National Marine Sanctuaries capture enhanced abundance and diversity of the California Current Ecosystem avifauna

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ABSTRACT

Quantifying the spatial patterns of marine predators, such as seabirds, reveals areas of ecological importance and associated food web characteristics, upon which marine conservation and management plans can be based. Owing to high productivity, the California Current Ecosystem (CCE) harbors an abundant and diverse avifauna comprised of resident and migratory species. With a goal of protecting habitats in three biogeographic regions — North, Central, and South CCE — a network of marine protected areas have been designated, including five National Marine Sanctuaries (NMS). Using an extensive at-sea survey dataset (1980 to 2017), we characterize spatial patterns of seabirds, and compare mean relative abundance, diversity, and community composition both within and outside the NMSs. We found that within the CCE, seabird abundance and diversity increase linearly from south to north ($R^2 = 0.54$ and $R^2 = 0.55$, respectively) and decrease linearly with distance from the coast ($R^2 = 0.16$ and $R^2 = 0.23$, respectively). The avifauna of the North and South regions are the most distinct, with the Central region being transitional between the two. The CCE avifauna shows limited overall diversity, with just 10 species contributing >93% of abundance totals. In addition, certain foraging guilds and prey preference groups were dominant: pursuit-feeding and piscivorous species in the North and surface feeding generalists in the South. Overall, seabird relative abundance and diversity are higher within NMS boundaries compared to outside. Although relative abundance and diversity of seabirds within NMSs were broadly representative of corresponding biogeographic regions, the overall NMS network captures a range of distinct seabird communities. The analysis of this extensive dataset provides a better understanding of seabird spatial patterns and their ecological roles within different regions, thus facilitating more effective, adaptive management of CCE biotic resources.

1. Introduction

The spatial patterns of mesopredator abundance and diversity provide insights into the structure and functioning of an ecosystem (Hairston et al., 1960; Heithaus et al., 2008; Griffin et al., 2008). Characterizing broad patterns of these indices identifies areas of persistent, ecological importance, i.e. 'hotspots' at the mesoscale, and provides valuable information for further investigation into ecological impacts from resource extraction and climate change (Ives and Carpenter, 2007), as well as those from species recovery (Ainley et al., 2018; Ainley, 2019). In addition, the spatial patterns of the abundance and diversity of upper trophic level species can indicate broad patterns in food webs on which they depend, indicating what might be the most appropriate attributes for monitoring and protections (Schmitz et al., 2010). Collecting broad spatial data on most marine predators is difficult and costly. On the other hand, seabirds are conspicuous, spending most of their time above the sea surface and, therefore, are a prime study group for characterizing broad spatial patterns among predators in marine ecosystems. Given that seabirds are not apex predators, referring to them as mesopredators would be more appropriate, with that trophic position being most directly affected by variation in the forage fish and invertebrates at middle trophic levels.

Seabird relative abundance, diversity, and community composition can be distinct within different oceanographic regions, determined by the physical and biological characteristics present (Ainley, 1976; Briggs et al., 1987; Ballance et al., 2001). At sea, seabird habitat use is often closely tied to the distribution of their prey, i.e., middle trophic level organisms; therefore, seabird abundance patterns provide information on prey availability (Fauchald, 2009). Seabird diversity reveals the abundance and breadth of ecological niches — more diverse faunas have increased complexity of species interactions which presumably allows them to be more resilient to ecosystem disturbances (i.e., diversity-stability hypothesis, McCann, 2000). Avifaunal community composition can indicate ecological importance/uniqueness of a region within a broader area (Ives and Carpenter, 2007). Seabirds have exhibited significant decreases in numbers in many parts of the world, mirroring, in some cases, a reduction in food web resources (Estes et al., 2011; Croxall et al., 2012; Paleczny et al., 2015; Grémillet et al., 2018), and understanding broad patterns of their distribution is important for their continued and future conservation (Dias et al., 2019).

Due to its elevated overall productivity, a characteristic of upwelling-driven, eastern boundary currents, the California Current Ecosystem (CCE) provides foraging grounds for not just abundant breeding or non-breeding, seasonal resident species, but also for a substantial number of migratory species, many of which travel large distances to target CCE habitats (Ainley, 1976; Briggs et al., 1987; Block et al., 2011). In the CCE, the intensity and timing of upwelling varies at multiple spatial and temporal scales (e.g., seasonal, interannual, decadal), yet there are persistent patterns, with the onset of upwelling progressing seasonally from south to north; one result is the presence of three distinct biogeographic regions: South, Central, and North (Fig. 1; Checkley and Barth, 2009). Upwelling in the South is comparatively weak, though still seasonally recurring, but it increases in intensity and persistence from the Central to the North (Huyer, 1983; Checkley and Barth, 2009). With the lessened upwelling, the South is more influenced by oceanic, rather than continental shelf, processes. Thus, along with latitudinal heterogeneity, cross shelf gradients of ocean properties also exist with primary productivity typically decreasing from inshore to offshore, more so in
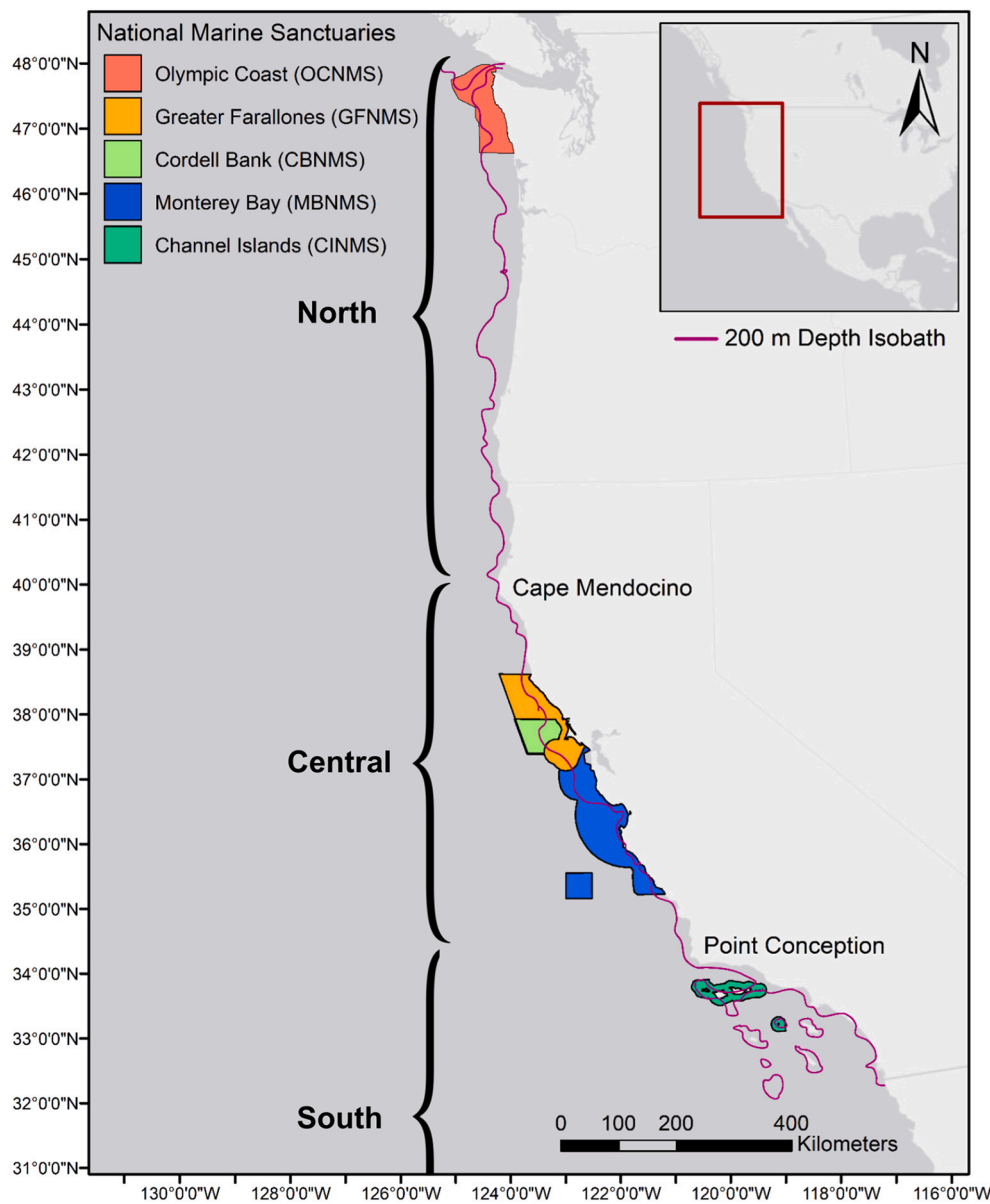

Fig. 1. The biogeographic regions and West Coast National Marine Sanctuaries within the California Current Ecosystem. The North and Central are separated by Cape Mendocino, California, while the Central and South are separated by Point Conception. The South bioregion extends south to Point Eugenia in Baja, California, Mexico (not shown). The 200 m isobath separates the off-shelf (> 200 m) and on-shelf (< 200 m) regions.

the South. However, this general large-scale pattern is broken up by mesoscale (radius of <100 km) upwelling plumes carrying coastal water far offshore (Batchelder et al., 2005; Ainley et al., 2009).

Within the CCE, a number of marine protected areas and underwater parks have been designated, including five National Marine Sanctuaries (NMS) managed by the National Oceanographic and Atmospheric Administration (NOAA). The boundaries of NMSs were designed to protect diverse and productive habitats, including their recreational, cultural and historical value. These NMSs are found in all three of the biogeographic regions, providing well-defined segments of the CCE in which to compare seabird patterns. NMSs undergo routine monitoring and have an existing framework that could facilitate the establishment of further legal protections (Nur et al., 2011; McGowan et al., 2013; Smith et al., 2014). If seabird communities within NMSs are representative of respective biogeographic regions, ongoing monitoring within the sanctuaries could provide insight on seabirds at various spatial scales (NMS and biogeographic) within the CCE.

