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Spatiotemporal trends of Seabirds in the California Current Ecosystem

A Dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy

in

Oceanography

by

Tamara M. Russell

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2024

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University of California San Diego

2024

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LIST OF ABBREVIATIONS

ACCESS	Applied California Current Ecosystem Studies
CalCOFI	California Cooperative Oceanic Fisheries Investigations
CBNMS	Cordell Bank National Marine Sanctuary
CINMS	Channel Islands National Marine Sanctuary
EEZ	Exclusive Economic Zone
ENSO	El Niño Southern Oscillation
GAM	Generalized additive model
GFNMS	Greater Farallones National Marine Sanctuary
MBNMS	Monterey Bay National Marine Sanctuary
MEI	Multivariate El Niño Southern Oscillation Index
MHW	Marine Heatwave
NMS	National Marine Sanctuary
NOAA	National Oceanic and Atmospheric Administration
NPGO	North Pacific Gyre Oscillation
OCNMS	Olympic Coast National Marine Sanctuary
ONI	Oceanic Niño Index
PCA	Principal component analysis
PDO	Pacific Decadal Oscillation
SST	Sea surface temperature

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ABSTRACT OF THE DISSERTATION

Spatiotemporal trends of Seabirds in the California Current Ecosystem

by

Tamara M. Russell

Doctor of Philosophy in Oceanography

University of California San Diego, 2024

Maria Vernet, Chair

Seabirds are integral predators in marine ecosystems and ideal indicators of ocean health and productivity. Along the west coast of North America, the dynamic California Current Ecosystem (CCE) provides vital foraging habitat to a variety of resident and migratory marine birds. The CCE is a complex current system that is highly variable over different spatial and temporal scales. Within the CCE, there is a web of different marine protected areas, including five National Marine Sanctuaries (NMS). These NMSs are found in the southern, central and northern portion of the CCE and provide well-defined regions to compare patterns and changes in seabird distributions throughout the CCE.

Although seabirds within the CCE are well studied, it is only recently that the majority of at-sea data on seabirds in the CCE have been consolidated into one dataset that spans from

1980 to 2017. In addition, there are broad spatial patterns and temporal trends that remain unresolved about seabirds within the CCE. Understanding such trends will provide valuable information on how seabird density, diversity, and community composition may change in association with natural environmental variability and long-term impacts from climate change. Here, I use the most extensive data available on seabirds at-sea in the CCE to: (1) describe broad spatial patterns of seabird indices of density, diversity and community composition, (2) determine fine scale temporal trends of these seabird indices within NMSs, and (3) use diverse sources of data, including citizen science, to investigate relationships between range shifts of tropical species and environmental variables.

I found higher seabird abundance and diversity within higher latitudes and nearshore habitats, and that west coast NMS capture important seabird habitats, with greater abundance and diversity than outside the sanctuary boundaries. However, I found that the abundance of avifauna within the NMS in the CCE has decreased since the 1980's, with greater declines in the south. Decreases were largely due to a decline in non-CCE breeding species, which have decreased in abundance within all five NMS. Relationships between the abundance of seabirds with environmental conditions varied among the NMS, indicating that there are distinct drivers within each of these regions. Through investigation into five tropical species within the Sulidae family, I found that all of these species had increased in the CCE and their rise in abundance was linked with the two intense marine heatwaves that occurred in the 2010's. With these increases, there were some species that persisted at high abundances, and others that did not remain at high numbers after warm water events. This research results in a detailed description of the spatial patterns of seabirds in the CCE, trends of seabirds within NMS, and documented the northward range expansion of five tropical species.

INTRODUCTION

Seabirds

Seabirds are integral species within ocean ecosystems. As top marine consumers, seabird habitat use is inextricably tied to the health of the marine ecosystem and they can serve as important ecosystem indicators (Hyrenbach & Veit 2003; Piatt et al., 2007; Ballance 2007; Sydeman et al., 2009; Lyday et al., 2015). The term "seabird" describes a diverse group of bird species that all share the following characteristic: they obtain all of their food from the ocean while flying, swimming, or diving (Ashmole 1971; Ainley 1980; Furness & Monaghan 1987). Within this diverse group, there exists many different foraging guilds, such as surface foragers, plunge divers, pursuit feeders, etc. (Ashmole 1971; Nelson 1980; Furness & Monaghan 1987). Seabird species can be generalists (feeding on many types of prey species) or specialists (feeding on a particular prey species or group), with main prey species including forage fishes, euphausiids and squid (Furness & Monaghan 1987; Jodice et al., 2003). As marine predators, seabird distribution at sea is tied to their prey, which typically have a patchy distribution as schooling or swarming species (Weimerskirch 2007). To adapt to these foraging conditions, seabirds have developed distinct foraging strategies and morphological attributes that allow them to be successful hunters at sea (Nelson 1980; Furness & Monaghan 1987). Their distribution, and patterns of abundance and diversity can be used as conservation planning and management tools, and provide deeper insights into the spatiotemporal dynamics of marine food webs and ecosystem health (Fauchald & Erikstad, 2002).

Although seabirds are highly conspicuous, spending the majority of their time above the sea surface, understanding their at-sea distribution and habitat use is challenging (Ballance 2007). Seabirds are highly mobile and can quickly cover large regions during migration or

transiting between foraging sites. There have been tremendous advances in biologging tags that can collect data on fine scale movements of individual birds, but there are limitations to the number of birds that can be tagged due to cost, access to catching the birds, and it can be labor intensive (Ballance 2007). To understand broad patterns and trends of seabird density (number per area) and habitat use at the population and community level, the data need to be collected in a way that covers a large area and collects information on all species present, essentially, integrating the fine-scale movements of individual birds. Ship and aerial transect surveys are an excellent ways to collect such data (Spear et al., 2004). Such surveys have been conducted within the CCE for many decades and are ideal for long-term analysis on seabird trends, as well as broad, persistent patterns of seabird distribution. Many of these ongoing survey efforts have been revisiting the same transect lines for many years, and these repeated and overlapping surveys smooth the variation of individual habitat use and environmental heterogeneity of potential drivers of distribution that exists at multiple scales throughout the CCE (Ballance et al., 1997; Hyrenbach et al., 2007). These large-scale data allow the broad spatial patterns of seabirds, along with a more accurate depiction of the community composition, to be determined (Ballance 2007).

California Current Ecosystem

The highly productive waters of the CCE contain vital foraging habitats for many resident and migratory seabird species. The CCE is a complex and productive eastern boundary upwelling ecosystem along the west coast of North America. This equatorward-flowing current stretches roughly 2,800 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 1,000 km

offshore (Kämpf & Chapman 2016; Checkley & Barth 2009). The intensity and timing of upwelling in the CCE is spatially and temporally variable on multiple scales. Within the CCE, the currents, Coriolis force, variability in the atmospheric pressure that affects winds, and shape of the coastline all impact upwelling in this region (Checkley & Barth 2009). Along the coasts, wind-driven upwelling supplies nutrients and supports high primary production, while broad and less intense upwelling occurs offshore due to wind-stress-curl-driven upwelling (Checkley & Barth 2009). The increased primary productivity in the CCE supports large commercial fisheries and foraging habitat for large numbers of marine predators, such as seabirds.

The spatiotemporal variability within this system results in heterogeneous distributions of primary productivity and foraging hotspots that impact the habitat use of marine predators. Across latitudes, there are three distinct regions within the CCE, the northern and central sector are divided by Cape Mendocino, and the central and southern portion are separated by Point Conception (Checkley & Barth 2009). These regions are distinct due to the differences in oceanography and many biological distributions are consistent with these boundaries, such as forage fishes (Ainley et al., 2015; Allen et al., 2006).

Along with latitudinal heterogeneity, there are also onshore-offshore gradients of oceanographic processes and primary productivity, with stronger upwelling and therefore, higher productivity along the coastal regions than offshore. In ecology, there is often an inverse relationship between primary production and diversity, with lower productivity (e.g., tropical regions) having higher diversity (Grady et al., 2019; Tittensor et al., 2010). The number of species (species richness) and the proportion of each species within a community (species evenness) are used to determine a region's diversity. In line with this principle, seabird diversity should be higher in more equatorial and offshore regions, yet this has not been examined in the

CCE (Grady et al., 2019; Jablonski et al., 2006; Tittensor et al., 2010). As seabird's prey connects these marine predators to changes in oceanographic conditions, understanding the patterns of seabird abundance and diversity, and the relationships between seabirds and environmental variables is extremely informative (Sydeman et al., 2015).

In addition to the spatial heterogeneity in the CCE, the ecosystem is highly variable on multiple temporal scales (Sydeman et al., 2009). Temporal modes of variation include diel and weather, seasonal, interannual to decadal and long-term changes (Checkley & Barth 2009). The intensity of the temporal variability also changes with latitude, for example, interannual variation is higher in lower latitudes, while decadal processes are more variable in higher latitudes (Lluch-Cota et al., 2003). Therefore, the correlations between oceanographic dynamics of different temporal scales with ecosystems in the CCE may differ between regions. Within the entire CCE, dynamics at the interannual to decadal scales are the dominant forces; in particular, El Niño–Southern Oscillation (ENSO) is a dominant mode here and can shift quickly and impact the entire CCE (Mysak 1986). ENSO is a recurring climate pattern that shifts from a cool phase (La Niña) to warm phase (El Niño) every two to seven years. These shifts affect water temperature, rainfall and winds that further impact upwelling intensity in the CCE. During El Niño, the easterly winds weaken, which decreases upwelling along the CCE resulting in less nutrients to drive ocean primary productivity. The decreased food availability and shift to warm water can affect predator foraging success, and affect the distribution of species that track sea surface temperature (SST; Mysak 1986; Velarde et al., 2015). Variation that occurs over multiple decades is often associated with major shifts in the ecosystem. Indices that characterize this longer-term variation are the Pacific Decadal Oscillation (PDO; Mantua et al., 1997), which describes SST patterns, and the North Pacific Gyre Oscillation (NPGO; Di Lorenzo et al., 2008),

which describes sea-level pressure over the North Pacific (Checkley & Barth 2009). In addition to the natural variability within the CCE, the impacts from climate change, such as long-term warming, acidification, and deoxygenation, are altering each of the dynamics mentioned above, and changing the overall oceanography and related ecosystems over time.

National Marine Sanctuaries in CCE

National Marine Sanctuaries (NMS) are regions of ecological or cultural importance with well-defined boundaries, making them ideal spatial units for monitoring ecosystem changes and testing ecological relationships. Although some protections are in place (restrictions on seabed mining, discharging materials, etc.), NMSs are open to recreational and commercial fishing, which may place additional pressures on these designated regions. Despite their limited protections, the designation and management of NMSs provide a framework that could facilitate the establishment of further legal protections (Nur et al., 2011; Smith et al., 2014; McGowan et al., 2013). Each sanctuary is re-evaluated every 5 years to assess the resources and environmental health of the region therefore research on patterns and trends within the NMS boundaries can aid sanctuary managers with condition reports and information for ecosystem-based management of the sanctuaries (McGowan et al., 2013). Understanding species distributions and trends within and outside of the NMSs can aid in the prioritization of conservation efforts and highlight gaps in protections or monitoring. Seabirds are not only inherently valuable and important members of the marine ecosystem, but their at-sea distributions can be used to highlight important ecological areas for other species or species groups that may have limited data or be difficult to detect (McGowan et al. 2013). The CCE contains five National Marine Sanctuaries (NMS) managed by National Oceanographic and

Atmospheric Administration (NOAA): Channel Islands (CINMS), Monterey Bay (MBNMS), Cordell Bank (CBNMS), Greater Farallones (GFNMS), and Olympic Coast (OCNMS). These sanctuaries are located in the southern (CINMS), central (MBNMS, CBNMS, GFNMS), and northern (OCNMS) region of the CCE.

Seabirds in California Current Ecosystem

The productive waters of the CCE provide vital foraging grounds for breeding seabird species, along with non-breeding resident and migratory seabirds; supporting an estimated 6.4 million birds annually (Briggs et al., 1987). The major seabird nesting locations in the CCE are on nearshore rocky islets and cliffs of Oregon and Washington, offshore islands located off the central coast (Farallon Islands, Año Nuevo Island) and Southern California (Channel Islands). The CCE provides nesting habitat to several endemic species, species that only breed within the CCE, such as Brandt's Cormorant and ashy storm-petrels (Sydeman et al., 2001; Carter et al., 2007). When breeding, seabirds are central place foragers, meaning that while they are nesting and rearing chicks their foraging range is constrained by the time needed forage and return to regularly provide for their offspring (Orians & Pearson 1979). The CCE also provides essential habitat to migratory seabirds. For example, the Pacific flyway, a major migratory pathway for birds, tracks the west coast of North America through the CCE region (Barton et al., 2018). The heterogeneity of the CCE also provides habitat to vagrant seabirds, species that are rarely seen within a region due to it being outside of its typical range and not because the species is inherently rare (Stake 2012; Roberson 2002; Taylor et al., 1994). The proportion of these different species, or the seabird community composition, within a region can indicate ecological importance and/or uniqueness within the broader CCE.

The seabirds of the CCE are well-studied, with several long-term research programs that continue to collect valuable data on seabirds at sea (Ainley 1976; Briggs et al., 1987; Tyler et al., 1993; Ainley et al., 2005; Spear & Ainley 2008). The substantial and ongoing seabird research in this region provides the opportunity for new data compilations to grow richer and more informative. Such extensive datasets allow broader understanding of seabird distributions, potential impacts from climate change and investigations into how species compositions are changing overtime. In addition, newly compiled data provide an opportunity to confirm previous findings and test ecological principles on seabirds in this region, such as latitudinal gradients of diversity and relationships between diversity and primary productivity. With the common use of seabirds as ecological indicators and their use in marine spatial planning, understanding broad patterns and temporal trends in their density and diversity are valuable for continued management of marine resources in the CCE.

RESEARCH OBJECTIVES

Chapter 1: Spatial patterns of seabirds in the CCE and west coast NMSs.

1. Describe spatial patterns of relative abundance, diversity, and community composition within the CCE and west coast NMSs.
2. Compare relative abundance, diversity and community composition inside NMSs boundaries with the broader CCE and their corresponding biogeographic regions.

Chapter 2: Trends in relative abundance and community composition of seabirds within National Marine Sanctuaries of the California Current Ecosystem

1. Describe temporal trends of relative abundance of CCE-breeding and non-CCE breeding seabirds, and select dominant species.
2. Investigate correlations between environmental variables with seabird trends
3. Assess the relationship between environmental variables and community composition

Chapter 3: The increase of tropical seabirds (Sulidae) in the California Current Ecosystem with warmer ocean conditions

1. Describe temporal trends of Sulidae distribution and abundance in the CCE
2. Investigate the relationship between environmental variables and Sulidae abundance.

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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.

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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

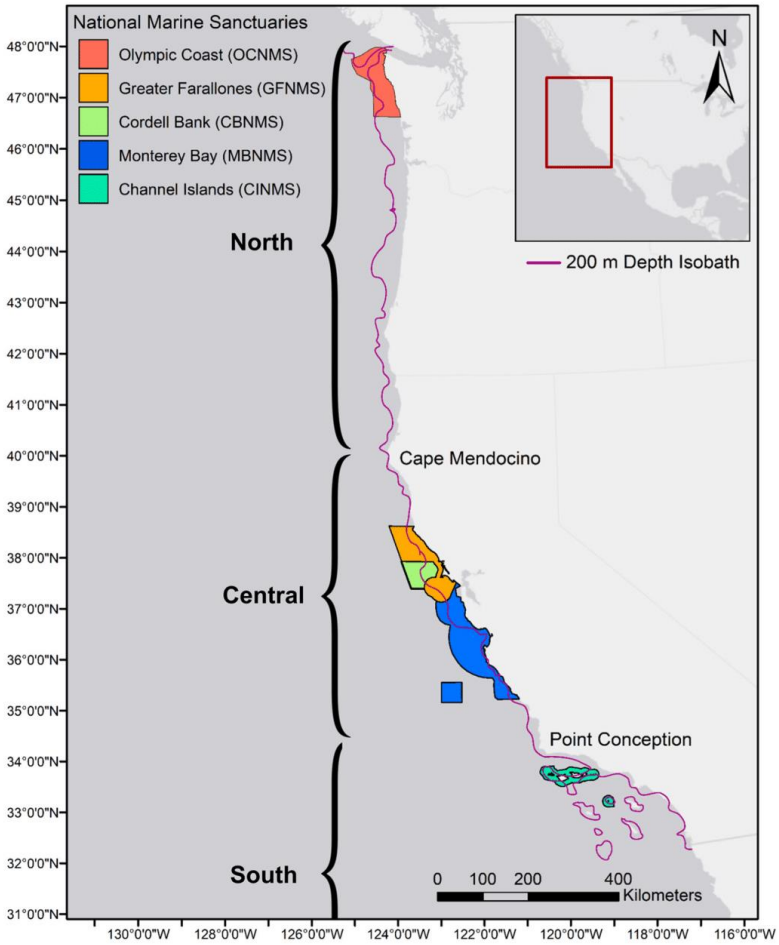


Fig. 1. The biogeographic regions and West Coast National Marine Sanctuaries within the California Current Ecosystem. The North and Central are separated by Cape Mendocino, California, while the Central and South are separated by Point Conception. The South bioregion extends south to Point Eugenia in 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
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 'specaccum,' 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

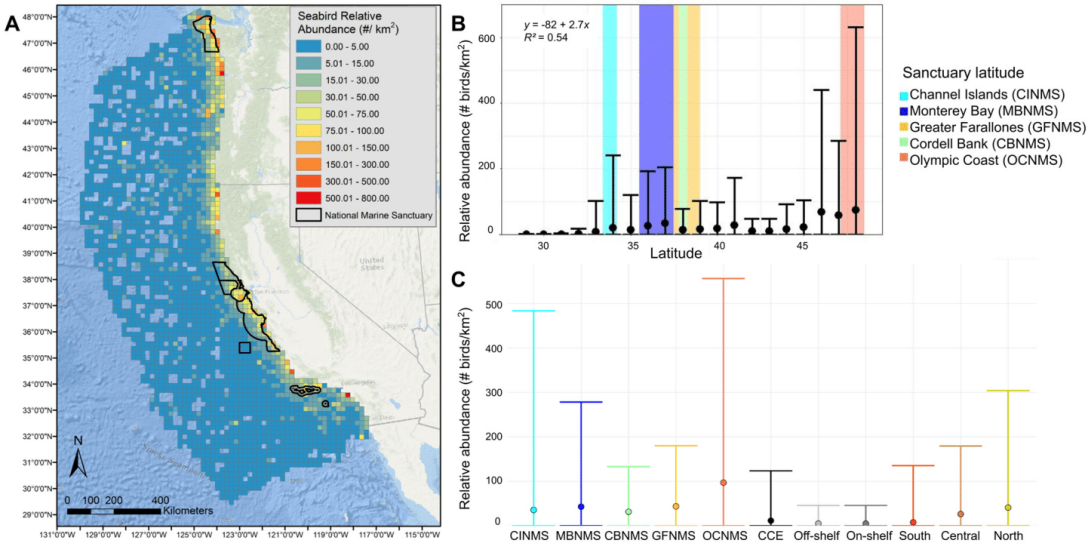


Fig. 2. (A) Map of average seabird relative abundance (number of birds/km^2) within 20 × 20 km^2 grids in the California Current Ecosystem. (B) Seabird relative abundance (mean +/− SD) within transect segments gauged for each degree of latitude. Colored bars indicate the latitudes overlapping each corresponding 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.

