current during March–April (Hyrenbach et al., 2002). This species was essentially absent from the study area in 1998–2000 (Fig. 4), which may be explained by later breeding in those years. For shearwaters and

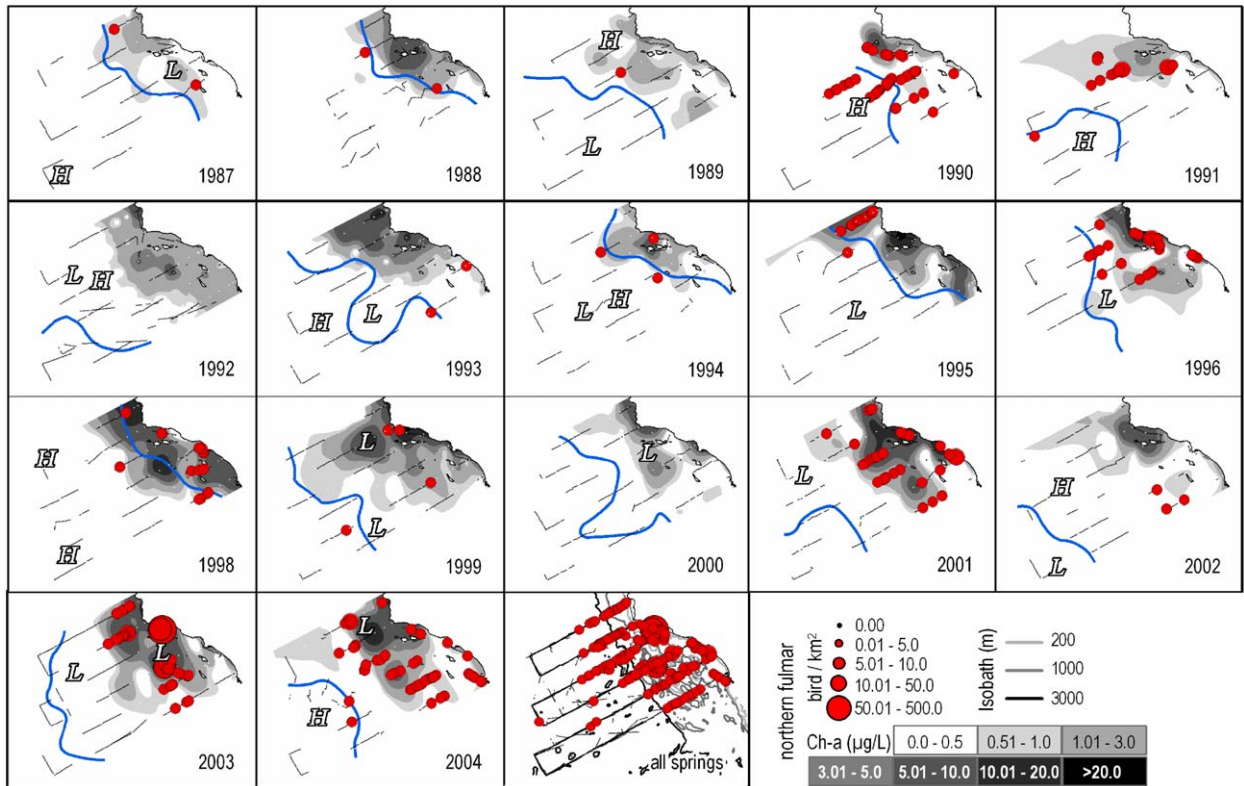


Fig. 8. Northern fulmar distribution and abundance over 17 years.