Previous studies in the CCE have found that seabird abundance and diversity are highly variable across latitudes and longitudes, as abundance varies with distance from shore (Ainley, 1976; Briggs et al., 1987; Tyler et al., 1993; Santora et al., 2018; Hyrenbach et al., 2007). Important habitats exist in waters overlying the shelf, shelf break, and slope, facilitated by fronts, eddies, and upwelling plumes that enhance primary productivity and/or act to concentrate prey (Ashmole, 1971; Hunt Jr., 1991; Ballance et al., 1997; Yen et al., 2004; Ainley et al., 2005, 2009; Nur et al., 2011). Seabird abundance at the large and smaller scales is correlated with high chlorophyll, which can identify fronts that support greater overall seabird abundance compared to less productive waters (Briggs et al., 1987; Tyler et al., 1993; Ainley et al., 2009; Suryan et al., 2012; Nur et al., 2011). As central place foragers, the presence of breeding colonies also affects abundance patterns of breeding residents, as their foraging distance is constrained by the location of their colony during the breeding season (Orians and Pearson, 1979). The availability of foraging and breeding locations may also result in higher regional diversity, and previous work has found that seabird diversity increases with latitude (Ainley, 1976; Briggs et al., 1987). By identifying these particular regions of high abundance and diversity, we can test the degree to which seabird habitat is 'captured' by NMSs and highlight whether there are other yet-to-be protected areas that seabirds are indicating to be important.

Seabirds are tied spatially to the prevalence of their prey, and so groups that have similar foraging strategies or preferred prey may have similar distribution patterns, unless competition is particularly strong (Spear and Ainley, 2008; Ainley et al., 2009). These assemblages may exist at large (e.g., water mass), moderate (e.g., sea surface temperature) or smaller (e.g., bathymetric feature) spatial scales (Ashmole, 1971; Hunt Jr. and Schneider, 1987; Scales et al., 2014). Avifaunal community composition may also be affected by migration patterns as well as breeding location (Tyler et al., 1993). Locally breeding species may be larger components of the community inshore than offshore, depending on the distribution of islands, islets and headlands where they nest. In contrast, species that migrate into and/or through the CCE may play a larger role in the offshore community. For example, the highly abundant, nesting common murre (*Uria aalge*), predominant in North waters, appears to displace the even more abundant, visiting sooty shearwater (*Ardenna grisea*) to forage farther offshore (Ainley et al., 2009). In addition, productivity of habitats likely plays a role, with more diving species in highly productive areas and more surface-feeding seabirds in regions of lower productivity (Ainley, 1977; Ballance et al., 1997; Spear et al., 2001). Comparing community composition among different spatial scales (CCE, latitude, NMSs) can quantify these patterns and identify regions of unique seabird communities.

In this study, we used a large-scale (>200,000 km^2) and long-term (37 years) at-sea seabird data set to assess seabird spatial variability of abundance, diversity, and community within the CCE, with reference to NMS boundaries. We hypothesize that seabird abundance and diversity will be higher in more productive regions, and unique avifauna communities will reflect the biogeographic regions of the CCE. As the NMS were designated, in part, for their ecological importance, the NMS should capture important habitat for marine birds.

2. Materials and methods

2.1. Survey region

The CCE is a complex and productive eastern boundary current, upwelling ecosystem along the west coast of southcentral North America. This equatorward-flowing current stretches roughly 2800 km from the North Pacific Current (~50°N), near the U.S.-Canada border, down to Baja California (23–25° N) and from the coastline to approximately 1000 km offshore (Kämpf and Chapman, 2016; Checkley and Barth, 2009). Although upwelling in the CCE is spatiotemporally variable, there are persistent biogeographic patterns, with the strongest, yet seasonal, upwelling in the North, strong, persistent upwelling in the Central, and weaker, seasonal upwelling in the South. Along with their distinct oceanographic conditions, these three biogeographic regions host unique biological attributes, such as forage fishes (Ainley, 1976; Ainley et al., 2015; Schipper et al., 2016). The South and Central regions are separated by Point Conception (34.448°N) and the Central and North by Cape Mendocino (40.438°N; Fig. 1; Checkley and Barth, 2009). Within the CCE, five National Marine Sanctuaries (NMS) are managed by the National Oceanographic and Atmospheric Administration (NOAA): Channel Islands (CINMS), Monterey Bay (MBNMS), Cordell Bank (CBNMS), Greater Farallones (GFNMS), and Olympic Coast (OCNMS). There is at least one of these NMSs within each of the CCE biogeographic regions (South: CINMS; Central: MBNMS, CBNMS, GFNMS; and North: OCNMS; Fig. 1).

2.2. At-sea data

Although seabirds are conspicuous, they are highly mobile and understanding their at-sea distribution is still challenging (Ballance, 2007). Ship and aerial at-sea transect surveys are suitable to this task as they cover a large area within a short time span and collect information on all species present (Briggs et al., 1987; Ballance et al., 1997; Croll et al., 1998; Spear et al., 2004).

In the CCE, systematic seabird surveys began in 1980, though serendipitous observations were made beforehand (Ainley, 1976; Stallcup, 1976; Briggs et al., 1987; Tyler et al., 1993; Hyrenbach and Veit, 2003; Ainley et al., 2005; Ford et al., 2004, 2021; Spear and Ainley, 2008; Nur et al., 2011). The data set used in this study was derived from 21 distinct sources, previously compiled into a common format by a Bureau of Ocean Energy Management (BOEM)-funded research project (Leirness et al., 2021). Having different goals than the latter, we used a subset of these data from within the CCE (Fig. S1) and added additional years from California Cooperative Oceanic Fisheries Investigations (2016 & 2017, Table 1). These data now span 37 years (1980–2017), capturing the environmental heterogeneity characteristic of the CCE (Veit et al., 1996; Ballance et al., 1997; Hyrenbach et al., 2007; Santora and Veit, 2013). The data set includes observations from all 12 months within each of the biogeographic regions, logging over 2.1 million individual seabird observations within a total 208,735.5 km^2 of strip transect survey effort (Fig. S1.A-D). Observations were collected from both aircraft- and vessel-based platforms (Tasker et al., 1984; Ballance, 2007; Mason et al., 2007). Although these platforms differ, efforts using either provide species counts and the number of birds per km^2 from which relative abundance can be determined (Henkel et al., 2007). Without correcting for the effects of seabird motion relative to the survey platform (i.e., "seabird flux"; Spear et al., 1992) absolute seabird densities could not be determined from these data (Clarke et al., 2003), except for stationary seabirds detected on the water or those flying slow enough to be considered essentially 'stationary' relative to the motion of

Table 1

Survey data used in this study and compiled by Leirness et al. (2021).

Survey Name	Current Principal Investor(s)	Organization(s)	Type	Years Included
Applied California Current Ecosystem Studies (ACCESS)	Jaime Jahncke	Point Blue Conservation Science, Cordell Bank National Marine Sanctuary (NMS), Greater Farallones NMS	Ship	2010–2015
California Cooperative Oceanic Fisheries Investigations (CalCOFI)	Richard Veit, David Hyrenbach; William Sydeman	Scripps Institution of Oceanography, California Department of Fish and Wildlife (CDFW), Farallon Institute	Ship	1987–2017
California Current Cetacean and Ecosystem Assessment Survey (CalCurCEAS)	Lisa Ballance	NOAA Southwest Fisheries Science Center	Ship	2014
California Seabird Ecology Study	Kenneth Briggs	UC Santa Cruz, Minerals Management Service (MMS)	Aerial	1985
Collaborative Survey of Cetacean Abundance and the Pelagic Ecosystem (CSCAPE)	Lisa Ballance	NOAA Southwest Fisheries Science Center	Ship	2005
Equatorial Pacific Ocean Climate Studies (EPOCS)	David Ainley, Larry Spear	H. T. Harvey & Associates, NOAA Environmental Research Laboratories	Ship	1980–1995
Juvenile Salmon Ocean Ecosystem Survey (JSOES)	Jeannette Zamon	NOAA Northwest Fisheries Science Center	Ship	2005–2017
Marine Mammal and Seabird Surveys of Central and Northern California	Thomas Dohl, Kenneth Briggs	UC Santa Cruz, MMS	Aerial	1980–1983
Northwest Forest Plan Marbled Murrelet Monitoring Program Zone 2	Scott Pearson, William McIver	USFS Pacific Northwest Research Station, Washington Department of Fish and Wildlife (WDFW)	Ship	2000–2013
Northwest Forest Plan Marbled Murrelet Monitoring Program Zones 3–5	Craig Strong, William McIver	USFS Pacific Northwest Research Station, CDFW	Ship	2000–2017
Olympic Coast NMS Seabird and Marine Mammal Surveys	C. Edward Bowlby, Liam Antrim, Jenny Waddell	Olympic Coast NMS	Ship	2002–2004
Olympic Coast NMS Pelagic Seabird Surveys	Liam Antrim, Jenny Waddell	Olympic Coast NMS	Ship	2006–2016
Oregon and Washington Marine Mammal and Seabird Surveys	G. A. Green, Michael Bonnell, Kenneth Briggs	Ebasco Environmental, Ecological Consulting, Inc., MMS	Aerial	1989–1990

Table 1 (*continued*)

Survey Name	Current Principal Investor(s)	Organization(s)	Type	Years Included
Oregon, California, and Washington Line-transect Expedition (ORCAWALE)	Lisa Ballance	NOAA Southwest Fisheries Science Center	Ship	1996–2008
Pacific Coast Winter Sea Duck Survey	Joseph Evenson	WDFW, Sea Duck Joint Venture	Aerial	2011
Pacific Continental Shelf Environmental Assessment (PaCSEA)	Josh Adams	USGS Western Ecological Research Center	Aerial	2011–2012
Pacific Orca Distribution Survey (PODS)	Bradley Hanson, Dawn Noren, Jeannette Zamon	NOAA Northwest Fisheries Science Center	Ship	2006–2012
Pelagic Juvenile Rockfish Recruitment and Ecosystem Assessment Surveys	David Ainley; William Sydeman	Point Blue Conservation Science, and H.T. Harvey & Associates; Farallon Institute	Ship	1986–2015
Santa Barbara Channel Surveys	Michael L. Bonnell	UC Santa Cruz, CDFW Office of Spill Prevention and Response, MMS	Aerial	1995–1997
Southern California Bight Surveys	Josh Adams, John Takekawa	USGS Western Ecological Research Center, MMS	Aerial	1999–2002
Wind to Whales	Donald Croll, James Harvey	UC Santa Cruz, Moss Landing Marine Laboratories	Ship	1997–2007

the platform (Ford et al., 2021). Species codes were standardized across surveys and observations were subdivided into smaller transect segments (mean = 4.03 km long) with counts spatially associated with the coordinates of each transect segment midpoint.

2.3. Regional data designation

For data manipulation, analyses, and most graphics, we used R programming (R Core Team, 2021, version 4.0.3), with maps made in ArcMap (version 10.7.1).

