Persistence of trophic hotspots and relation to human impacts within an upwelling marine ecosystem

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Abstract. Human impacts (e.g., fishing, pollution, and shipping) on pelagic ecosystems are increasing, causing concerns about stresses on marine food webs. Maintaining predator–prey relationships through protection of pelagic hotspots is crucial for conservation and management of living marine resources. Biotic components of pelagic, plankton-based, ecosystems exhibit high variability in abundance in time and space (i.e., extreme patchiness), requiring investigation of persistence of abundance across trophic levels to resolve trophic hotspots. Using a 26-yr record of indicators for primary production, secondary (zooplankton and larval fish), and tertiary (seabirds) consumers, we show distributions of trophic hotspots in the southern California Current Ecosystem result from interactions between a strong upwelling center and a productive retention zone with enhanced nutrients, which concentrate prey and predators across multiple trophic levels. Trophic hotspots also overlap with human impacts, including fisheries extraction of coastal pelagic and groundfish species, as well as intense commercial shipping traffic. Spatial overlap of trophic hotspots with fisheries and shipping increases vulnerability of the ecosystem to localized depletion of forage fish, ship strikes on marine mammals, and pollution. This study represents a critical step toward resolving pelagic areas of high conservation interest for planktonic ecosystems and may serve as a model for other ocean regions where ecosystem-based management and marine spatial planning of pelagic ecosystems is warranted.

Key words: anchovy; fisheries; food web; krill; oil; primary productivity; retention; sardine; seabirds; shipping; spatial management; upwelling.

Introduction

The design of coastal Marine Protected Areas (MPA) has focused on the recovery of depleted populations and conservation of biodiversity (Game et al. 2009, Gleason et al. 2013). Estimating connectivity metrics for tracking interactions between potential protected areas is critical to evaluate the size and spacing of MPA networks for sustaining marine populations (Botsford et al. 2003, Shanks et al. 2003). A key attribute of current MPA networks is that many target relatively sedentary species (e.g., invertebrates, corals, and demersal fish); therefore, estimating larval dispersal provides a direct connectivity link to size and spacing decisions (Mace and Morgan 2006, Botsford et al. 2009). Coastal and open ocean, plankton-based, pelagic

systems are fundamentally different than nearshore communities in that most species are highly mobile through their entire life history (e.g., sardine, anchovy, salmonids, seabirds, marine mammals) and thus may require larger protected areas based on different design criteria (Hyrenbach et al. 2000, Game et al. 2009), or alternatively with a different set of presumed results or outcomes from management actions. Moreover, pelagic ecosystems are forced by large-scale, dynamic, ocean–climate processes (e.g., ENSO) that promote complex relationships among trophic levels, from primary producers to secondary and tertiary consumers (Schwing et al. 2010). Within eastern boundary upwelling ecosystems (EBUE), mechanisms regarding spatial organization of multiple trophic levels within pelagic ecosystems are conceptualized by Bakun's "Triad" (Bakun 1996), which emphasizes the role of physical forces that affect nutrient enrichment, concentration, and retention of primary producers and secondary consumers. Upwelling in eastern boundary current systems

is a physical process that is frequently critical for supporting the triad, especially around topographic and bathymetric features.

The California Current Ecosystem (CCE) is a highly productive EBUE that sustains a substantial plankton-based food web (McGowan et al. 1998, Checkley and Barth 2009), a high diversity of top predator species (Block et al. 2011), and important fisheries (McEvoy 1986, MacCall 1996, Kaplan et al. 2012, Lindegren et al. 2013). In the CCE, several assessments of biological hotspots have been made of seabirds, zooplankton, and fish (Reese and Brodeur 2006, Yen et al. 2006, Nur et al. 2011, Santora et al. 2011), and evaluated relative to human impacts (Maxwell et al. 2013). These analyses and associated pelagic hotspots have been defined mainly as areas of high species diversity and/or abundance of single species or functional groups (e.g., krill; Santora et al. 2011); indeed, studies directly linking trophic levels and oceanographic drivers have rarely been accomplished (Hazen et al. 2013). Hotspots of forage nekton (e.g., krill, schooling fish) used by multiple upper-level predators may be considered areas of enhanced trophic interactions or *trophic hotspots*. In EBUE, trophic hotspots may form due to features related to upwelling (Bakun 1996, Ainley et al. 2009, Santora et al. 2011, Reese and Brodeur 2015), but the careful consideration and analysis of the spatial overlap and functional relationships across multiple trophic levels has rarely been rigorously evaluated. Moreover, regions that represent trophic hotspots across multiple trophic levels are not typically considered in the context of human activities and impacts in the marine environment. Thus, examining the nexus between ocean processes and populations across multiple trophic levels should help to understand spatiotemporal aspects of trophic hotspots, and their susceptibility to human impacts.

To date, most studies of pelagic hotspots lack estimation of *persistence*, a key statistic based on the frequency of positive standardized anomalies that provides information on the likelihood of hotspot recurrence (Suryan et al. 2012, Santora and Sydeman 2015, Welch et al. 2015). Here we define trophic hotspots in pelagic ecosystems as areas with high persistence of elevated concentrations of primary producers and secondary and tertiary consumers. Estimating persistence is especially important given the high variability and spatial patchiness that is characteristic of most coastal and open ocean ecosystems (Benoit-Bird and McManus 2012, Hazen et al. 2013, Bertrand et al. 2014). We hypothesize that the persistence of trophic hotspots in upwelling ecosystems is the result of physical forces that affect enrichment (nutrients and primary production), concentration, and retention of lower trophic levels (Bakun 1996). We further suggest these locations are recurring principally down-current of strong upwelling zones within comparatively stronger retention zones (Santora et al. 2011), supporting enhanced concentrations of zooplankton,

forage fish, and seabird density and diversity. We test these ideas using data from the southern CCE and apply a persistence metric to address the following objectives: (1) quantify persistence of multiple trophic levels to resolve recurring trophic hotspots and characterize the ocean conditions under which they occur, (2) assess functional relationships between the persistence of top predators and lower trophic levels, and (3) place trophic hotspots in context with spatial patterns of human activities, such as shipping traffic and historical fishery extraction.