	Logistic Model		Gamma Model		Combined Model	
Region	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 ($F_{(1,1132)} = 1392$, $R^2 = 0.552$, $p < 2.2e\text{-}16$).

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).

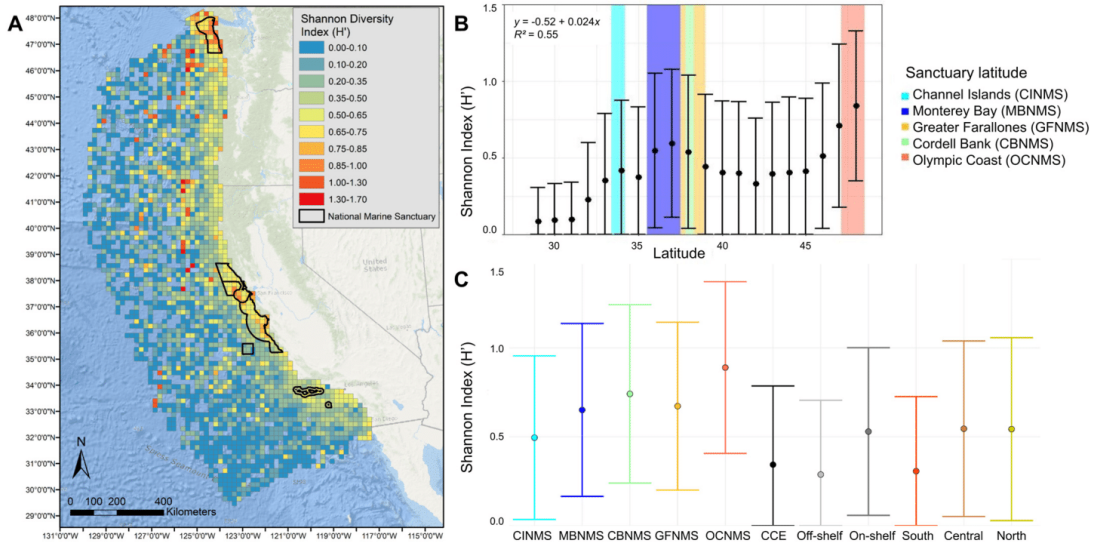


Fig. 3. (A) Map of average Shannon Index ('H) of transect segments within 20 × 20 km^2 grids within the California Current Ecosystem. (B) The Shannon Index (mean +/− SD) of seabirds within transect segments for each degree of latitude along the U.S. West Coast. Colored bars indicate the range of latitudes 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.

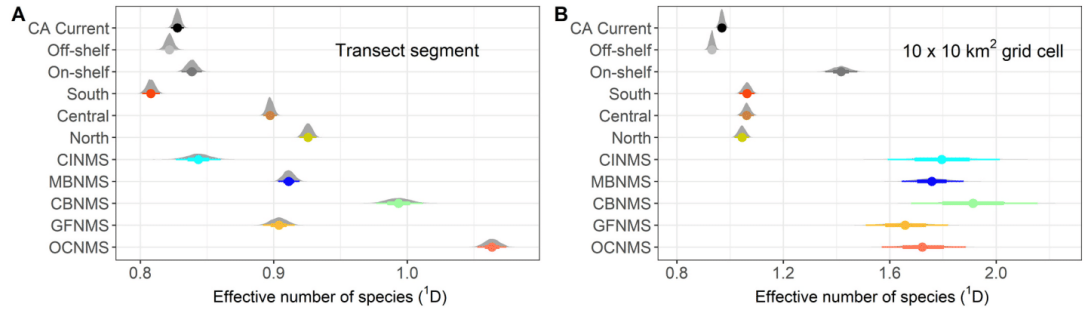


Fig. 4. The 95% credible intervals or posterior distributions of effective number of species (^{1}D) for each region. (A) Estimates from transect segment values, and (B) estimates from 10 × 10 km^2 grid cell values. Over fine spatial scales (i.e. transect segment) (A), the highest diversity is in the 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; $F_{(1,1288)} = 275.7$, $R^2 = 0.176$, $p < 2.2e\text{-}16$). The relationship between relative abundance and diversity decreased as scale decreased with no relationship between the two indices at the transect segment scale ($F_{(1, 80,534)} = 58.7$, $R^2 = 0.0007$, $p = 1.85e\text{-}14$).

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 ± 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

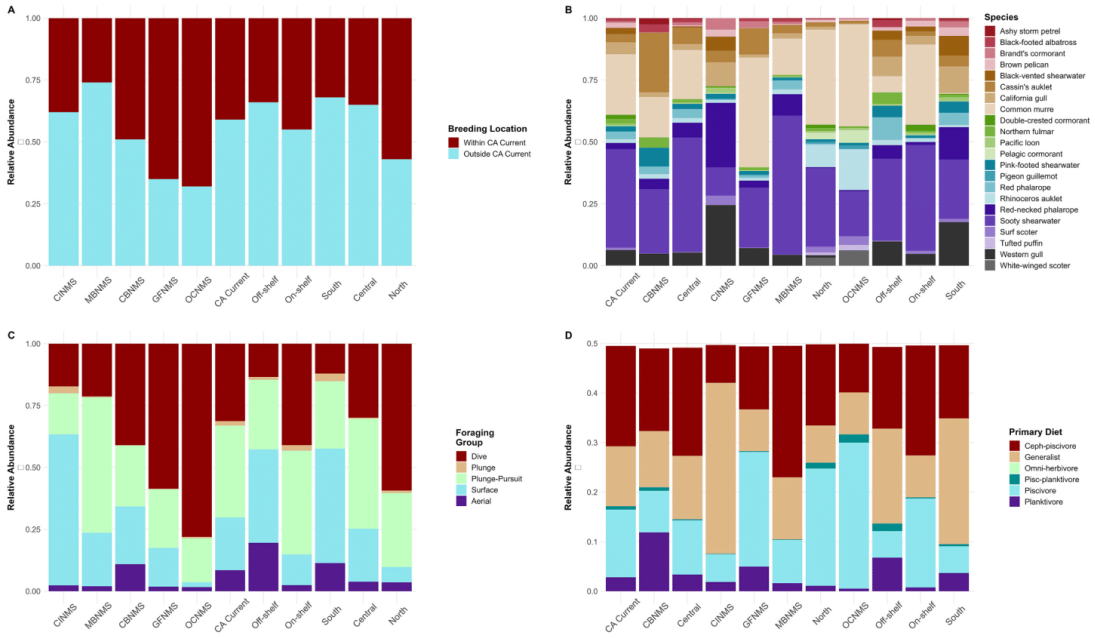


Fig. 5. Relative abundance plots of different seabird groups within National Marine Sanctuaries (NMS) and outside of NMS (CA Current, Off-shelf and On-shelf), by overall biogeographic regions (South, Central, North). Species and functional groups included are: (A) Birds that breed within and those that 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 other regions, except GFNMS. The other NMSs captured communities that were highly dissimilar to most regions, including other NMS.

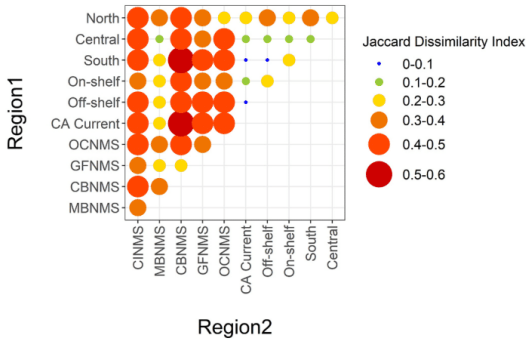


Fig. 6. Bubble heat plot of the Jaccard Dissimilarity Index among regions and National Marine Sanctuaries. This Index uses presence/absence data and calculates the proportion of unique species between communities. The more similar regions are to each other, the smaller the index value.

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

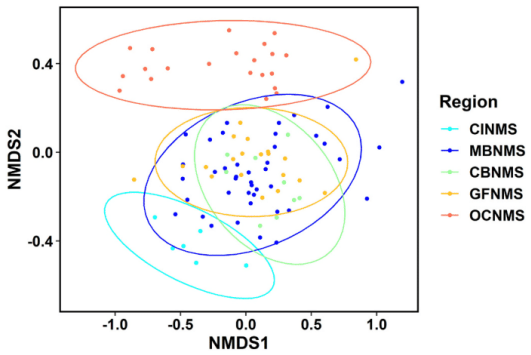


Fig. 7. Non-metric Multi-dimensional Scaling (NMDS) showing the ordination of the Bray-Curtis dissimilarity metric (a measure of community composition) within each 20 × 20 km^2 grid cell among the National Marine Sanctuaries (NMS). Points that are closer to one another are more similar to each other 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 km^2 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 km^2, largest grid size), relationships existed between diversity and relative abundance that were not apparent at finer spatial scales (~1.2 km^2, 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

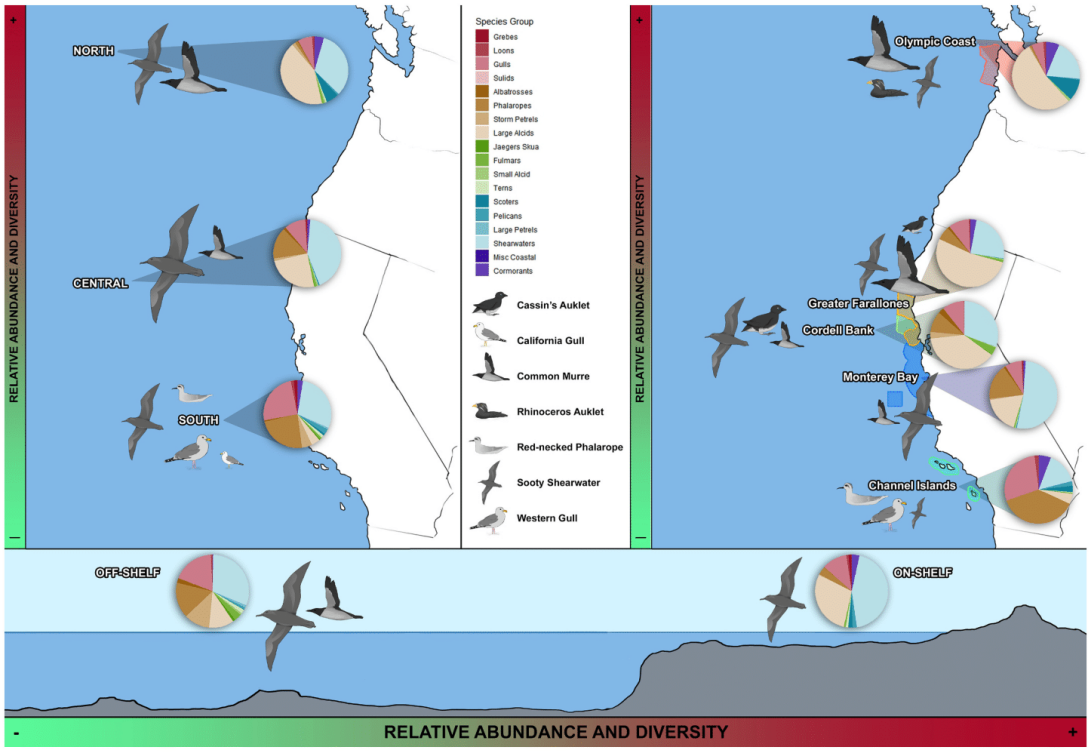


Fig. 8. Spatial patterns of seabirds in the California Current Ecosystem and within west coast National Marine Sanctuaries. The x and y axes of the maps highlight that seabird density (number of birds/km^2) and diversity (effective number of species) decrease both with latitude (north to south) and distance 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 subarctic 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.

Author contributions

T.M.R.: Conceptualization, Methodology, Formal analysis, Writing-original draft, Visualization.
A.S.: Software.
T.J.: Data Curation.
D.G.A.: Investigation.
L.B.: Conceptualization, Methodology, Supervision.
All authors involved in Writing-Review & Editing of manuscript.

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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).

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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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Chapter 1, in full, is a reprint of the material as it appears in the Journal of Marine Systems. Russell, Tamara M., Szesciorka, Angela R., Joyce, Trevor W., Ainley, David G., and Lisa T. Ballance, 2023. The dissertation author was the primary investigator and author of this paper.

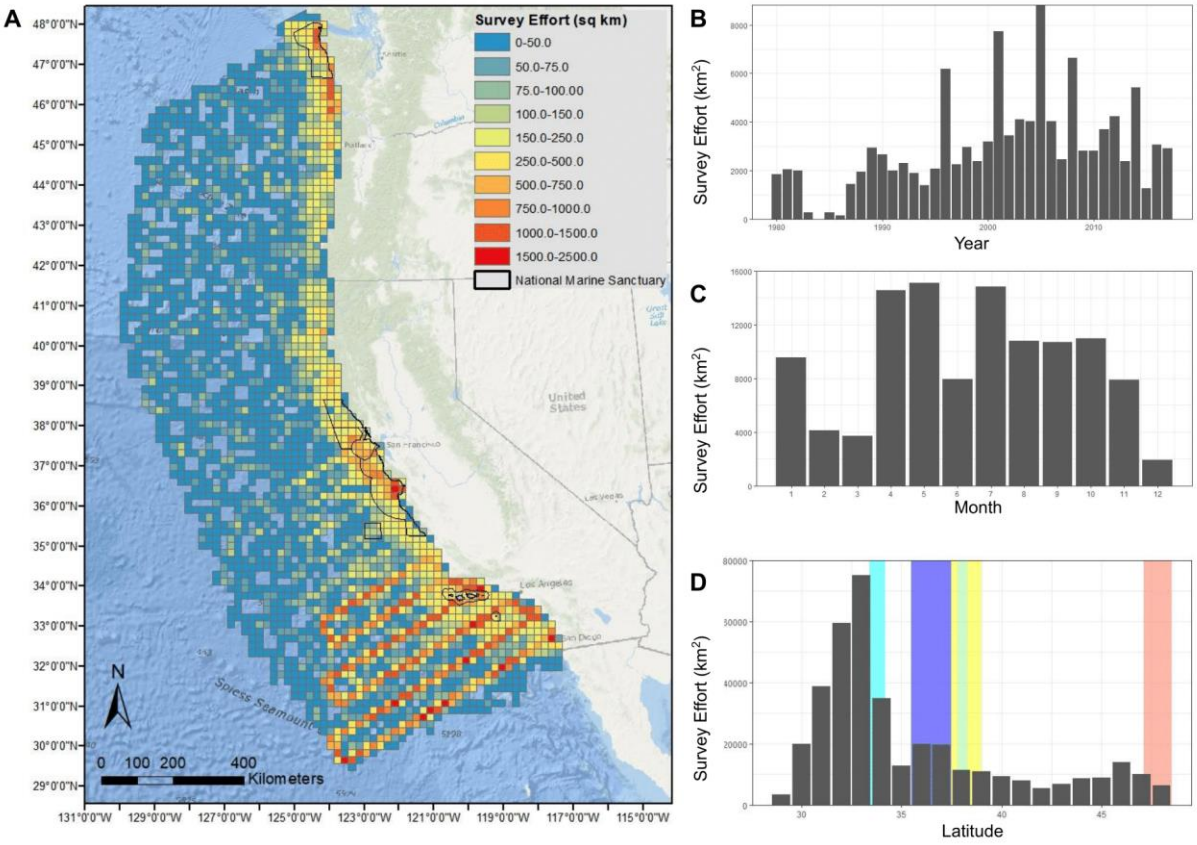


Figure S1.1: Summaries of survey effort (km^2). (A) Surveyed area within each 20 x 20 km^2 grid cell, (B) per year, (C) per month, and (D) per latitude. The colored bars indicate overlapping latitudes among the National Marine Sanctuaries (NMSs): Channel Islands NMS in teal, Monterey Bay NMS in blue, Greater Farallones NMS in yellow, Cordell Bank NMS in green, and Olympic Coast NMS in pink.