We grouped data into different biogeographic regions (by latitude, South, Central and North), and within each of the five NMSs (progressing south to north: CINMS, MBNMS, GFNMS, CBNMS, OCNMS). Patterns of seabirds recorded outside of NMS boundaries were also considered (CA Current outside of NMSs, and by bathymetric habitat: off-shelf and on-shelf).

We assigned data to these various regions using two methods. First, midpoints of each transect segment were assigned to a region if they were within or intersected the region boundary. Second, we created three different-sized grid cells (10×10 km^2, 20×20 km^2, 30×30 km^2) and assigned each transect midpoint to a grid and then assigned the grid midpoint to a region if it fell within or intersected the region boundary. As each sized grid cell would encompass a different number of transect midpoints, we used all three grid sizes in analyses to determine if differences in seabird patchiness affected our results. Indeed, seabirds do have patchy distributions influenced by the spatial patterns of productivity multiple scales and, therefore, both the use of spatial means and sorting into three different grid sizes aim to smooth over this variability

(Fauchald, 2009; Hyrenbach et al., 2000).

We extracted ETOPO1 bathymetry data at one-arc minute geographic resolution in order to classify transect segments and grids into two depth bins using the 'getNOAA.bathy' function in the marmap package in R (Pante and Simon-Bouhet, 2013, version 1.0.6). Data were considered off-shelf if the transect segment or grid midpoints were in waters >200 m, the continental shelf-break, and on-shelf if the transect segment or grid midpoints were in waters <200 m. The 200-m isobath has been used in previous studies (Kämpf and Chapman, 2016; Ainley and Hyrenbach, 2010; Ainley et al., 2005, 2009; Santora et al., 2012; Ford et al., 2021). We calculated distance from shore for each grid midpoint to test for trends between the distance from shore (~3 m resolution, osmdata package, Eugster and Schlesinger, 2012) and seabird indices using the 'st_nearest_feature' in the sf package (Pebesma, 2018, version 1.0–8).

Before analysis, we removed grids with no survey effort and, for diversity analyses, we removed transect segments and grids with zero species.

2.4. Seabird indices

To characterize broad patterns of seabird occurrence, we calculated relative abundance and diversity indices, and regional community composition metrics by determining the long-term spatial mean of transect segments and grid cells within a region over the entire 1980 to 2017 period.

2.4.1. Relative abundance

We used all species and species groups to derive a measure of relative abundance (number of birds/ km^2, Table S1). Given that we did not correct for seabird flux (Clarke et al., 2003), nor did we address potential effects of ship avoidance/attraction that varies by species, or the fact that aerial counts are generally collected by a single observer while ship-based ones usually had multiple observers (Spear et al., 2004), our relative abundance estimates can only be considered a density index. Single observers detect fewer small birds and, depending on ship and wind speed, fast-flying species (e.g., auks, shearwaters) can be disproportionately tallied relative to slow species (e.g., storm-petrels) depending on relative bird-vessel speed and direction.

Transect width varied between surveys (50–300 m) and is either set at a default width or determined beforehand due to conditions and size of species, and height above the sea of the observer (lower the observer, narrower the strip; Ballance, 2007). These differences in transect width were documented in our data — for surveys that had default widths the value was the same for small and large species, while surveys that accounted for conditions occasionally had different widths for small and large species. We accounted for this by calculating the relative abundance of small and large birds per segment. These two densities were summed to determine total segment seabird relative abundance, from which we calculated mean relative abundance per region and the mean relative abundance per grid cell in each region for each sized grid.

2.4.2. Diversity

There are many diversity indices and ways to examine regional diversity, therefore we used several methods in our analysis to thoroughly test for spatial trends in seabird diversity. First, we investigated species richness and evenness separately, and then we tested diversity between regions using both the Shannon Index (H'; Shannon and Weaver, 1949) and the Simpson's Index (1-D; Simpson, 1949). Both the Shannon and Simpson indices are a measure of species richness and evenness but are sensitive to different components of a community. The Shannon Index is a measure of entropy, as it determines the uncertainty in predicting the species of an individual that is taken at random from the population, where the higher the index, the more diverse (higher uncertainty). The Simpson's Index (D) is an estimate of the probability that two randomly drawn individuals would be the same species and is a measure of

dominance as it is heavily skewed by the abundance of the most common species. The Simpson's Index delivers a number, where zero is higher diversity and one is low diversity, and therefore 1-D is used so that the higher the number, the greater the diversity.

For most diversity analyses, we used the vegan package (Oksanen et al., 2018, version 2.6–2). Only counts of birds that could be identified to species were included, and species that had zero sightings within a region were removed prior to analysis. To account for the disparate survey effort among regions, we used species accumulation curves to determine regional species richness (May, 1988; White, 2007). We constructed a species accumulation curve using the function 'spe-caccum,' with 100 permutations, to compute expected species richness via sample-based rarefaction and allow for appropriate comparisons among regions (Colwell and Coddington, 1994; Heck et al., 1975; Chiarucci et al., 2003). The curve is produced by drawing a random sample of transect segments and producing, by interpolation, the expected number of species added with each additional segment surveyed. We used the minimum surveyed effort within the regions (on/off-shelf: 20,000 segments; biogeographic regions: 27,558 segments; regions compared with NMSs: 2208 segments) to extract expected species richness within each region with that amount of survey effort in order to compare differences among regions.

To examine species evenness, we constructed Whittaker plots to show the ranked abundance curve within each region and calculated Pielou's (evenness) Index. Whittaker plots display the ranked relative abundance of species and we used the slope of the line that fits the curve to compare species evenness (Whittaker, 1965). Regions with a steeper slope have lower species evenness than regions with a flatter slope. Pielou's Index is the Shannon Index divided by the maximum possible value of Shannon Index within a region (Pielou, 1975). Both Whittaker slopes and Pielou's Index showed the same trends among regions, and, therefore, we only report on Whittaker slopes.

We used the 'diversity' function to compute the Shannon and Simpson's indices for each region. Shannon and Simpson's values were not normally distributed and both were slightly skewed (Shannon: skewness = 0.77; Simpson's: skewness = −0.56). After preliminary analysis, we determined that the Simpson's Index was less informative than the Shannon Index, due to the prevalence of a few super abundant species throughout the California Current.

2.4.3. Community composition

To investigate the differences in avifaunal composition among regions, we determined the regional dominant species by calculating each species' relative abundance (number of individual birds of a species/ total counts of seabirds within a region) and identified the 10 species having the greatest abundance. We also investigated the relative abundance of species that breed within the CCE compared to those that do not, the primary foraging methods, as well as the preferred prey of seabirds in our dataset (Table S1).

To quantify and compare the species composition between regions, we used two indices of beta diversity, the Jaccard and Bray-Curtis Dissimilarity Indices. The Jaccard Dissimilarity Index calculates the proportion of unique species between communities (Jaccard, 1901). This index uses presence/absence data, making it suitable for analysis between regions with disparate amounts of survey effort. The higher the index, the less similar the regions are to each other. We produced Jaccard Dissimilarity Index values between each region using the 'beta.pair' function in the betapart package (Baselga and Orme, 2012 version 1.5.6). The Bray-Curtis metric uses the number of species and number of individuals in each region to calculate any difference. The value ranges from zero to one, with a value of zero meaning the two regions are the same and a value of one meaning that they do not share any species. The Bray-Curtis values were calculated using the 'metaMDS' function in the vegan package (Oksanen et al., 2018, version 2.6–2).

2.5. Statistical analyses

2.5.1. Relative abundance

We used generalized linear regression models to test for correlations between seabird relative abundance with distance from shore and across latitudes. We tested this relationship at each spatial scale, including all three grid sizes (small scale) and by transect segment (fine scale).

The relative abundance data was zero-inflated (proportion of zeros: 0.451) and overdispersed (skewness: + 70.31), representing the patchy nature of seabirds at-sea distribution. As the data had a zero-inflated gamma distribution, we used hurdle models on the seabird relative abundance for each region. Hurdle models are well suited for zero-inflated data, as they first analyze the data by presence/absence, and then conduct a separate analysis on all non-zero data (Cragg, 1971). First, we fit a logistic regression to predict the probability of a non-zero value within a transect segment, and then we fit a gamma generalized linear model (GLM) with a log link to predict the mean of the non-zero data. A combined relative abundance and confidence intervals on these prediction are derived by adding the two means (logistic model and gamma model) on a log scale and re-exponentiating them. We used non-parametric bootstrap method with 10,000 replicates to obtain confidence intervals around this predicted mean (boot package, version 1.3–28, (Canty and Ripley, 2021).

2.5.2. Diversity

As diversity indices are nonlinear, they are not directly comparable between regions (e.g. H' = 2.4 vs H' = 1.2 is not twice as diverse). To allow for direct comparisons, we used the effective number of species, or Hill number, ^1D, which is the exponential of H' (Macarthur, 1965; Hill, 1973). The effective number of species result in the number of equally common species required to give a particular diversity index (Hill, 1973). We used ^1D values to evaluate differences in diversity between regions and in linear models on spatial trends.

We used Bayesian methods to estimate seabird diversity (^1D) by constructing posterior distributions, by which to evaluate differences among regions. We used the 'brms' package to develop and run our Bayesian model in Stan (Bürkner, 2017, version 2.17.0; Stan Development Team, 2020) and extracted the posterior distributions. We tested several different combinations of priors on the slope, intercept, and variance of the model, but they did not affect the posterior distributions because of the data richness in our analysis. Therefore, we present the results from the default priors, which is a flat prior over the values in the data. Our model used the default priors and gamma distribution with log link function, along with four chains with 2000 iterations each to draw our posterior distributions of effective number of species (^1D) per region.

2.5.3. Relative abundance and diversity

To test for diversity trends across space, we used simple linear regression to evaluate the relationship of relative abundance and ^1D with distance from shore and latitude. We also tested for relationships between seabird relative abundance and diversity (using ^1D) using a simple linear regression.

2.5.4. Community composition

To inspect differences between communities, we first visualized the Jaccard dissimilarities with a heatmap. We then used the Bray–Curtis dissimilarity metrics to visualize differences in community compositions by producing a Non-metric Multidimensional Scaling (NMDS) plot using the 'metaMDS' function in the vegan package (Oksanen et al., 2018, version 2.6–2). Plots were created using transect segments, all three grid sizes, and by biogeographic region. We evaluated the NMDS plots by examining their corresponding Shepard diagrams for a coherent curve or line and a stress value below 0.20 (Kruskal, 1964). We then used a PERMANVOA to test if differences between groups are meaningful (Anderson, 2001).