METHODS

Study area

The core of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey area is approximately 300000 km^2 and consists of a grid of sampling stations following six parallel lines that extends 400–700 km offshore (Fig. 1). Within this study area, the 2000-m isobath delineates the Southern California Bight (SCB), a region characterized by a complex bathymetry that includes eight major islands (many with considerable continental shelf habitat), 12 major basins, and numerous canyons and seamounts (Genin et al. 1988, Hickey 1992) as well as a dramatic change in the angle of the coastline associated with consequent changes in wind-forced upwelling (Genin et al. 1988, Checkley and Barth 2009). These factors contribute to an oceanographically complex region in which large-scale features, such as the equatorward flowing California Current in offshore waters and the poleward-flowing Southern California Countercurrent, interact with the bathymetry and with local and basin-scale forcing that results in mesoscale complexity in oceanographic conditions (Hickey 1992, Checkley and Barth 2009, McClatchie 2013). Point Conception promontory, an upwelling center located at the northern boundary of the SCB, is a major influence on the region's down-current ocean productivity and an important biogeographic breakpoint (Blanchette et al. 2008, Checkley and Barth 2009, Gottscho 2014). Furthermore, persistent upwelling-favorable winds around Point Conception influence thermal gradients and biological productivity throughout the SCB waters to the south, particularly at the northwestern portion of the Santa Barbara Channel, due in part to the considerably weaker influence of wind forcing and local upwelling within the SCB (Hickey 1992, Hickey et al. 2003, Jacox et al. 2014). Moreover, the semi-permanent gyre circulation within the SCB and Santa Barbara Channel is an important factor for the concentration and retention of upwelled nutrients and zooplankton (Bakun 1996, Hickey et al. 2003, Woodson and Litvin 2015). Four distinct domains have been identified in the SCB: (1) a southern coastal domain influenced by northward movement of warm waters from the subtropics,
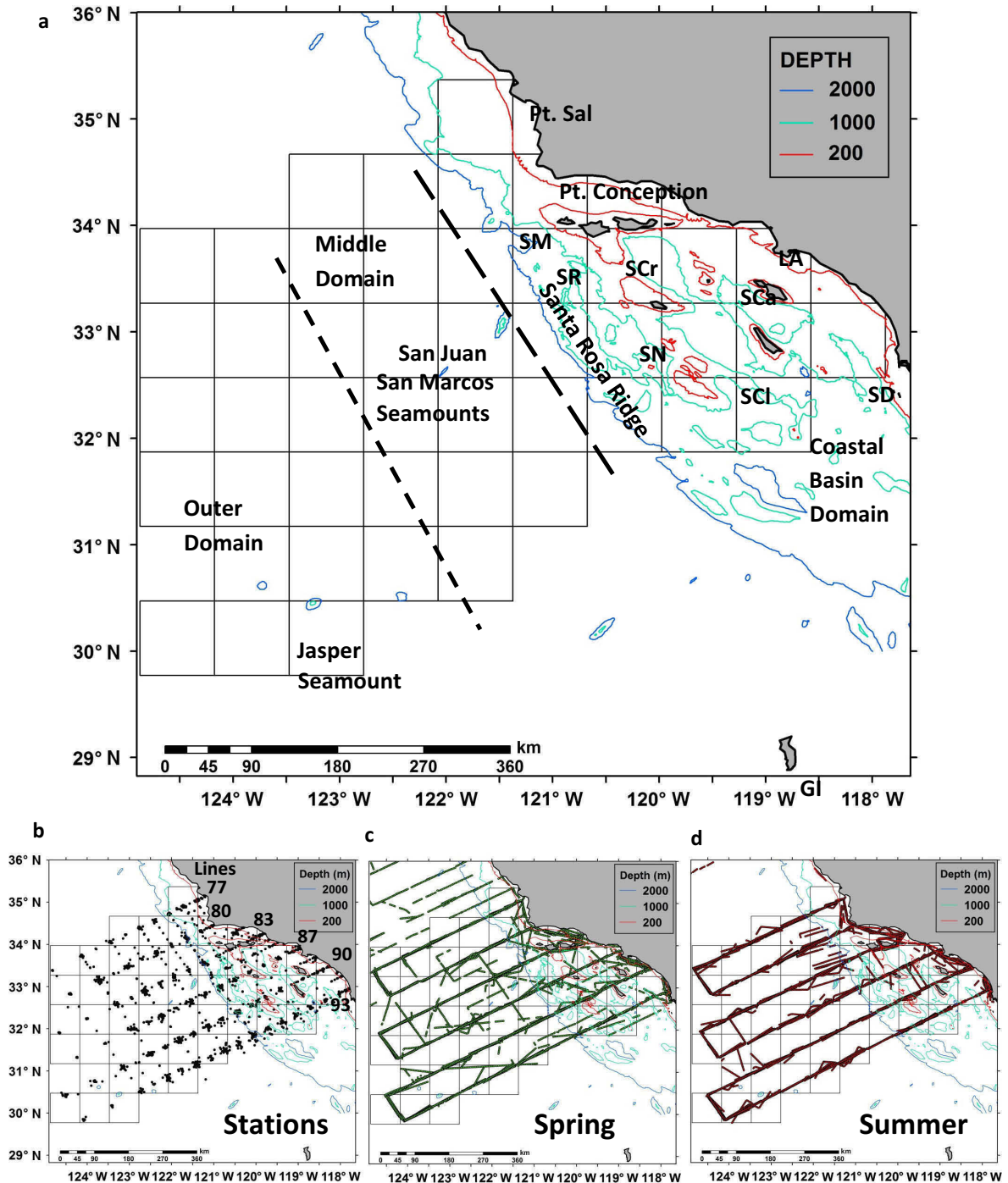
Fig. 1.　(a) The southern California Current region, CalCOFI survey domain, and location of grid cells used to assess physical ocean conditions and persistence of trophic hotspots; dashed lines indicate the approximate boundaries separating the coastal basin, middle, and outer domains; GI, Guadalupe Island; LA, Los Angeles; SM, San Miguel Island; SR, Santa Rosa Island; SCr, Santa Cruz Island; SCa, Santa Catalina Island; SCl, San Clemente Island; SN, San Nicholas Island; SD, San Diego. (b) Location of hydrographic and biological stations sampled during CalCOFI surveys and (c, d) distribution visual survey effort for seabirds during spring and summer CalCOFI surveys, 1987–2012. Contour lines are the 200-, 1000-, and 2000-m isobaths. Figure derived from Santora and Sydeman (2015). (Color figure can be viewed at wileyonlinelibrary.com.)