Leach’s storm-petrel, Hyrenbach and Veit (2003) demonstrated negative and positive correlations with 10-m water temperature at lags of 6–9 months and 0–3 months, respectively. They hypothesized that these species responded differently to short-term oceanographic variability via different mechanisms: localized productivity for the shearwater (as described above relative to the spring transition) and shifting water mass distributions for the storm-petrel. Additionally, inter-annual species re-distributions have been documented for these species in the southeastern Gulf of Alaska. Yen et al. (2005) described a shoreward shift of sooty shearwater distributions during years of warm-water. Year-to-year changes in shearwater numbers and distributions also have been documented in the Gulf of the Farallones, California, another productive coastal upwelling domain in the northern CCS (Oedekoven et al., 2001; Yen et al., 2004). Therefore, this study and others show that bio-geographic affinities, timing of migrations and survey dates, and water-mass distributions and patterns of coastal productivity all influence the relative abundance of seabirds in a study region. This highlights the need for

considering temporal environmental variability when quantifying seabird–ocean habitat relationships.

4.3. Marine bird distributions

Our results corroborate previous studies on the distributions of the focal species in the southern California Current (Briggs et al., 1987). The “coastal” species included shearwaters, northern fulmar, and red-necked phalarope. The “pelagic” species included black-footed albatross, Leach’s storm petrel, Cook’s petrel, and red phalarope.

For the coastal species in our study, shearwaters remained largely shoreward of the core of the California Current (Fig. 7, see “all springs”). Similarly, Briggs et al. (1987, p. 62) showed the shearwater distribution as between the coastal and oceanic realms in regions of high gradients in hydrographic characteristics. We found exceptions to this generalized habitat understanding in 1995 and 1998, two years when shearwaters in our study were found far offshore. In these years, a coastal upwelling jet appeared to be well formed in the

