New approach for using remotely sensed chlorophyll *a* to identify seabird hotspots

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ABSTRACT: Satellite imagery of chlorophyll *a* concentration (chl *a*) provides the only holistic perspective of productivity in marine ecosystems worldwide, yet its utility for understanding and predicting the distribution of upper trophic-level predators remains equivocal. We tested the hypothesis that remotely sensed chl *a* measurements spanning a decade can predict marine bird movements and distributions and provide insight into persistent seabird 'hotspots'. To test this hypothesis, we developed a temporally and spatially explicit chl *a* variance metric that explained up to twice the variation (90 %) in seabird distributions than mean chl *a* values in our model system, the California Current. Our chl *a* variance metric—the frequency of chlorophyll peaks index (FCPI)—quantifies the frequency of chl *a* anomalies that exceed 1 standard deviation from the mean, relative to a spatial model for the ecosystem. Using the FCPI, we identified locations of high chl *a* anomaly persistence amidst considerable habitat heterogeneity from British Columbia, Canada, to Baja California, Mexico. Calculating variance and persistence metrics such as FCPI over large temporal scales may be preferable to analyzing mean or median chl *a* values over shorter time scales if understanding or predicting predator distributions is a goal of the research. As a static habitat layer, we suggest that the FCPI integrates time lags, physical forcings, and food web processes that can thwart attempts to link primary productivity and predator distributions in pelagic ecosystems. Additionally, identifying important ecological areas reflecting persistently elevated productivity and predator abundance is critical to marine spatial management and conservation.

KEY WORDS: Biological aggregations · Blooms · Marine protected areas · Persistence · Trophic transfer

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INTRODUCTION

On both land and sea, satellite remote sensing has emerged as a powerful tool for measuring, monitoring, and assessing the quantity and quality of biological resources (Hardman-Mountford et al. 2008, Hansen et al. 2010). In marine environments, satellite remote sensing has provided unprecedented insight into global spatio-temporal patterns of primary productivity (Field et al. 1998) and patterns of human use (Halpern et al. 2008). However, while primary productivity can be inferred from satellite data, extrapolating

this information to secondary or tertiary productivity, or inferring spatial and temporal variability in biological activity from these data, has produced mixed results (Worm et al. 2005, Suryan et al. 2006, Gremillet et al. 2008, Kappes et al. 2010, Block et al. 2011). Understandably, advection of surface waters, and variation in grazing rates, water column, or chlorophyll *a* (chl *a*) maximum is not detected by surface sensors, and time lags in the responses of secondary and tertiary consumers to primary productivity all contribute to apparent spatial and temporal mismatches between chl *a* concentrations and consumer distributions.

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Despite these challenges, if appropriate metrics and integrative statistics can be developed, coupling remotely sensed data on primary productivity with consumer distributions could be a powerful tool for understanding the spatial organization of large marine ecosystems. Indeed, there is a need to expand the use of marine satellite imagery for ecosystem-based approaches to management, including marine spatial planning, as well as conservation more generally. In particular, in light of new efforts to safeguard and balance the needs of marine ecosystem structure, functions, and services (e.g. fisheries), deriving indicators for sites of potential energy transfer from primary producers (phytoplankton) to tertiary consumers (e.g. seabirds) has broad resource management implications. Various tools are under consideration for ecosystem protection, including marine protected areas (Halpern et al. 2008), but more information, especially on the ecosystem-wide scale, and integration of spatial data layers on continental shelf fauna and flora, is needed to make wise choices about the locations of potential protected sites or regions.

To that end, our objective was to design and implement a large marine ecosystem-scale metric of primary productivity within the California Current System (CCS) that could depict areas of enhanced trophic transfer and thus of importance to top marine predators. We conceptualized a metric analogous to certain static bathymetric features, such as sea mounts (Yen et al. 2004) and canyons (Croll et al. 2005), that are predictably associated with bio-physical processes that enhance productivity, concentrate prey, and cause an aggregative response in predators (Bakun 1996). Given that high chl *a* mesoscale variability may be as important as chl *a* biomass in determining the potential productivity for higher trophic levels (Henson & Thomas 2007a), we hypothesized that accounting for the persistence (consistent or frequent occurrence) of anomalies, integrated over time, could provide a metric for sites of elevated and predictable trophic transfer needed to understand and predict predator distributions. To test this hypothesis, we developed and tested an analytical technique that expands upon the traditional use of remotely sensed chl *a* data to understand and provide predictions of marine consumer 'hotspots' or regions of consistently high abundance of predators (and presumably prey at the scale of $>100 \text{ km}^2$) relative to the surrounding area in the open ocean. We used seabird abundance from vessel-based surveys in 2 distinct regions and time periods, as well as satellite-tracked movements of an endangered spe-