3. Results

3.1. Seabird relative abundance

Seabird relative abundance was greater on-shelf and decreased with distance from the coast (linear model: $F_{(1, 1264)} = 244.2$, $R^2 = 0.162$, $p < 2.2e-16$, Fig. 2). From our hurdle model, which provides the probability of seeing a bird, the relative abundance if a bird is present, and a combined predicted relative abundance, we found there was a 34.9% greater probability of seeing a bird within a transect segment, with predicted relative abundance 82.2% higher on-shelf compared to off-shelf (Table 2). The relationship between relative abundance and distance from shore was greatest within the first 200 km from the coastline ($F_{(1, 530)} = 178.6$, $R^2 = 0.252$, $p < 2.2e-16$); beyond 200 km the relationship was weak ($F_{(1, 732)} = 22.24$, $R^2 = 0.0295$, $p < 2.88e-06$).

Seabird relative abundance increased with latitude from south to north ($F_{(1,18)} = 21.49$, $R^2 = 0.544$, $p = 0.0002$): greatest seabird relative abundance was in the North, followed by Central, and then South biogeographic regions (Fig. 2). The results of the hurdle model for the biogeographic regions showed a greater probability of seeing a bird within a transect segment in the North (71.4%) and Central (70.5%) regions compared to the South (42.5%, Table 2). The combined results of the model, which accounted for the probability of seeing a bird and estimated relative abundance if a bird was present, showed that seabird abundance in the North were 1.56 times greater than the Central and 5.44 times greater than in the South.

From our hurdle model, all NMSs had a greater probability of observing a seabird within a transect segment compared to the overall CCE, off-shelf and their corresponding biogeographic region, and all but CINMS were also higher than within the on-shelf region (Table 2). The probability of seeing a bird within a transect segment was greatest in the North (OCNMS), followed by Central (GFNMS, CBNMS, MBNMS), then the South region (CINMS). If a bird was present (gamma model), densities in the North were substantially greater within transect segments and the Central and South regions had similar densities (Table 2). The combined prediction resulted in greater relative abundance within NMSs, the North region, and on-shelf habitat.

Variability in seabird relative abundance and diversity is consistent with their patchy distribution. For example, consider the densities within the CINMS compared to the CBNMS. The CINMS is a mix of on-shelf and off-shelf habitat that is close to the coast, with greater intrusions of subtropical water, while CBNMS has a higher proportion of off-shelf habitat and is farther from the coast. Within the CINMS, there was a lower probability of seeing a bird within a transect segment than within the CBNMS (73.2% compared to 88.3%, Table 2). Yet, if a bird was present within a segment, the relative abundance of birds was 3.6–28.9% higher in CINMS. This may indicate that there is greater patchiness of seabirds within the CINMS, with lower probability of seeing a bird, yet denser patches, consistent with warm-water ecosystems. The variability of patchiness and seabird relative abundance within regions was also reflected in the standard deviation among regional densities (Fig. 2).

3.2. Seabird diversity

A total of 105 seabird species were recorded. Diversity was greater in on-shelf habitats compared to off-shelf. Expected species richness was higher on-shelf (78.6 ± 1.7) compared to off-shelf (72.7 ± 2.3), although species evenness was greater within off-shelf habitats (Whittaker slope = −0.219) compared to on-shelf (Whittaker slope = −0.389). On-shelf habitat had a greater Shannon Index within transect segments (0.425 ± 0.47) than off-shelf habitats (0.137 ± 0.32, Fig. 3), although Simpson's Index (1-D) was higher off-shelf (0.664 ± 0.43) than on-shelf (0.481 ± 0.37). Seabird diversity decreased with distance from shore, with less effective number of species (^1D) moving from the coast to offshore ($F_{(1,1132)} = 337.3$, $R^2 = 0.230$, $p < 2.2e-16$) and increased
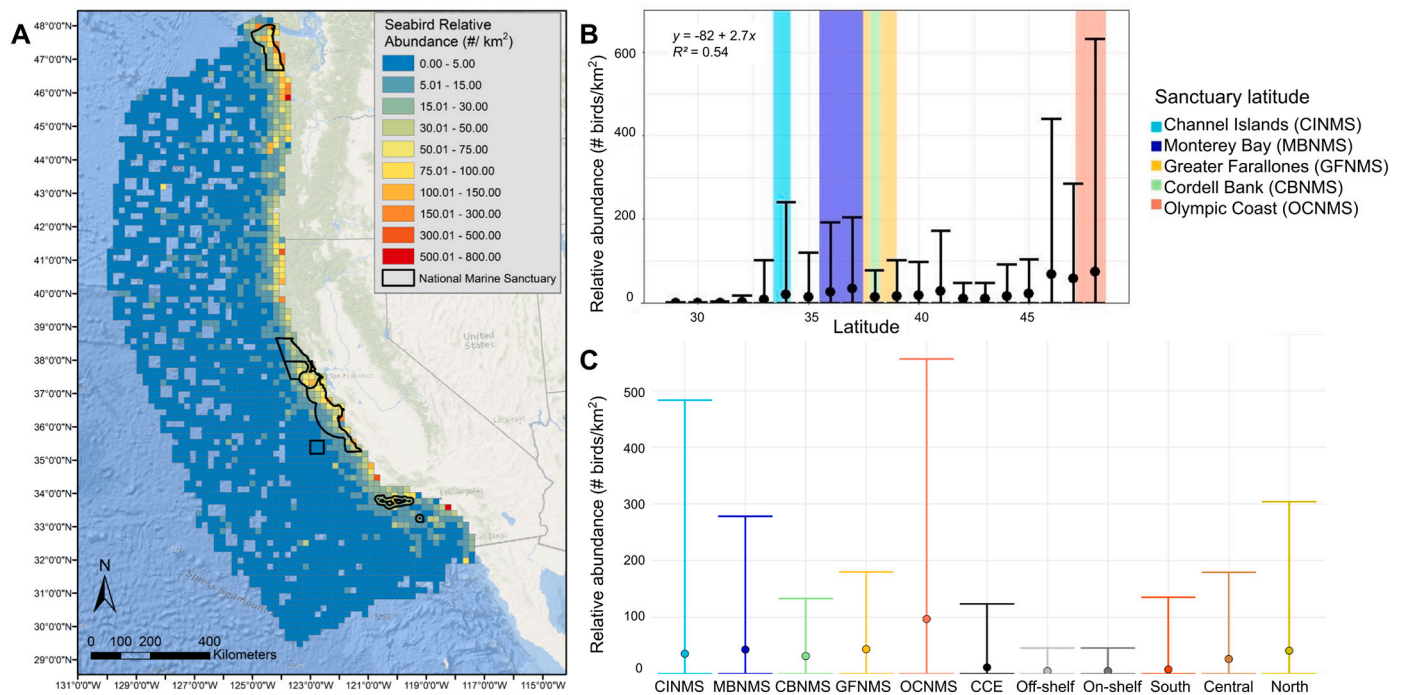
Fig. 2. (A) Map of average seabird relative abundance (number of birds/km^2) within 20×20 km^2 grids in the California Current Ecosystem. (B) Seabird relative abundance (mean $+/-$ SD) within transect segments gauged for each degree of latitude. Colored bars indicate the latitudes overlapping each corresponding National Marine Sanctuaries (NMS). Seabird relative abundance increased with latitude (R^2 = 0.544). (C) Seabird relative abundance (mean $+/-$ SD) within transect segments within NMSs compared with regions outside of sanctuary boundaries (CA Current, Offshore and Onshore) and overall biogeographic regions (South, Central and North). Seabird relative abundance is higher within NMSs compared to overall CA Current and Offshore, and their corresponding biogeographic regions.

Table 2

Results of Hurdle models, which first use a logistic regression to predict the probability of a non-zero value (probability of seeing a bird within a transect segment), and then use a gamma general linear model (GLM) with a log link to predict the mean of the non-zero data (density of birds if a bird is present). We calculated a combined estimated density and confidence intervals on these prediction by adding the two means (logistic model and gamma model) on a log scale and re-exponentiating them. A non-parametric bootstrap method with 10,000 replicates provided confidence intervals around this predicted mean.

Region	Logistic Model		Gamma Model		Combined Model	
	Mean probability of observing a non-zero value	95% confidence intervals	Mean density, given a non-zero value	95% confidence intervals	Combined predicted density	Bootstrapped 95% confidence intervals
CINMS	0.732	0.718–0.746	48.25	33.31–73.63	35.31	25.95–59.83
MBNMS	**0.858**	**0.852–0.864**	49.76	45.13–55.05	42.70	39.28–48.21
CBNMS	**0.883**	**0.869–0.896**	35.38	31.01–40.61	31.23	27.89–36.96
GFNMS	**0.898**	**0.889–0.906**	48.36	44.33–52.90	43.41	40.01–47.99
OCNMS	**0.944**	**0.937–0.950**	**102.53**	**89.91–117.64**	**96.81**	**87.67–117.54**
CCE	0.481	0.478–0.484	23.46	22.10–24.93	11.28	10.62–11.94
Off-shelf	0.446	0.443–0.450	11.95	11.34–12.62	4.72	4.498–4.991
On-shelf	0.795	0.788–0.801	**67.00**	**61.45–73.23**	**53.24**	**48.68–58.09**
North	0.714	0.709–0.720	57.01	52.88–61.57	40.72	38.00–43.89
Central	0.705	0.701–0.709	36.99	35.03–39.10	26.07	24.76–27.64
South	0.425	0.421–0.428	17.63	15.60–20.03	7.49	6.598–8.539

with latitude, with greater ^{1}D moving from south to north (F$_{(1,1132)}$ = 1392, R^2 = 0.552, p < 2.2e-16).

There was higher expected species richness in the North compared to the Central and South regions (Fig. S2). The South had greater species evenness (Fig. S3, Whittaker slope = −0.175), while the Central region had the highest species dominance (Whittaker slope = −0.428) (Table S2). The North and Central regions had similar Shannon Index values that were greater than the South (Fig. 3), and Simpson Index (1-D) values overlapped among all three regions. There was greater ^{1}D in the North, followed by the Central, and then the South regions (Fig. 4).