(2) northern coastal domains influenced by upwelling at Point Conception, (3) a transition (middle) domain associated with the generalized core location of the California Current, and (4) an oceanic (outer) domain (Hayward and Venrick 1998, McClatchie 2013, Bograd et al. 2015; Fig. 1).
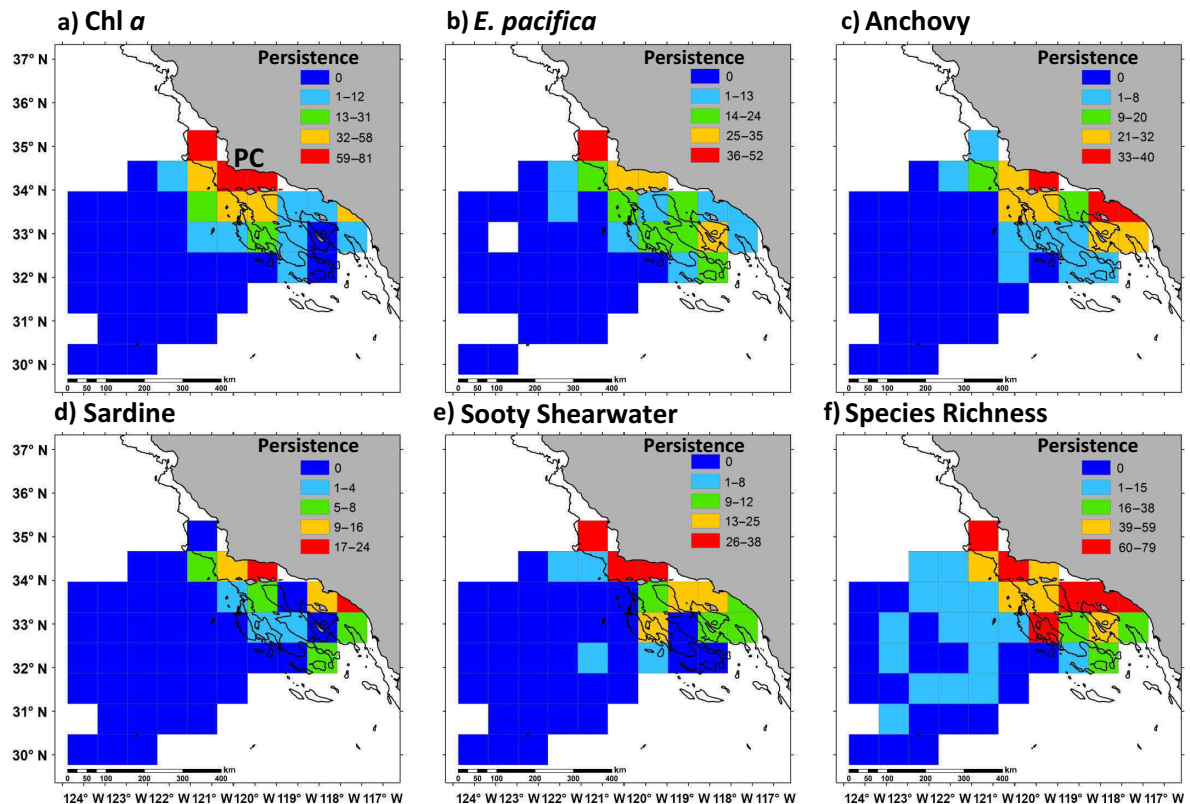
Fig. 2. (a–f) Persistence of representative trophic levels off Southern California (summer; for spring see Fig. S1): (a) chlorophyll *a*, (b) *Euphausia pacifica* (krill), (c) northern anchovy, (d) Pacific sardine, (e) Sooty Shearwater, and (f) seabird species richness; PC is Point Conception. Persistence values (color bar) are based on the percentage of time a grid cell is >1 standard deviation above the grand mean (all sampled cells). (Color figure can be viewed at wileyonlinelibrary.com.)

Data sources and analysis

To assess the distribution and persistence of trophic hotspots, we examine 26 yr (1987–2012) of simultaneous shipboard sampling of ocean conditions, Chlorophyll *a* (chl *a*), krill, forage fish, and seabird biodiversity (species richness) and abundance (Fig. 2). Data are available from the CalCOFI website (*available online*).[7] For a description of the sampling design see Bograd et al. (2015); Hyrenbach and Veit (2003) provide a description of the methods used for seabird surveys. Spring and summer surveys (*N* = 47) are analyzed in this study (seabird sampling began in 1987). We conform to the spatial resolution of CalCOFI by integrating continuous visual survey effort (seabirds) with discrete station sampling (hydrographic, zooplankton, forage fish). Seabird observations were mapped continuously during daylight hours while the ship was in transit between biophysical sampling stations (Fig. 1). A station consists of a vertical profile of the water column to assess hydrographic conditions (collected via a CTD), primary production, and nutrients (Bograd et al. 2015), while net hauls (bongo) were collected to enumerate the density of zooplankton and larval fish species (Brinton and Townsend 2003, Koslow et al. 2013).

7 http://www.calcofi.org/new.data/index.php

Data were gridded (55 cells; each cell ~4500 km^2) to integrate continuous sampling of seabirds with station samples; the gridding procedure was predetermined by the extent of continuous shipboard survey effort (Santora and Sydeman 2015). If more than one station was sampled per cell, then the mean of all stations sampled was calculated; generally two stations occurred in coastal grid cells due to the sampling design (McClatchie 2013). For each grid cell (per survey), we summarized the following biological variables: (1) chl *a* concentration (per mg^3) at 10 m, (2) density (individuals/m^2) of the euphausiid, *Euphausia pacifica* (total adults), (3) density (individuals/m^2) of larval northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*), (4) density (individuals/km^2) of Sooty Shearwaters (*Puffinus griseus*; most abundant migrant seabird in the CCE), and (5) species richness of seabirds. Since adult krill samples are only available for spring surveys and their geographic distribution is consistent (Brinton and Townsend 2003), their springtime abundance is also included in summer descriptions and analyses of trophic hotspots (krill are present during summer but were not enumerated). While accounting for the amount of time a cell was sampled (total surveys), the persistence for each variable is measured by calculating a standardized spatial anomaly for each cell (*z* score; specific to each

survey), and then we enumerated the percentage of time (frequency likelihood) a cell's value is >1 standard deviation above the grand mean (all sampled cells); for further review of the persistence metric in the CalCOFI study area, see Santora and Sydeman (2015). We use generalized additive models (GAM) to investigate the functional relationship between lower and upper trophic levels (e.g., krill, larval fish, and seabirds). As an example, bivariate GAMs (e.g., seabird persistence vs. *E. pacifica* persistence) are used to investigate how the persistence of seabird species richness, which is correlated with Sooty Shearwater abundance (Santora and Sydeman 2015), may be functionally related to the persistence of lower trophic levels. GAMs were implemented using the mgcv package in the R statistical program (R Development Core Team 2016) and smoothness parameters were estimated using generalized cross-validation (Zuur et al. 2009). The effect of each covariate (e.g., chl *a*, *E. pacifica*, anchovy, and sardine) included in each GAM was plotted to visually inspect the functional form and assess seabird hotspots vary in relation to geospatial covariates (Zuur et al. 2009).

The persistence of each biological variable per grid cell was stored in a matrix and principal component analysis (PCA) was used to examine coherence of persistence among biological variables (biological PC) to establish a spatial index of hotspots across trophic levels. We compared the biological PC results to a station-specific climatology of ocean conditions (spatial mean) to assess how they influence the mesoscale spatial organization of trophic hotspots. Physical variables include temperature (°C), potential density (kg/m^3) at 10 m, dynamic height relative to 500 m (m), and depth of the pycnocline as determined by the depth of the maximum Brunt-Väisällä Frequency (m) (Kim and Miller 2006). Bilinear interpolation was used to link these variables to the biological grid and their long-term means per grid cell was calculated for describing a regional spatial climatology of mesoscale ocean conditions (Bograd et al. 2015). We averaged grid cells to the east and west of the 2000-m isobath (Figs. 1, 2) to characterize temporal variability of physical variables within the SCB in comparison to waters beyond the core of the California Current (Bograd et al. 2015). Subsequently, we implemented a PCA of ocean conditions (physical PC) using a data matrix of the temporal means (1987–2012) of the four physical variables over the 48 grid cells to characterize ocean conditions. Since wind-driven upwelling plays a critical role in structuring biological productivity in the CCE (Bakun 1996), we compare biological hotspots with a climatological spatial index derived from a decade (2000–2009) of remotely sensed ocean wind measurements (QuikScat satellite) to characterize the regions frequency of strong wind events (percentage of days >15 knots), zonal Ekman mass transport (kg·m^{-1}·s^{-1}), and upwelling velocity (m·d^{-1}). Upwelling velocity is calculated by combining wind stress curl and coastal upwelling using alongshore winds adjacent to the coast (Rykaczewski and Checkley 2008) and Ekman transport is derived from Santora et al.

