Persistence of hotspots and variability of seabird species richness and abundance in the southern California Current

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Abstract. Aggregations of seabirds at sea may provide information on centers of enhanced trophic interactions and concentrating mechanisms, however, to date most studies lack quantification of persistence, a key hotspot characteristic. Persistence statistics may reduce uncertainty about seabird habitat use, improve understanding of the spatio-temporal scales of pelagic food web dynamics, and inform conservation planning. Using 26 years (1987–2012, 47 surveys) of shipboard surveys from a 300K km² study area within the southern California Current Ecosystem, we conduct a spatial assessment of the inter-annual and seasonal dynamics of the persistence of seabird hotspots and identify recurring sites of elevated seabird species richness and abundance. Previous studies document declines in abundance, but were based on broad spatial standardizations to assess where declines may have occurred. Here, we refine the hypothesis that seabird populations have declined off southern California by focusing on persistently used habitats in nearshore or offshore domains. We demonstrate that spatio-temporal variability of seabird distribution and abundance is characterized by anomalous events embedded within trends. In addition to identifying the locations of persistence of seabird aggregations, we found significant declines in species richness and the density of sooty shearwater (Puffinus griseus) and Leach’s storm petrel (Oceanodroma leucorhoa); in contrast, black-footed albatross (Phoebastria nigripes) abundance appear to be increasing. This assessment provides a spatially-explicit framework for future evaluations of biophysical drivers of seabird hotspots and their associations and impacts on forage fish and zooplankton populations.

Key words: albatross; CalCOFI; hotspot persistence; shearwater; spatial ecology; species richness; trend assessment.

INTRODUCTION

Seabird population and community dynamics respond to local to large spatio-temporal scales in marine ecosystems (e.g., fronts to ocean basins and days to decades), such that their distribution and abundance at sea can serve as indicators of marine ecosystem variability (Veit et al. 1997, Hyrenbach and Veit 2003, Ainley et al. 2009, Platt et al. 2007, Sydeman et al. 2009, 2015). Many seabird species exhibit long-distance migrations among disparate marine ecosystems and hemispheres to feed on seasonally abundant forage species (Veit et al. 1996, Shaffer et al. 2006), and therefore may affect marine food webs regionally and globally. Quantifying interannual spatial variability of seabirds at sea also provides valuable indicators of ecosystem health and habitat quality (e.g., pollution), as well as information on key scales of variability concern-
ing trophic interactions in pelagic ecosystems (Ainley et al. 2009, Sigler et al. 2012, Santora and Veit 2013). Quantifying the persistence of seabird hotspots (i.e., the reoccurrence of locales of high abundance and/or diversity) may reduce uncertainty about seabird habitat requirements (e.g., marine Important Bird Areas; Lascelles et al. 2012), and facilitate future investigations of seabird-forage interactions needed for improving ecosystem-based fishery management (Santora et al. 2014), yet is rarely accomplished. In this study, we use an extensive shipboard data set (26 years) to quantify persistence of seabird hotspots within the southern California Current Ecosystem (CCE; Fig. 1).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program maintains one of the longest marine sampling programs in the world, and since 1987 includes routine counting of seabird abundance (Veit et al. 1996, 1997, Hyrenbach and Veit 2003). The CalCOFI program has quantified the influence of climate states on marine ecosystem functions (McGowan et al. 2003, Di Lorenzo et al. 2008), as well as long-term trends in physical oceanographic features (Bograd and Lynn, 2003, Bograd et al. 2008) and populations of zooplankton (Rommich and McGowan 1995, McGowan et al.1998), larval fishes (Hsieh et al. 2009, Koslow et al. 2011), and seabirds (Veit et al. 1997, Sydeman et al. 2015). Changes in oceanographic conditions and key zooplankton and larval fish relate to changes in seabird abundance (Sydeman et al. 2015), but changes in distributional statistics and potential trophic linkages between seabirds and their prey have yet to be examined. Therefore, an assessment of the spatio-temporal variability of seabird population and community dynamics will facilitate future spatial integration of the important CalCOFI data set (Fig. 1).