cies, the short-tailed albatross *Phoebastria albatrus*, covering over half of the CCS, as model test cases to demonstrate potential consumer relationships with our new chl *a* persistence metric. We then applied this understanding to the entire ecosystem to describe likely consumer hotspots for $>2000 \text{ km}$ of coastline along the US west coast. These concepts and techniques may be applicable to other large marine ecosystems worldwide.

MATERIALS AND METHODS

Study area

The CCS is a highly productive eastern boundary current system in the North Pacific Ocean. The CCS is well studied via satellite remote sensing. Spatial and temporal patterns in primary productivity include latitudinal and longitudinal (onshore/offshore) variation and trends through time, interannual and decadal-scale variability, and relationships with bathymetry and coastal geomorphology (e.g. Strub et al. 1991, Thomas & Strub 2001, Legaard & Thomas 2006, Palacios et al. 2006, Henson & Thomas 2007a, b). None of these studies, however, quantified the persistence of chl *a* concentrations, nor examined the relationships of persistence metrics to consumer (e.g. seabird) distribution and abundance. Furthermore, despite many similarities in statistical treatments, there is considerable variation in analytical approaches such as initial data standardization (i.e. removing temporal means, spatial means, and/or seasonal cycles), which greatly affects the results. Given our focus on identifying persistent features and their relevance to upper trophic-level species, our analytical approach is considerably different from previous studies.

Chl *a*

We used 9 yr (January 1998 through December 2006) of monthly Level 3 chl *a* concentration ($9 \text{ km} \times 9 \text{ km}$ resolution; $29\,504 \text{ pixels}$, with $108 \text{ mo pixel}^{-1}$) from SeaWiFS (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>) to characterize primary productivity and chlorophyll persistence. Some small, short-lived phytoplankton blooms are no doubt missed at this spatial and temporal resolution; however, monthly 9 km composites minimized data loss from periodic cloud cover while permitting seasonal comparisons. We excluded data from inland waters (e.g. Strait of Juan de Fuca, San

Francisco Bay, Sea of Cortez) so that our results, especially calculations of anomalies and persistence, reflect, specifically, the coastal and offshore CCS. While higher mean chl *a* values or positive anomalies are indicative of primary productivity, we were explicitly interested in the variance in chl *a* concentrations. Therefore, we used a 3-step process to quantify the temporal and spatial variance and anomaly persistence in pixel-specific chl *a*. (1) We first standardized monthly chl *a* values for each pixel using a $\log_{10}$ transformation and a z-score, i.e. the 108-mo mean for each pixel was subtracted from each monthly pixel value, then divided by the standard deviation (SD) for the pixel. Using z-score-standardized data allowed for results to be comparable between nearshore (higher chl *a*) versus offshore (lower chl *a*), and northern latitudes (higher chl *a*) versus southern (lower chl *a*). (2) We next computed the spatial mean for the entire study area and created a CCS-scale model of monthly chl *a* (including periodic seasonal cycles and linear trend) using the following least-squares linear regression equation ($R^2 = 0.45$, $F = 20.970$, $p < 0.001$; Fig. S1 in the supplement at www.int-res.com/articles/suppl/m451p213_supp.pdf).

$$\text{chl } a = \beta_0 + \beta_1 \sin(2\pi f_1 t) + \beta_2 \cos(2\pi f_1 t) + \beta_3 \sin(2\pi f_2 t) + \beta_4 \cos(2\pi f_2 t) + \beta_5 t \quad (1)$$

where β are the coefficients estimated by least squares, f_1 and f_2 are the frequency of annual and semi-annual cycles (12 and 6 mo, respectively; Legaard & Thomas 2006), and t is time (108 mo). A positive, linear time trend in untransformed chl *a* was evident in some regions, such as continental shelf waters of central and southern CCS (Figs. S2 & S3 in the supplement) and, therefore, retained in the final model (see the supplement for additional details on model development and testing). (3) Finally, we calculated the proportion of months that each pixel had a positive anomaly > 1 SD above the CCS-wide model (roughly 80% confidence interval [CI], i.e. highly anomalous). This analytical procedure integrates both variability and anomaly persistence (frequency) into a single metric that we will refer to as the frequency of chlorophyll peaks index (FCPI). In mapping this metric, we have produced a spatially explicit seascape of seasonally and annually resolved (adjusted) peak chl *a* values.