(2011). Furthermore, to assess how biological variables are spatially related to enhanced nutrients due to regional upwelling, we compared them to a spatial climatology of nitrate (μmol·L^{-1}·kg^{-1}), a key upwelled nutrient for promoting enhanced primary production (Palacios et al. 2013, Bograd et al. 2015), at a vertical integration depth of 0–25 m and linked to the grid. Therefore, we predict that upwelling velocity, nitrate, and the physical PC are positively related and should provide a regional scalar for understanding how trophic hotspots are functionally related to environmental conditions.

Last, to evaluate trophic hotspot associations with human activities, we report geospatial information on commercial shipping intensity (obtained from Halpern et al. 2009), location of oil platforms, and the regional distribution of commercial fishery extraction of coastal pelagic fish (northern anchovy, Pacific sardine, and mackerel spp.) and groundfish (e.g., *Sebastes* rockfish). Fishery extraction data is from both historical and contemporary California Department of Fish and Wildlife block summary data (note that these data are coarsened from the original 10' by 10' [3 × 3 m] block summary data). Miller et al. (2014) provide further details and methods on the estimation of historical (1930–2000) fishery extraction patterns off California. For the purposes of this study, we summarized the total extracted metric tons (per km^2 of the appropriate habitat) of fish of each taxonomic group to the CalCOFI grid, and examined their relationship with the trophic hotpot index (biological PC).

RESULTS

Trophic hotspots

Quantifying persistence of different trophic levels resolved the spatial organization of the pelagic ecosystem of the southern CCS (Fig. 2; Appendix S1: Fig. S1). During summer, all trophic levels exhibited persistent hotspots shoreward of the 2000-m isobaths with hotspots clustered around the Point Conception and Santa Barbara Channel region (chl *a*, *E. pacifica*, anchovy, sardine, Sooty Shearwater, and seabird species richness), and to a lesser extent to the southeast along the southern California Coast (anchovy, sardine, Sooty Shearwater, and seabird species richness; Fig. 2). The persistence of different trophic levels is spatially coherent among spring and summer, except for sardines, whose persistent hotspots were distributed further offshore during the spring coinciding with their primary spawning habitat locations (Fig. 2; Appendix S1: Fig. S1). Furthermore, the functional relationship among persistence of seabird species richness and persistence of trophic levels suggests an asymptotic response, indicating a threshold amount of persistence at each trophic level is required to achieve maximum species richness within hotspots (Fig. 3).

A PCA applied to persistence of biotic variables yielded a dominant component (PC) that explained 64% and 74% of the total spatial variance during spring and summer,
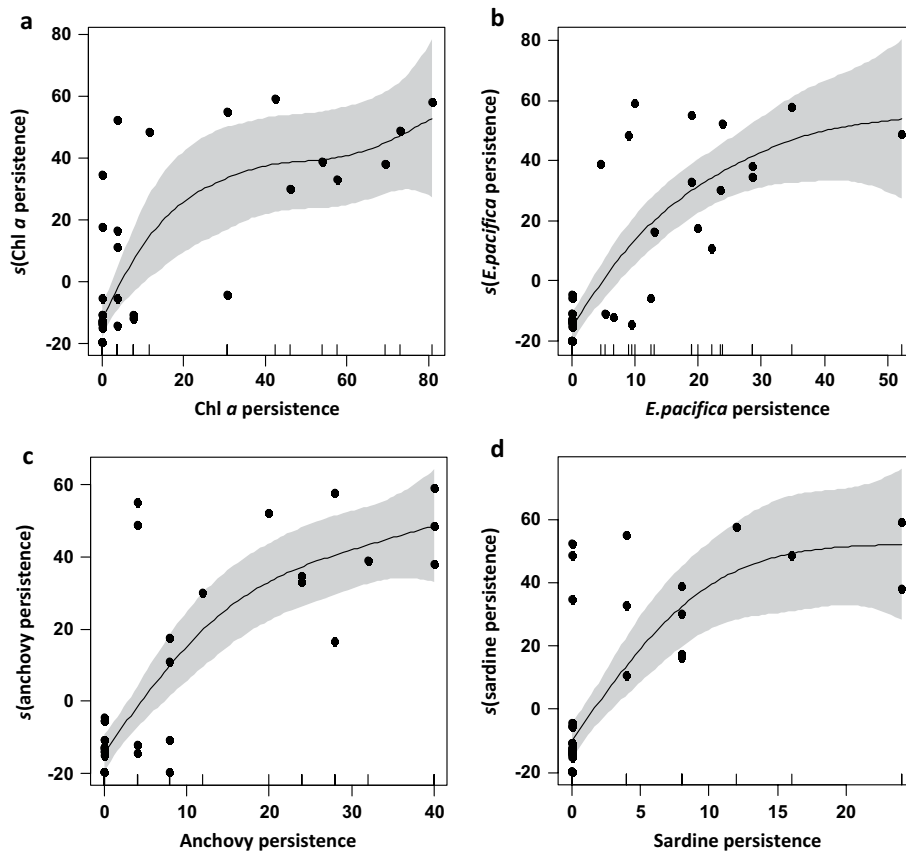
Fig. 3. Functional relationships, derived from GAMs, illustrate numerical responses between the persistence of summertime seabird species richness and persistence of (a) chl *a*, (b) *Euphausia pacifica*, (c) anchovy, and (d) sardine; *s* is a smoothing function representing the effect of each variable on the persistence of seabird species richness, and shaded area indicates 95% confidence intervals.

respectively (Table 1). On mapping the component scores over space, we are able to resolve the spatial distribution of trophic hotspots (Fig. 4a, b), and in doing so demonstrate that during spring and summer, two of the highest trophic hotspots are located in the vicinity (down-current) of Point Conception within the Santa Barbara basin. Moreover, during summer months additional trophic hotspots are located to the north of Point Conception and to the southeast near 33.5°N. These trophic hotspots are locations where at least five or six of all biological variables exhibited high persistence, indicating these locations are characterized as having relatively high reoccurring concentrations of primary production and secondary and tertiary consumers.

Oceanographic determinants of trophic hotspots

The interaction between coastal geomorphology, gyre recirculation, and frequency of strong equatorward winds at Point Conception is largely responsible for regional upwelling conditions and influences transport patterns and retention of nutrients down-current, where upwelling winds are generally weaker, throughout the coastal waters

of the SCB (Figs. 4c, 5a–c; Appendix S1: Fig. S2). The first one-half of the ocean condition time series (1987–1998) is characterized by a period of warm conditions (along with

TABLE 1. Factor loadings resulting from principal component analysis (PCA) to examine coherence among trophic levels to index trophic hotspots locations in (a) spring, and (b) summer.