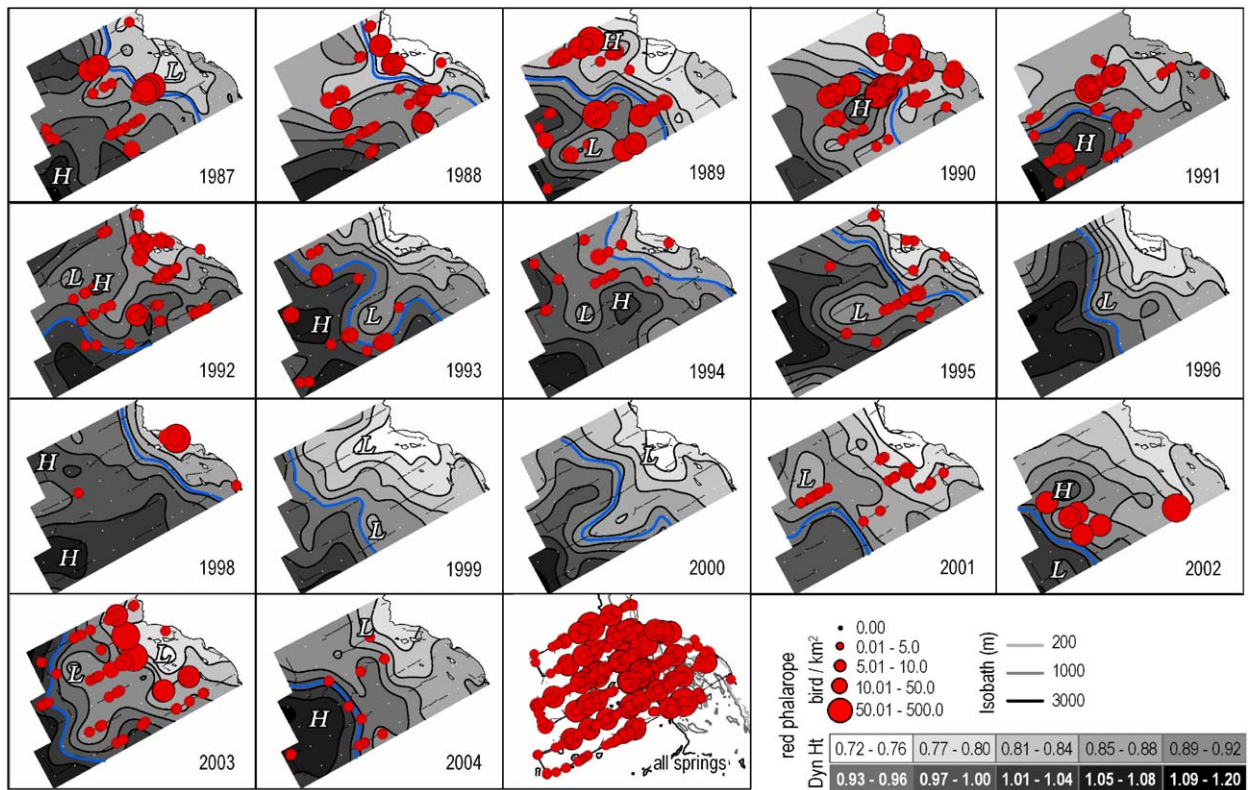


Fig. 9. Red phalarope distribution and abundance over 17 years.

study region. Moreover, ocean conditions were transitioning from warm El Niño to cool La Niña conditions. As shearwaters are known to concentrate in regions of strong hydrographic gradients (Briggs et al., 1987; Hoefler, 2000; Oedekoven et al., 2001), particularly along coastal upwelling jets (Ainley et al., 2005), it is not surprising that they can be found further offshore under certain conditions. Briggs et al. (1987) indicated that only red phalaropes were found offshore; they also suggested associations with hydrographic gradients for both phalarope species. Similarly, we found a clear nearshore distribution for red-necked phalarope (Fig. 10) and a mixed distribution, from coastal to pelagic, for red phalaropes (Fig. 9). We found northern fulmars distributed coastally and occasionally offshore. Briggs et al. (1987, p. 17) similarly found most fulmars on the shelf and shelf-break/slope regions, but indicated finding them as far as 460-km offshore. We also found fulmars in the pelagic realm, but rarely beyond 300-km from shore (Fig. 8, “all springs”).

For the pelagic species in our study, we associated Leach’s storm petrel with areas of high DyHt,

generally offshore of the core of the California Current in deep waters >3000-m (Fig. 6, “all springs”). Briggs et al. (1987, p. 62) showed that this species selected offshore habitats of relatively homogeneous and warm SST. Briggs et al. (1987, p. 23) also noted that “thermal and optical fronts marking the outer edges of coastal upwellings coincided with the shoreward distribution” of this species. In our study, a region of high density for this species was observed southwest of Point Conception above the shelf-break/slope. In addition to the possible connection between Leach’s storm-petrels and the San Juan Seamount (previously mentioned), it seems likely that this area reflects the outermost boundary of the Point Conception upwelling jet, thus supporting these earlier ideas concerning the distribution of this species relative to recently upwelled waters. Black-footed albatross were distributed from the mid-shelf to deep waters, with relatively homogeneous abundance out to edge of our study area, ~700 km from shore in the southwestern sector (Fig. 4, “all springs”). There was one high density area in deep water, but this was due to a single sighting of 50+ birds in one