We also created a standard ecosystem-wide, 9 yr climatology using arithmetic means of chl *a* for comparison to the persistence metric. Depending on the analysis being conducted, mean chl *a* climatologies were either annual, including all 12 mo, or seasonal, including only the 2 mo corresponding to the 3

seabird survey seasons. In contrast, our calculation of FCPI required us to use a single climatology (9 yr, including all months) for all analyses. This also allowed us, however, to test the robustness of the single metric compared to various mean chl *a* layers. Remote sensing data analysis was conducted using Matlab (MathWorks).

Seabird distribution

We used seabird at-sea distribution data from 2 study regions within the CCS and during 3 time periods: the Gulf of the Farallones (GOF) off central California during May-June (surveys conducted in conjunction with NOAA-National Marine Fisheries Service Juvenile Rockfish Survey) and the Southern California Bight (SCB; surveys conducted in conjunction with California Cooperative Oceanic Fisheries Investigations) in March-April and July-August (Fig. 1). The at-sea distribution and abundance of birds was estimated using a standardized strip-transect survey technique (300 m; Tasker et al. 1984). In the GOF, 9 annual surveys were conducted during May and June in 1996, 1997, and from 2000 to 2006. The survey occurred from Pt. Arena south to Monterey Bay, and typically sampled waters across the continental shelf (50 to 200 m depth) to deep oceanic zones (> 3000 m; Fig. 1). In the SCB study area, 18 strip-transect surveys were conducted annually during March-April ($n = 9$) and July-August ($n = 9$) from 1998 to 2006. The SCB survey grid is a series of 6 parallel transects perpendicular to shore, and like the GOF surveys, extending from shallow inner continental shelf 50 to 200 m depth to deep offshore oceanic waters (> 3000 m). The SCB study area, however, does encompass a much larger offshore ocean domain than the GOF study area (Fig. 1). The same grid of transects were sampled each year in both areas; details of data collection methods are provided in prior publications (Yen et al. 2004, 2006). We calculated total bird density per 3 km of transect length by 0.3 km survey strip (0.9 km^2 bins), for a total of 4092 sampling units over 9 yr (number of 3 km bins yr^{-1} , mean $\pm$ SD: 455 ± 221) in the GOF, and 14 281 sampling units over 9 yr (mean number of 3 km bins yr^{-1} : 1298 ± 459) in the SCB study areas. As illustrated in prior studies (Briggs et al. 1987, Yen et al. 2004, 2006), total seabird density in the GOF region chiefly (89% of total density) reflects the abundance of 4 species or genera (local breeders: common murre *Uria aalge* and Cassin's auklet *Ptychoramphus aleuticus*; and seasonal migrants: sooty shearwater *Puffinus griseus*

Fig. 1. Marine-bird utilization distributions (no. km⁻²) within the Gulf of the Farallones (GOF) and Southern California Bight (SCB). Seabird surveys in the GOF were conducted in May and June in 1996, 1997, and from 2000 to 2006; and in the SCB during spring (March–April) and summer (July–August) from 1998 to 2006. See ‘Materials and methods’ for dominant seabird species

and phalaropes *Phalaropus* spp.). Total seabird density in the SCB region for both time periods combined chiefly (80 % of total density) reflects the abundance of 6 species or groupings (local breeders: gulls *Larus* sp., common murres, Leach’s storm-petrel *Oceanodroma leucorhoa*, brown pelicans *Pelecanus occidentalis*; and seasonal migrants: shearwaters [primarily *Puffinus griseus*] and phalaropes). Yen et al. (2004, 2006) and Rintoul et al. (2006) provide maps of individual species distributions.

We also tested whether the movements of satellite-tagged, endangered short-tailed albatrosses *Phoebastria albatrus* were correlated with chl *a* mean and FCPI. Six satellite-tagged albatrosses in total were tracked during 2003, 2006, and 2009 in the CCS. All individuals were tagged outside the study region (in Alaska or Japan), but spent a portion of the tracking period in the CCS (including all months except January and June to August) and only the CCS portion of the movement path were used in the analysis. Several tracking devices were used, but all data were standardized prior to utilization distribution analysis.