Factor	PC1	PC2
a) Spring	(3.84, 64.01)	(0.78, 13.04)
Chlorophyll *a*	0.83	0.10
Euphausia pacifica	0.80	0.30
Northern anchovy	0.69	−0.12
Pacific sardine	0.56	0.79
Sooty Shearwater	0.90	0.19
Seabird species richness	0.95	0.03
b) Summer	(4.45, 74.25)	(0.80, 13.32)
Chlorophyll *a*	0.86	−0.15
E. pacifica	0.83	−0.46
Northern anchovy	0.86	0.43
Pacific sardine	0.80	0.54
Sooty Shearwater	0.88	−0.29
Seabird species richness	0.95	−0.04

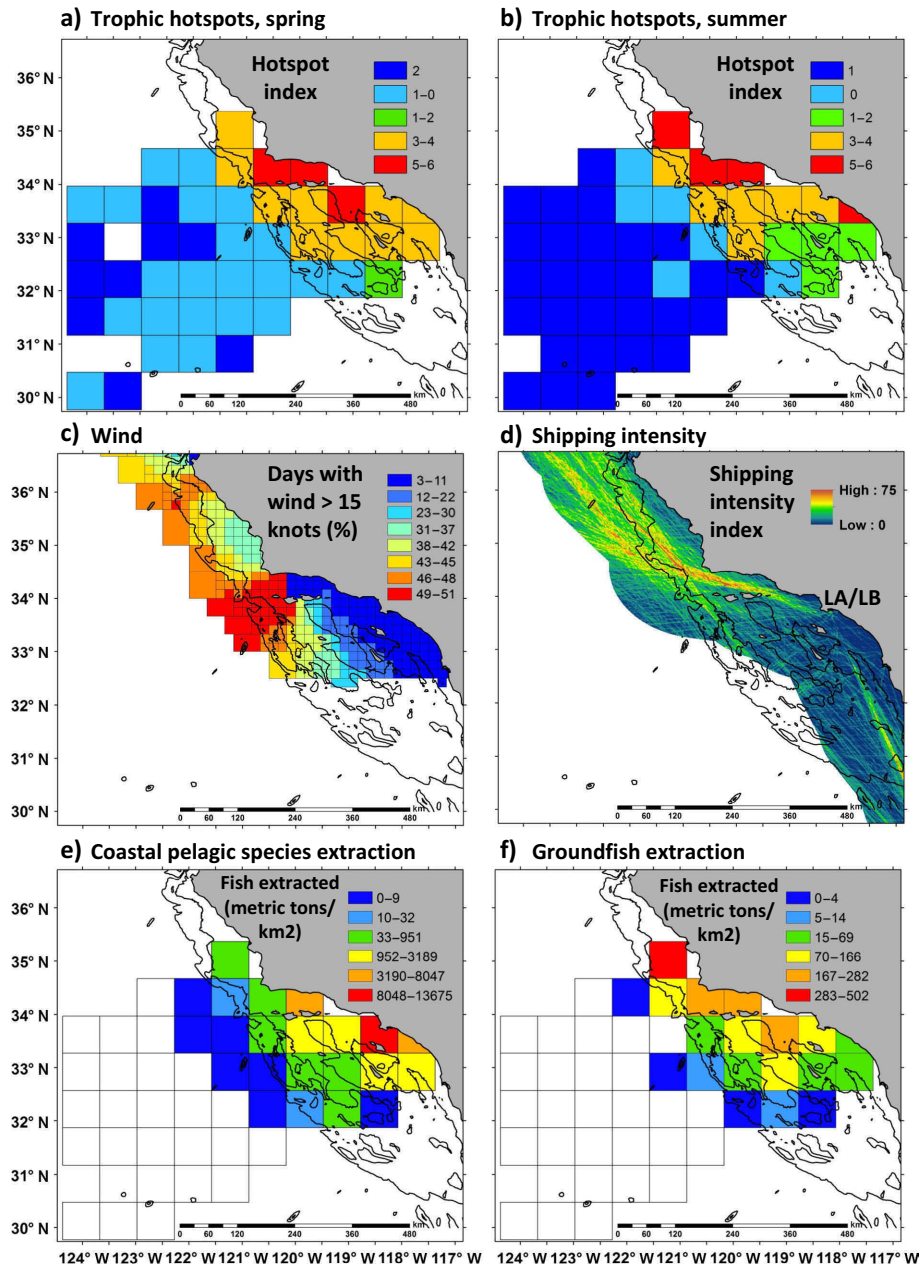*Note:* Values in parentheses are the eigenvalue and percent variance, respectively.

FIG. 4. Distribution of the trophic hotspot index representing the persistence of biological variables during (a) spring and (b) summer (positive values indicate areas with higher coherence of persistence among variables; yellow and red grid cells are considered meso-scale hotspots). (c) Persistence of remotely sensed winds as indexed by the percentage of days with winds >15 knots, (d) shipping intensity index highlights areas with heavy commercial shipping traffic (from Halpern et al. 2009), and total metric tons (per km^2; 1930–2000) of historical fish extraction of (e) coastal pelagic species and (f) groundfish and rockfish, aggregated to CalCOFI grid. LA/LB is Los Angeles and Long Beach port complex. (Color figure can be viewed at wileyonlinelibrary.com.)

higher dynamic height and deeper pycnocline depth), and the second one-half (1999–2012) generally reflects cooler ocean conditions (along with lower dynamic height, shallow pycnocline depth) nearer the coast (Appendix S1: Fig. S3). The PCA applied to the spatial climatology of ocean conditions yielded a first component that explained 84% and 75% of the total variance during spring and summer, respectively (Table 2; Appendix S1: Fig. S4).

Physical PC1 loads very strongly on temperature, density, dynamic height, and pycnocline depth, highlighting differences between offshore vs. SCB waters, separating cold, dense, shallow, mixed-layer waters inshore, from warm, low-density, and deep mixed-layer waters offshore. Due to the upwelling associated nutrient enrichment and concentration down-current in more relaxed regions (Fig. 5), it is clear that the trophic hotspot index is positively correlated
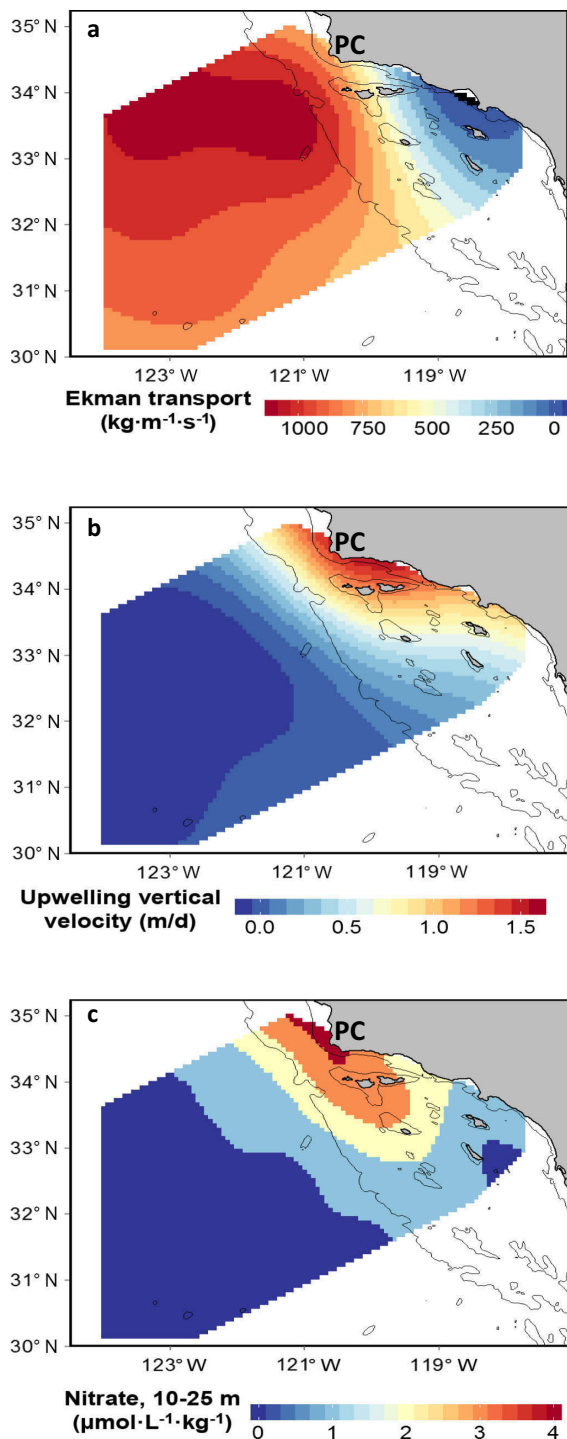
TABLE 2. Factor loadings resulting from PCA to examine coherence among physical variables in (a) spring, and (b) summer.