Higher expected species richness (from species accumulation curves) occurred in the CCE and on-shelf compared to all NMSs, and only OCNMS and MBNMS had greater expected species than off-shelf (Fig. S2). Expected species richness within NMSs was greatest in the North

(OCNMS), then Central, on-shelf NMS (GFNMS, MBNMS), and then South or off-shelf NMS (CINMS, CBNMS). Species evenness varied among NMSs (Table S2, Fig. S3), with CINMS and CBNMS having similar evenness as off-shelf (Whittaker slope = −0.234 and − 0.223, respectively). Species diversity within NMSs generally reflected broad trends of the CCE, with increasing Shannon Index within NMSs from south (CINMS) to north (OCNMS, Fig. 3.C). The Shannon Index was greater within all NMSs compared to the CCE and off-shelf (transect and grid), and most had higher values than on-shelf as well. The Simpson's Index (1-D) was slightly greater in all NMS (transect and grid) but there was a large overlap between all regions.

At fine scales (i.e., transect segments) the model showed 95% confidence that the effective number of species (^{1}D) was greater (higher diversity) in all NMS compared to the CCE, off-shelf and on-shelf (Fig. 4).
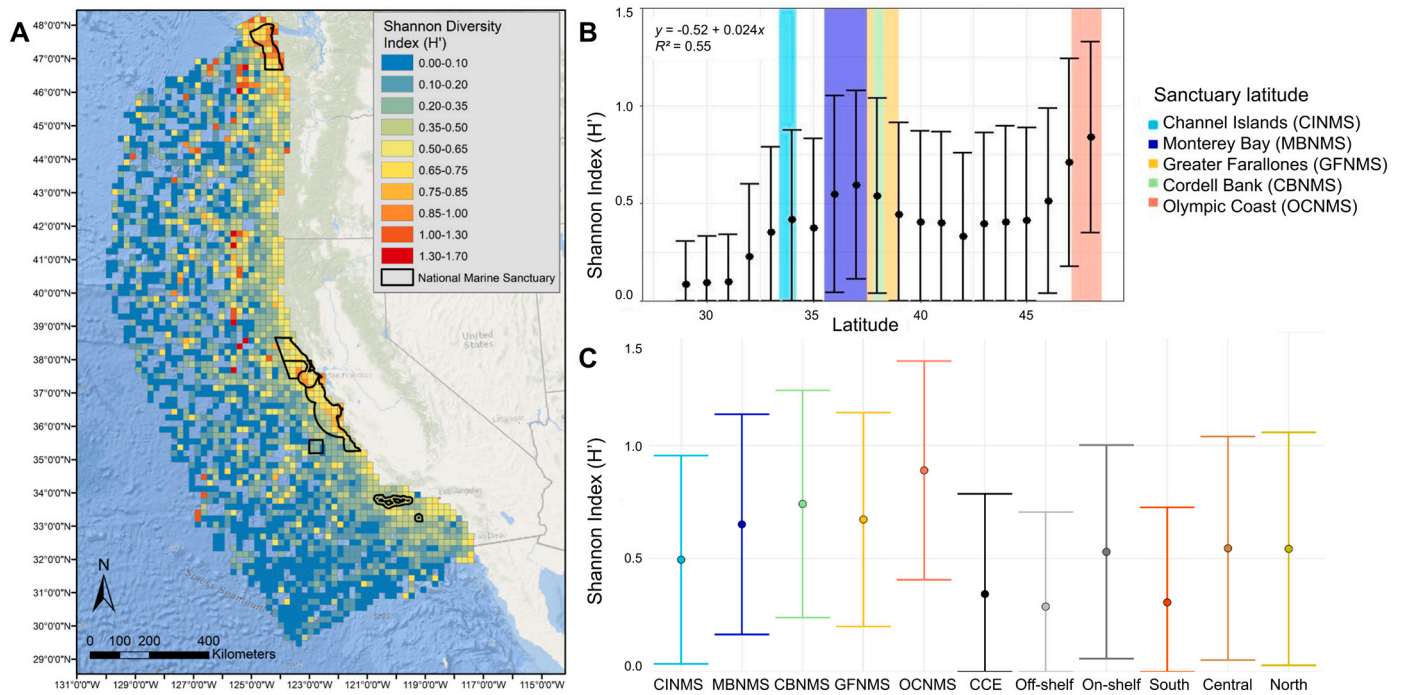
Fig. 3. (A) Map of average Shannon Index ('H) of transect segments within 20×20 km^2 grids within the California Current Ecosystem. (B) The Shannon Index (mean $+/-$ SD) of seabirds within transect segments for each degree of latitude along the U.S. West Coast. Colored bars indicate the range of latitudes within each National Marine Sanctuary (NMS). Seabird diversity increased with latitude (R^2 = 0.552). (C) Shannon Index (mean $+/-$ SD) of seabirds within transect segments among the NMSs compared with regions outside of sanctuary boundaries (CA Current, Off-shelf and On-shelf) and overall biogeographic region (South, Central and North). Seabird diversity is higher within NMSs compared to overall CA Current, Offshore, and most are higher than Onshore, as well as their corresponding biogeographic regions.
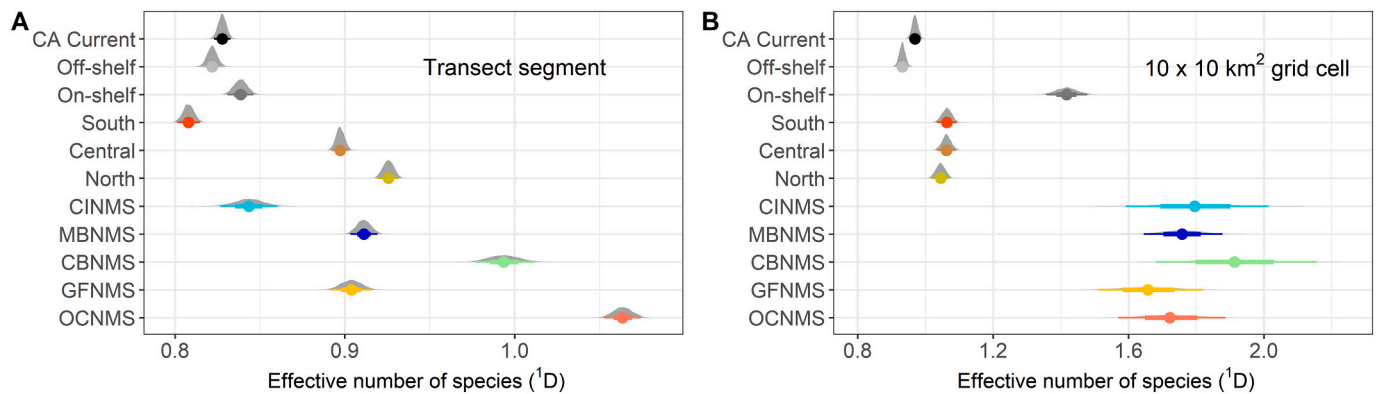
Fig. 4. The 95% credible intervals or posterior distributions of effective number of species (^{1}D) for each region. (A) Estimates from transect segment values, and (B) estimates from 10×10 km^2 grid cell values. Over fine spatial scales (i.e. transect segment) (A), the highest diversity is in the North, then Central bioregion. Diversity was also higher in Olympic Coast National Marine Sanctuary (OCNMS) and then Cordell Bank NMS (CBNMS) in the comparison between waters inside and outside NMS boundaries. At small spatial scales (i.e. 10×10 km^2 grids) (B), diversity was similar among all three biogeographic regions, overlapping among all NMSs, yet all were higher compared to outside NMS boundaries and their corresponding biogeographic regions.

At small spatial scales (i.e., 10×10 km^2), similar diversity existed among all NMSs, yet we were 95% confident they were higher than outside NMS boundaries. There were not enough grid cell midpoints within the NMS boundaries to produce meaningful model results from larger grid sizes (>20×20 km^2 grid cells).

3.3. Relative abundance and diversity

A linear relationship existed between relative abundance and diversity (^{1}D) at larger scales of the 30×30 km^2 grids (Fig. S5; $F_{(1,1288)}$ = 275.7, R^2 = 0.176, p < 2.2e-16). The relationship between relative abundance and diversity decreased as scale decreased with no

relationship between the two indices at the transect segment scale ($F_{(1, 80,534)}$ = 58.7, R^2 = 0.0007, p = 1.85e-14).

3.4. Seabird community composition

The proportional species composition and the most dominant species varied by region. On average, the 10 most abundant species among all regions (totaling 22 species) made up 93 $\pm$ 0.07% of all birds recorded (Fig. 5). The most dominant species overall were restricted to just five species: sooty shearwater, common murre, red-necked phalarope (*Phalaropus lobatus*), western gull (*Larus occidentalis*), and Cassin's auklet (*Ptychoramphus aleuticus*). When we grouped species, the dominant
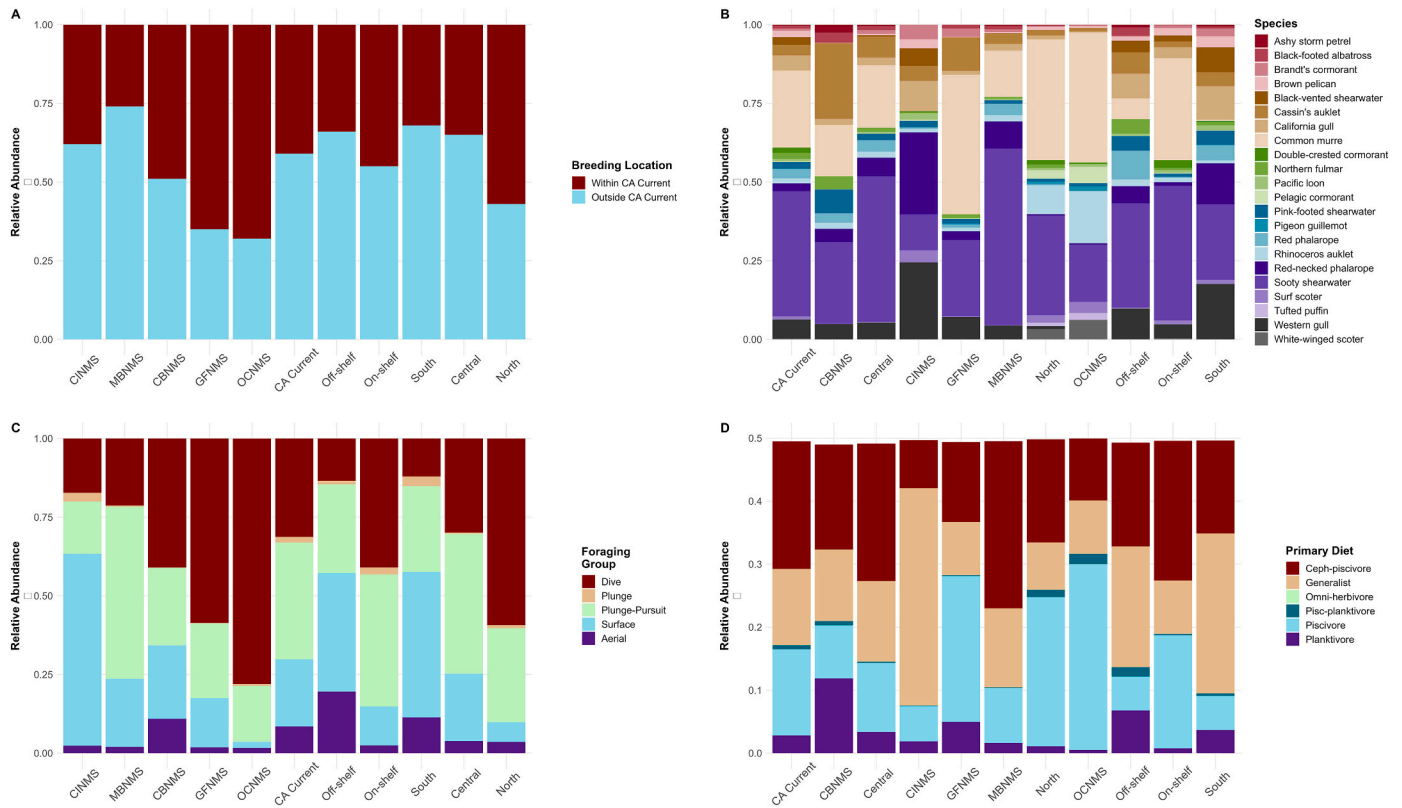
Fig. 5. Relative abundance plots of different seabird groups within National Marine Sanctuaries (NMS) and outside of NMS (CA Current, Off-shelf and On-shelf), by overall biogeographic regions (South, Central, North). Species and functional groups included are: (A) Birds that breed within and those that breed outside of the CA Current; (B) the 10 most abundant species within each region ($N = 22$); (C) foraging method; and (D) primary diet. Graphs A and B used only observations identified to species, while C and D used observations that were identifiable to species groups that had the same foraging or diet characteristics.