In 2003 and 2006, position-only satellite transmitters were used with duty cycles of 8 h on and 16 or 24 h off (Suryan et al. 2006, Suryan & Fischer 2010). In 2009, satellite-linked GPS receivers (22 g, Microwave Telemetry) were attached using tape or harness. The GPS units acquired 6 fixes d⁻¹ at 2 to 4 h intervals and transmitted these positions via Service Argos every 3 d. All data were filtered using standard algorithms for Argos (Suryan & Fischer 2010) and GPS (R. M. Suryan unpubl.) acquired position fixes to remove locations with detectable positional error (<5 % of all positions were removed, n = 5425 positions post-filtering). We standardized tracking data among tracking devices by linearly interpolating along the movement paths with positions spaced at hourly intervals (n = 2040 hourly locations within our study area).

Data treatment and analysis

We used generalized additive models (GAM) to quantify similarities and dissimilarities in the spatial pattern of overall mean chl *a* (all months) and FCPI. We independently modeled the relationships of mean chl *a* and FCPI versus seafloor depth (m), slope (degrees), and spatial coordinates (longitude, latitude). Bathymetric data (m; 0.016° resolution) were obtained from the ETOPO1 Global Relief Model (www.ngdc.noaa.gov/mgg/global/global.html), and a digital elevation model in GIS was used to estimate slope. The fitted GAM for chl *a* or FCPI was specified with a Gaussian distribution and an identity-link function: chl *a* (or FCPI) ~ *s*(depth) + *s*(slope) + *te*(latitude, longitude), where *s*() and *te*() are regression splines (R Development Core Team 2010, package mgcv). Furthermore, we examined the spatial coherence between maps of mean chl *a* and FCPI. We used a GAM [FCPI ~ *s*(chl *a*)] to directly compare mean chl *a* to FCPI. The effect of each spatial covariate included in a GAM was plotted to visually inspect the functional form to determine whether mean chl *a* and FCPI exhibit similar changes in relation to depth and slope.

To identify habitats of predictably higher densities of birds, we used 9 yr of seabird survey data each for

GOF and SCB, and 3 yr of albatross tracking data for analysis. We used the kernel density tool in the Spatial Analyst extension of ArcGIS 9.3 (Environmental Systems Research Institute) to interpolate seabird density (ind. km⁻²) as percent utilization distributions (5% to 95%). We used a 3 km search radius for GOF, a 10 km radius for the larger SCB study area, and a 25 km search radius for the even broader albatross distribution. Selection of search radii for kernel smoothing was based on the geographic extent of the data set and the distance separation of grid cells for surveys (generally ~3 km) or albatross tracking locations. The number of contour intervals between the 5% to 95% utilization distributions varied depending on study area size, with fewer intervals for smaller areas. We used 12 partially irregular percent contour intervals (5%, 10%, 15%, 20% to 80% by increments of 10%, and 95%) within the smallest region, GOF; 18 regular intervals (5% to 90% by increments of 5%) for the larger SCB region; and 19 regular intervals (5% to 95% by increments of 5%) for the albatross data that spanned over half of the CCS. The kernel distributions were used to represent the location and extent of probable seabird hotspots.

We merged the gridded chl *a* data set with bird utilization distributions to test whether chl *a* was related to seabird distributions. We spatially averaged chl *a* attributes (mean and FCPI) in relation to bird utilization distributions to assess the spatial co-variation between chl *a* and bird densities. We conducted a bootstrap and Monte Carlo analysis (10 000 randomizations) to estimate linear correlation coefficients, and confidence limits and explanatory power (R^2) to

test whether mean chl *a* or FCPI was a better predictor of bird density. Relationships between area use by albatrosses and chl *a* were nonlinear. Therefore, we fitted single-parameter GAMs, albatross ~ $s(\text{chl } a)$ and albatross ~ $s(\text{FCPI})$, specified with a Gaussian distribution and an identity-link function, where $s()$ is a regression spline (R Development Core Team 2010, package mgcv), to determine the explanatory power (R^2) of the relationships.