The assessment of seabird populations at sea is dependent on the size of an area surveyed and the consistency and repeatability of surveys across many years (Nur et al. 2011, Lascelles et al. 2012, Santora and Veit 2013). Seabirds tend to concentrate in suitable foraging habitat; some species concentrate near the coast, whereas others are more oceanic and found 500-km offshore (Hyrenbach and Veit 2003). Therefore, deriving simple means or total counts of seabirds over a large survey area such as CalCOFI (Sydeman et al. 2015) without adjusting for variability in spatially referenced survey effort can lead to an increase in uncertainty about trends in species populations. Here, we focus on the spatio-temporal variability of seabirds and conduct an assessment of their inter-annual and seasonal dynamics, and apply an application for the identification and location of persistent seabird species richness and abundance hotspots (i.e., reoccurring areas of high abundance and species; Suryan et al. 2012, Santora and Veit 2013). With more than double the length (26 years; 1987–2012) of previously published time series on individual species (Hyrenbach and Veit 2003) we apply a spatial standardization (e.g., grid-based approach) to investigate the hypothesis that seabird densities have declined in the southern CCE (Veit et al. 1997, Sydeman et al. 2015). Specifically, we assess whether the spatio-temporal variability of seabirds is characterized by anomalies (events; influxes of migrants), long-term trends or both. This assessment will benefit seabird conservation and marine spatial management of the CCE and will provide a spatially explicit framework for future evaluation of biophysical drivers of seabird hotspots.

**METHODS**

*Study area*

The CalCOFI sampling of the Southern California Bight includes 6 parallel survey lines (east to west) that extend from the coast out to 470–700 km (northern most line is shorter) offshore (Fig. 1). The survey area covers approximately 300,000 km². The 2000 m isobath runs southeast (~135°) and represents a distinct change in bathymetry (e.g., Santa Rosa Ridge), moving from the coastal Channel Islands and deep basins onshore to the abyssal plain offshore, which is punctuated by the location of seamounts (Fig. 1). Four distinct hydrographic and biogeographic domains have been described: (1) southern coastal domain influenced by northward movement of warm waters from the subtropics, (2) northern coastal domains influenced by upwelling at Pt. Conception, (3) the transition (middle) domain associated with the generalized core location of the California Current, and (4) oceanic (outer) domain (Hayward and Venrick 1998; Fig. 1). Jasper seamount, an underwater volcano with
Fig. 1. (Top panel) The southern California Current region, CalCOFI survey domain and location of grid cells used to assess seabird hotspots; dashed lines indicate the approximate boundaries separating the coastal basin, middle and outer domains; GI = Guadalupe Island, LA = Los Angeles, SM = San Miguel Island, SR = Santa Rosa Island, SCr = Santa Cruz Island, SCa = Santa Catalina Island, SCI = San Clemente Island, SN = San Nicholas Island, SD = San Diego. (Bottom left panel) Location of hydrographic and biological stations sampled during CalCOFI (illustration purposes only) and (bottom middle and right panels) distribution visual survey effort for seabirds during spring and summer CalCOFI surveys, 1987–2012. Contour lines are the 200 m, 1000 m and 2000 m isobaths.
a summit depth of ~700 m is located in the southwest study region (~30.5° N, 123.4° W) and is likely an attractive area for top predators. Offshore of Point Sal and Point Conception (prominent headlands that influence upwelling and hydrographic variability), the southward flowing California Current moves along the coast and also meanders offshore (via jets) where it meets sub-tropical waters that are characteristic of the far western CalCOFI survey region (McClatchie 2013). At approximately 32° N, the California Current moves towards the east and forms the southern boundary of cyclonic gyre known as the Southern California Eddy (Cher- eskin and Niiler 1994); a feature that influences upwelling dynamics, including frontal development, within the onshore coastal domain. Comparatively, the coastal domain has less shelf habitat (indexed by the 200 m isobath contour) and upper slope depth (indexed by area within the 200–500 m isobaths) along the coast than offshore around the islands (McClatchie 2013; Fig. 1). Furthermore, the coastal domain contains numerous deep basins, which adds to the bathymetric complexity and hydrographic circulation of the region.