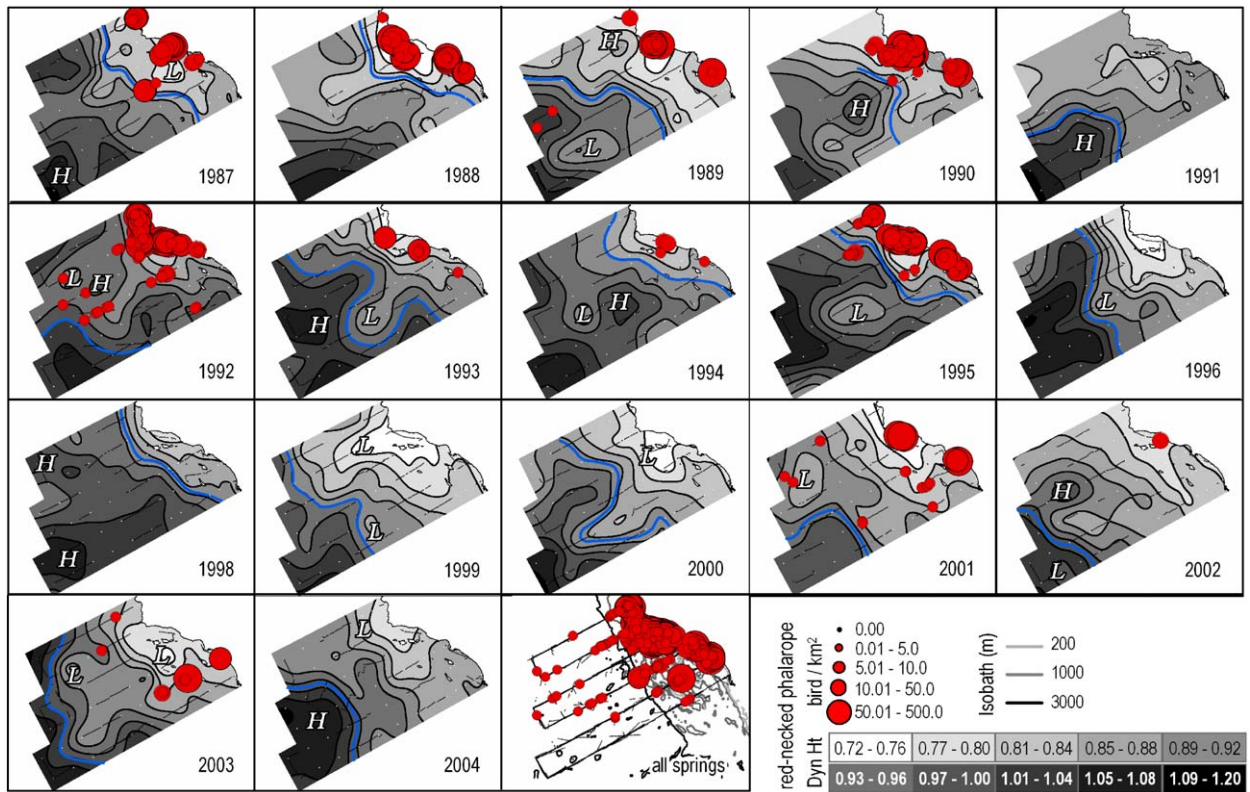


Fig. 10. Red-necked phalarope distribution and abundance over 17 years.

year, 2003. Briggs et al. (1987, p. 15) indicated that this albatross was more numerous over the slope than either shelf or offshore waters, a result not supported by our data. Finally, Cook’s petrel was distributed in deep waters with few sightings closer than 200 km from shore. Briggs et al. did not have sufficient sightings to characterize the distribution of this species off southern California.

4.4. Seabird associations with eddies/meanders of the California Current

Previously, we and others have established that marine bird distribution and abundance in the CCS is influenced by fixed shallow-water topographies such as seamounts (Yen et al., 2004, 2005), dynamic hydrographic habitats such as fronts (Briggs et al., 1987; Hofer, 2000; Ainley et al., 2005), specific habitat characteristics such as temperature and thermocline depth, and indices of primary production (Oedekoven et al., 2001; Ainley et al., 2005; Yen et al., 2005), and prey fields (Ainley et al., 2005; Vlietstra, 2005). In this study, we quantified associations of these migratory marine birds with

eddies and/or meanders of the California Current, and described the temporal consistency of habitat affinities over the span of 17 springs. To our knowledge, this study documents, for the first time, eddy associations for black-footed albatross, Leach’s storm-petrel, and red phalarope. Notably, the fourth pelagic species, Cook’s petrel, did not show an affinity for eddies in the region. Briggs et al. (1987, p. 17) suggested that black-footed albatross may have been associated with eddies off northern California, but did not document this relationship. However, Briggs et al. made the important point that albatross may have been attracted to complex and dynamic interactions between upwelling jets and warm California Current eddies. Indeed, our results suggest that the three species with statistical eddy associations were distributed in a region where interactions with the inner edges of the California Current and upwelling filaments were possible.