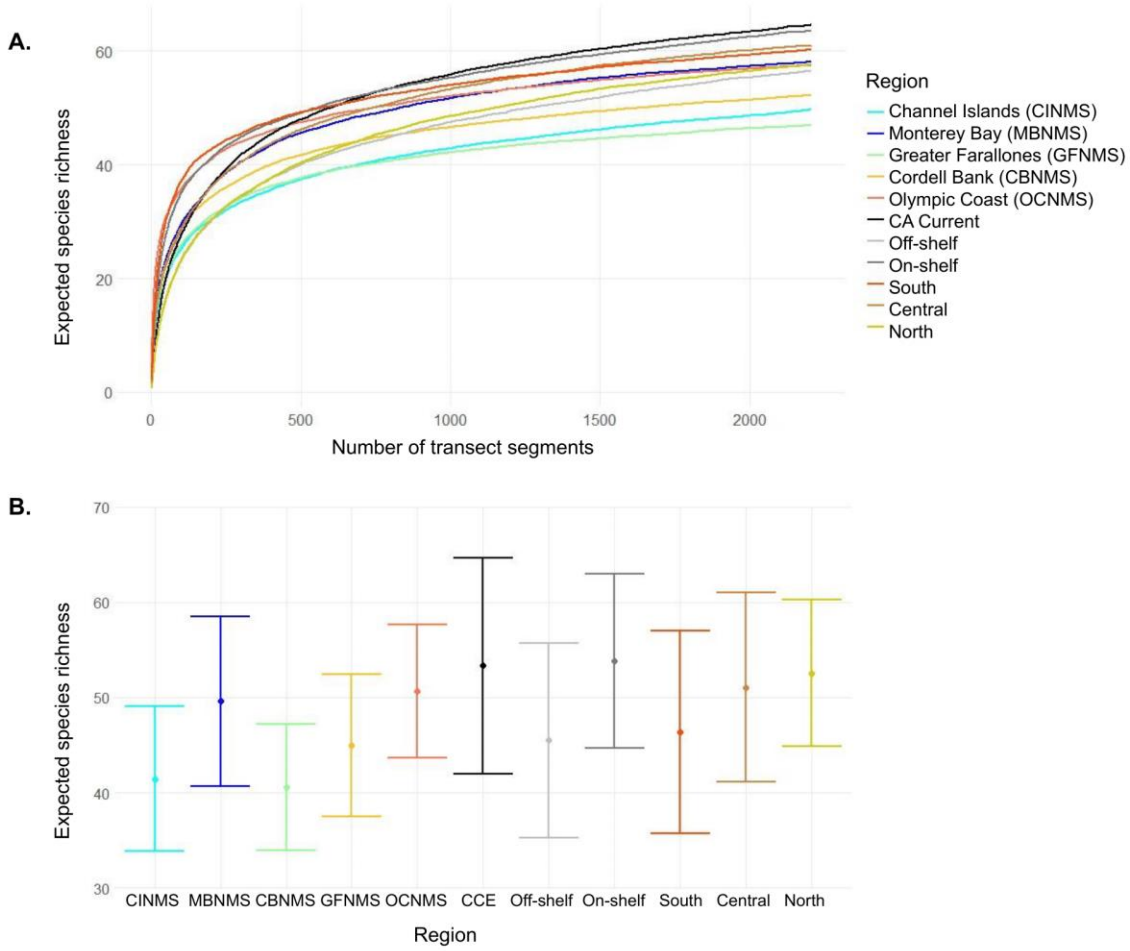


Figure S1.2: (A) Species accumulation curves, standardized to the minimum effort within a region (2,208 transect segments). (B) Mean and standard deviation of expected species richness (100 permutations) within each region.

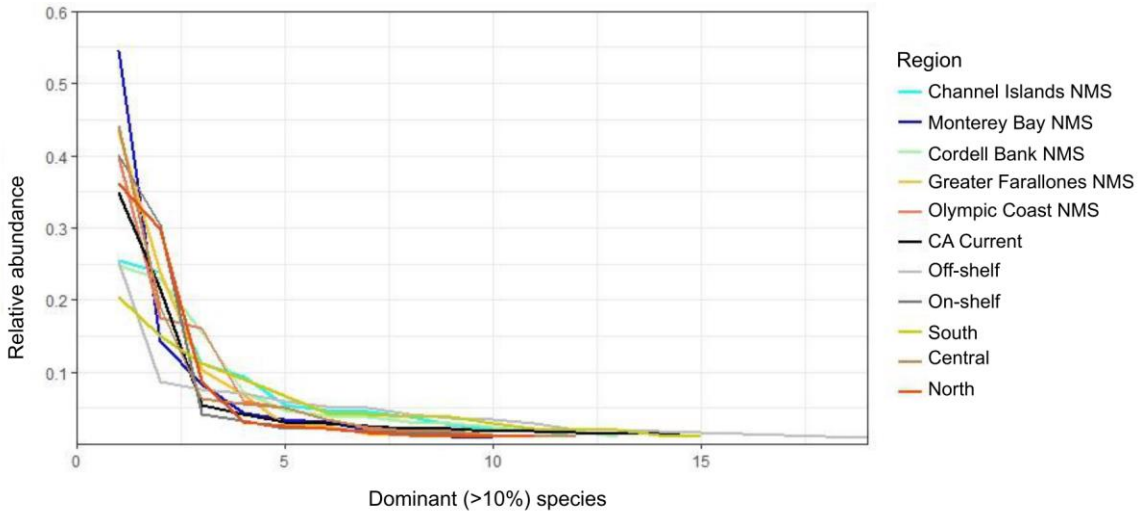


Figure S1.3: Whittaker plot of the relative abundance of the dominant (> 10%) species in each region. The slope of these lines indicates species evenness (e.g., greater slope, lower evenness).

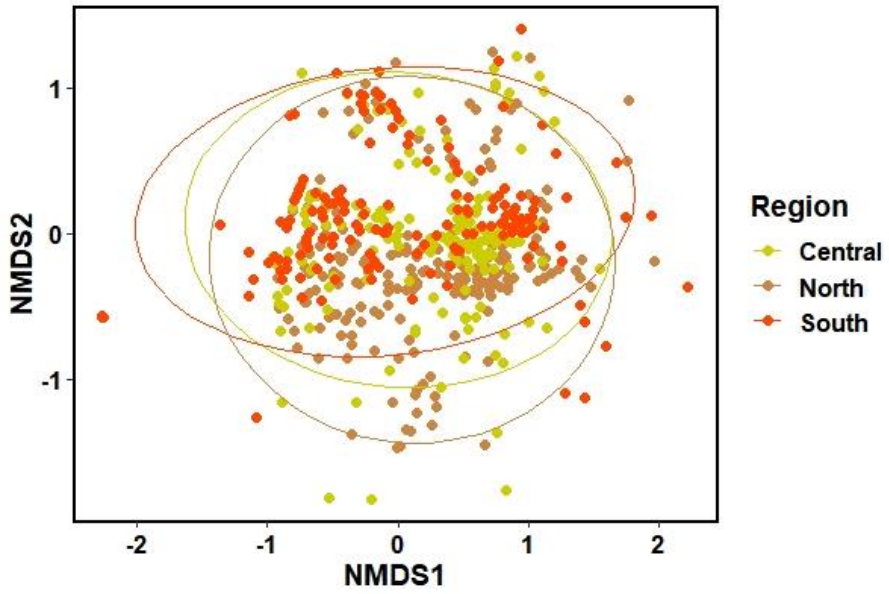


Figure S1.4: Non-metric Multi-dimensional Scaling (NMDS) showing the ordination of the Bray-Curtis dissimilarity metric within each 30 x 30 km^2 grid cell within each biogeographic region. Although there is some separation of points between the south and north, we did not find distinct communities through this analysis (Stress = 0.159, PERMANOVA: $F_{(4)} = 53.31$, $R^2 = 0.696$, $p < 0.001$). Displayed grid size selected for aesthetics, all three grid sizes showed no definitive trend among biogeographic regions.

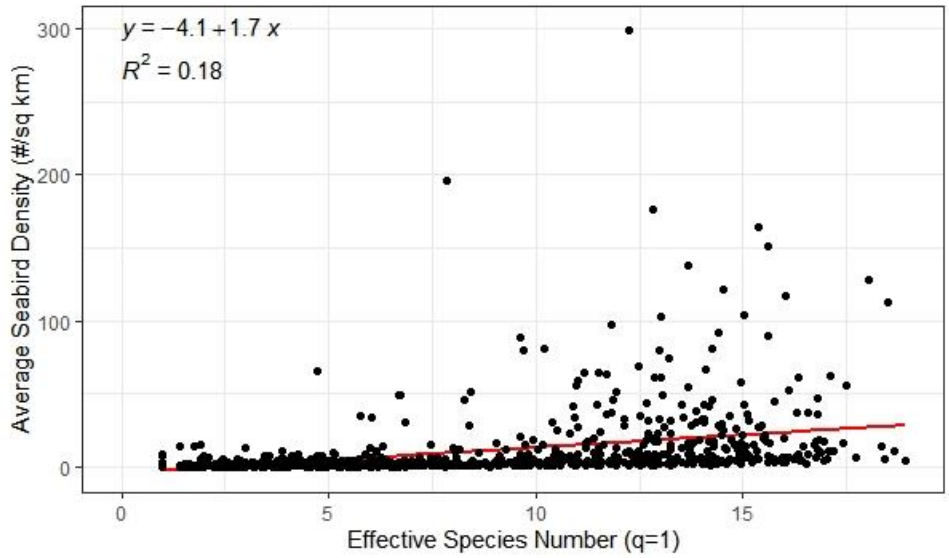


Figure S1.5: The relationship between the average seabird relative abundance (number of birds/km^2) and the effective number of species (^{1}D, the exp(Shannon index)) within 30 x 30 km^2 grid cells.

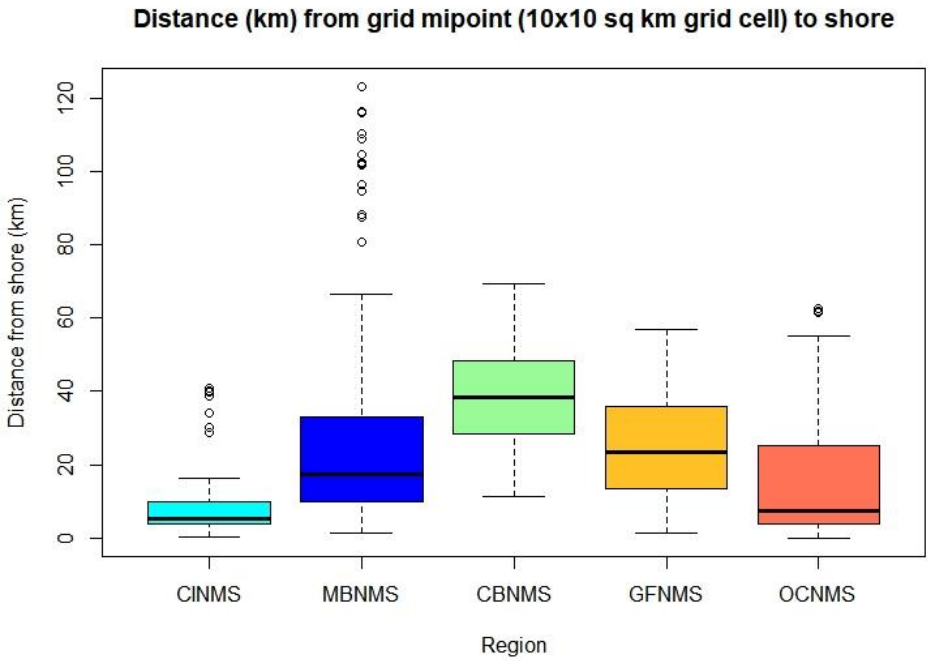


Figure S1.6: Distance (km) from the grid cell (10 x 10 km^2) midpoint from coastline within each National Marine Sanctuary (NMS). The outliers in MBNMS represent the Davidson Seamount.

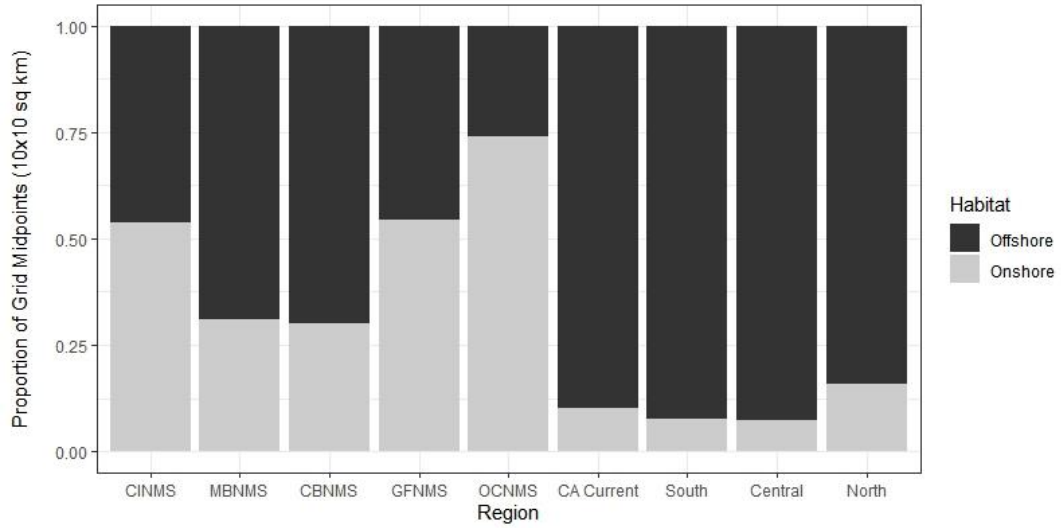


Figure S1.7: The proportion of grid cell (10 x 10 km^2) midpoints that are classified as On-shelf (< 200 m) or Off-shelf (> 200 m) within each National Marine Sanctuary, CA Current Ecosystem and biogeographic regions.

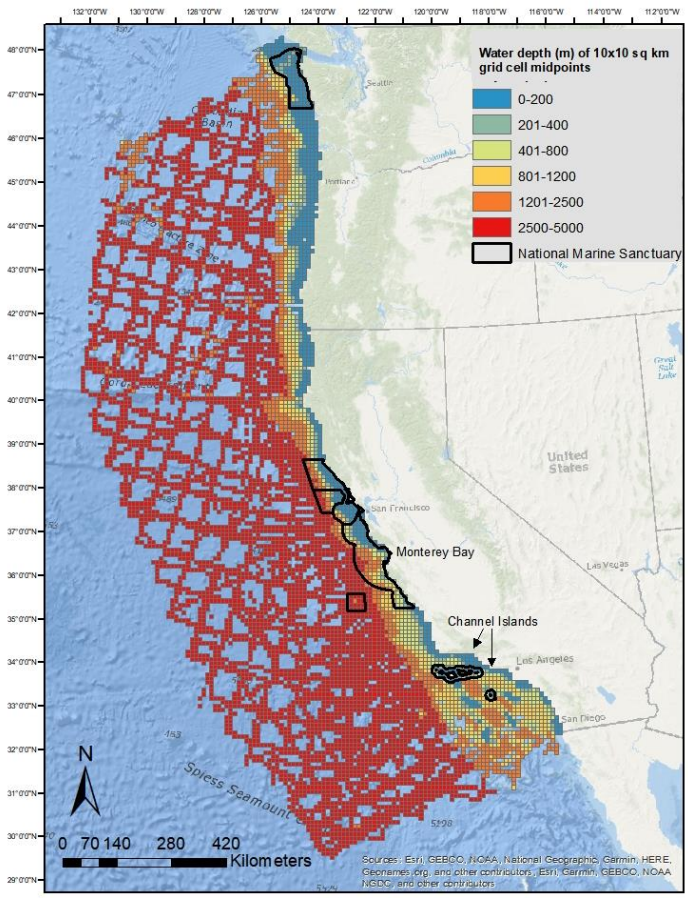


Figure S1.8: The water depth (m) of the midpoints of 10 x 10 km^2 midpoints. In the North, there is a wider continental shelf compared to southern regions. The continental shelf constricts to the coast at Monterey Bay, resulting in less On-shelf (< 200 m) habitat in the Central region and expands outward around the Channel Islands in the South.