Seabird surveys and species selection

The methodology for counting seabirds on CalCOFI surveys is detailed by Veit et al. (1996) and Hyrenbach and Veit (2003). Briefly, standardized counts are conducted during daylight hours while the vessel was underway at speeds >5 knots between hydrographic sampling stations. All seabirds sighted within a 300 m arc from the bow to 90° to the side with the best visibility (least glare) are identified to species and enumerated (Tasker et al. 1984). Survey effort and counts of seabirds are aggregated in 3 km intervals and stored in a relational database (http://sccoos.org/data/seabirds/). This study investigates spring and summer CalCOFI surveys. Spring and summer surveys provide important information due to seasonal upwelling (Checkley and Barth 2009) as well as the presence of migrants in the system (Hyrenbach and Veit 2003, Yen et al. 2006). The months of the spring and summer surveys are March–April and July–August, respectively; 47 surveys were conducted over the years 1987–2012. We omitted the 1991 survey from the spring survey list because it occurred a month earlier (February) than the mean spring start date (first week of April) and it should probably be considered a winter survey. There were no seabird surveys conducted in summer 1994 and spring of 1997 and 2007. There was an error in the GPS assigned to the seabird data logging computer and the coordinate data were not available for the 2009 spring survey resulting in this year being omitted from this synthesis.

Species included in the species richness calculations were predetermined by Appendix A provided by Hyrenbach and Veit (2003), which includes 68 species/taxa. For individual species assessments, we focused on the most numerous migratory species encountered during spring and summer CalCOFI surveys (Hyrenbach and Veit 2003, Yen et al. 2006), including sooty and pink-footed shearwaters, Leach’s storm petrel (Oceanodroma leucorhoa), Cook’s petrel and black-footed albatross (Phoebastria nigripes). These species also represent a variety of life history and feeding behaviors, including trans-hemisphere migrants (shearwaters, Cook’s petrel), surface-feeding and diving (Table 1). Furthermore, the International Union for the Conservation of Nature (IUCN; Rodrigues et al. 2006) classifies some of these species as either near threatened and/or vulnerable (Table 1); assessing the persistence of

Table 1. Biological aspects and conservation status of species examined in this study; weight and feeding ecology derived from Hyrenbach and Veit (2003). IUCN is International Union for Conservation of Nature; website accessed on 9 March 2015.

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight (g)</th>
<th>Feeding method</th>
<th>IUCN status</th>
<th>IUCN population trend</th>
</tr>
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<td>Sooty shearwater (Puffinus griseus)</td>
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<td>surface and diving</td>
<td>near threatened</td>
<td>decreasing</td>
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<tr>
<td>Pink-footed shearwater (Puffinus creatopus)</td>
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<td>surface and diving</td>
<td>vulnerable</td>
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<td>Cook’s petrel (Pterodroma cookii)</td>
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<td>surface</td>
<td>vulnerable</td>
<td>increasing</td>
</tr>
<tr>
<td>Black-footed albatross (Phoebastria nigripes)</td>
<td>3148</td>
<td>surface</td>
<td>near threatened</td>
<td>increasing</td>
</tr>
</tbody>
</table>
migratory species hotspots will provide geographic reference points for their conservation.

Analysis

The first objective of this study is to assess the spatio-temporal persistence of seabird species richness and abundance hotspots. The CalCOFI program samples a fixed grid of stations that is highly replicated using consistent methodology (Bograd et al. 2003; Fig. 1). Integrating seabird observations with station data requires a grid-based approach to resolve spatially explicit time series that account for survey effort over time. All shipboard tracklines, indexed by 3 km intervals (Yen et al. 2006; Fig. 1), was linked to a GIS, as we have done for other studies in the CCE (Santora et al. 2011a, b, 2012a, b). The extent of the shipboard trackline (total survey effort) and CalCOFI sampling stations determined the extent and size of grid cells. This was accomplished using the create fishnet command in ArcView to project the individual 3km sampling points onto a grid with cells size of $0.7^\circ \times 0.7^\circ$ (~4500 km$^2$). The size of cells was chosen to account for total trackline effort (Fig. 1) and to reflect the layout of the CalCOFI hydrographic and biological sampling stations (Fig. 1) in order to permit future integration with those data sets. The grid process resolved the location of consistently sampled cells during 1987–2012 with 45 and 48 cells in spring and summer, respectively (Fig. 1).