It appears that these seabirds use both cyclonic and anticyclonic eddies (Table 3). Black-footed albatross and red phalarope were associated with high (anticyclonic) eddies, and Leach’s storm-petrel

Table 3
Likelihood ratio statistics (LRS) for univariate models of habitat covariates accounting for Julian date, latitude, and year (not shown) effects

	Coefficient													
	Black footed albatross	Cook's petrel	Leach's storm-petrel	Dark shearwaters	Northern fulmar	Red phalarope	Red-necked phalarope	Black footed albatross	Cook's petrel	Leach's storm-petrel	Dark shearwaters	Northern fulmar	Red phalarope	Red-necked phalarope
<i>(a) Logistic (n = 8713)</i>														
Julian day	2.85	20.00	0.33	156.05	14.83	13.38	109.74	+	+	+	+	+	+	+
Latitude	3.82	301.38	105.85	695.66	134.26	16.21	387.64	-	-	-	-	-	-	-
CC jet	24.24	7.60	54.99	13.76	0.02	31.83	26.12	+	+	+	+	+	+	+
Dyn ht mean	8.97	62.45	14.74	162.94	49.04	0.25	114.59	+	+	+	+	+	+	+
Dyn ht CI	15.36	19.53	22.57	0.88	31.63	30.27	6.75	+	+	+	+	+	+	+
Chlo. <i>a</i>	5.15	46.73	96.16	35.11	22.30	0.48	61.17	-	-	-	-	-	-	-
NO ₃	6.86	30.49	72.00	105.00	7.08	11.04	29.96	-	-	-	-	-	-	-
Eddy	24.11	5.99	34.76	1.77	6.17	62.28	15.23	+	+	+	+	+	+	+
L eddy	2.51	3.51	24.14	4.07	0.72	4.92	2.59	-	-	-	-	-	-	-
H eddy	14.08	5.33	43.82	14.79	12.56	54.53	13.60	-	-	-	-	-	-	-
<i>(b) Ordered logistic</i>														
Positive bins	204	315	629	767	256	536	268							
Julian day	0.83	0.54	0.00	31.67	0.01	0.96	1.91	+	+	+	+	+	+	+
Latitude	0.12	0.90	2.63	72.76	1.34	7.30	34.22	+	+	+	+	+	+	+
CC jet	1.59	0.42	1.04	9.90	3.45	1.21	9.05	-	-	-	-	-	-	-
Dyn ht mean	0.37	4.05	0.57	28.28	5.16	0.62	38.47	+	+	+	+	+	+	+
Dyn ht CI	2.07	1.99	0.71	4.63	5.05	0.94	0.12	-	-	-	-	-	-	-
Chlo. <i>a</i>	1.43	0.96	3.00	1.92	7.67	0.20	13.02	-	-	-	-	-	-	-
NO ₃	3.76	6.23	1.44	20.99	4.57	1.35	7.62	+	+	+	+	+	+	+
Eddy	1.12	2.29	1.16	2.40	5.11	0.17	4.39	-	-	-	-	-	-	-
L eddy	2.91	0.86	1.08	1.92	1.84	2.86	4.18	-	-	-	-	-	-	-
H eddy	3.17	4.22	1.17	0.95	5.25	2.71	2.24	-	-	-	-	-	-	-

LRS values and coefficient signs are reported for (a) logistic models on occurrence (presence/absence), and (b) ordered logistic models on density for presence only. All df = 1. Bold LRS values and shaded boxes show significance at $P < 0.001$.

with both high and low eddies. However, because eddy structures often occurred in pairs (e.g., 1992–1994, Fig. 3), it is difficult to ascribe seabird–eddy associations to a specific type of eddy (cyclonic or anticyclonic). Cyclonic (low) eddies are characterized by surface divergence and interior upwelling (McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998). Therefore, seabird associations with cyclonic eddies may be a response to enhanced local productivity due to small-scale upwelling (Haney, 1986). Anticyclonic (high) eddies are characterized by surface convergence and downwelling at the core and may have reduced productivity at their centers (Ribic et al., 1997). However, due to the inherent temporal lags involved in plankton growth and seabird food web dynamics, productivity arguments are difficult to accept as explaining these habitat relationships. Moreover, the association with both cyclonic and anticyclonic structures does not support a productivity explanation. Instead, it seems likely that eddy associations for seabirds result from mechanisms that aggregate prey. It may be the edges of the eddy/meander features that are important to foraging seabirds (Nel et al., 2001; Weimerskirch et al., 2004). In the case of these species, all feed primarily in the neuston layer on zooplankton (e.g., amphipods) and possibly squid, which could be concentrated on eddy/meander edges.