types contained these species: gulls, phalaropes, large alcids and shearwaters. There were 13 species having only one sighting, including a wandering albatross (*Diomedea exulans*) in 2008 off the coast of San Francisco (Table S1). The communities in the off-shelf, on-shelf, and overall CCE, showed little dissimilarity among each other (Fig. 6). The North and South were most distinct from each other compared to the Central region. Most of the NMS were very dissimilar to regions outside of NMS boundaries. Although, MBNMS captured the most similar community to the CCE and most other regions, except the North, OCNMS, and CBNMS. While CBNMS was the most distinct from the CCE and all
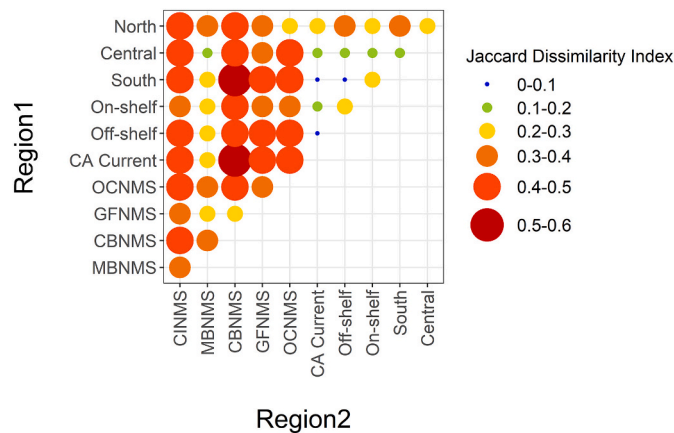

Fig. 6. Bubble heat plot of the Jaccard Dissimilarity Index among regions and National Marine Sanctuaries. This Index uses presence/absence data and calculates the proportion of unique species between communities. The more similar regions are to each other, the smaller the index value.

other regions, except GFNMS. The other NMSs captured communities that were highly dissimilar to most regions, including other NMS.

Plots of Non-metric Multi-dimensional Scaling (NMDS), using the Bray-Curtis dissimilarity metric on biogeographic regions, showed no clear differences in community patterns among regions (Fig. S4). Among NMSs, the NMDS plots show distinct communities in the North (OCNMS), Central (MBNMS, CBNMS, GFNMS) and South components (CINMS) of the CCE (Fig. 7). All grid sizes showed spatial trends among communities within the NMSs. The 30×30 km^2 had the lowest stress (stress = 0.132), yet the 20×20 km^2 had enough points in each NMS to draw an ellipse (stress = 0.159, PERMANOVA: $F_{(4)} = 53.31$, $R^2 = 0.696$, $p < 0.001$).

The regions were characterized by different proportions of residents/migrants, foraging guilds, and supposed diets, as well as dominant species (Fig. 5). The main foraging guilds in the CCE were birds that dive, plunge-pursuit, or surface feed (Fig. 5.C). Surface and aerial feeders decreased with latitude, the opposite trend of divers. There were greater proportions of surface and aerial feeders off-shelf, while divers were documented in greater proportions on-shelf. There were similar proportions of plunge-pursuit species within the NMSs, except for MBNMS, which had a greater proportion of these birds (e.g. aquatic shearwaters; as defined by Kuroda, 1954). Plunge feeders made up a small component of the birds in the South, CINMS, and in both on-shelf and off-shelf habitats.

The supposed, primary diet of birds in the CCE varied (Fig. 5.D). There were more generalist species in the South, CINMS, and off-shelf, with similar proportions in other regions. More birds that consume primarily micronekton were greatest in the Central region and corresponding NMSs (MBNMS, CBNMS, GFNMS). The proportion of likely piscivores was greater on-shelf, increased from south to north, and were greatest in OCNMS and North region. Zooplanktivores were documented
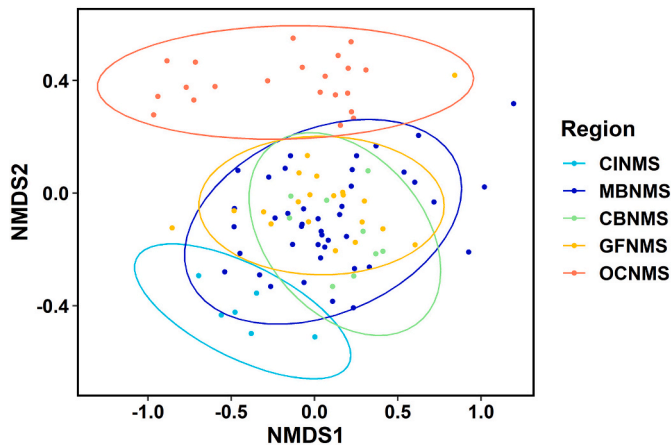
Fig. 7. Non-metric Multi-dimensional Scaling (NMDS) showing the ordination of the Bray-Curtis dissimilarity metric (a measure of community composition) within each 20 × 20 km² grid cell among the National Marine Sanctuaries (NMS). Points that are closer to one another are more similar to each other compared to those further away. There are similar communities in the central California NMSs, while the most northern (OCNMS) and southern (CINMS) sanctuaries have distinct seabird communities (stress = 0.159, PERMANOVA: $F_{(4)} = 53.31$, $R^2 = 0.696$, p < 0.001). All three grid sizes produced this pattern, but the 20 × 20 km² grid size was selected for aesthetics.

in greater proportions in the off-shelf and CBNMS regions.

4. Discussion

We characterized broad spatial patterns of seabirds using data from ship and aerial at-sea surveys by evaluating spatial means of seabird relative abundance, diversity, and community composition. Overall, seabird relative abundance and diversity was greater in productive regions, such as higher latitudes, within on-shelf habitats and closer to the coast within the CCE (Checkley and Barth, 2009; Hayward and Vennck, 1998; Fig. 8). In addition, the boundaries of the west coast NMSs captured habitat that had high seabird relative abundance and diversity compared to larger scale regions outside of the NMSs. The distribution of these NMSs also captured a variety of distinct seabird communities, with different proportions of species, species groups, resident and migratory birds, foraging guilds, and differing diets (Figs. 7 & 8). At small scales (900 km², largest grid size), relationships existed between diversity and relative abundance that were not apparent at finer spatial scales (~1.2 km², transect segments), reflecting the patchy distributions of seabirds within the CCE.

4.1. Broad spatial patterns of relative abundance

Seabird relative abundance was variable throughout the CCE, yet we found strong spatial patterns that confirm previous work and highlight broad relationships between seabird relative abundance and areas of
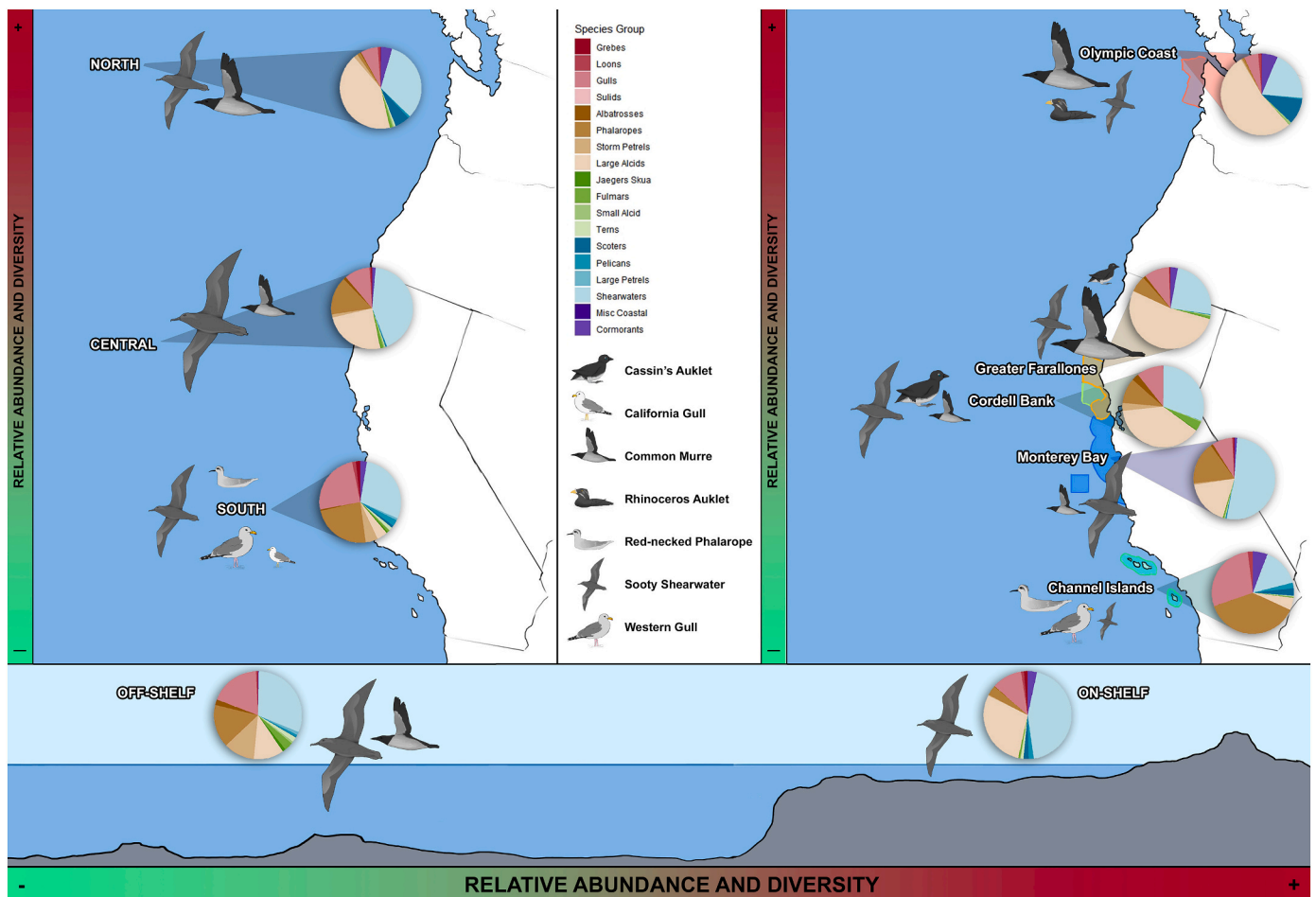