Factor	PC1	PC2
a) Spring	(3.37, 84.28)	(0.57, 14.16)
Dynamic height	−0.97	−0.22
Pycnocline depth	−0.88	−0.48
Potential density (10 m)	0.96	−0.22
Temperature (10 m)	−0.86	0.49
b) Summer	(2.99, 74.77)	(0.93, 23.17)
Dynamic height	−0.94	−0.30
Pycnocline depth	−0.77	−0.63
Potential density (10 m)	0.94	−0.31
Temperature (10 m)	−0.80	0.59

Note: Values in parentheses are the eigenvalue and percent variance, respectively.

with upwelling velocity and nitrate concentration at depths related to the pycnocline (Appendix S1: Table S1; Fig. 6). The relationship between the trophic hotspot index and physical PC1 is linear; indicating the spatial distribution of trophic hotspots corresponds to an inshore–offshore gradient, where higher persistence relates to areas of greater upwelling, cooler sea surface temperature, shallow pycnocline depth, and lower dynamic height (Fig. 6).

Associations with shipping and fishing

We compared the distribution of trophic hotspots with spatial patterns of human impacts within the southern CCE to illustrate the importance of these hotspots as ecosystem resources and potentially benefit their management (Fig. 4d–f). Trophic hotspots located within the Santa Barbara Basin overlap with the intensive commercial vessel activity (Fig. 4d; shipping vessels transiting to and from the Los Angeles and Long Beach port complex, the largest port complex in the United States), especially in the vicinity of Point Conception. The trophic hotspots identified in this study overlap with historical fishery extraction patterns off southern California (Fig. 4). For example, the spatial distribution of total metric tons per km^2 of fish extracted (1930–2010) of coastal pelagic species and groundfish clearly overlaps with trophic hotspots (Figs. 4e, f, 6e, f). Moreover, the association between the total extracted amount of fish and the trophic hotspot index suggests a functional relationship, indicating a few locations that account for high fishery extraction that occurred at moderate trophic hotspots (Figs. 4e, f, 6e, f).

DISCUSSION

Persistence and trophic hotspots

We document the temporal persistence and cooccurrence of hotspots of abundance for chl *a*, krill,

FIG. 5. Climatological summer ocean conditions reflecting mesoscale spatial patterns of enrichment, concentration, and retention (i.e., Bakun's Triad) within the greater Point Conception (PC) region: (a) Ekman transport, (b) upwelling vertical velocity, and (c) nitrate distribution derived from CalCOFI sampling stations. (Color figure can be viewed at wileyonlinelibrary.com.)
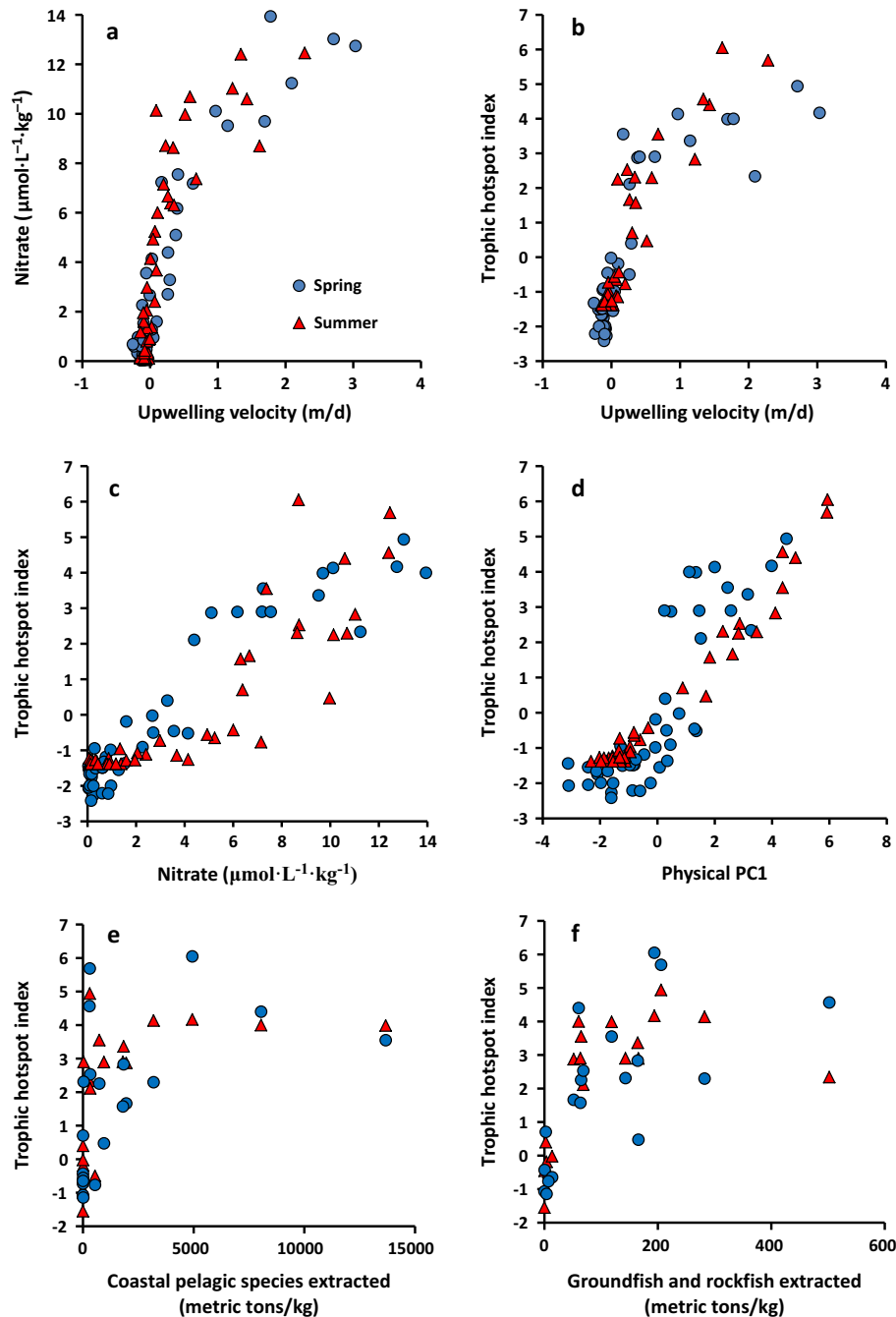
Fig. 6. Physical and biological relationships during spring and summer: nitrate (integrated from 25 to 50 m) and upwelling vertical velocity, (b) trophic hotspot index and upwelling vertical velocity, (c) trophic hotspot index and nitrate (integrated from 25 to 50 m), (d) trophic hotspot index and physical PC1, and trophic hotspot index and the amount of fish extracted for (e) coastal pelagic species and (f) groundfish and rockfish. (Color figure can be viewed at wileyonlinelibrary.com.)