R CODING

Density Hurdle Model

Modified code from https://seananderson.ca/2014/05/18/gamma-hurdle/

```
# hurdle_data is a dataframe of species counts (across columns) per region (rows)
# Change relative abundance values to only 0 and 1
hurdle_data$non_zero <- ifelse(hurdle_data$Relative_abundance > 0, 1, 0)
#Fit a logistic regression to predict the probability of a non-zero value
model1 <- glm(non_zero ~ 1, data = hurdle_data, family = binomial(link = logit))
#Fit a Gamma GLM with a log link to predict the mean of the non-zero data.
model2 <- glm(Density ~ 1, data = subset(hurdle_data, non_zero == 1), family = Gamma(link =
log))
m1_coef <- plogis(coef(model1)[[1]]) # mean probability of observing a non-zero value
M2_coef <- exp(coef(model2)[[1]]) #mean density when there is a non-zero value
plogis(confint(model1)) #confidence intervals
exp(confint(model2)) #confidence intervals
# take the two means, add them on a log scale and re-exponentiate them to get overall predicted
mean
pred <- exp(log(bin_coef) + log(gamma_coef))
```

Effective number of species Bayesian model

Using the brms package (Bürkner, 2017), we developed a model to produce the posterior distributions of effective number of species (^{1}D=exp(Shannon index)) between regions. We used a gamma distribution with log-link function and default priors (a flat prior over the values in the data), along with four chains with 2000 iterations each to draw our posterior distributions of effective number of species (^{1}D) per region. We had first tried several model priors, yet because of the extensive data, it did not affect our results.

```
library(brms)
#Data file is a column with region and Shannon Index for every transect segment (rows)
#Calculate effective number of species
Data$EffectiveSp <-exp(Data$Shannon)
set.seed(123)
Model  <- brm(
   EffectiveSp ~ 0 + Region,
  data = Data,
  family=Gamma(link="log"),
  cores = 4,
  chains = 4,
  iter = 2000,
  warmup = 1000)
```

ADDITIONAL CODING

Calculate Distance from shore for each grid midpoint.

```
# ‘grid_10’ is a dataframe with ‘grid_id’ as the midpoint ID, latitude and longitude of the midpoint
library(dplyr)
library(sf)
library(osmdata)
# Convert data to sf object
df <- grid_10 %>%
        st_as_sf(coords = c('lon','lat')) %>%
        st_set_crs(4269)
# Created bounding box and change coordinates to the extent of the data
bbox <- getbb ("california")
bbox[1,c(1:2)] <-c(-131.1, -117.2)
bbox[2,c(1:2)] <-c(29.8, 49.00)
# Pull the coastline within our bounding box. Along the U.S. west coast, the resolution is ~3 m.
coast <- opq (bbox = bbox, timeout = 100) %>%
        add_osm_feature (key = "natural", value = "coastline") %>%
        osmdata_sf (quiet = FALSE)
# Pull the coordinates from our grids and the coastline and make into data frame
p_df <- as.data.frame (st_coordinates(df))
line_df <-as.data.frame(st_coordinates(coast$osm_lines)[,1:2])
# Create row_ID's for midpoint and line data, and make into a simple, spatial feature
p_sf <- p_10 %>%
        mutate( id = row_number() ) %>%
        st_as_sf( coords = c("X", "Y"), crs=4269)
line_sf <- line_df %>%
        mutate( id = row_number() ) %>%
        st_as_sf( coords = c("X", "Y"), crs = 4269)
# Find the nearest distance between the line and the midpoint coordinates and calculate distance
near_dist <- p_sf %>%
        group_by( id ) %>%
        mutate( np = st_nearest_feature( geometry, line_sf),
       dist_np = as.numeric(st_distance( geometry, line_sf [np,] ) ) )
# Output is in meters. Next, connect this back to the main data by the ‘grid_id.’
```

Table S1.1: List of species codes, common names and scientific names of all species treated in this study. Their primary diet, foraging guild, whether they are a resident breeder in the CCE and species groups are listed. Foraging methods are surface, plunge, plunge-pursuit, diving, and aerial feeding. Some birds may utilize multiple types of foraging methods, we compared only primary foraging methods. The primary diets of seabirds are piscivores (only fishes), ceph-piscivores (cephalopods and fishes), planktivore (only zooplankton), pisc-planktivore (fishes and zooplankton), generalists (combination of fishes, squid, and zooplankton) and omni-herbivore (organisms and/or vegetation). Small and Large alcid separation is by survey detectability methods, not necessarily size.

Common Name	Scientific Name	Foraging method	Diet	Local Breeder	Species Group	Total number
Unidentified alcid	*N/A*	Dive	Pisc-planktivore	N/A	Large alcid	2175
Unidentified albatross	*N/A*	Surface	Ceph-piscivore	No	Albatross	6
Ancient murrelet	*Synthliboramphus antiquus*	Dive	Pisc-planktivore	No	Small alcid	1681
Arctic tern	*Sterna paradisaea*	Aerial	Piscivore	No	Tern	2869
Ashy storm petrel	*Oceanodroma homochroa*	Aerial	Planktivore	Yes, Endemic	Storm petrel	4413
American white pelican	*Pelecanus erythrorhynchos*	Surface	Piscivore	No	Pelican	1
Black-footed albatross	*Phoebastria nigripes*	Surface	Ceph-piscivore	No	Albatross	13352
Blue-footed booby	*Sula nebouxii*	Plunge	Piscivore	No	Sulid	1
Black-legged kittiwake	*Rissa tridactyla*	Surface	Generalist	No	Gull	10712
Black scoter	*Melanitta americana*	Dive	Generalist	No	Scoter	273
Black skimmer	*Rynchops niger*	Aerial	Piscivore	Yes	Tern	1
Black storm petrel	*Oceanodroma melania*	Aerial	Pisc-planktivore	Yes	Storm petrel	2736
Black tern	*Chlidonias niger*	Aerial	Pisc-planktivore	No	Tern	3
Bonaparte's gull	*Chroicocephalus philadelphia*	Surface	Generalist	No	Gull	11049
Brandt's cormorant	*Phalacrocorax penicillatus*	Dive	Piscivore	Yes	Cormorant	16293
Brant	*Branta bernicla*	Surface	Omni-herbivore	No	Misc	219
Brown booby	*Sula leucogaster*	Plunge	Piscivore	Yes	Sulid	31
Brown noddy	*Anous stolidus*	Aerial	Piscivore	No	Tern	5
Brown pelican	*Pelecanus occidentalis*	Plunge	Piscivore	Yes	Pelican	20221
Band-rumped storm petrel (Harcourt's)	*Oceanodroma castro*	Aerial	Planktivore	No	Storm petrel	3
Buller's shearwater	*Ardenna bulleri*	Aerial	Ceph-piscivore	No	Shearwater	2807
Buller's or pink-footed shearwater	*Ardenna sp.*	Aerial	Ceph-piscivore	No	Shearwater	6
Black-vented shearwater	*Puffinus opisthomelas*	Plunge-Pursuit	Ceph-piscivore	No	Shearwater	23652
Cassin's auklet	*Ptychoramphus aleuticus*	Dive	Planktivore	Yes	Small alcid	69364
California gull	*Larus californicus*	Surface	Generalist	No	Gull	53740
Caspian tern	*Hydroprogne caspia*	Aerial	Piscivore	Yes	Tern	5122
Clark's grebe	*Aechmophorus clarkii*	Dive	Piscivore	No	Grebe	32
Common loon	*Gavia immer*	Dive	Piscivore	No	Loon	1748
Common merganser	*Mergus merganser*	Dive	Piscivore	No	Misc	9
Common murre	*Uria aalge*	Dive	Piscivore	Yes	Large alcid	457201
Unidentified Cookilaria	*Pterodroma sp.*	Surface	Generalist	N/A	Large petrel	10

Table S1.1: List of species (continued)

Cook's petrel	*Pterodroma cookii*	Surface	Generalist	No	Large petrel	3323
Unidentified cormorant	*Phalacrocorax sp.*	Dive	Piscivore	N/A	Cormorant	11792
Common tern	*Sterna hirundo*	Aerial	Piscivore	No	Tern	299
Craveri's murrelet	*Synthliboramphus craveri*	Dive	Pisc-planktivore	No	Small alcid	85
Double-crested cormorant	*Phalacrocorax auritus*	Dive	Piscivore	Yes	Cormorant	13455
Unidentified duck	*N/A*	Dive	N/A	N/A	Misc	186
Eared grebe	*Podiceps nigricollis*	Dive	Generalist	No	Grebe	83
Elegant tern	*Thalasseus elegans*	Aerial	Piscivore	Yes	Tern	2752
Elegant or royal	*Thalasseus sp.*	Aerial	Piscivore	Yes	Tern	450
Flesh-footed shearwater	*Ardenna carneipes*	Plunge-Pursuit	Ceph-piscivore	No	Shearwater	75
Forster's tern	*Sterna forsteri*	Aerial	Piscivore	No	Tern	269
Franklin's gull	*Leucophaeus pipixcan*	Surface	Generalist	No	Gull	13
Fork-tailed storm petrel	*Oceanodroma furcata*	Aerial	Pisc-planktivore	Yes	Storm petrel	9828
Glaucous gull	*Larus hyperboreus*	Surface	Omni-herbivore	No	Gull	8
Unidentified grebe	*Podicipediformes sp.*	Dive	Piscivore	N/A	Grebe	168
Unidentified gull	*Larus sp.*	Surface	Generalist	N/A	Gull	39854
Greater scaup	*Aythya marila*	Dive	Omni-herbivore	No	Misc	7
Glaucous-winged gull	*Larus glaucescens*	Surface	Generalist	No	Gull	3762
Hawaiian petrel	*Pterodroma sandwichensis*	Surface	Ceph-piscivore	No	Large petrel	19
Heermann's gull	*Larus heermanni*	Surface	Generalist	No	Gull	5090
Herring gull	*Larus argentatus*	Surface	Generalist	No	Gull	10004
Horned grebe	*Podiceps auritus*	Dive	Generalist	No	Grebe	4
Horned puffin	*Fratercula corniculata*	Dive	Piscivore	No	Large alcid	42
Unidentified jaeger	*Stercorarius sp.*	Aerial	Piscivore	N/A	Jaeger/Skua	360
Parasitic/long-tailed jaeger	*S. parasiticus/S. longicaudus*	Aerial	Piscivore	N/A	Jaeger/Skua	15
Juan Fernandez petrel	*Pterodroma externa*	Aerial	Ceph-piscivore	No	Large petrel	1
Kelp gull	*Larus dominicanus*	Surface	Omni-herbivore	No	Gull	1
Kermadec petrel	*Pterodroma neglecta*	Surface	Ceph-piscivore	No	Large petrel	8
Laysan albatross	*Phoebastria immutabilis*	Surface	Ceph-piscivore	No	Albatross	588
Laughing gull	*Leucophaeus atricilla*	Surface	Generalist	No	Gull	1
Long-billed murrelet	*Brachyramphus perdix*	Dive	Pisc-planktivore	No	Small alcid	1
Leach's storm petrel	*Oceanodroma leucorhoa*	Aerial	Planktivore	Yes	Storm petrel	24357
Leach's or ashy storm petrel	*Oceanodroma sp.*	Aerial	Planktivore	Yes	Storm petrel	16
Least tern	*Sternula antillarum*	Aerial	Generalist	Yes	Tern	158
Unidentified loon	*Gavia sp.*	Dive	Piscivore	N/A	Loon	3363
Least storm-petrel	*Oceanodroma microsoma*	Aerial	Planktivore	No	Storm petrel	517
Long-tailed jaeger	*Stercorarius longicaudus*	Aerial	Piscivore	No	Jaeger/Skua	1167
Marbled murrelet	*Brachyramphus marmoratus*	Dive	Pisc-planktivore	Endemic	Small alcid	3521
Manx shearwater	*Puffinus puffinus*	Plunge-Pursuit	Piscivore	No	Shearwater	64
Mew gull	*Larus canus*	Surface	Generalist	No	Gull	330
Mottled petrel	*Pterodroma inexpectata*	Surface	Generalist	No	Large petrel	149

Table S1.1: List of species (continued)

Murphy's petrel	*Pterodroma ultima*	Surface	Generalist	No	Large petrel	239
Xantus's murrelet (Guadalupe)	*Synthliboramphus hypoleuca*	Dive	Pisc-planktivore	Yes	Small alcid	386
Xantus'/Craveri's murrelet	*S. hypoleuca/S. craveri*	Dive	Pisc-planktivore	Yes	Small alcid	295
Northern fulmar	*Fulmarus glacialis*	Surface	Generalist	No	Fulmar	20458
Parakeet auklet	*Aethia psittacula*	Dive	Planktivore	No	Large alcid	379
Parasitic jaeger	*Stercorarius parasiticus*	Aerial	Piscivore	No	Jaeger/Skua	694
Pacific loon	*Gavia pacifica*	Dive	Piscivore	No	Loon	13682
Parkinson's petrel (black petrel)	*Procellaria parkinsoni*	Surface	Ceph-piscivore	No	Large petrel	17
Pelagic cormorant	*Phalacrocorax pelagicus*	Dive	Piscivore	Yes	Cormorant	23531
Dark-rumped petrel	*P. sandwichensis/P. phaeopygia*	Aerial	Ceph-piscivore	N/A	Large petrel	5
Solander's petrel (providence)	*Pterodroma solandri*	Surface	Ceph-piscivore	No	Large petrel	2
Pink-footed shearwater	*Ardenna creatopus*	Aerial	Ceph-piscivore	No	Shearwater	32705
Unidentified phalarope	*P. fulicarius/P. lobatus*	Surface	Generalist	N/A	Phalarope	98924
Pigeon guillemot	*Cepphus columba*	Dive	Piscivore	Yes	Large alcid	7296
Pomarine jaeger	*Stercorarius pomarinus*	Aerial	Piscivore	No	Jaeger/Skua	2348
Unidentified Pterodroma	*Pterodroma*	Surface	Ceph-piscivore	No	Large petrel	60
Ring-billed gull	*Larus delawarensis*	Surface	Generalist	No	Gull	501
Red-breasted merganser	*Mergus serrator*	Dive	Piscivore	No	Misc	14
Red-billed tropicbird	*Phaethon aethereus*	Plunge	Ceph-piscivore	No	Tern	158
Red phalarope	*Phalaropus fulicarius*	Surface	Generalist	No	Phalarope	38942
Red-footed booby	*Sula sula*	Plunge	Piscivore	No	Sulid	1
Rhinoceros auklet	*Cerorhinca monocerata*	Dive	Piscivore	Yes	Large alcid	93255
Ringed storm petrel (Hornby's)	*Oceanodroma hornbyi*	Surface	Planktivore	No	Storm petrel	1
Red-necked grebe	*Podiceps grisegena*	Dive	Piscivore	No	Grebe	23
Red-necked phalarope	*Phalaropus lobatus*	Surface	Generalist	No	Phalarope	75833
Royal tern	*Thalasseus maximus*	Aerial	Piscivore	No	Tern	246
Red-throated loon	*Gavia stellata*	Dive	Generalist	No	Loon	1258
Red-tailed tropicbird	*Phaethon rubricauda*	Plunge	Ceph-piscivore	No	Tern	147
Sabine's gull	*Xema sabini*	Surface	Generalist	No	Gull	5445
Slaty-backed gull	*Larus schistisagus*	Surface	Omni-herbivore	No	Gull	1
Scripps's murrelet	*Synthliboramphus scrippsi*	Dive	Planktivore	Yes	Small alcid	92
Unidentified shearwater	*Puffinus sp.*	Dive	Ceph-piscivore	No	Shearwater	54578
Sooty/slender-billed shearwater	*P. griseus/P. tenuirostris*	Dive	Ceph-piscivore	No	Shearwater	13438
Unidentified skua	*Stercorarius sp.*	Surface	Generalist	No	Jaeger/Skua	239
Sooty shearwater	*Ardenna grisea*	Plunge-Pursuit	Ceph-piscivore	No	Shearwater	631235
Dark-rumped storm petrel	*Oceanodroma sp.*	Aerial	Planktivore	N/A	Storm petrel	3
Leach's/Harcourt's storm petrel	*O. leucorhoa/O. castro*	Aerial	Planktivore	Yes	Storm petrel	1
South polar skua	*Stercorarius maccormicki*	Surface	Generalist	No	Jaeger/Skua	273
Unidentified storm petrel	*Oceanodroma sp.*	Aerial	Planktivore	No	Storm petrel	708
White-rumped storm petrel	*Oceanodroma sp.*	Aerial	Planktivore	N/A	Storm petrel	4
Short-tailed shearwater	*Ardenna tenuirostris*	Plunge-Pursuit	Generalist	No	Shearwater	1081

Table S1.1: List of species (continued)

Short-tailed albatross	*Phoebastria albatrus*	Surface	Ceph-piscivore	No	Albatross	3
Stejneger's petrel	*Pterodroma longirostris*	Surface	Piscivore	No	Large petrel	24
Streaked shearwater	*Calonectris leucomelas*	Aerial	Ceph-piscivore	No	Shearwater	4
Surf scoter	*Melanitta perspicillata*	Dive	Generalist	No	Scoter	24652
Thick-billed murre	*Uria lomvia*	Dive	Piscivore	No	Large alcid	6
Arctic/common tern	*S. paradisaea/S. hirundo*	Aerial	Piscivore	No	Tern	419
Unidentified tern	*Tern sp.*	Aerial	Piscivore	No	Tern	272
Thayer's gull	*Larus gaucoides thayeri*	Surface	Piscivore	No	Gull	116
Unidentified tropicbird	*Phaethon sp.*	Plunge	Ceph-piscivore	No	Tern	7
Tufted puffin	*Fratercula cirrhata*	Dive	Pisc-planktivore	Yes	Large alcid	9698
Unidentified small alcid	*N/A*	Dive	Pisc-planktivore	N/A	Small alcid	4898
Unidentified kittiwake	*Rissa sp.*	Surface	Generalist	No	Gull	1
Unidentified large alcid	*N/A*	Dive	N/A	N/A	Large alcid	941
Unidentified puffin	*Fratercula sp.*	Dive	Pisc-planktivore	N/A	Large alcid	61
Unidentified scoter	*Melanitta sp.*	Dive	Generalist	N/A	Scoter	12796
Wandering albatross	*Diomedea exulans*	Surface	Generalist	No	Albatross	1
Western/Clark's grebe	*A. occidentalis/A. clarkii*	Dive	Piscivore	N/A	Grebe	88
Western grebe	*Aechmophorus occidentalis*	Dive	Piscivore	No	Grebe	11070
Western gull	*Larus occidentalis*	Surface	Generalist	Endemic	Gull	88196
Western x Glaucous-winged gull	*Larus occid. x glauces.*	Surface	Generalist	No	Gull	6583
Wilson's phalarope	*Phalaropus tricolor*	Surface	Generalist	No	Phalarope	1
Wilson's storm petrel	*Oceanites oceanicus*	Aerial	Pisc-planktivore	No	Storm petrel	15
Wedge-rumped storm petrel	*Oceanodroma tethys*	Aerial	Piscivore	No	Storm petrel	17
Wedge-tailed shearwater	*Ardenna pacifica*	Aerial	Piscivore	No	Shearwater	28
White-winged scoter	*Melanitta fusca*	Dive	Generalist	No	Scoter	27814
Yellow-billed loon	*Gavia adamsii*	Dive	Piscivore	No	Loon	1

Table S1.2: Summary of seabird indices in each region. The total survey effort (transect segment length*segment width), relative abundance (number of birds/km^2), expected species richness standardized to the minimum amount of transect segments (n=2208), Whittaker slope (great slope=lower species evenness), Pielou's Index (greater value=greater evenness), transect Shannon Index (H', greater value=higher diversity), transect effective number of species (the number of even species needed to obtain the Shannon Index).