We standardized sampling effort by assessing the number of times the ship visited a cell and the amount of survey effort collected within that cell, relative to all cells in a given season over the entire length of the time series (Santora and Veit 2013). To determine a threshold to use as a cut off, we calculated the mean ± SD of cell visits and effort per season, then omitted all effort less than 1 SD below the mean. For spring surveys, it was determined that a cell required at least 7 visits for 24 km of survey effort; resulting in a total of 573 cells visited, with a mean ± SD of 55.29 ± 9.55 km per cell and total of 31,911 km.

There was more effort during summer, so a cell required at least 9 visits for 24 km of survey effort; resulting in a total of 736 cells visited, with a mean ± SD of 55.09 ± 10.82 km per cell and total of 40,800 km.

We quantified the spatio-temporal mean, variance, anomaly and persistence of a cell’s value for species richness as species per unit effort (SPUE) and abundance as individuals per unit effort (IPUE; Santora and Veit 2013). For each survey, rates of SPUE and IPUE are calculated by dividing the total number of species (out of 68 species; Hyrenbach and Veit 2003) or individuals by the number of 3 km samples per cell. For spatio-temporal comparison of SPUE and IPUE among surveys, each survey and cell was standardized by subtracting its spatial mean and dividing by its standard deviation to determine an overall time series for each survey as well as a spatial anomaly per cell (computed from the grand spatial mean and standard deviation). Moreover, we estimated the spatio-temporal persistence for SPUE and IPUE by calculating the percentage of time a cell exhibited a value that was greater than the grand spatial mean by 1 SD. We then mapped the spatial anomaly and persistence index per cell to determine the location and persistence of SPUE and IPUE hotspots. Cells with higher percentages are locations where SPUE and IPUE are persistently higher than the baseline standardized anomaly and are considered hotspots. For mapping hotspots and to facilitate comparison among species, persistence is classified into 5 classes using the Jenks natural breaks optimization method in ArcView; those cells greater than 30% and 50% are considered medium and high hotspots, respectively; Santora and Veit (2013) describe all of these methods in greater detail.

The second objective is to determine trends in the anomalies of seabird species richness and abundance based on habitat persistence data. This was accomplished by (1) fitting generalized additive models (GAM) to seabird anomalies for the entire region, and (2) correlating (Spearman Rank) seabird anomalies within each grid cell over time and mapping significant ($p < 0.05$) correlations to reveal locations where trends are apparent. The GAM was fit to annual seabird anomalies by including a smoothed term (spline) for year with a Gaussian link function (seabird anomalies were normally distributed; J. Santora, unpublished data). Results of each GAM is plotted to describe the overall fit of the seabird anomaly time series for elucidating whether there are declines and/or periods of years with higher anomalies of particular species (i.e., events). A Monte-Carlo randomization procedure assesses
the significance of spatial correlations (time series within cells) for seabird anomalies. Locations with significant \((p < 0.05)\) correlations were mapped to provide additional context for understanding change of seabird abundance within particular habitat and their potential association with bathymetric topographies (e.g., seamounts; Fig. 1).

**Results**

**Interannual and seasonal variability of species richness hotspots**

The spatial anomaly and persistence of species richness during spring and summer displayed coherence in space and time, with higher values located near the coast/islands and declining with increasing distance offshore (Fig. 2). All persistent areas of species richness (>30%) were located near or shoreward of the 2000 m isobath. More high persistence cells (>50%) were found during spring \((n = 9)\) than in summer \((n = 6)\), and spring hotspots were broadly clustered along the coast (Fig. 2). However, the spatial anomaly of species richness during summer was clustered and exhibited higher anomalies than spring spatial anomalies (Fig. 2). In general, summer-time richness anomalies were positive during the beginning of the time series (1987–1993) and were generally negative from 1995 onwards, except for 2000, 2006 and 2012 (Fig. 2). Spring anomalies tended to exhibit fluctuations with alternating years of positive and negative anomalies (Fig. 2).

**Interannual and seasonal variability of species abundance hotspots**

The abundance of sooty shearwaters was spatially clustered along the coast and around the Channel Islands (Fig. 3). Interestingly, as the numerically dominant species, sooty shearwaters displayed no persistent hotspots during spring (weak persistence of 15–30%) and only three medium persistent hotspots during summer (E1, F2 and G2) located near Pt. Conception. High spatial anomalies of shearwaters during spring were located in the northeastern portion of the study area near the Channel Islands and Pt. Conception. Compared to spring, there were comparatively fewer areas of high spatial anomalies during summer (Fig. 3). In both spring and summer time series, the anomaly of shearwater abundance was characterized by a relatively few number of high positive anomalies at the start of the series; years 1987 and 1990 during spring and 1988 in summer (Fig. 3).