Fig. 8. Spatial patterns of seabirds in the California Current Ecosystem and within west coast National Marine Sanctuaries. The x and y axes of the maps highlight that seabird density (number of birds/km²) and diversity (effective number of species) decrease both with latitude (north to south) and distance from shore. Dominant species (>10% of the total birds) are shown alongside each region. The proportion of species groups within each region are indicated by the associated pie charts. (© Freya Hammar).

higher upwelling and primary production (Fig. 8). Our findings support the broad trend that more productive, on-shelf waters support higher seabird densities, while also highlighting the linear relationship involving distance from shore (Briggs et al., 1987; Tyler et al., 1993). The presence of large breeding colonies also affects the relative abundance of birds, with these areas having higher abundances, even compared to nearby regions (such as GFNMS compared with CBNMS). The high proportion of migratory species in certain regions, such as MBNMS, highlight those areas that are important stopovers along migratory pathways, and can increase relative abundance in those regions dramatically. Some species, such as sooty shearwaters, arrive in the hundreds of thousands. We also found that seabird relative abundance was highly correlated with latitude, given that northern regions were more productive. In addition, there was a greater probability of seeing a bird in the North and then Central region compared to the South, a pattern that confirms overall higher abundance (ultimately, densities) in these regions. The regional trends of patchiness (the probability of seeing a bird) warrant further investigation, as understanding the regional seabird patchiness provides information on potential foraging competition and resources use.

4.2. Broad spatial patterns of diversity

Contrary to global patterns of diversity with other organisms (Tittensor et al., 2010; Hillebrand, 2004; Jablonski et al., 2006), there is higher diversity (species richness and Shannon Index) within on-shelf regions and in higher latitudes, already established with smaller datasets (Briggs et al., 1987; Tyler et al., 1993; Santora and Sydeman, 2015; Grecian et al., 2016; Santora et al., 2018; Grady et al., 2019;). Other studies on the diversity of marine predators, including seabirds, found that diversity is low at high latitudes, moderate at low latitudes, and peaks within intermediate latitudes (20–30° N and S), where temperate and tropical species overlap (Pitman, 1986; Worm et al., 2003; Spear and Ainley, 2008). The reason for this disparity is likely to be related to the fact that the CCE, owing to its high productivity, is where many seabirds spend their non-breeding period (Block et al., 2011), and is true for other eastern boundary currents, e.g., the Peru Current (Spear and Ainley, 2008) and Benguela Current (Abrams and Griffiths, 1981).

Although the patterns of species richness and Shannon Index showed higher diversity in more productive regions, this was not the case for species evenness. The latter was higher off-shelf and in the South. Although both evenness and richness are used in calculating overall diversity, these two measurements may not be correlated, or be negatively correlated, with one another or with patterns of relative abundance (Bock et al., 2007). This difference between seabird richness and evenness was driven by the regions with high evenness being those in which all or most species present were similarly uncommon (Ainley, 1976; Briggs et al., 1987). Therefore, species richness and Shannon Index highlight overall diversity better than evenness alone, whereas evenness highlights regions of unique communities or habitat that supports rare or uncommon species.

4.3. Relative abundance and diversity

At the mesoscale scales (900 km^2), diversity and relative abundance were correlated and both increased northward along the latitudinal gradients and with decreasing distance from shore. They also were higher on-shelf. These patterns were consistent with the findings of Ainley (1976) and Briggs et al. (1987). Gradients help explain why there are higher seabird indices in different regions and within NMSs (see also Ballance et al., 1997). In the North, the continental shelf is wider (greater on-shelf habitat; Fig. S7 & S8) and exhibits stronger more persistent upwelling leading to the higher relative abundance of seabirds (Checkley and Barth, 2009). In the Central region, the shelf is narrow, dropping to greater depths (>2500 m) near the coast (Fig. S8). Although seasonal upwelling is strong in the Central region, which may explain

the moderately high seabird relative abundance, this region also encapsulates the ecological transition between the South and North (Huyer, 1983; Checkley and Barth, 2009), which resulted in relatively higher seabird diversity than expected. Again, this had much to do with the CCE being the target for seabirds from breeding locations occurring elsewhere (Ainley, 1976; Briggs et al., 1987). The exception to the on-shelf trend was within the South, where the shelf extends around and out from the Channel Islands (Fig. S8). Even though the South region has a high proportion of on-shelf habitat (Fig. S7), it has lower relative abundance and diversity that may result from different conditions, such as the weaker, seasonal upwelling (Checkley and Barth, 2009).

4.4. Broad patterns of community composition

The three biogeographic regions in the CCE host disparate seabird communities and proportions of functional groups (Fig. 8). Our findings support previous work showing the North and South regions to be the most distinct. The Central region is a transition zone between the other two communities (McGowan and Williams, 1973; Polovina et al., 2001; Sydeman et al., 2009).

The North region had the highest diversity, while also capturing a unique community of birds, and provides habitat that attracts more sub-arctic species, such as scoters (*Somateria* spp.) and tufted puffins (*Fratercula cirrhata*), as well as southern, temperate ones. The northern community was dominated by large alcids (common murres and rhinoceros auklets, *Cerorhinca monocerata*) and, from the Southern Hemisphere, sooty shearwaters (Fig. 8). These alcids are divers, while sooty shearwaters feed by plunge-pursuit, and both feed extensively on micronekton (though at times, zooplankton as well). In the North, pelagic trawls of surface waters have found a dominance of forage fishes (Brodeur et al., 2005), a finding that supports why these birds dominate there. Although a linear trend existed between relative abundance and diversity with latitude, the Central region had higher indices than the regions to the South and regions just to the North in accord with its transitional properties. The Central region is important for both migratory and resident species, such as sooty shearwaters and common murres, respectively (Fig. 8). The community in the South region captured higher proportions of gulls (Laridae) and phalaropes (Phalaropidae) than other regions, and the highest proportion of surface and aerial feeding seabirds (Fig. 8). The South had high species evenness (therefore low dominance) compared to other regions and provides habitat to migrant cold- and warm-water species (e.g. cold: sooty shearwater, northern fulmar (*Fulmarus glacialis*); warm: Cook's petrel (*Pterodroma cooki*), black-vented shearwater (*Puffinus opisthomelas*). The high evenness, and presence of cold- and warm-water species, may be due to the heterogeneity of this region's oceanography, in which cold, upwelled water meets warm sub-tropical waters intruding from the south (Hayward and Vennck, 1998).

4.5. Dominance in the CCE

Although regions differed in species evenness, overall there was high species dominance in the CCE, with only two species, sooty shearwater and common murre, making up over half of birds recorded (29.5% and 21.3%, respectively). The fact that the CCE avifauna is dominated by a non-resident species, sooty shearwater, is noteworthy, especially as Veit et al. (1997) found their abundance had decreased markedly during the first half of our study period. Species dominance within upwelling regions has been previously recorded in small planktivorous fishes (Glantz and Thompson, 1981; Cury et al., 2000) and seabirds (Ainley, 1976; Wiens and Scott, 1975; Briggs et al., 1987; Tyler et al., 1993; Ainley et al., 2005; Spear and Ainley, 2008). Foraging guild and prey preference groups also exhibited patterns of dominance within regions of the CCE. For example, in the North, diving and piscivorous species dominated the community, while in the South surface feeding, generalists were dominant. This pattern of proportionally more surface feeders in

the South, compared with more diving feeders in more productive regions has been previous noted (Ainley, 1977; Ainley and Boekelheide, 1983; Hyrenbach and Veit, 2003). Diving is energetically costly and these species need larger, more predictable aggregations of prey and are therefore found predominantly in productive, upwelling regions (Ainley and Boekelheide, 1983; Hodum et al., 1998). On the other hand, surface feeding enables species to take advantage of a variety of food resources in lower productive regions and is energetically less costly (Ainley and Boekelheide, 1983; Ballance et al., 1997). Surface feeders tend to be more aerial, thus to cover wider areas, than divers (Ainley, 1977).

While the spatial distribution of dominant species is important for characterizing regional communities and informing management, the presence of less common species is also important (McCann et al., 1998). Most of the species in the CCE were uncommon, with 83 species making up only 6.9% of the total (Table S1). Most previous studies on seabird communities within the CCE have focused on the dominant species to characterize a region, yet the occurrences of uncommon, or even rare species (<5 sightings), should not be ignored (McCann et al., 1998; Spear and Ainley, 2008). Although the dataset used in this study is extensive, with surveys spanning seasons and years, as well as throughout the CCE, the sighting of a species only once is a valuable data point and should be included when quantifying a regions' seabird diversity. For example, while the lone wandering albatross had to have come from the south (Southern Hemisphere), it was detected in the Central region, possibly owing to the higher productivity in that region being more attractive, keeping this bird longer (thus to be detected).