Region	Total survey effort (km^2)	Relative abundance (#/km^2)	Expected species richness	Whittaker slope	Pielou's Index	Shannon Index	Effective number of species (^{1}D)
CINMS	4396.71	35.31± 448.3	49.38± 1.8	-0.234	0.564	0.50±0.46	1.83±0.92
MBNMS	18608.8	42.69±235.6	58.43± 2.34	-0.535	0.411	0.65±0.49	2.16±1.10
CBNMS	3160.51	31.23±101.6	40.59± 6.6	-0.224	0.591	0.74±0.50	2.38±1.20
GFNMS	6753.78	43.41±136.4	52.12± 1.7	-0.422	0.454	0.67±0.47	2.19±1.07
OCNMS	10055	96.81±459.5	57.56± 1.7	-0.390	0.482	0.89±0.48	2.72±1.28
CCE	164278	11.28±112.2	64.35± 2.9	-0.330	0.537	0.34±0.44	1.58±0.87
Off-shelf	145675	4.72±40.9	56.38± 3.1	-0.219	0.634	0.29±0.42	1.48±0.79
On-shelf	18602.7	53.24±283.7	63.84± 2.2	-0.389	0.450	0.53±0.47	1.91±1.01
South	114783.6	7.49±127.7	46.34± 10.6	-0.175	0.609	0.31±0.42	1.50±0.78
Central	63592.51	26.07±153.2	51.05±9.9	-0.428	0.461	0.55±0.49	1.96±1.06
North	41975.03	40.7±263.3	52.54±7.7	-0.350	0.482	0.54±0.52	1.98±1.15

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CHAPTER TWO

Trends in relative abundance and community composition of seabirds within National Marine Sanctuaries of the California Current Ecosystem

ABSTRACT

Climate change is altering the distribution and abundance of marine organisms. The California Current Ecosystem (CCE) has experienced increased water temperatures, climatic variability, and marine heatwaves due to anthropogenic climate change. This increased variability is likely to influence the distributions of predator abundance and diversity through direct and indirect impacts to their prey. Understanding how the avian predator community has changed can inform us about the underlying food web and how the structure of the ecosystem is changing in relation to the environment. Due to the dynamic nature of the CCE, testing overall trends and environmental relationships can be difficult across the entire ecosystem. However, previous research found that west coast NMSs had similar patterns of seabird relative abundance and community composition within their corresponding biogeographic regions (i.e., North, Central, and South); therefore, the NMSs provide smaller subunits along the latitudinal gradient of the CCE to test for temporal trends. Here, we use an extensive compilation of at-sea seabird sightings derived from 21 different survey programs to investigate how seabird relative abundance and community composition have changed over time (1980-2018) and in association with environmental conditions within NMS in the CCE. To disentangle patterns among different groups of seabirds, we investigate birds that breed within the CCE, those that breed outside, and three species that are commonly used as ecosystem indicators (common murres, sooty shearwaters, and Cassin's auklets). Overall, the abundance of avifauna within the NMS in the CCE has decreased since the 1980's, with greater declines in the south. These declines were

largely due to a decline in non-CCE breeding species, which had decreased in abundance within all five NMS. Relationships between the abundance of seabirds with environmental conditions varied among the NMS, indicating distinct drivers, such as warm water events like El Niño, within each of these regions. This work provides an overview of the trends in seabird abundance within NMS and highlights that comparisons to similar data from outside sanctuary boundaries are needed to fully understand these dynamics in order to use seabird data to better-determine habitat use and ecosystem health.

INTRODUCTION

Eastern boundary currents, like the California Current Ecosystem (CCE), are highly productive regions that cover only a small proportion of the world's oceans (Pauly & Christensen 1995). The enhanced upwelling in these areas have a bottom-up effect on productivity, making them hotspots of primary production and predator abundance (Arístegui et al., 2009, Block et al., 2011). Eastern boundary currents are also projected to be substantially impacted by climate change, due to shifts in atmospheric pressure that impact wind-driven upwelling intensity and timing, along with increased stratification due to warming (Bakun 1990, Bakun et al., 2015, Sydeman et al., 2014, García-Reyes et al,. 2015). However, the effects of climate change in the CCE are uncertain and vary regionally. For example, there may be upwelling-favorable winds in the northern CCE, and uncertainty of impacts in the south due to disproportionate land warming, which can shift the pressure gradients, and therefore winds (García-Reyes et al., 2015, Bakun 1990, Schwing & Mendelssohn 1997). Yet, this ecosystem has experienced warming and changes in the stratification, both of which can affect productivity (Schwing et al., 2010, Kämpf & Chapman 2016). Additionally, climate change has been linked with increases in extreme warm water events,

or marine heatwaves, which has severe impacts on several components of the ecosystem (Bond et al., 2015, Cavole et al., 2016).

Within the CCE, there are three well-established biogeographic regions –North, Central, South–each with distinct upwelling patterns and biological communities (Figure 1). There is seasonal upwelling in the North, strong, seasonal upwelling in the Central, and weak, persistent upwelling in the South (Checkley & Barth 2009). In addition to the spatial heterogeneity in the CCE, the ecosystem is highly variable on multiple temporal scales (Sydeman et al., 2009). Temporal modes of variation include diel and weather, seasonal, interannual to decadal and long-term changes (Checkley & Barth 2009). The intensity of the temporal variability also changes with latitude. For example, interannual variation is higher in lower latitudes, while decadal processes are more variable in higher latitudes (Lluch-Cota et al., 2003). Therefore, the correlations between oceanographic dynamics of different temporal scales with ecosystems in the CCE may differ between regions. Within the entire CCE, dynamics at the interannual to decadal scales are the dominant forces; in particular, El Niño–Southern Oscillation (ENSO), which can affect the entire CCE (Mysak 1986, McGowan et al., 1998). ENSO is a recurring climate pattern that shifts from a cool phase (La Niña) to warm phase (El Niño) every two to seven years. These shifts affect water temperature, rainfall, and winds that further impact upwelling intensity. During El Niño, the easterly equatorial winds weaken, which ultimately decreases upwelling along the CCE resulting in less nutrients to drive ocean primary productivity. The decreased food availability and shift to warm water can affect predator foraging success, and affect the distribution of species that track ocean temperatures (Mysak 1986, McGowan et al., 1998, Velarde et al., 2015). Variation that occurs over multiple decades, such as North Pacific Gyre Oscillation (NPGO), is often associated with major shifts in the ecosystem (Di Lorenzo et al., 2008). In addition to the natural variability

within the CCE, the impacts from climate change may alter these upwelling dynamics, which are projected to become more variable as the climate continues to change (Sydeman et al., 2009; Cai et al., 2021). Despite the uncertainty of overall changes in the CCE, it is clear that this ecosystem is likely to be affected by climate change. Already, significant impacts are becoming apparent, with a dramatic decline in zooplankton biomass in the Southern California Bight (SCB) over the past 60 years, which correlates with a warming trend that began in the 1940's (Roemmich & McGowan 1995, Kämpf & Chapman 2016). This increased variability and changing bottom-up processes in the food web may affect marine predators through direct and indirect impacts to their prey. Understanding how predator abundance and community composition have changed over time can inform us about the health and trajectories of an ecosystem.

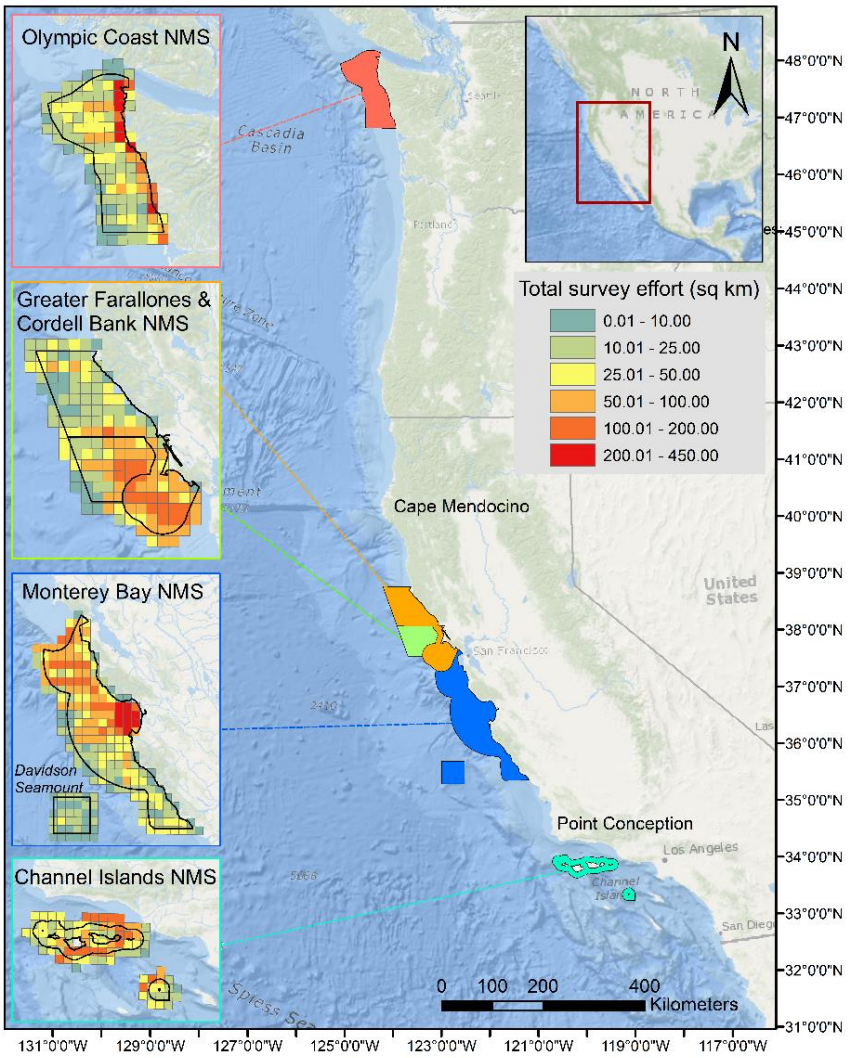


Figure 2.1: Location of the California Current Ecosystem and the five National Marine Sanctuaries (NMS) along the west coast of the United States. Map insets are 10x10 km^2 grids in each NMS with the total amount of survey effort (km^2) of data that was used in this study (Table S1). There are three biogeographic regions in the CCE (North, Central, and South). The North and Central are separated by Cape Mendocino, and the Central and South by Point Conception.

Seabirds are conspicuous marine predators, whose distribution can reflect underlying patterns of the marine ecosystem they are a part of and rely upon for their prey. The productive waters of the CCE provide vital foraging grounds for breeding seabird species, along with non-breeding resident and migratory seabirds (Briggs et al., 1987). The major seabird nesting locations in the CCE are on offshore islands located off the central coast (Farallon Islands, Año Nuevo

Island) and Southern California (Channel Islands), and along rocky cliffs and rocky outcrops along Oregon and Washington (Carter et al., 1995; Suryan et al., 2012). When breeding, seabirds are central place foragers, meaning that while they are nesting and rearing chicks their foraging range is constrained by their ability to travel for foraging and return to regularly provision for their offspring (Orians & Pearson 1979). The CCE also provides essential habitat to migratory seabirds. For example, the Pacific flyway, a major migratory pathway for birds, tracks the west coast of North America through the CCE region (Barton et al., 2018). Therefore, local seabird abundance can reflect conditions that would support resident, breeding birds and conditions that would attract and retain migratory or non-breeding species.

The seabirds of the CCE are well-studied, with several long-term research programs that continue to collect valuable data on seabirds at sea (Ainley 1976, Briggs et al., 1987, Tyler et al., 1993, Hyrenbach & Veit 2003, Ainley et al., 2005, Ford et al., 2004, Spear & Ainley 2008). Such extensive datasets allow additional and new understandings of seabird trends, the influence of environmental conditions on seabird abundance and communities, and potential impacts from climate change. With the common use of seabirds as ecological indicators and their use in marine spatial planning, understanding these trends are valuable for continued management of marine resources in the CCE (Parsons et al., 2008; Piatt, Sydeman & Wiese 2007; Roletto, Lindquist, & Broughton 2016).

Although monitored seabird populations worldwide have declined considerably since the mid-1900s, regional research within the CCE has shown variable trends in seabird density (Paleczny et al., 2015, Hyrenbach & Veit 2003). During a short-term study, overall seabird density throughout the CCE had declined by 40% from 1987 to 1994, which occurred alongside increases in SST (Veit et al., 1996). In the southern sector, there has been an overall decrease in seabird

density, with an estimated 2 % decrease per year between 1987 and 2011 (Mason et al., 2007, Sydeman et al. 2009, Sydeman et al. 2015). In contrast, studies have found seabird density to be increasing in northern regions (Sydeman et al., 2009).

There have also been variable trends in regional avifauna within the CCE. Some studies have found increases in species richness in the northern sector and decreases within the SCB region (Sydeman et al., 2009, Hyrenbach & Veit 2003, Santora & Sydeman 2015). In particular, avifauna in the southern sector may be highly impacted by increasing water temperatures. The SCB seabird community has shifted from a cool, "high productivity" community to a warm, "low productivity" community (Hyrenbach & Veit 2003). The complex oceanography of the CCE complicates analyses, while finer spatial scale analyses can be used to examine regional trends and environmental relationships and inform larger-scale analyses in the future.

The avifauna in the CCE experience high species dominance (i.e., species that make-up a high proportion of the community), several of which are used as ecosystem indicators, and some of these dominant species have shown significant shifts over time (Ainley et al., 2005). Throughout the CCE, multiple studies found that three cool water, dominant species had decreased over time; Sooty shearwaters (*Puffinus griseus*), Cassin's Auklet (*Ptychoramphus aleuticus*), and Rhinoceros Auklet (*Cerorhinca monocerata*; Hyrenbach & Viet 2003, Veit et al., 1996, Mason et al., 2007, Sydeman et al., 2009). Sooty shearwaters are important members of the seabird community as they are one of the most abundant seabird species in the CCE (Briggs et al., 1987). There was an estimated 90% decrease in sooty shearwaters between 1987 and 1994 in the overall CCE (Veit et al., 1997, Mason et al., 2007), yet, more recent studies have not been able to detect if this decrease has accelerated, reversed, or become stable (Sydeman et al., 2009). The occurrence of marine heatwaves, which are predicted to increase with the changing climate, have caused mass mortality

events of breeding seabirds, such as Cassin's auklets and common murres (*Uria aalge*), along the west coast and are likely to exacerbate any potential density declines in the CCE (Jones et al., 2018, Piatt et al., 2020).

As seabirds are highly mobile and respond to short and long scale variability, detecting trends in seabird density and community composition requires repeated and long-term surveys that can distinguish temporary patterns from long-term trends. Due to the dynamic nature of the CCE, testing overall trends and environmental relationships can be difficult across the entire ecosystem. However, the placement of west coast National Marine Sanctuaries (NMS) provides smaller-scale areas with distinct boundaries within each of the CCE biogeographic region (i.e. North, Central, and South) that capture similar regional abundance and diversity patterns as observed in their corresponding biogeographic region (Russell et al., 2023; Nur et al., 2011). Therefore, the NMS provide unique subunits along the latitudinal gradient of the CCE that allow clearer analysis of temporal trends in abundance and diversity, and their relationships with the environment. Here, we examine how seabird relative abundance and community composition have changed overtime and in association with environmental conditions within the U.S. west coast NMS. Seabirds are diverse, and there are two main drivers affecting the presence of seabirds in the CCE; breeding and foraging. Species may either breed in the CCE and forage here only during breeding or are restricted to the CCE year around, or they breed outside of the CCE and migrate here to feed during the juvenile or non-breeding stage (Ainley 1980). These two groups may have different drivers of their abundance and relationship to the environment; therefore, we parse seabirds into CCE-breeding and non-CCE breeding species to investigate their potential trends separately. We also investigate trends for three species that are commonly used in management as ecosystem indicators: common murres, sooty shearwaters, and Cassin's auklets.