Compared to sooty shearwaters, pink-footed shearwaters (Fig. 4) displayed more medium and high persistence located during spring near the outer 2000 m isobath and within the central basin during summer (Fig. 4); these areas are not sooty shearwater hotspots. Spatial anomalies of pink-footed shearwaters during spring occurred along the outer 2000 m isobaths near the Channel Islands (cells E2, F3 and G3) and closer to shore near Catalina Island (cells I3–4). Summer spatial anomalies of pink-footed shearwaters were located to the south of the Channel Islands (cells G3–4) and to the east (cells H3 and I3; Fig. 4). The spring anomaly time series of pink-footed shearwaters displayed only one positive peak anomaly, during 2010 (Fig. 4). However, their summer temporal anomalies display substantial variability with multiple positive peaks throughout the study period (Fig. 4), suggesting their occurrence during summer may relate to climate events (e.g., ENSO).

Leach’s storm petrel displayed high spatial anomalies and persistent hotspots throughout the middle and outer domains (Fig. 5). Interestingly, there is an apparent geographic shift in their distribution from spring to summer. During spring, high spatial anomalies and persistent cells are located to the west of 2000 m isobath, but during summer, spatial anomalies and persistent hotspots are concentrated along the 2000 m isobath (Fig. 5). Spring temporal anomalies of Leach’s storm petrel are generally negative with only a few positive years (Fig. 5), whereas the summer anomalies display a number of consecutive positive years earlier in the time series (Fig. 5).

Cook’s petrels are oceanic species and their high spatial anomalies and hotspots are located in the outer domain (except for one spatial anomaly during summer that located off Pt. Conception; Fig. 6). During spring and summer, persistent hotspots (medium and high) for Cook’s petrels are found near and around Jasper’s Seamount (cell C4). The spring anomaly time series of Cook’s petrels exhibited only one positive peak coinciding with the 1997 ENSO
Fig. 2. Species richness: (A–D) spatial anomalies and persistence of hotspots and (E–F) standardized time series (anomaly, mean and standard deviation) during spring and summer. Contour lines are the 1000 and 2000 m isobaths.
Fig. 3. Sooty shearwater: (A–D) spatial anomalies and persistence of hotspots and (E–F) standardized time series (anomaly, mean and standard deviation) during spring and summer. Contour lines are the 1000 m and 2000 m isobaths.
Fig. 4. Pink-footed shearwater: (A–D) spatial anomalies and persistence of hotspots and (E–F) standardized time series (anomaly, mean and standard deviation) during spring and summer. Contour lines are the 1000 m and 2000 m isobaths.
Fig. 5. Leach’s storm petrel: (A–D) spatial anomalies and persistence of hotspots and (E–F) standardized time series (anomaly, mean and standard deviation) during spring and summer. Contour lines are the 1000 m and 2000 m isobaths.
Fig. 6. Cook’s petrel: (A–D) spatial anomalies and persistence of hotspots and (E–F) standardized time series (anomaly, mean and standard deviation) during spring and summer. Contour lines are the 1000 m and 2000 m isobaths.
event (Fig. 6), whereas during the summer anomaly time series, numerous positive peaks occurred, some of which coincide with the 1992, 1997 and 2009 ENSO events.

Black-footed albatrosses exhibit a greater number of high spatial anomalies and persistent hotspots during spring compared to summer (Fig. 7). In general, highly persistent hotspots of black-footed albatross were more dispersed during spring and more clustered during summer within the outer domain (Fig. 7), possibly indicating a redistribution pattern after the onset of the spring upwelling transition. The anomaly time series of black-footed albatross during spring displayed numerous positive peaks prior to 2002 and was generally negative afterwards. During summer, anomalies of black-footed albatross were generally negative up to 1999; afterwards they tended to be positive, suggesting an increase in their abundance.