4.6. Spatial patterns within National Marine Sanctuaries

Overall, our results confirm and support the contention that west coast NMSs, and more than just the Central coast ones (NCCOS, 2003), capture important seabird habitat. There was higher seabird relative abundance and diversity within the NMSs compared to regions outside their boundaries, and the trends in these indices were consistent with their biogeographic regions, yet they captured distinct seabird communities (Fig. 8). In part, these patterns result from the NMSs encompassing the waters adjacent to many of the important nesting habitats along the coast of the CCE. In addition, their general location captures a high proportion of on-shelf habitat, which we found to capture higher seabird relative abundance and diversity throughout the CCE. Contributing additionally, are distinct localized upwelling and/or unique circulation that affects the distribution and availability of prey, and often associated with capes, i.e., upwelling plumes (e.g., Ainley et al., 2005, 2009).

On average, there was a 38.1% greater probability of seeing a bird within a NMS compared to outside their boundaries and 41.6% greater probability than in off-shelf regions (Table 2). The probability of seeing a bird was impacted by the relative abundance of birds (more birds, higher probability), but also informs us about the patchiness of birds present (more patchiness, lower probability). All NMSs had a higher predicted relative abundance than CCE and off-shelf, whereas the on-shelf region has a higher predicted relative abundance than all but the northern NMS. The lack of a NMS in the North-Central region may explain this difference, as there are high densities along the Northern California and Oregon coastline but no NMS (e.g. Briggs et al., 1987; Ainley et al., 2009; Nur et al., 2011). The distance from shore and proportion of on and off-shelf habitat within each NMS may also influence predicted densities (Figs. S6 and S7). OCNMS, which had the highest proportion of on-shelf habitat, had the highest predicted densities, while CBNMS, which is further from shore and has a high proportion of off-shelf habitat, showed lower predicted densities. The outliers to this trend were MBNMS and CINMS. Because of the Monterey Canyon and Davidson Seamount, MBNMS has a high proportion of off-shelf habitat, yet this large sanctuary also hosts coastal habitats, as well as higher local productivity. Even though CINMS has a high proportion of on-shelf habitat, lower predicted densities within CINMS may

be due to its location within the South where there is weaker upwelling. The probabilities of seeing a bird within all NMSs were higher than their respective biogeographic regions (average 21.2% higher). The higher predicted densities of seabirds within NMSs compared to their biogeographic regions emphasizes their ideal placement along the productive coastline.

All NMSs had higher Shannon Index values than CCE and off-shelf, and all except the NMS in the south had higher diversity than the on-shelf region. An overall increase in NMS seabird diversities occurred with latitude reflecting the latitudinal trend of seabird diversity in the CCE (Fig. 3). Although there was overall higher diversity, the NMSs had lower expected species richness than regions outside their boundaries. Larger regions encompass more latitudes, bathymetric variability and thus microhabitats, which explains why these larger regions would have a greater number of species. Therefore, species richness alone is not a thorough measure for overall diversity of a region. For example, both MBNMS and OCNMS encompass a larger area than the other three NMS, containing a higher expected number of species than the smaller NMSs.

NMSs exhibit distinct regional seabird community patterns (Fig. 7). This is contrary to results of comparisons between biogeographic regions (Fig. S4). At biogeographic scales, seabirds within the CCE may not align with current biogeographic definitions, or these trends may only be present at regional scales or in certain habitats (on-shelf).

Most of the NMSs captured highly dissimilar seabird communities compared to regions outside their respective boundaries (Fig. 6). The MBNMS captured the most similar community to the CCE, while CBNMS captured the most distinct. The MBNMS contains the region within and around Monterey Bay, including a submarine canyon that comes very close to the coast, and an off-shelf grid around Davidson Seamount. The combination of the on-shelf and off-shelf components of this NMS mean that it contains a diverse community of seabirds, including both pelagic and coastal species, and migratory and resident birds. This may be due to the deep marine canyon, which is a target for birder trips to maximize number of species seen in a day (Stallcup, 1976; Ford et al., 2021). Although the habitat within CBNMS is mostly off-shelf and further from the coast, the avifauna was dissimilar to the overall off-shelf community, and clearly captures a unique offshore community within the CCE. Interestingly, although CBNMS had lower expected species richness, it had higher Shannon Index, effective number of species, and species evenness than the other two central NMSs. These differences may be driven by the off-shelf location of CBNMS, including its seamount character, yet still within the productive Central region. The amount of data may also affect different indices, as the CBNMS is one of the smallest NMSs and had the least amount of survey effort. These results highlight the need to use multiple indices to investigate trends in regions, as Jaccard does not use abundance and is therefore not affected by difference in effort, while Bray-Curtis does. This may account for the lack of detection of the NMDS plot to CBNMS unique community in the Central region (Fig. 6). The other NMSs captured communities that had high dissimilarity to most regions, including other NMS and their corresponding biogeographic regions, highlighting the diverse set of communities captured within each of the NMS along the central coast.

The seabird community within OCNMS reflected the overall biogeography in the North region. The dominant species was the common murre, owing to a high proportion of resident breeding birds and, in accord, the diving foraging guild. The abundance of piscivores, such as common murres, in this region reflects overall trends in the North and highlights the availability of dense aggregations of forage fishes in this region (Brodeur et al., 2005; Ainley et al., 2005, 2009, 2021).

The three NMS in the Central region all captured different seabird communities. Even though the MBNMS and GFNMS have similar seabird densities and diversity, they differ in composition. Lacking significant breeding habitat, MBNMS was dominated by seasonally resident and migratory sooty shearwaters, as well as other migratory species. In contrast, the GFNMS, which is home to the largest breeding colony of seabirds along the contiguous U.S. West Coast, the Farallon Islands

(Ainley and Boekelheide, 1990), had high community dissimilarity compared to all regions. It had a high proportion of CCE breeding species, dominated by common murres. The CBNMS is further from the coast and has proportionally more off-shelf habitat than the other central NMSs (Fig. S7). Seabird communities within the CBNMS differ greatly from those of other regions, including its NMS neighbors, with high species evenness, and a variety of primary foraging methods and preferred diets (Fig. 8). The higher proportion of planktivores in the CBNMS compared to all other regions supports findings that it contains a krill hotspot (Santora et al., 2011). Overall, the placement of sanctuaries appears to matter in order to capture distinct communities within relatively small regions.

Despite seabird relative abundance and diversity in the South being similar to the CCE, on-shelf and off-shelf, the CINMS captured a seabird community that was dissimilar to all regions, including the South region. The CINMS had high species evenness, with the primary groups being gulls and phalaropes, as well as other surface feeding birds and generalists. The flight capabilities of these species allow them to take advantage of limited resources in this less productive region (Ainley, 1977; Ainley and Boekelheide, 1983; Ballance et al., 1997). The CINMS is also within the South, a region that is characterized by heterogeneous ocean conditions (cooler in the north, warmer in the south) that provides habitat for both cool- and warm-water species. The result is higher species evenness and lack of single species dominance as found in other regions.

In summary of this section, west coast NMSs are regions that capture seabird relative abundance and diversity that are similar to their respective biogeographic regions yet are comprised of distinct communities. The NMSs capture communities that are different along a latitudinal gradient and their placement captures a variety of habitat and seabird communities along the U.S. West Coast. In addition, the three central NMSs are a prime example of how placement of a sanctuary matters, as all three are in the Central region but capture distinct seabird communities. Although west coast NMSs are in all three biogeographic regions, there remains a large gap between the central NMSs and OCNMS in the north. We found that the region along the Oregon coast, particularly in the vicinity of the Columbia River mouth (~46° N; Phillips et al., 2018), may be a good candidate for future NMS nominations. In this region, the seabird relative abundance was similar to the coastal regions in the North and the diversity was similar to the central NMSs. Although there is a gap in NMS placement, the diverse placement of current NMSs and existing infrastructure are valuable tools in monitoring seabirds within the CCE.

5. Conclusions

5.1. Future directions and limitations

The goal of this paper was to characterize the seabird communities within the CCE using a newly compiled, rich dataset of seabirds at-sea. We did not exhaust all of the comparisons possible, but rather focused on larger comparisons (e.g. compare on-shelf, close to the coast locations within a NMS to other regions). The breadth of these data permits the opportunity for further questions to be answered and our broad characterizations provide a baseline to develop a more thorough understanding of seabird distribution patterns in the CCE.

Although survey data were extensive and throughout the CCE, some areas had much higher survey effort (e.g., CalCOFI lines in the South region) compared to others (off-shelf in the North and off northern California/southern Oregon. We standardized data using survey effort, but additional surveys in these regions will better provide insights into spatial patterns of seabirds and ecological importance in these regions, as judged by seabird use. We also acknowledge that the drivers of regional differences (or lack of them) may be driven by seasonal or yearly differences. The addition of more fine scale surveys and the continuation of existing monitoring programs will continue to

contribute to our understanding of seabirds at-sea in the CCE, eventually to identify other areas of significance (cf. Nur et al., 2011).

Additional integrative research, such as occurred in GLOBEC (Batchelder et al., 2005) is needed to understand how these distinct communities function within their ecosystems, the relationship between seabird diversity and the diversity of their preferred prey, and if there is higher ecosystem functioning and stability within more diverse regions. There may also be differences in the patterns of diversity among different scales or additional regions. For example, are there differences in latitudinal patterns of diversity in off-shelf vs on-shelf regions? In addition, there now looms the question on how these patterns have changed in relation to prey resources, as affected by fisheries and climate (Ainley et al., 2018; Warzybok et al., 2018). What are the elements of intra- and interspecific (including fisheries) competition that are at play? In addition, we highlight the relationship between relative abundance and diversity and further work is needed to investigate this connection and test how the strength of this relationship changes over time. Understanding such fundamental ecological trends of seabirds in the CCE will help determine how climate change, impacts from fisheries, and overlap with offshore wind energy will impact their distribution, shifts in habitat, or changes in community overtime. It is important to continue to monitor seabird occurrence in the CCE using aerial and ship-based surveys because of the incredibly high prevalence of species arriving from breeding areas elsewhere in the Pacific (e.g., Spear and Ainley, 2008), where there may not be monitoring. Seabirds are exceedingly sensitive to ocean and food web change, and such data collection can highlight ecological change or areas in need of further protections.

Declaration of Competing Interest

The authors declare no conflict of interest.

Data availability

Some of this data are publicly available online (see referenced table below), remaining data may be requested from survey program principal investigators (Leirness et al., 2021, Appendix A, Table A-1, https://espis.boem.gov/final%20reports/BOEM_2021-014.pdf).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.jmarsys.2023.103887.

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