METHODS

Survey region

The CCE spans from the U.S.-Canada border south to Baja California and has three distinct biogeographic regions (Kämpf and Chapman, 2016; Checkley and Barth, 2009). The North and Central regions are separated by Cape Mendocino, while the Central and South regions are separated by Point Conception, and the South extends down to Point Eugenia. Within each of these biogeographic regions, there is at least one NMS, which are managed by the National Oceanographic and Atmospheric Administration (NOAA) Office of National Marine Sanctuaries (Figure 1).

In the South, the Channel Islands NMS (CINMS; 3,807 km^2) is located offshore within the Southern California Bight. The CINMS contains five of the northern Channel Islands –Anacapa, Santa Cruz, Santa Rosa, San Miguel, and Santa Barbara– which are breeding locations for twelve seabird species (ONMS 2019**).** The CINMS is south of the transition zone of Point Conception, and contains cool, nutrient-rich waters from the north and warm currents from the south (ONMS 2019**)**.

There are three NMSs in the Central region: Monterey Bay (MBNMS), Cordell Bank (CBNMS), and Greater Farallones (GFNMS). MBNMS (15,783 km^2) includes nearshore and above-canyon waters of the Monterey Bay, as well as the offshore location of Davidson's Seamount (ONMS 2009A). In addition to complex bathymetry, MBNMS is a region of enhanced upwelling due to the shape of the bay's coastline. Davidson seamount is located 1,250 m below the sea surface and is one of the largest seamounts in U.S. waters, at approximately 42 km long, 20 km wide, and 2,280 m above the seafloor (ONMS 2009A; Newton & DeVogelaere 2013). Although it is a deep seamount, and likely does not affect local upwelling, it enhances primary productivity within its vicinity due to horizontal flux from internal waves and results in

aggregations of animals over the seamount (Lucas et al., 2011, Newton & DeVogelaere 2013). CBNMS (3330 km^2) is located offshore from Point Reyes, California where it borders both MBNMS to the south and Greater Farallones NMS (GFNMS) to the west. CBNMSs main feature is Cordell Bank, an underwater, rocky seamount just below the ocean's surface (37 m) that drops off at the continental slope to over 3,600 m (ONMS 2009B). The CBNMS encompasses the seamount, continental shelf and deep offshore waters, providing a rich variety of habitats (McGowan et al., 2013, Haver et al., 2020). GFNMS (3,312 km^2) is located off the coast of San Francisco, California and includes coastal and offshore waters around the Farallon Islands, which hosts the largest concentrations of breeding seabirds in the contiguous United States (ONMS 2010, McGowan et al., 2013).

In the North, OCNMS (8,572 km^2) is located along the coast of northern Washington State and includes coastal and offshore waters spanning across the continental shelf and the heads of three submarine canyons (ONMS 2008). Within the sanctuary boundaries, are three national wildlife refuges, collectively called the Washington Island National Wildlife Refuges. These refuges protect over 600 offshore rocky outcrops and islands that provide nesting habitat for 16 seabird species (ONMS 2008).

Seabird data

We used data on the at-sea distribution of seabirds collected using the ship, strip transect method (Tasker et al., 1984; Ballance, 2007) or aerial, strip survey method (Mason et al. 2007). There have been systematic surveys in the CCE for decades and Leirness et al. (2021) compiled data from 21 of these into a common format (1980-2017). We enhanced the temporal resolution of these data with additional years from California Cooperative Oceanic Fisheries Investigations (CalCOFI; 2016-2018), Applied California Current Ecosystem Studies (ACCESS; 2016-2018),

and NOAA's Southwest Fishery Science Centers California Current Ecosystem Survey (CCES; 2018) resulting in almost 40 years of data (1980 to 2018; Table 1S). We then extracted data from this compilation from within each of the five west NMS boundaries (Figure 1). In certain NMSs, there were limited surveys done earlier in the dataset, so those were truncated; thus, two NMS have a shorter time span, OCNMS (1989 to 2018) and CINMS (1987 to 2018). Data from strip surveys from both aircraft- and vessel-based platforms provide species counts and the number of birds per km^2 (Henkel et al., 2007). During compilation, the species codes were standardized across the different surveys. We subdivided observations into smaller segments (4 km plus transect ends) and assigned coordinates to each segment midpoint. To prevent overestimates of abundance, we only used transect segments over 0.5 km long (overall segment mean=3.95 km).

We used data on species and species groups to calculate seabird relative abundance (number of birds/ km^2). These calculations did not correct for the effect of seabird movement through the transect ("seabird flux"; Spear et al., 1992, Clarke et al., 2003), the potential effect from ship avoidance or attraction, or differences in single vs. multiple observers (Spear et al., 2004); therefore, the relative abundance calculations are density estimates. To calculate the area surveyed, the transect length was multiplied by the transect width, which varied by survey. The transect width used during data collection is either set at a default width for the survey program or determined beforehand based on the species (e.g., small vs. large species), ocean conditions, visibility, or height of the observer above the sea (Ballance, 2007). To account for these differences, we calculated the relative abundance of small and large species separately for each transect segment, and then used the sum of these two relative abundance amounts.

Seabird abundance and diversity in a region can vary depending on species that breed and migrate through a region. Therefore, we accounted for this by separating species into those that

breed within the CCE and those that do not. Species were considered a CCE-breeding species if there was documented breeding within one of our biogeographic regions during our study period, and a non-CCE breeding species if there was no documentation of sustained breeding (Table S2). We only included species groups (categories for birds that could not be identified to species) if all species considered in that group were CCE or non-CCE breeding species. In addition, we also investigated trends among three abundant species that are often used as ecosystem indicators – common murres, sooty shearwaters, Cassin's auklets. Common murres are a CCE-breeding species that feeds on forage fishes and euphausiids (krill), and they migrate from central California up through Alaska (Ainley et al., 1996; Sydeman et al., 2001). Cassin's auklets are a small, diving seabird that breeds in the CCE and feeds on a variety of zooplankton and larval fishes (Sydeman et al., 2001). Sooty shearwaters are a long-distance migratory species in the CCE, breeding off New Zealand and migrating to the CCE during the non-breeding season to feed on euphausiids, squid, and forage fishes (Briggs and Chu, 1986; Adams et al., 2012).

Environmental data

As seabirds are indirectly linked to the environment through conditions that affect their prey, seabird distributions can correlate with environmental variables (Ainley and Hyrenbach, 2010, Ainley et al., 2005, Serratosa et al., 2020). As each region has distinct oceanographic conditions, each NMS may have different environmental conditions that affect the abundance and distribution of important seabird prey, such as forage fishes, squid and krill. To investigate potential environmental linkages with seabirds, we used monthly means of large-scale climate indices and local-scale sea surface temperatures (SST; Figure 1S).

The climate and upwelling indices used in analyses are the Pacific Decadal Oscillation (PDO), Oceanic Niño Index (ONI), North Pacific Gyre Oscillation (NPGO), Multivariate El Niño-

Southern Oscillation (ENSO) INDEX (MEI) and the Bakun Upwelling Index. The PDO is a long-lived pattern of ocean-atmosphere variability that is calculated from the first principal component of monthly SST north of 20˚C in the North Pacific. The PDO describes SST patterns within the North Pacific Basin, with positive values indicating warm conditions along the west coast of North America, and negative values indicating cool conditions (Mantua, 1999; Wen et al., 2014). The ONI is an indicator for ENSO climate pattern, that is calculated by a three-month running average of SST over the Niño 3.4 region (5˚N-5˚S, 120˚-170˚W), where high values (> 0.5) are El Niño, or warmer conditions, and lower values (< -0.5) are La Niña, or cooler conditions (NOAA, 2023A). The NPGO is calculated from sea surface height anomalies across the North Pacific (180°W–110°W; 25°N–62°N; Di Lorenzo et al., 2008). The NPGO describes sea-level pressure over the North Pacific and correlates with patterns of water characteristics in the CCE (e.g., salinity, nutrients and chlorophyll-a; Di Lorenzo et al., 2008). MEI is an alternative index that describes ENSO, by combining oceanic and atmospheric conditions: sea level pressure, SST, surface winds and longwave radiation across the tropical Pacific basin (30°S-30°N and 100°E-70°W; NOAA 2023B). The MEI, PDO, NPGO, and ONI data were downloaded using the data retrieval package, 'rsoi' (Albers 2023; version 0.5.5). The Bakun Upwelling Index calculates Ekman transport to estimate upwelling intensity, with positive values implying upwelling and negative values indicating downwelling (Bakun 1973). We used the mean of 1˚ Bakun Upwelling Calculations from each latitude available that was near or intersected a NMS (Bakun 1973). Although there are a variety of other indices and environmental data through these regions (e.g. Biologically Effective Upwelling Transport Index (BEUTI), satellite-derived chlorophyll-a, in-situ prey data, etc.), none of these data cover the timespan and/or extent of all five NMS. Therefore, we used only variables

that were available during all of the years corresponding to our available avifaunal data (1980-2018).

For local SST data, we used the HadISST Average Sea Surface Temperature (downloaded from NOAA ERDDAP). We used the 1° Monthly measurements, which are calculated from a combination of in-situ and adjusted satellite-derived measurements (Rayner et al., 2003). The SST provides information on advection and upwelling in a region, both of which influence ocean productivity which can support potential seabird prey (Abraham & Sydeman, 2004; Sydeman et al., 2006).

Data Analyses

We conducted all statistical analyses in the R environment (version 4.0.3 R Core Team 2020). We used the relative abundance (number of birds/km^2) of transect segments in all analyses.

Relative abundance models

To determine appropriate time series analysis and examine the variables before analysis we followed protocols by Zuur et al. (2012). We first tested the relative abundance data for outliers and zero-inflation, which were present in each NMSs. Seabirds have a patchy distribution which results in data with a high proportion of zeros, and highly skewed with large outliers (e.g., large flocks that went through the transit). As the zeros and outliers are true data, both were retained in the analyses, and log transformations were used on positive data to de-emphasize outliers.

Oceanographic variables can be autocorrelated (i.e., past conditions influence current conditions) and cross-correlated (e.g., local conditions are influenced by broader spatial scale processes), therefore, we could not add all these data into our analyses as independent variables. To take each of these variables into account, while decreasing the dimensions of our data, we used principal component analysis (PCA) to reduce these data into a few multi-variate environmental

values. We only included principal components (PCs) with eigenvalues >1 and/or that explained > 60% of the variance, which resulted in selecting PC1, PC2 and PC3.

After removing collinearity of variables with PCA, we investigated the relationships between the PCs and seabird relative abundance. They displayed non-linear patterns; therefore, linear models were not appropriate for analysis. In addition, typical time series analysis was inappropriate, as they required one value over regularly spaced intervals, and we have many grouped data points scattered inconsistently throughout our study period.

In summary, the data are zero-inflated, highly skewed, have non-linear relationships with covariates, and irregularly spaced in time. Because of these characteristics, we used Bayesian hurdle generalized additive models (GAM) to investigate relationships between seabird relative abundance and the final selected variables of Year, PC1, PC2, PC3, and transect ID as a random intercept. The use of GAMs overcomes the non-linear relationships between relative abundance and the covariates, as it allows for potentially complex, non-linear relationships, can handle the irregular spacing of samples in time and estimate temporal trends as smooth functions (Hastie and Tibshirani 1986). We utilized the smoothing functions of GAMs within a hurdle model, which is suitable for zero-inflated data, as it evaluates the processes generating the excess zeros as well as the processes generating the non-zero data (Cragg, 1971). We used a hurdle model that first estimates the probability of seeing zero birds per year using a logistic model (hu), and the predicted relative abundance if a bird is present using a lognormal model (μ).

These hurdle GAMs were run using a Bayesian framework to make inferences about the posterior probabilities of these two trends (presence/absence and predicted relative abundance), and an overall predicted relative abundance that incorporates both parts of the hurdle model (hu and mu). Bayesian inference is a powerful tool that produces posterior distributions of the additive

relationships, giving us credible intervals for these relationships. For all Bayesian analyses, we used the *brms* package in R (Bürkner 2017). Models were fitted with a logistic (hu) and lognormal (μ) distribution and run using four Monte Carlo Markov chains with 4,000 iterations (including 1,000 warm-up iterations) per chain. A random intercept effect of transect segment was included in all models, allowing observations made along the same transect to be correlated. Convergence of all chains was diagnosed by ensuring the Gelman–Rubin convergence diagnostic ($\hat{R}$) for each parameter was <1.05 (Gelman and Rubin, 1992). We used weakly informative priors for each parameter, as seabird density was highly variable, therefore was only constrained to positive values. The smooth weights (spline coefficients) of each of the variables, which determines the amount of 'wiggliness' of the smooth, were checked to ensure that they did not contain or cross zero, which would indicate they were better suited for linear analysis. The goodness of fit of our models was assessed by evaluating graphical posterior predictive checks. We first computed posterior draws from our model posterior estimates using the 'posterior_predict' function. We then visually compared the distribution of the seabird relative abundance in our data to the distribution derived from 1,000 draws from the posterior predictions using the 'ppc_dens_overlay' function in the bayesplot library (Gabry & Mahr 2024). We extracted the posterior distributions from the models using the 'conditional_effects' function (*brms*) for the hu, μ, and combined models.

In addition to our models, we also tested for differences in the seabird relative abundance of CCE-breeding and Non-CCE breeding species, and our three indicator species, between the first and last 10 years of available data within each NMS. These periods varied among NMS due to differences in data availability, but were compared to show broader patterns of changes in abundances. We calculated the percentage change (Hyrenbach and Veit, 2003) in relative abundance between periods and the difference in relative abundance means (+95% confidence

intervals) between periods using the 'MeanDiffCI' function in the DescTools package (version 0.99.5; Signorell et al., 2024). We also calculated the proportion of zeros between the first and last 10 years of data. The proportion of zeros can be an indicator of changes in patchiness and the presence/absence during different periods. Therefore, this is a helpful measure to evaluate the abundance and distribution of seabirds during different periods. This function calculates the 95% confidence intervals with 999 bootstrapped samples. We also compared the data on our dominant, indicator species to describe changes within each NMS.

Community composition

For community composition analysis, we retained data that had more than 10 transect segments per year within a NMS to reduce skewed effects in species proportions. To compare the community composition between different periods, we used Bray-Curtis Dissimilarity Index, which uses the number of species and number of individuals each year to calculate any difference between years. The value ranges from zero to one, with a value of zero meaning the two years are the same and a value of one meaning that they do not share any species. The annual Bray-Curtis values were calculated using the 'metaMDS' function in the *vegan* package (Oksanen et al., 2018, version 2.6–2). To determine what years had similar communities to each other and if similar years reflected different environmental conditions, we conducted a cluster analysis on the Bray–Curtis dissimilarity index values and visualized results using a dendrogram. We used the 'hclust' function to conduct the hierarchical cluster analysis on the dissimilarity values, and the 'as.dendrogram' function (both in stats package, R Core Team 2020) to produce dendrograms. We used functions within the dendextend package to extract these components and make customized plots (version 1.17.1; Galili 2015). Years with similar SST conditions were colored to visualize potential trends within the dendrograms. SST categories were classified using the 1st and 3rd quantiles for the cut-

offs for low, moderate and high classifications. To further investigate differences in communities, we also plotted the proportion of each species/species group within each NMS during different SST categories.

RESULTS

Environmental Conditions

The first three principle components (PC1, PC2, and PC3) explained 66.4-76.8% of the variance of environmental variables within the NMS. Using the variables with moderate to strong loadings (>0.5), we describe the PCs, as follows (Figure 2, Table 1). PC1 and PC2 were similar among NMS environmental conditions (1980-2018), with PC1 associated with longer time-scaled dynamics (positive with PDO) and/or ENSO conditions (positive with MEI and/or ONI) and PC2 associated with seasonal, local upwelling with the Bakun Upwelling Index. The exception with PC2 was a strong positive association with SST in OCNMS, in addition to the Bakun Upwelling Index. The PC3 associations varied among NMS, with PC3 in OCNMS positively associated with NPGO, GFNMS and CBNMS negative with MEI, and MBNMS and CINMS positive with SST.