Notably, for each of these species, occurrence decreased with increasing distance from the eddy/meander structure. However, the functional relationship for red phalaropes was different than that for black-footed albatrosses and Leach's storm-petrels (Table 2). The red phalarope–eddy relationship was best described by a linear function, whereas that of the albatross and storm-petrel was best modeled by a square transformation with distance, indicating a “threshold” response. We believe this reflects flight and possibly daily foraging distances for these species. The red phalarope is a shorebird wintering and/or migrating through the offshore realm. Sustained flight for this species is possible only by constant flapping, whereas both the albatross and storm-petrel are capable of sustained flight by gliding.

4.5. Associations with proxies for productivity and prey

The species that were clearly associated with our proxies of primary productivity (chlorophyll *a* and

nitrate) were the coastal species, including the shearwaters, fulmars, and red-necked phalaropes (Table 3). None of the species in this study, however, feed on phytoplankton; instead mid-trophic-level fish, squid, and zooplankton are taken (Hunt et al., 2000). The underlying mechanisms responsible for enhanced spring-time primary productivity in the southern CCS, particularly within the coastal domain, have been well established (Hayward and Venrick, 1998; Bograd and Lynn, 2003). Additionally, there is evidence that the location and the extent of the spring-time spawning and developmental habitats of fish that the seabird consume (e.g., Pacific sardine *Sardinops sagax*, and northern anchovy *Engraulis mordax*) are similarly influenced by hydrographic habitat gradients (Checkley et al., 2000; Lynn, 2003; Jacobson et al., 2005). Nonetheless, more research is required for understanding seabird predator–prey relationships in this region. For example, while larval fish distributions provide an indication of the spatial distributions of prey fields, vertically integrated tows cannot characterize prey patchiness, a critical issue for seabirds foraging in this dynamic ecosystem (Briggs et al., 1987).

4.6. Conservation and management implications

In considering methods to manage protected species and their habitats, spatially explicit conservation approaches are taking center stage. In particular, marine protected areas (MPAs) are becoming a widely accepted tool for conservation and management of marine ecosystems and protected species (Murray et al., 1999; Hyrenbach et al., 2000; Halpern, 2003; Hooker and Gerber, 2004). Of the habitats we considered herein, the coastal region of Point Conception appears to be an important site of sustained primary production and large seabird aggregations. It is well known that a substantial upwelling plume is produced at Point Conception, which provides a well-understood mechanism for its significance as a “hotspot” of ocean productivity and marine bird activity. The seabird species in this study associated with Point Conception were dark shearwaters, red-necked phalaropes, and northern fulmars, but other migratory and locally breeding species are also known to forage here (PRBO unpublished data). Ainley et al. (2005) provide an excellent study of how seabird predator–prey relationships are influenced by upwelling off

Oregon, and similar mechanisms are probably at work off Point Conception.

Some “hotspots” are not permanent, but change location and extent seasonally and interannually (this volume). Indeed, the mesoscale features we characterized in this study were ephemeral (eddies), persistent yet dynamic (core of the California Current), and constant (Point Conception upwelling). Ephemeral and dynamic hydrographic habitats pose a challenge for protection because they are spatially and temporally unpredictable (Hyrenbach et al., 2000). While some protected areas have been designated to protect marine birds, most are delineated as buffers around breeding colonies (Hooker and Gerber, 2004). This study has demonstrated the importance of a coastal promontory to migratory seabirds inhabiting a dynamic upwelling-dominated ecosystem. As such, the greater Point Conception coastal region may warrant consideration as potential protected area to enhance the foraging opportunities for marine birds and other top predators. This approach may be applicable to other coastal promontories in the California Current and other eastern boundary current systems worldwide.

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