Evaluation of trends in space and time

The grand annual anomaly (computed over all cells per season and year) of species richness displayed a significant declining trend during summer (Figs. 8A and 9A), but not spring (not shown). Within the long-term trend, there is autocorrelation in the anomaly of summer species richness, with significant lags at 3–7 years. There is no temporal autocorrelation in the spring species richness. Relating changes over time within grid cells revealed specific areas where summer species richness significantly declined (Fig. 9A). For example, there are four areas displaying significant declining trends in species richness: (1) cells off Pt. Conception extending outwards along the upwelling jet (cells C2, D3, and E2), (2) central basin (cells G3–4), (3) middle domain (cells E5 and F5) and (4) the warm oceanic region coinciding with the location of and waters north of Jasper Seamount (cells B6, C6–7).

Of the five species analyzed, three (sooty shearwater, Leach’s storm petrel and black-footed albatross) exhibited trends in abundance over time and space (Figs. 8 and 9). GAM fits to anomalies of seabird abundance were non-linear and suggest that temporal variability of these species may be best characterized as a series of autocorrelated years that are embedded within trends over time. The anomaly of sooty shearwater abundance decreased over time during spring, but not summer (Fig. 8B). However, it is important to note 2 years (1987, 1990) at the beginning of the spring time series should be characterized as anomaly events and are likely responsible for decreasing linear trend. Spatially, significant declines in sooty shearwater abundance are located near Pt. Conception (F2), the coastal basin (H4) and within the middle domain (F6) and outer domain near Jasper Seamount (C7; Fig. 9). The anomaly of Leach’s storm petrel abundance decreased during summer, but not spring (Fig. 8C). The GAM for Leach’s storm petrel clearly shows several years (1990–1992) where abundance of this species was anomalously high (Fig. 8C). Significant declines of storm petrels are located throughout the outer domain with a clustered distribution of cells located to the north of Jasper Seamount (Fig. 9C). Storm petrels also exhibited declines near the Channel Islands (F3) and within the coastal basin (H4; same cell as sooty shearwater). In contrast, the anomaly of black footed shearwater. However, the fitted GAM for albatross clearly shows that 1999–2003 was a sustained period of anomalous albatross abundance; the highest anomaly occurs in 2012 and is likely influencing the apparent increase (Fig. 8D). Significant increases of albatross abundance are located in the outer domain and near Jasper Seamount (Fig. 8D).

DISCUSSION

Quantifying the spatio-temporal variability of seabird distributions at sea by accounting for spatially explicit survey effort and habitat utilization, resolved persistent hotspots and trends in species richness and abundance. Analysis of these seabird time series provide evidence that variability of seabird densities at sea is best characterized by years of autocorrelated conditions as well as lower frequency trends. In particular, we found a significant long-term decline of species richness and confirmed that the abundances of sooty shearwater and Leach’s storm petrel declined during spring and summer, respectively. In contrast, and somewhat surprisingly, abundance increases of black-footed albatross are apparent during summer within the
Fig. 7. Black-footed albatross: (A–D) spatial anomalies and persistence of hotspots and (E–F) standardized time series (anomaly, mean and standard deviation) during spring and summer. Contour lines are the 1000 and 2000 m isobaths.
outer domain. All of these trends are specific to particular areas and each requires further research to elucidate causal factors driving population change. In particular, we found declines in species richness and sooty shearwaters near Pt. Conception (an important upwelling zone and previously identified biological hotspot), so the biophysical drivers of and trophic interactions within this hotspot require further study to elucidate possible mechanisms for the long-term change. This study also highlights the importance of Jasper Seamount in the offshore domain as a species richness and abundance hotspot.

**Persistence of seabird hotspots**

No previous CalCOFI study conducted a spatio-temporal assessment of seabird populations at sea that accounts for the persistence of species richness and abundance hotspots. Here, persistence indicates the probability of a hotspot reoccurring over 26 years, and the results of this synthesis suggests some hotspots are clearly more likely than others to persist between seasons and among years. For example, species richness hotspots exhibited some of the highest levels of persistence (60–90%) and fidelity to coastal locations. The described onshore to offshore gradient in species richness hotspots is likely a relatively stable spatial aspect of the CalCOFI seabird data set due to bathymetry and positioning of the California Current. Our results also indicate that the persistence of abundance hotspots is dependent on season, whereby some species shifted geographically between spring and summer. This may relate to migratory movement patterns of bird species during spring and redistribution of migratory species (e.g., shearwaters) from southern to northern California. Both sooty and pink-footed shearwaters displayed an increase in persistence and the number of hotspots between spring and summer, while sooty hotspots appeared to shift from south to north (toward Pt. Conception), hotspots of pink-footed shearwaters shifted in spring from the 2000 m isobath to shoreward around the Channel Islands. Leach’s storm petrel hotspots