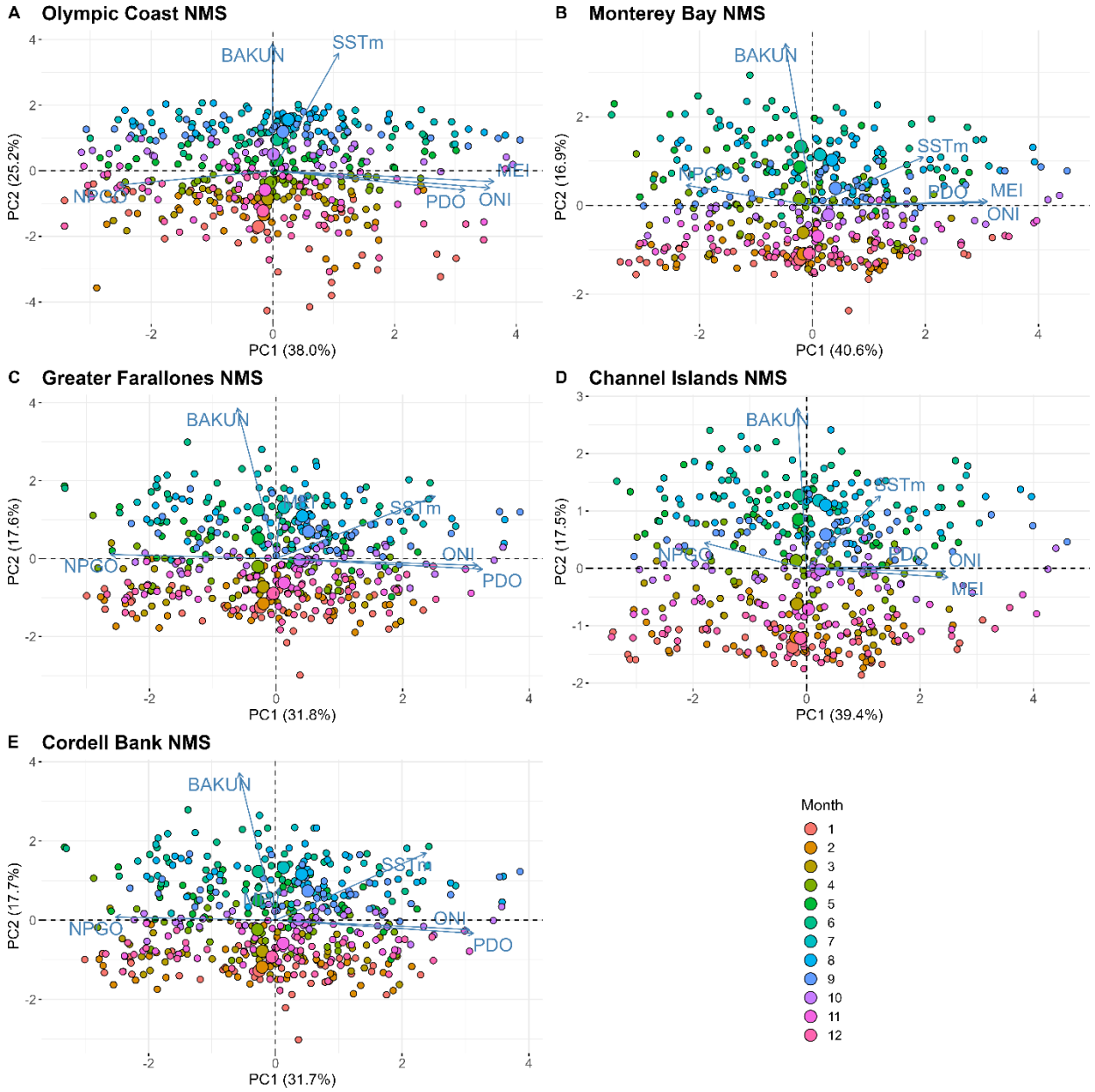


Figure 2.2: Results of the Principal Component Analysis on the environmental variables within each National Marine Sanctuary (NMS). Arrows that are closer together indicate high correlation. PC's were similar among NMS environmental conditions (1980-2018), with PC1 associated with longer time-scaled dynamics (positive with PDO) and upwelling conditions (positive with MEI and/or ONI) and PC2 associated with season and local upwelling with the Bakun Upwelling Index. Relationships with SST were variable within PC1, PC2, and PC3.

Table 2.1: Results of principal component analysis showing the loadings of environmental variables of the six multivariate components, the eigenvalues, and the proportion of the variance explained by each component (strong loadings >0.5 are in bold, moderate loadings between 0.4 – 0.5 are in italics). Environmental variables included sea surface temperature (SST), Pacific Decadal Oscillation (PDO), Oceanic Niño Index (ONI), North Pacific Gyre Oscillation (NPGO), Multivariate El Niño-Southern Oscillation (ENSO) INDEX (MEI), and Bakun Upwelling Index (BAKUN).

NMS	Variable	PC1	PC2	PC3	PC4	PC5	PC6
OCNMS	SST	0.164	**0.667**	0.314	0.127	**0.600**	0.231
	PDO	*0.480*	-0.110	0.159	**0.814**	-0.265	0.003
	ONI	**0.541**	-0.098	0.306	-0.345	0.137	**-0.683**
	NPGO	-0.382	-0.081	**0.873**	-0.048	-0.279	0.068
	MEI	**0.552**	-0.062	0.073	*-0.440*	-0.276	**0.645**
	BAKUN	-0.001	**0.723**	-0.121	-0.082	**-0.630**	-0.242
	Eigenvalue	**2.28**	**1.51**	0.81	0.61	0.44	0.34
	% variance explained	38.03	25.18	13.55	10.20	7.30	5.74
GFNMS	SST	*0.429*	0.368	0.281	0.088	**0.769**	0.058
	PDO	**0.557**	-0.062	-0.121	0.292	-0.214	**-0.735**
	ONI	**0.544**	-0.040	-0.124	0.354	-0.331	**0.673**
	NPGO	*-0.447*	0.025	-0.087	**0.873**	0.171	-0.029
	MEI	0.009	0.268	**-0.928**	-0.138	0.220	0.018
	BAKUN	-0.105	**0.887**	0.152	0.017	*-0.420*	-0.050
	Eigenvalue	**2.36**	**1.05**	0.91	0.73	0.60	0.35
	% variance explained	39.42	17.47	15.09	12.22	9.93	5.88
CBNMS	SST	*0.424*	*0.405*	0.253	0.055	**0.766**	0.051
	PDO	**0.557**	-0.079	-0.117	0.302	-0.201	**-0.733**
	ONI	**0.545**	-0.056	-0.121	0.369	-0.304	**0.675**
	NPGO	*-0.449*	0.019	-0.092	**0.863**	0.209	-0.030
	MEI	0.010	0.195	**-0.945**	-0.151	0.214	0.017
	BAKUN	-0.102	**0.888**	0.076	0.039	-0.437	-0.049
	Eigenvalue	**1.90**	**1.06**	**1.02**	0.77	0.71	0.54
	% variance explained	31.70	17.68	16.97	12.88	11.79	8.98
MBNMS	SST	0.330	0.284	**0.714**	**0.523**	0.160	0.028
	PDO	*0.461*	0.012	-0.152	0.167	**-0.856**	0.068
	ONI	**0.510**	0.018	-0.383	0.133	0.314	**-0.690**
	NPGO	-0.375	0.118	*-0.461*	**0.779**	0.046	0.153
	MEI	**0.521**	0.023	-0.297	-0.088	0.372	**0.703**
	BAKUN	-0.080	**0.951**	-0.140	-0.256	-0.057	-0.033
	Eigenvalue	**2.43**	**1.01**	0.85	0.75	0.60	0.36
	% variance explained	40.56	16.89	14.15	12.44	10.04	5.92
CINMS	SST	0.280	*0.407*	**0.736**	*0.421*	0.175	0.075
	PDO	*0.458*	0.017	-0.326	-0.106	**0.816**	0.084
	ONI	**0.526**	-0.018	-0.239	0.325	-0.276	**-0.695**

Table 2.1: Results of principal component analysis (continued)

NPGO	-0.385	0.143	*-0.426*	**0.779**	0.128	0.165
MEI	**0.535**	-0.050	-0.195	0.092	*-0.436*	**0.689**
BAKUN	-0.035	**0.900**	-0.275	-0.300	-0.145	-0.037
Eigenvalue	**2.36**	**1.05**	0.91	0.73	0.60	0.35
% variance explained	39.42	17.47	15.09	12.22	9.93	5.88

Relative Abundance

Comparison between periods

Trends in seabird relative abundance varied between CCE-breeding and non-CCE breeding species within U.S west coast NMS (Table 2). Between the first ten years and the last ten-year period in our data, CCE-breeding species have experienced declines in CINMS in the south, and MBNMS and CBNMS in the central region. However, there were moderate increases within GFNMS (14.2%), and massive increases within OCNMS (233.1%). Non-CCE breeding species (migratory species) declined within every NMS (mean decline -29.7% ± 13.3). The greatest declines occurred in the south (CINMS; 54.4%), followed by similar declines in MBNMS (25.5%), GFNMS (29.13%), and OCNMS (25.2%), and the lowest declines in CBNMS (14.4%).

Table 2.2: Comparison of seabird relative abundance (number of birds/surveyed area, km^2) between the first 10 years of available data to the last 10 years (in grey) of CCE and Non-CCE breeding species within each National Marine Sanctuary. We report the range of years used for each time period, the number of transect segments, the percent of transects with no seabird sightings, the mean and the mean difference along with 95% confidence intervals, and the percentage difference between periods.

CCE-breeding species

National Marine Sanctuary	Year	n	% Zeros	Mean relative abundance (95% CI)	Mean difference between periods (95% CI)	% Difference
Olympic Coast	1989-1998	784	40.1	18.12 [14.05 22.19]	42.24 [34.17 50.31]	233.1
	2009-2018	1642	6.1	60.36 [53.40 67.31]		
Greater Farallones	1980-1989	1548	35.6	29.17 [23.44, 34.90]	4.12 [-2.62, 10.85]	14.1
	2009-2018	2901	12.3	33.30 [29.76, 36.82]		
Cordell Bank	1980-1989	699	42.2	20.03 [15.26, 24.79]	-2.92 [-8.41, 2.58]	-14.6
	2009-2018	1202	22.2	17.11 [14.39, 19.83]		
Monterey Bay	1980-1989	3244	54.3	16.06[12.07, 20.04]	-7.66 [-11.73, -3.60]	-47.7
	2009-2018	3939	28.9	8.40 [7.60, 9.19]		
Channel Islands	1987-1996	542	17.7	19.77 [11.70, 27.83]	-11.00 [-19.55, -2.45]	-55.6
	2009-2018	572	23.5	8.77 [5.98, 11.56]		

Non-CCE breeding species

National Marine Sanctuary	Years	n	% Zeros	Mean relative abundance (95% CI)	Mean difference between periods (95% CI)	% Difference
Olympic Coast	1989-1998	784	39.4	50.74 [17.65, 83.82]	-12.79 [-46.62, 21.05]	-25.2
	2009-2018	1642	15.5	37.95 [31.12, 44.79]		
Greater Farallones	1980-1989	1548	44.1	19.40 [14.81, 23.98]	-5.65 [-11.62, 0.32]	-29.1
	2009-2018	2901	43.3	13.75 [9.93, 17.57]		
Cordell Bank	1980-1989	699	40.1	15.27 [10.89, 19.64]	-2.19 [-8.76, 4.38]	-14.4
	2009-2018	1202	26.1	13.08 [8.18, 17.97]		
Monterey Bay	1980-1989	3244	40.8	35.04 [25.33, 44.75]	-8.93 [-21.13, 3.26]	-25.5
	2009-2018	3939	28.9	26.11 [18.73, 33.49]		
Channel Islands	1987-1996	542	33.2	49.28 [-3.44, 102.01]	-26.83 [-81.74, 28.08]	-54.4
	2009-2018	572	43.7	22.45 [7.52, 37.39]		

Within CINMS, for both CCE-breeding and non-CCE breeding species, there was a decrease in the mean abundance, but also an increase in the number of zero birds found within a transect. Within the remaining NMS, the proportion of zero birds within a transect decreased, indicating changes in patchiness as well as occurrence of seabirds within these sanctuaries.

When we compare the first and last 10 years of our data on our three dominant species, we see variable trends across the different NMS (Table S3). The mean abundance of sooty shearwaters had increased within all central and southern NMS (GFNMS 33%, CBNMS 41%, MBNMS 38%, CINMS 103%), and showed a decline in OCNMS in the north (-38%; relative abundance changed from 31.9±31.7 to 19.8±5.8). However within all NMS, the proportion of zero sightings in our data had decreased (OCNMS -17%, GFNMS -18%, CBNMS -25%, MBNMS -22%, CINMS -9%), indicating possible changes in the patchiness of their distribution, or that the presence of sooty shearwaters in all NMS are increasing, even though mean relative abundance has decreased in the north. Within the NMS where sooty shearwaters increased, these estimates of change in relative abundance between the first and last 10 years include zero, therefore are not robust (Mean difference between periods: GFNMS 2.31c[-2.29, 6.92], CBNMS 1.19 [-1.52, 3.90], MBNMS 4.21 [-3.50, 11.92], and CINMS 2.65 [-0.65, 5.95]

Common murres increased by a tremendous amount in the north (OCNMS 243%) and within two of the central NMS near/around the Southeast Farallon Islands (GFNMS 65%, CBNMS 39%), and declined within MBNMS (-38%). Common murres are not commonly found as far south as CINMS, therefore we did not include estimates. Within all central and northern NMS, the proportion of zeros decreased (OCNMS 48%, GFNMS 35%, CBNMS 29%, MBNMS 19%). The change in relative abundance estimates between the first and last 10 years within OCNMS (24.65

[17.80, 31.50]) and GFNMS (9.38 [5.08, 13.68]) were robust and did not cross zero; however both CBNMS (2.19 [-1.04, 5.41]) and MBNMS (-3.10 [-5.26, -0.94]) did.

Cassin's auklets have declined in all five NMS (OCNMS -53%, GFNMS -30%, CBNMS -47%, MBNMS -28%, CINMS -91%). Within the central NMS, there was very little change in the proportion of zeros, therefore trends were driven only by changes in the number of birds per sighting (GFNMS -2.23 [-4.59, 0.12], CBNMS -5.35 [-9.19, -1.51], MBNMS -0.54 [-1.13, 0.04]). However, estimates in the change in relative abundance between the first and last 10 years within GFNMS and MBNMS were not robust and crossed zero. Within OCNMS, the abundance within transect segments were low, therefore small changes in detections of this species may overestimate trends (-6% change in proportion of zeros, mean difference between periods was -1.44 [-2.35, -0.53]). Within CINMS, the substantial decline was a combination of an increase in the proportion of zeros, as well as a decrease in the mean relative abundance (-2.86 [-5.03, -0.68]).

Bayesian hurdle GAM: seabird relative abundance

All models successfully converged, and none of the smooth weights crossed zeros, therefore, we retained smoothers for all variables. When assessing model performance, most models captured the distribution of our seabird data well (Figure S2 & S3). Models on CCE-breeding species performed well, however, the models on non-CCE breeding species consistently failed to capture when relative abundance was low (Figure S3; e.g., one bird observed in a transect). This may be due to the diversity of non-CCE breeding species and the array of potential drivers of a single occurrence of an individual within these NMS. For individual species, the models also had a hard time capturing when there were 1-2 individuals, but captured the proportion of zeros and overall shape of the abundance curves (Figures S4, S5, S6).

Overall, the trends of seabird abundance in NMSs were highly variable, with oscillations of different frequency, and opposing longer-term trends among some NMS and species/species groups. Within the central NMS, there was relatively high uncertainty in CCE-breeding species abundance during the 1980's due to sporadic and highly variable data during these years (Figure 3). Although there was an increase between the first and last 10 years of CCE-breeding species within OCNMS, these species increased between 2001 and 2012, until their abundance leveled off in 2006, and then declined up until 2018. There were similar CCE-breeding species patterns within GFNMS and CBNMS, with two oscillations in relative abundance during our study period. The peak periods of abundance were during the mid-1980's and around 2010. Within MBNMS, CCE-breeding species varied with ~10 year oscillations in their relative abundance. Since 2008, there has been a decline in the abundance of these species in MBNMS. We also found oscillations of CCE-breeding species within CINMS, with one full cycle of 14 years captured in our study period (between 1996 and 2010). Peaks in abundance occur during the late 1980's and early 2000's; however, there is an overall decline even as relative abundance of these species oscillates.

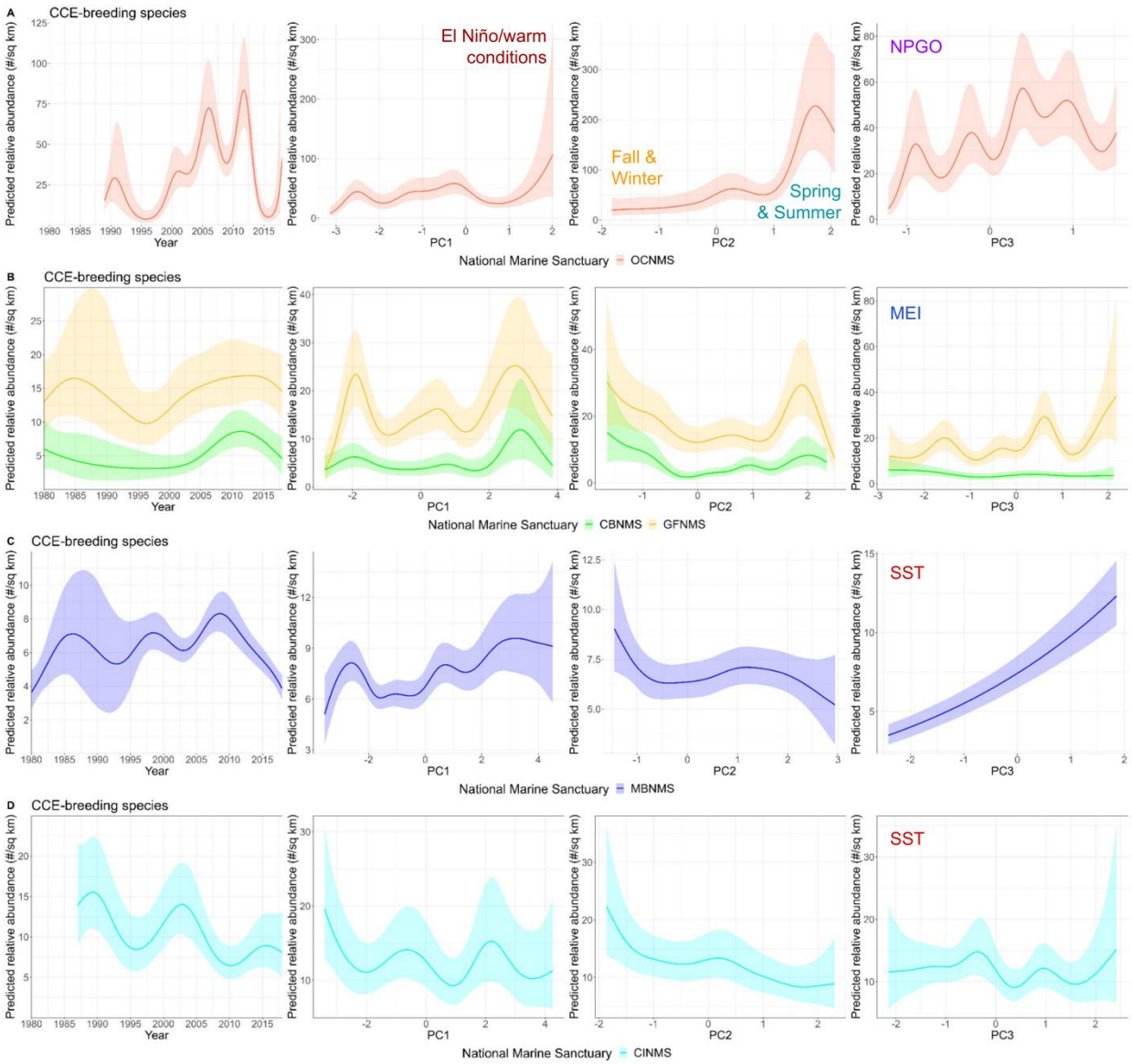


Figure 2.3. The results of the Bayesian hurdle, GAM using the relative abundance of CCE-breeding seabirds within transects in the Olympic Coast National Marine Sanctuary (OCNMS), Greater Farallones NMS (GFNMS), Cordell Bank NMS (CBNMS), Monterey Bay NMS (MBNMS), and Channel Islands NMS (CINMS). Model covariates include PC1, PC2, and PC3 of the Principle Component Analysis of environmental variables within each NMS.