larval forage fishes, and seabirds in relation to upwelling in the Point Conception, California region. This headland is a biogeographic transition zone between the subtropical ecosystem of the SCB to the south and the temperate upwelling region to the north (Blanchette et al. 2008, Gottscho 2014). To demonstrate the existence of trophic hotspots off Point Conception, we applied a

persistence metric to measurements of the relative abundance of key species of a trophic chain from phytoplankton to krill to forage fish to seabirds eating forage fish (Wells et al. 2008, Santora et al. 2012, Sydeman et al. 2015). Our analysis of spatial persistence associations therefore reflects the underlying trophic dynamics of this pelagic ecosystem. Marine mammals also use this area

preferentially for foraging (Redfern et al. 2013, Irvine et al. 2014, Kuhn and Costa 2014), so they may be considered part of the trophic equation as well, though we did not include them in our analyses. The seabirds may therefore serve as a surrogate for the upper trophic level community, including species whose abundance and distribution patterns are more difficult to quantify in this dynamic environment.

Our application of a simple metric of persistence across trophic levels shows that a multivariate description of potential trophic hotspots can be developed by pooling existing data sources in order to better understand the spatial relationships among a wide range of physical properties and biological assemblages (Suryan et al. 2012, Santora and Sydeman 2015). Furthermore, we have shown that some human uses of the marine environment, such as fisheries extraction, are associated with trophic hotspots. We have also shown associations between shipping lanes and oil platform and trophic hotspots, but these relationships are spatially coincidental rather than causally related to underlying food web dynamics that may support fisheries. There are, however, at least two important caveats in our approach. First, the derivation of a persistence metric requires long time series, to account for the inter-annual variability in biophysical relationships that drive the variation in persistence metric (Edwards et al. 2010). In this case, we used 26 yr of synoptic observations to assess ocean conditions and trophic hotspots. This temporal resolution was appropriate as it covered a variety of ENSO to quasi-decadal-scale ocean-climate variation (Bograd et al. 2015). For example, the biological persistence patterns we describe developed during a period characterized by a relative warm ocean state (1987–1998) and a cool state (1999–2012), as indicated by the physical variables we quantified within and outside of the SCB (Appendix S1: Fig. S3). The second caveat involves the spatial extent and spatial resolution of our study: (1) we were limited to where the ship consistently surveyed, and this did not include nearshore habitats and (2) the regional focus resulted in widely spaced survey tracks (~40 km in latitude). Consequently, the trophic hotspots we derived are relatively coarse in spatial resolution; there may be subregions within hotspots that warrant consideration, but we cannot address this scale with the data at hand. That said, our spatial resolution may be justified by the fact that highly mobile predators require vast oceanic areas that contain dense concentrations of forage species for sustenance (Block et al. 2011, Maxwell et al. 2013).

Scaling and mechanistic considerations

At the regional-scale, the trophic hotspots we describe may represent a network of smaller-scale "meso-hotspots," which are connected due to the high mobility of organisms utilizing these areas as well as the oceanographic drivers of hotspot formation in this region (Suryan et al. 2012, Hazen et al. 2013). For most species, contouring would likely reveal a smooth surface of abundance from Point Conception to the south, but with seasonal variation. For example, sardine hotspots are found further offshore in spring due to spawning, but inshore, albeit at lower density in summer. For the most part, anchovy are concentrated near Point Conception during summer, with a secondary concentration off the Palos Verde peninsula during spring. Even with this variation, the Point Conception "macro-hotspot" is almost certainly related to upwelling as well as eddy structures that form to the north and south of the Point Conception upwelling cell (Dong et al. 2009, Woodson and Litvin 2015). Furthermore, hotspots located within the Santa Barbara Channel are influenced by the interaction of the cold southward flowing California Current and the warm westward flowing nearshore countercurrent, which results in a persistent thermal gradient within the channel (Hickey 1992, Hickey et al. 2003). Conceptually, we envisage that the strong upwelling at Point Conception stimulates nutrient enrichment over the broad geographic zone composed of the SCB and offshore domains (Rykaczewski and Checkley 2008, Jacox et al. 2014), with retention of primary production, plankton, and forage fish causing top predator (seabird) aggregative behavior in the lee (upwelling shadow; Graham and Largier 1997) as well as upstream from the headland (Figs. 4, 7). Although we did not examine the finer-scale physical mechanisms of hotspot formation (presumably fronts, eddies, and gyre recirculation; Dong et al. 2009, Woodson and Litvin 2015), we hypothesize that the combination of enrichment from upwelling, and concentration and retention from the circulation in the lee of Point Conception within SCB, provides the basis for enhanced primary productivity and a food chain of krill and forage fish that ultimately attracts dense aggregations of Sooty Shearwaters and a diverse seabird community. Therefore, we conclude that the network of trophic hotspots in the Point Conception region is in keeping with Bakun's Triad model of ecosystem dynamics for EBUE where mechanisms of enrichment, concentration, and aggregation by consumers determine spatial associations. In this manner, we have described aspects of the functional ecology of the "macro-hotspot" of Point Conception and the SCB region of California.

Extension of trophic hotspots to other EBUE

Our concept of regional to mesoscale trophic hotspots, as identified off southern California, may be applicable to other upwelling ecosystems where krill, anchovy, and sardine form the base of the food web (e.g., Benguela and Humboldt Currents), especially in bight regions off Africa, Chile, and Peru (Bakun and Parrish 1982, Bakun 1996). Our results highlight how geomorphology of bights and upwelling set up basic ocean conditions where trophic hotspots are likely to be formed and maintained. Located downstream from large-scale equatorward flows, coastal promontories/capes and strong upwelling regions, bights are locations where turbulent mixing
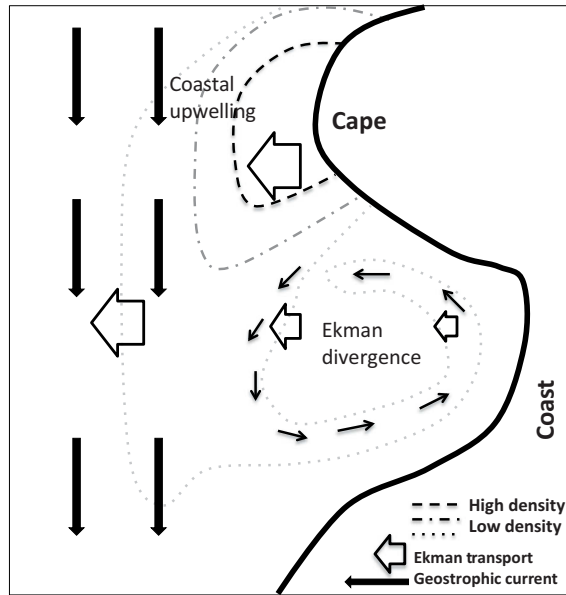
Fig. 7. This figure, modified from Bakun (1996), illustrates the generalized dynamics of eastern boundary upwelling ecosystems and the formation/maintenance of enriched trophic conditions due to coastal upwelling. The combination of winds, broad-scale equatorward flow along the coastline, and the coastal configuration generates high-density/nigh-nutrient water near capes that is drawn into nearby areas that are characterized by weaker Ekman transport and increased gyral retention and other recirculation processes. This diagram may be extended to other upwelling ecosystems that contain coastal bights and capes (e.g., eastern coastline of Africa and South America) to locate trophic hotspots.