Fig. 8. GAM fit to standardized anomaly time series of (A) summer species richness, (B) spring sooty shearwater, (C) summer Leach’s storm petrel, and (D) summer black-footed albatross.
are principally concentrated in the offshore domain during spring, but strikingly, their hotspots shifted toward the outer edge of the 2000 m isobath during summer. Further research should assess the apparent shifts of these species hotspots, and in particular, how persistence of hotspots may relate to changes in ocean physics and seasonal to longer-term availability of forage fish species.

**Declines in species richness and abundance**

We have demonstrated that summertime species richness has declined substantially over 26 years and this clearly warrants further research. This corroborates the findings of Sydeman et al. (2009) in which we described initial trends in seabird richness and demonstrated declines may depend on season. The decline of seabird species richness adds to the collection of physical and biological variables displaying long-term changes that collectively exemplify changes occurring within this marine ecosystem. Ocean warming and shoaling of the oxygen minimum layer (Bograd et al. 2003, 2008) have coincided with declines of mesopelagic fish (Hsieh et al. 2009, Koslow et al. 2011), and it now seems that the entire seabird community may be responding to variability of forage fish populations (Sydeman et al. 2015). The decline of species richness is puzzling, but may relate to either long-term climate change in local breeding seabird populations, and/or declines in populations that originate outside of the CCE. In their comprehensive analysis of seabird time series from CalCOFI surveys, Hyrenbach and Veit (2003) determined that variability of seabird community structure reflected years of warm and cool ocean temperatures, with warmer years having higher numbers of seabird species originating from the eastern tropical Pacific. Their study occurred from 1987 to 1998, a period now considered as generally warm (PDO+) ocean conditions. After the 1997/1998 El Niño event, conditions in the CCE during 1999 transitioned to La Niña (Bograd and Lynn 2001) and the following decade was characterized as an extended period of cool
ocean conditions (Bjorkstedt et al. 2010). Therefore, the decline in species richness could be due to a decline in the number of seabird species with warm water affinity that visit the southern CCE. For example, Leach’s storm petrel, the most common pelagic bird in the middle and outer domains, exhibited increases in their abundance during the warm decade (prior to 1999; Figs. 5 and 9). As well, several other warm water affinity species, such as Cook’s petrel, pink-footed shearwater, black storm petrel (Oceanodroma melanian) and Heerman’s gull (Larus hermanni) exhibited positive pulses in the southern CCE during El Niño years (Veit et al. 1996, Hyrenbach and Veit, 2003). Since seabird community structure relates to inter-decadal scale variability of ocean conditions, then perhaps the long-term decline in species richness reported here, may in fact indicate that ocean conditions within CalCOFI study area are becoming less hospitable to migrant seabirds. Nevertheless, the drastic decline in species richness reported here requires further evaluation with respect to changes in physical and biological conditions sampled by the CalCOFI program.

Migratory seabird populations at sea exhibit large abundance fluctuations and most perceived declines are either result of changes in spatial distribution (i.e., shifts out of restricted sampling areas; Hyrenbach and Veit 2003), reflective of ocean conditions, or declines at breeding colonies (Ainley and Hyrenbach 2010). Substantial evidence exists for many species that suggest seabird populations have declined at breeding colonies to threatened and endangered levels (Rodrigues et al. 2006). Populations of sooty shearwaters have declined at their breeding colonies in New Zealand (Jones 2000, Scott et al. 2008), and it is likely that migrating populations to the CCE should also reflect this decline. However, their interannual abundance off the U.S. West Coast is often highly variable in space and time (Briggs and Chu 1986, Veit et al. 1997, Santora et al. 2011a, Adams et al. 2012). It is also of concern that the early sooty shearwater anomalies in the CalCOFI time series may be attributed to a few observations of dense aggregations (shearwaters are gregarious and patchy) within a coastal area that may have been infrequently surveyed. Furthermore, the low spatio-temporal persistence of sooty shearwater hotspots reported here likely indicates that high-density shearwater aggregations are spatially variable. The GAM fit to the anomaly of sooty shearwater abundance suggests there is still an apparent decline during spring (no decline during summer). Given the high variability and infrequent strong anomalies that characterize the sooty shearwater time series, the significant decline of sooty shearwaters may need further assessment with longer time series, and especially from combining multiple observations collected throughout the CCE (Veit et al. 1997, Adams et al. 2012).