RESULTS

Chl *a* variance and FCPI

The number of pixels with positive anomalies varied by month and year (Fig. 2). A seasonal signal is evident, with the months of most frequent positive anomalies occurring during the spring and summer when chl *a* concentrations were generally highest (Fig. 2A). It is clear, however, that FCPI is not driven exclusively by spring and summer patterns. The years with the lowest occurrence of positive anomalies were 1998, during a strong El Niño-Southern Oscillation, and 2005, when productivity in the northern CCS was anomalously low due to delayed upwelling (our Fig. 2B; Peterson et al. 2006).

Associations among chl *a*, FCPI, and bathymetry

Chl *a* and FCPI show distinct patterns in functional form with respect to seafloor depth and slope.

Fig. 2. Number of pixels with positive chl *a* anomalies by (A) month and (B) year within the California Current System. Box plots depict median (horizontal line), interquartile range (box), $1.5 \times$ interquartile range (error bars), and outlying data (+)

Throughout much of the CCS, the 0 to 200 m depth range represents the continental shelf. The model relationship between chl *a* versus depth shows that the chl *a* values were highest in shallow coastal water and steeply declined across the shelf into deeper offshore, oceanic waters, with tight 95 % CIs indicating that the relationship is consistent throughout the CCS (Fig. 3A). In contrast, FCPI shows a much more gradual decline with depth, and the effect of depth is positive out to nearly 1500 m (Fig. 3B), compared to <1000 m for chl *a* (Fig. 3A). Chl *a* and FCPI show a somewhat similar modeled response to slope (Fig. 3C,D). FCPI, however, reacts a bit more rapidly to initial changes in slope from zero and becomes negative at larger gradients, although CIs are also very broad at these higher slope values, and also include zero.

The modeled relationship between chl *a* and FCPI demonstrates that these 2 metrics are indeed quantifying different spatial patterns of the chl *a* field (Fig. 3E). The highest values of FCPI correspond to median chl *a* values ($\sim 3.5 \text{ mg m}^{-3}$, generally representing mid- to outer shelf; see Fig. 7) and are out of phase for chl *a* values $> 3.5 \text{ mg m}^{-3}$ (inner shelf, nearshore), but in phase for chl *a* values $< 3.5 \text{ mg m}^{-3}$ (offshore).

Spatial association between seabirds and chl *a*

For the GOF region (Fig. 4), high mean concentrations of chl *a* (for all months) occurred on the continental shelf west of San Francisco Bay and in Monterey Bay, north of Point Piños. In contrast, seabird utilization distributions depicted the highest densities generally west of these areas with high mean chl *a* (Fig. 4A). Mean chl *a* explained approximately half of the variance in seabird density within this region ($R^2 = 0.48$, $p = 0.012$; Fig. 4D). Using mean chl *a* restricted to the 2 mo of surveys (May and June) depicted a similar pattern in some areas, but also elevated chl *a* values within some of the higher density contours (Fig. 4B), which greatly improved the relationship with seabird density ($R^2 = 0.89$, $p < 0.001$; Fig. 4E). FCPI, in particular, showed distinct hotspots within inner, high-density contours, corresponding to regions of greatest seabird utilization (Fig. 4C) and explained 90 % ($R^2 = 0.90$, $p < 0.001$) of the variation in the seabird density distributions (Fig. 4F). As a composite surface, FCPI performed as well or better than chl *a* analyzed at 2 temporal scales.

In the SCB region, FCPI explained more than twice the variation in seabird density compared to mean

chl *a* restricted to the 2 survey months during both seasons. FCPI explained 73 % of the variation ($R^2 = 0.73$, $p < 0.001$) in seabird densities compared to 35 % ($R^2 = 0.35$, $p = 0.009$) for chl *a* during spring (March–April; Fig. 5A,B), and 27 % of the variation ($R^2 = 0.27$, $p = 0.02$) compared to no significant relationship ($R^2 = 0.07$, $p = 0.77$) for chl *a* during summer (July–August; Fig. 5C,D). As a composite surface, FCPI performed much better than mean chl *a* in this study region.