energy and Ekman transport declines and gyral circulation increases (Fig. 7). Higher density water upwelled near capes contains nutrients that are then transported downstream, retained, and concentrated within bights through gyre recirculation (Graham and Largier 1997, Hickey et al. 2003, Dong et al. 2009), promoting elevated primary production, and providing reproductive habitat for forage fish and shelter for fish larvae from alongshore wind stress (Bakun and Parrish 1982), thereby enriching trophic conditions for top predators (Santora et al. 2012). Persistence of elevated chl a levels, (along with krill and seabirds north of Point Conception) may also occur north of capes and promontories, and suggests upstream concentration mechanisms involving shelf-break upwelling fronts and meandering eddies are also important (Hickey 1992, Vander Woude et al. 2006, Dong et al. 2009, Woodson and Litvin 2015). Furthermore, curl-driven upwelling within the bights may also account for significant upwelling in pelagic ecosystems (Rykaczewski and Checkley 2008). Coupled ocean–ecosystem models may be used to confirm the mechanisms discussed here, as well as predict how and where trophic hotspots may be formed under different environmental conditions in EBUE worldwide (Cury et al. 2008).

Trophic hotspots, fisheries management, and human impacts

Eastern boundary upwelling ecosystems are some of the most productive marine ecosystems globally and account for a high proportion of the fish extracted by humans globally each year (Ryther 1969, Pauly and Christensen 1995). We found that trophic hotspots are important fishing areas for coastal pelagic and groundfish fisheries, although in the case of fisheries for coastal pelagic species in particular, the proximity to major ports may be another contributing factor regarding the spatial distribution of catches (Miller et al. 2014). While it is difficult to determine the full impacts of fishing on higher trophic level species that may compete with fisheries for prey, as well as the cumulative impacts on marine ecosystems more generally, one important first step is evaluating the spatial overlap between fisheries and key ecosystem components. The distribution and behavior of top predators and fishing vessels often depend on the aggregation and behavior of their prey, such that depletion of forage fish patches may trigger regional changes in predator foraging and sometimes demographic traits (Bertrand et al. 2007). If fishing is shown to have detrimental impacts within trophic hotspots, spatially explicit harvest control rules may be applied to maintain sufficient resources for predator foraging (Anderson et al. 1980, Bertrand et al. 2007, Field et al. 2010, Cury et al. 2011). Conservation and management of upwelling ecosystems could account for the type of bottom-up trophic dynamics that regulate the persistence of trophic hotspots (Duffy et al. 2007, Kaplan and Leonard 2012). Our trophic hotspot persistence index provides information for specific grid cells and its trophic significance. As society continues to develop criteria for what defines healthy marine ecosystems (Halpern et al. 2009), knowledge of spatially explicit ecological functions may be used to improve ecosystem-based management (DeMaster et al. 2001, Grantham et al. 2011, Maxwell et al. 2015). In particular, assessing the relationship between trophic hotspots and fisheries extractions, especially of forage species, could help in risk and vulnerability assessments (Lester et al. 2010, Pikitch et al. 2012, Halpern et al. 2015) and benefit dynamic ocean management strategies focused on temporally varying closures of key trophic hotspots (Maxwell et al. 2015).

Vessel traffic in pelagic ecosystems increases the risk of marine pollution (e.g., fuel leakage and oil spills) and direct impacts on upper trophic level predators (e.g., ship-strike incidents with baleen whales and oiling of seabirds). Our study complements previous risk assessments on shipping and baleen whales (Redfern et al. 2013), in that we showed intense shipping traffic intersecting with persistent trophic hotspots in the Santa Barbara Channel, adjacent to Point Conception. Knowledge of interannual and seasonal variation in trophic hotspots could help to inform habitat models and spatial management measures that might be

implemented to forecast or mitigate risk to marine mammals and other wildlife (Becker et al. 2012, Maxwell et al. 2013). Although static in time and space, oil platform distribution also overlaps with trophic hotspots in the region. There is an extensive offshore oil field within the Santa Barbara Channel (Appendix S1: Fig. S5), with many oil platforms located within or near trophic hotspots, presenting ongoing challenges for minimizing detrimental effects of oil extraction on the health of the ecosystem (Halpern et al. 2009, Andrews et al. 2014). However, the oil platforms off southern California are productive fish habitats (dense and diverse fish populations of mainly *Sebastes* spp.; Love et al. 2006, Clasisse et al. 2014) attractive to fisheries, and thereby may be considered human-facilitated hotspots.

Trophic hotspots and climate change

The trophic hotspots we describe are related to upwelling dynamics and the interaction between seasonal wind patterns, topography, and bathymetry. Upwelling is predicted to change with climate change, but it is unclear how it will impact all upwelling zones in EBUE throughout the world. In particular, upwelling favorable winds are predicted to intensify with global warming, and a recent meta-analysis of the literature suggests that this may already be occurring for poleward regions of the California Current (Sydeman et al. 2014). While upwelling intensification in the CCE may increase nutrient flux to the euphotic zone and primary productivity, sustained high levels of upwelling may lead to excessive offshore transport and displacement of plankton from coastal to offshore waters, destabilizing coastal trophic hotspots (Bakun et al. 2015). Alternatively, a northward shift in the distribution of upwelling centers could decrease overall productivity in this region (Rykaczewski et al. 2015). Biological communities that do not shift their distribution in response changes in upwelling may become more vulnerable to combined impacts of global change and other human impacts on the ecosystem. Moreover, in either scenario, increasing variability of climate–ocean conditions may lead to higher population variability for both lower and upper trophic levels (Sydeman et al. 2013), and change the persistence values that define trophic hotspots. Temporal shifts in forage fish abundance in the CCE (MacCall 1990, Asch 2015) may impact the aggregative responses of top predators with subsequent demographic consequences (Santora et al. 2014). Significant declines in seabird abundance and diversity have already occurred off southern California and may be related to climatic factors (Santora and Sydeman 2015).

Conclusion

In this study, we revealed bottom-up forcing due to upwelling generated spatial patterns of enrichment, concentration and retention of nutrients resulting in the distribution of persistent trophic hotspots. Previous work (Yen et al. 2006, Santora and Sydeman 2015) had shown the importance of the Point Conception and Santa Barbara Basin to migratory and resident seabirds, but here we related seabird species richness and abundance to the underlying food web of coastal pelagic species, as well as the physical mechanism driving hotspot persistence (i.e., upwelling driven concentration and retention of nutrients). Understanding these dynamics not only explains patterns of the distribution of marine wildlife, but is also related to fisheries extractions. Our persistence metric and trophic hotspots therefore have potential applications to both marine spatial planning (e.g., MPA development and temporally varying closures) and ecosystem-based fisheries management (Lester et al. 2010, Pikitch et al. 2012).

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SUPPORTING INFORMATION

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