Although Leach’s storm petrel displayed a few significant declines at locations within the middle and outer domains (Fig. 9), the GAM fit to their anomaly of abundance indicates this time series contains consecutive positive anomalies in the early to mid-1990s with little variability to 2012. This result is consistent with the findings of Hyrenbach and Veit (2003), which stated that anomaly of Leach’s storm petrel abundance relates to warm ocean conditions and perhaps variation in the flux of eastern tropical Pacific water into the CalCOFI study area. By comparison, the anomaly of black-footed albatross displayed significant increases over time in the outer and middle domains. The increases in albatross abundance may indicate that their populations are increasing (IUCN status; Table 1) or that foraging conditions with the southern CCE are improving for albatross, and/or foraging conditions are less favorable in areas outside of the CalCOFI study area. Further research is required to elucidate the interactive effects among ocean conditions and forage species for explaining variability and the apparent increase in albatross abundance.

Significance and future CalCOFI seabird assessments

Resolving persistence of seabird hotspots is important for at least three reasons. First, from a food web perspective, biological hotspots in pelagic ecosystems are ecologically important areas with high concentrations of marine species where high rates of trophic transfer may occur (Nur et al. 2011, Santora et al. 2011b, 2012, Sigler et al. 2012); thus, their identification will advance our understanding of how pelagic marine ecosystems are spatially organized. Moreover, little
is known about species richness patterns in marine ecosystems, so establishing where species richness hotspots form and are maintained is of great interest for advancing theory on how marine systems are structured (Myers et al. 2000, Worm et al. 2005, 2006). Second, migratory seabirds are abundant members of the CCE and may exert significant pressure on populations of forage species (Ainley and Hyrenbach 2010). For example, Chu (1984) estimated that 2 to 4 million sooty shearwaters migrate to the CCE every year and each individual requires 200–300 g of forage (fish, squid and krill) per day. A major objective of ecosystem-based fisheries management (EBFM) is balancing the dietary and consumption needs of seabirds while sustaining forage fisheries (Smith et al. 2011). Therefore, understanding trophic interactions within persistent seabird hotspots could benefit EBFM and development of harvest rules for forage fisheries. Third, marine spatial management in the CCE requires information on the distribution and connectivity of biological hotspots (Halpern et al. 2009, Nur et al. 2011, Santora et al. 2011b, Adams et al. 2012) in order to avoid potential negative interactions (e.g., seabirds and fishing vessels, oil spills; Hyrenbach et al. 2000, Hooker and Gerber 2004, Lascelles et al. 2012).

Our synthesis paves the way for integrated ecosystem science aimed at understanding biophysical processes and functional relationships among trophic levels and future variability of the CCE. Quantifying biophysical drivers of seabird-forage hotspots will reduce uncertainty about numerical responses between seabirds and forage fish (Cury et al. 2011, Santora et al. 2014), and promote identification of critical marine habitat important for sustaining seabird populations in the CCE (Nur et al. 2011, Adams et al. 2012). To that end, numerical response models should compare the spatio-temporal persistence of seabird hotspots to long-term changes in hydrographic conditions and forage fish abundance. Several locations exhibited long-term declines in species richness and abundance, but it is unknown how interactive changes in hydrographic conditions and forage species abundance may have varied within these areas of concern. Dynamic height in the CalCOFI area is important variable for predicting spawning locations of forage fish in the southern CCE (Asch and Checkley 2013), and may relate to the persistence of some seabird hotspots (Yen et al. 2006). Therefore, spatially-referenced numerical response models that combine ocean conditions and forage fish, should help illuminate the drivers of persistent hotspots (Santora et al. 2014).

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