Short-tailed albatrosses remained in the northern and central CCS, spending more time (more of the core density contours) in the northern areas and offshore of the highest-chl *a* zones (Fig. 6A), while at times overlapping regions of high FCPI in these areas (Fig. 6B). FCPI performed well, but was only slightly better than mean chl *a* in its association with the distribution of satellite-tracked short-tailed albatrosses. We used mean chl *a* for all months, since albatross data spanned 9 mo, and the 3 missing months were non-consecutive. The relationship was nonlinear, in contrast to ship-based surveys above, with the GAM (albatross utilization distribution versus a single FCPI or chl *a* term) for FCPI having a marginally better fit ($R^2 = 0.91$, $s(\text{FCPI}) F = 33.02$, $p < 0.001$) than for chl *a* mean ($R^2 = 0.83$, $s(\text{chlmean}) F = 16.48$, $p < 0.001$; Fig. 6C,D).

Mapping the chl *a* and FCPI fields

California Current-wide analyses show patterns of elevated chl *a* over the continental shelf, with a decline progressing offshore, and a prominent decline approaching the 200 m isobath along much of the coastline (Fig. 7). Elevated chl *a* was particularly evident and contiguous along the comparatively broad shelf of northern Oregon, Washington, and Canada and in the GOF (Fig. 7). Certain areas well known for their great abundance of mid- to upper-trophic-level consumers (e.g. Heceta and Cordell Banks; Yen et al. 2004, Ainley et al. 2009, respectively) showed lower mean chl *a* values than adjacent regions (Fig. 7). In contrast, our FCPI showed patchy chl *a* hotspots on the continental shelf, with relatively more contiguous hotspots along the continental shelf break/slope, particularly adjacent to broad sections of shelf, and near the heads of submarine canyons (e.g. west of Cape Flattery and Monterey Bay; Fig. 7). FCPI identified known hotspots at Heceta and Cordell Banks, despite having lower overall mean chl *a* relative to adjacent areas (Fig. 7). Furthermore, FCPI corresponded with high seabird densities in some areas

Fig. 3. Generalized additive model relationships ($\pm 95\%$ CIs) between bathymetric variables of (A,B) seafloor depth and (C,D) slope vs. (A,C) chl *a* mean and (B,D) frequency of chl *a* peaks index (FCPI), and (E) between chl *a* and FCPI directly. The models in (A) to (D) include a second variable of spatial coordinate (longitude, latitude), whereas (E) uses a single variable. Analyses were conducted for the California Current System, but restricted to waters ≤ 3000 m to minimize over-representation of the much broader deep-water, oceanic, southern region of the California Current System. The black vertical bars below curves depict sample sizes (n), showing consistently high values for n throughout the depth range (A,B), but reduced at higher values of slope (C,D) and higher values of both chl *a* and FCPI (E), as indicated by widening CIs

Fig. 4. Satellite-derived mean chl *a* concentration vs. frequency of chl *a* peaks index (FCPI) as predictors of seabird distribution. Seabird utilization distribution density contours (20 %, 50 %, and 90 % only are presented graphically for clarity) for the Gulf of the Farallones from 9 ship-based surveys (1996, 1997, and from 2000 to 2006) superimposed on a corresponding time-frame of mean chl *a* for (A) all months and (B) May-June, and (C) FCPI (% of all months with positive anomalies >1 SD). Association between seabird density within utilization distribution polygons (n = 12 polygons encompassing 5 % to 95 % utilization distributions) vs. mean chl *a* for (D) all months and (E) May-June, and (F) FCPI within each polygon. See 'Materials and methods' for description of regression analyses

lacking distinct geomorphological features such as the outer shelf north of Monterey Bay (Fig. 4).

DISCUSSION

In the present study, we derived maps of peak chlorophyll variability highlighting where the frequency of chl *a* peaks occur relative to an ecosystem-scale model for the California Current. By standardizing the value of each pixel using z-scores, we have created a metric that allows spatial and temporal comparisons, from north to south and onshore to offshore, while simultaneously quantifying variability. Moreover, by modeling chl *a* across multiple temporal

scales, our computation integrates variability in chl *a* across seasonal cycles and among years. Whereas our spatially explicit FCPI map provides a standardized representation of chl *a* peaks, the maps are still, in part, related to peak seasonal (i.e. during May-June in the central-northern California Current, earlier to the south and later to the north) and peak annual values.

FCPI, bathymetry, and seabird distributions

The FCPI showed markedly different spatial patterns than mean chl *a* throughout the CCS with respect to water depth and distance to shore. The most prominent difference was greater FCPI values over

Fig. 5. Associations between seabird density (no. km⁻²) vs. chl *a* mean and frequency of chl *a* peaks index (FCPI) for the Southern California Bight (1998–2006). Linear relationships of seabird density from line-transect surveys vs. (A) chl *a* mean and (B) FCPI during spring (March–April), and (C) chl *a* mean and (D) FCPI during summer (July–August) within utilization distribution polygons ($n = 18$ polygons, 5 % to 90 % utilization distributions by 5 % increments)

mid- to outer-continental shelf habitats versus greater mean chl *a* values over the inner shelf. FCPI may be greater offshore due to Ekman transport associated with upwelling favorable wind (Hickey 1989) or could be related to shelf-break fronts which concentrate phytoplankton biomass (Barth et al. 2005). The FCPI was an equivalent or better predictor of seabird distributions and movements than mean chl *a*. The equal or better performance of FCPI held true when analyzed with seabird distributions at progressively larger spatial and temporal scales and in different regions of the CCS. There are, however, cases for which mean chl *a* may be a better predictor of predator distribution than the FCPI, in particular for species having coastal distributions where mean chl *a* values are generally greater. For seabirds, these could include many species of gulls (Laridae) and possibly some alcids such as murres that show neritic distributions under certain conditions (Yen et al. 2004). Our maps of the climatology of mean chl *a* correspond well to

modeled California Current-wide seabird distributions for 16 species as reported by Nur et al. (2011). Yet, Nur et al. (2011) found that remotely sensed chl *a*, though matched closely in time to the seabird surveys, ranked poorly as an explanatory variable in comparison with static non-biological features such as water depth and distance to shore. Nur et al. (2011) did not evaluate variance in chl *a* concentration as a predictor variable or something equivalent to our FCPI or longer-term chl *a* means. In cases where prediction of seabirds fail, the FCPI could be used along with other environmental data layers, including mean chl *a* climatology, to develop multivariate predictors of seabird distributions. A particularly relevant result of our analyses common to both FCPI and mean chl *a* is that the use of longer time-series of chl *a* may be better than finer temporal-scale measurements (e.g. daily to monthly chl *a*) as indicators of productive habitats for upper-trophic-level predators, even when considering time lags.

Fig. 6. *Phoebeastria albatrus*. Short-tailed albatross (STAL) utilization distribution density contours (20%, 50%, and 85% [darker to lighter edge respectively] only are presented graphically for clarity) from 3 yr of tracking superimposed on a corresponding timeframe of (A) mean chl *a* and (B) frequency of chl *a* peaks index (FCPI). Nonlinear, generalized additive model relationships of STAL residence time within utilization distribution polygons ($n = 19$ polygons, 5% to 95% by 5% increments) vs. (C) mean chl *a* for all months and (D) FCPI

FCPI and food web dynamics

We interpret the association between FCPI and seabirds to reflect food web processes that promote seabird foraging and aggregation. The FCPI may reflect the triad of fundamental food-web mechanisms that Bakun (1996) postulated, including nutrient enrichment, concentration of prey, and aggregation of predators. The relationship between peak chl *a* and seabirds may have implications for energy transfer from lower- to other upper-trophic-level species including pelagic nekton in the CCS. For example, Ainley et al. (2009) showed spatial co-occurrence of seabirds, salmon, and pelagic nekton at frontal systems, which could be related to the FCPI, as an indicator of enhanced food web processes. Our re-

sults also support those of Henson & Thomas (2007a), who suggested that variability in chl *a* may be as important as biomass in determining biological productivity, which in turn is important to predator-prey interactions and the distribution and abundance of upper-trophic-level consumers.

The transfer of energy from primary productivity up the food web originates with zooplankton grazing, which, at times, can deplete phytoplankton standing stock (Behrenfeld & Falkowski 1997, Behrenfeld et al. 2006). More frequent phytoplankton production and subsequent grazing cycles could possibly create greater chl *a* variance signals. In turn, regions of persistent production-grazing cycles may indicate areas of abundant zooplankton and enhanced food webs for consumers, built on the

Fig. 7. (A,C,E) Mean chl *a* concentration and (B,D,F) chl *a* persistence for the California Current System (1998–2006): (A,B) southern Canada to southern Oregon, (C,D) southern Oregon to south-central California coast, and (E,F) south-central California to north-central Mexico. Depth contours denote the 200 m (continental shelf edge) and 3000 m (boundary of continental slope and oceanic waters) isobaths

reliability of prey resources. Spatial co-variation of krill *Euphausia pacifica* and seabirds in the central CCS (Santora et al. 2011) supports our suggestion that FCPI and seabird distribution reflect regions of elevated prey abundance. Furthermore, both the present study and that of Santora et al. (2011) highlight the significance of the outer continental shelf-slope region, especially adjacent to wider portions of the shelf, as important ecological areas for predators and their prey. Thus, we propose that the FCPI integrates spatio-temporal variability in lower- to mid-level trophic interactions that are key to persistently productive regions and enhanced trophic transfer to predators, such as seabirds.

FCPI across an ecosystem

The FCPI reveals different structure and heterogeneity in the marine environment of the California Current than mean chl *a* values (Fig. 7). While mean chl *a* concentrations show the well-known onshore-offshore gradient in primary productivity, the FCPI demonstrates alongshore gradients and ‘clusters’ of primary productivity not revealed by average chl *a* assessments. As such, the FCPI appears to integrate more information than mean chl *a* composites, and may therefore be of more value to important questions in pelagic marine conservation, such as ‘where are the ecological hotspots?’.

Some well-known hotspots have been suggested by this and other studies in the California Current (e.g. Heceta Bank, Oregon), with linkages established between primary productivity and a diversity of upper-trophic-level consumers (Tynan et al. 2005, Reese & Brodeur 2006, Ainley et al. 2009, Block et al. 2011). At Heceta Bank, fronts and eddies retain (concentrate) lower-trophic-level production (as evidenced by chl *a* persistence

calculated herein), and thereby attract (aggregate) mid- and upper-trophic-level consumers in a predictable fashion (Ainley et al. 2005, Barth et al. 2005, Reese & Brodeur 2006). In the SCB, immediately south of Pt. Conception (Fig. 7), a cyclonic gyre, coupled with strong stratification and calm winds, creates a retention center that favors larval fish survival and is used as a 'nursery' area for many species of fish (Dong & McWilliams 2007). This area is also important to seabirds (Fig. 1). Moreover, areas that concentrate mid- and lower-trophic-level production show persistence in space even though community composition may vary over time (Reese & Brodeur 2006). Persistence in chl *a* biomass and community structure, however, is rarely effectively quantified, and more of these kinds of analyses are needed to ascertain better understanding of ecological hotspots. Certain sites of persistent productivity may also be refugia for zooplankton, which could be important to top predators even during times of generally poor productivity, such as El Niño (Marinovic et al. 2002).

Implications for marine spatial planning and management

Identifying offshore and pelagic areas for management, including protection, is challenging, but possible, especially if the mechanisms of persistence can be identified (Hyrenbach et al. 2000). Benthic-pelagic coupling over seamounts is an example of the kind of compelling mechanism needed to understand regions of persistently elevated biological activity (Genin 2004). With this in mind, our objective was to identify relatively large areas (>100 km²) of predictably elevated chl *a* biomass that attracted abundant mid- to upper-trophic-level consumers, particularly seabirds, over long time scales (decades), despite the inherent variability in the system. Therefore, we used relatively coarse scales, monthly 9 km gridded chl *a* data, and smoothed density surfaces to compare chl *a* and bird distributions. While this smoothing approach removes variability and may increase R² values in our statistical analyses, the importance is in the relative comparison between results using FCPI versus mean chl *a*. A broad-scale application was appropriate for our purpose in identifying persistent primary productivity and seabird hotspots throughout the CCS. The FCPI, however, may also prove effective when applied at finer temporal and spatial scales.

CONCLUSIONS

Many ecological variables can affect the abundance and diversity of predators associated with a given hotspot of primary productivity. Thus, despite our findings of clear associations between FCPI and some upper-trophic-level predators of the California Current, predicting predator distributions from this relatively simple measure of ecosystem structure requires further testing. Furthermore, while the FCPI could be used independently, it may be more useful as one of many possible layers in habitat suitability models. That said, we have established that satellite-derived peak chl *a*, and not simply average chl *a* concentrations, is a robust predictor of seabird distributions in the CCS. The present study thereby provides a clear focus for future research of predator-habitat associations and the use of remotely sensed data products for endangered species and marine spatial management in the California Current and other marine ecosystems globally.

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