Non-CCE breeding species have distinct patterns and cycles of relative abundance within each NMS (Figure 4). In OCNMS, Non-CCE breeding species were abundant during 1989-1990, but afterwards they show a marked decline until 2002. The high uncertainty preceding this decline is due to limited surveys during this period. It was not until 2000 that data within OCNMS was

available annually. During this time (2000-2016), we see an increase in these species relative abundances until it peaked in 2016. Within both CBNMS and GFNMS, Non-CCE breeding species declined between 1980 and 1995, then increased to their peak within our survey period in 2002 and 2003, respectively. After these peaks in relative abundance, non-CCE breeding species began to decline in both NMS, more drastically within GFNMS. Non-CCE breeding species in MBNMS show a sustained decline since their peak in the mid-1990's. The large uncertainty of relative abundance from approximately 1985 to 1995 is due to sporadic sampling within this period, in addition to a wide distribution of recorded numbers. Although there is an overall decrease in these species, there are two pulses with heightened abundances, one in 2005 and another in 2015. In the CINMS, the abundance of non-CCE breeding species decreased into the early 2000s but may be increasing in more recent years. There is substantial data during this period of decline, due to the initiation of seabird observing by the CalCOFI program, however, there is high variance within relative abundance resulting in high uncertainty. After the low abundances in the early 2000's, these non-CCE breeding species began to increase within CINMS.

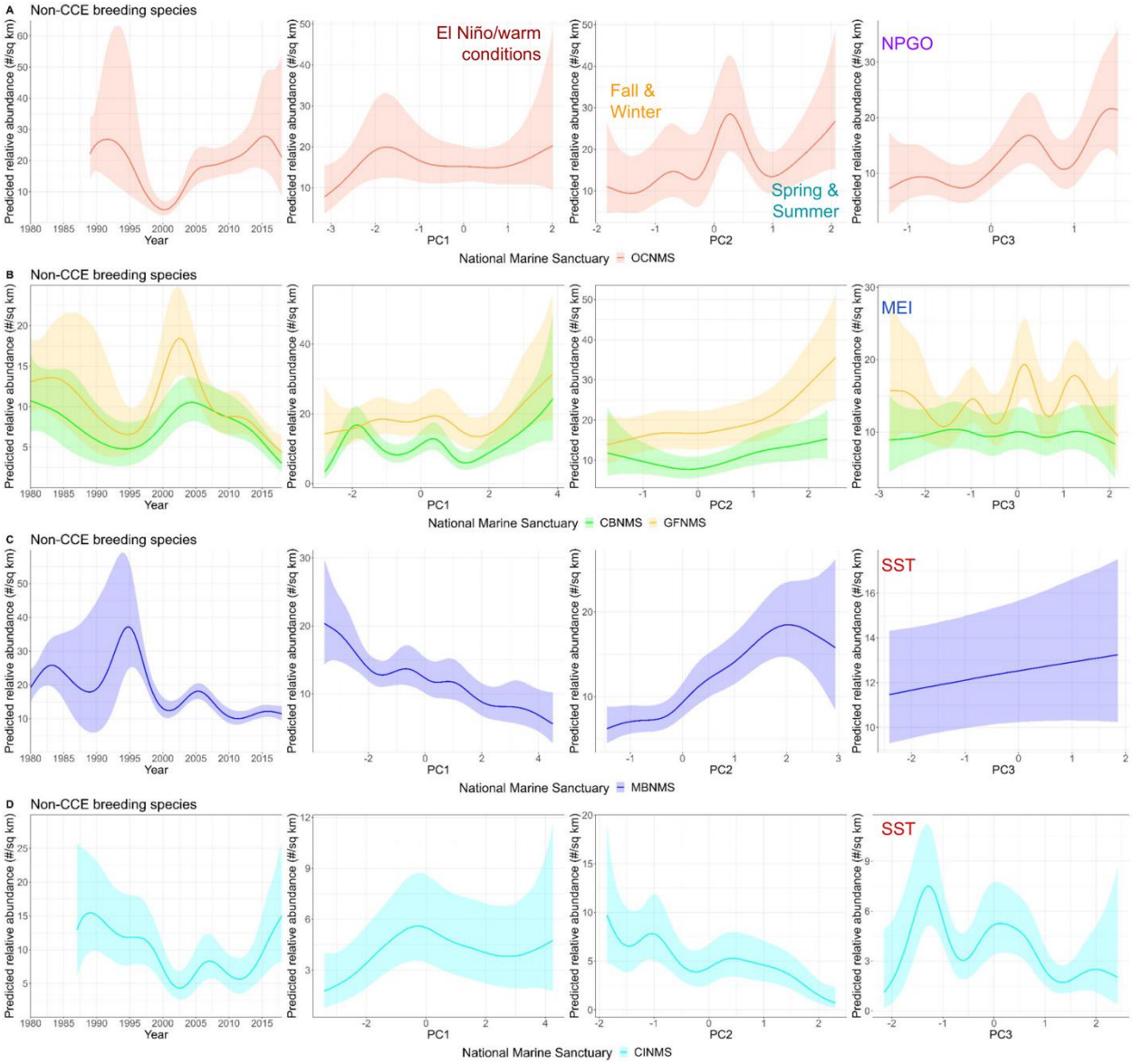


Figure 2.4. The results of the Bayesian hurdle, GAM using the relative abundance of Non-CCE breeding seabirds within transects in the Olympic Coast National Marine Sanctuary (OCNMS), Greater Farallones NMS (GFNMS), Cordell Bank NMS (CBNMS), Monterey Bay NMS (MBNMS), and Channel Islands NMS (CINMS). Model covariates include PC1, PC2, and PC3 of the Principle Component Analysis of environmental variables within each NMS.

Most of the trends of our indicator species in NMS were similar to the trends of their corresponding CCE-breeding or non-CCE breeding species groups. Within OCNMS, common murres increased through the 1990's until 2005, when their abundance leveled off and then began to decline from 2010-2018 (Figure 5). Within GFNMS and CBNMS, common murres

increased during the study period until the 2014 heatwave when their abundance declined until 2018. Within MBNMS, there were 5-10 year abundance cycles of common murres.

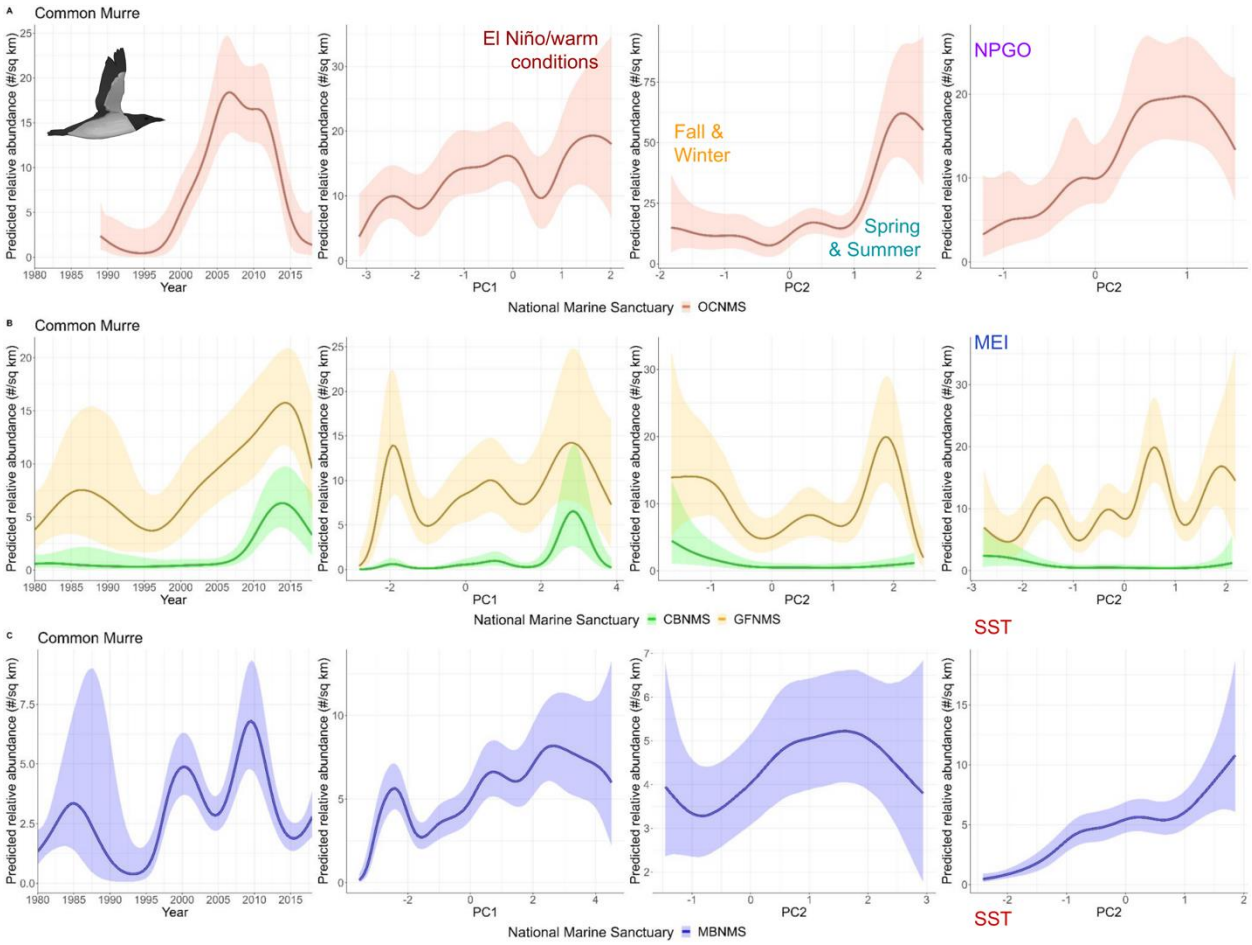


Figure 2.5. The results of the Bayesian hurdle, GAM using the relative abundance of common murres within transects in the Olympic Coast National Marine Sanctuary (OCNMS), Greater Farallones NMS (GFNMS), Cordell Bank NMS (CBNMS), and Monterey Bay NMS (MBNMS). Model covariates include PC1, PC2, and PC3 of the Principle Component Analysis of environmental variables within each NMS. Model results within Channel Islands NMS are not included due to their limited presence in this southern region (bird illustrations by Freya Hammar).

Sooty shearwaters within OCNMS had two abundance cycles with an initial decline between 1990 to the early 2000's and then increased to 2011 before declining again (Figure 6). Within GFNMS and CBNMS, sooty shearwater abundance increased until their peak during the early 2000's before declining until 2018. Within MBNMS, there was an apparent increase with

high variability during the mid-1980's to mid-1990's until declining to 2018. There were 5-year abundance cycles of sooty shearwaters within CINMS and overall remained stable.

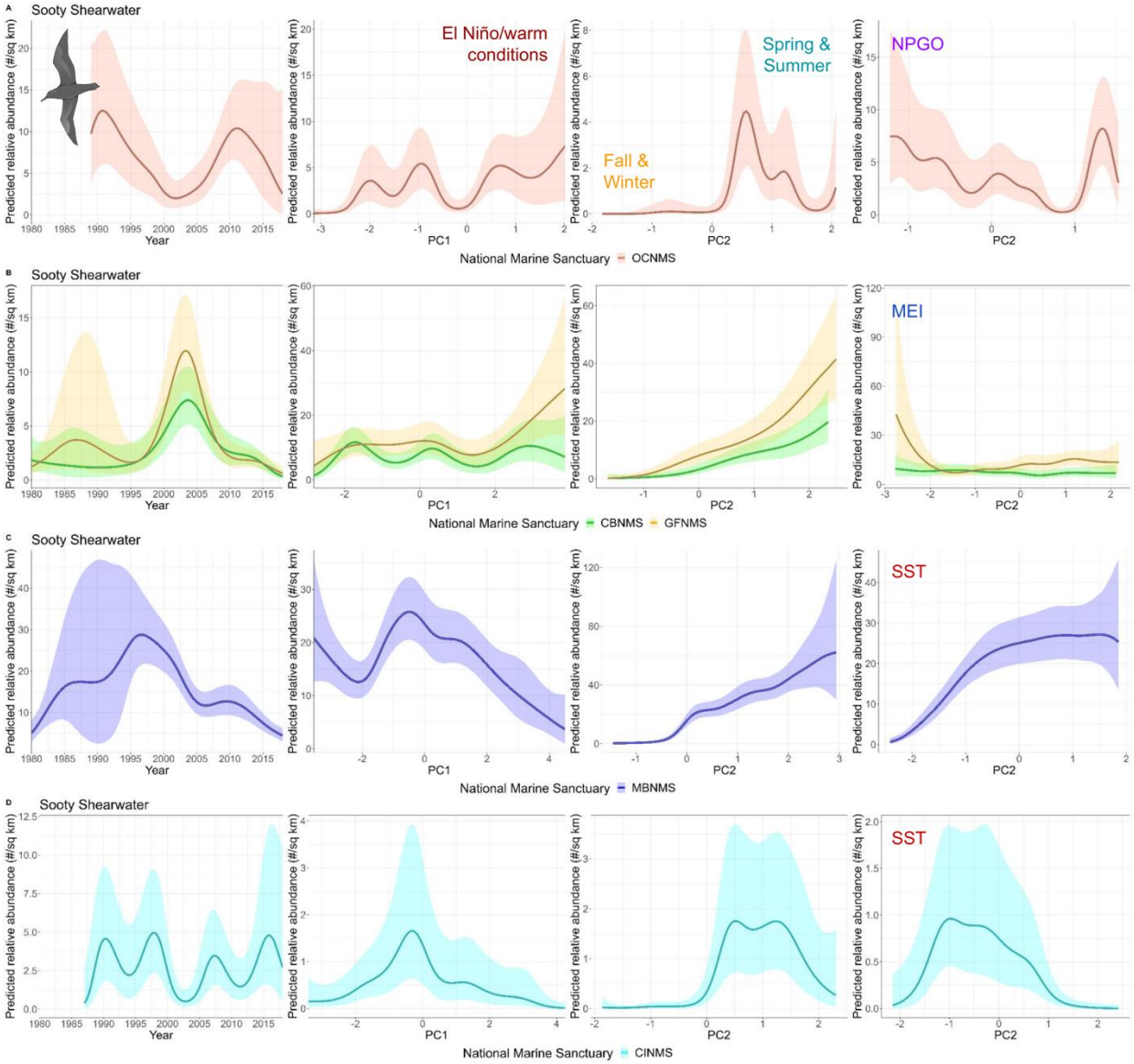


Figure 2.6. The results of the Bayesian hurdle, GAM using the relative abundance of sooty shearwaters within transects in the Olympic Coast National Marine Sanctuary (OCNMS), Greater Farallones NMS (GFNMS), Cordell Bank NMS (CBNMS), Monterey Bay NMS (MBNMS), and Channel Islands NMS (CINMS). Model covariates include PC1, PC2, and PC3 of the Principle Component Analysis of environmental variables within each NMS (bird illustrations by Freya Hammar).

Cassin's auklets were not abundant within OCNMS, however show increased abundance during the early 1990's and since 2015 (Figure 7). These auklets are decreasing within both

GFNMS and CBNMS, with 5-year cycles of high variability within GFNMS. Within MBNMS, there were two ≈15 year cycles in the abundance of Cassin's auklets. Cassin's auklets have precipitously declined in CINMS since 1987.

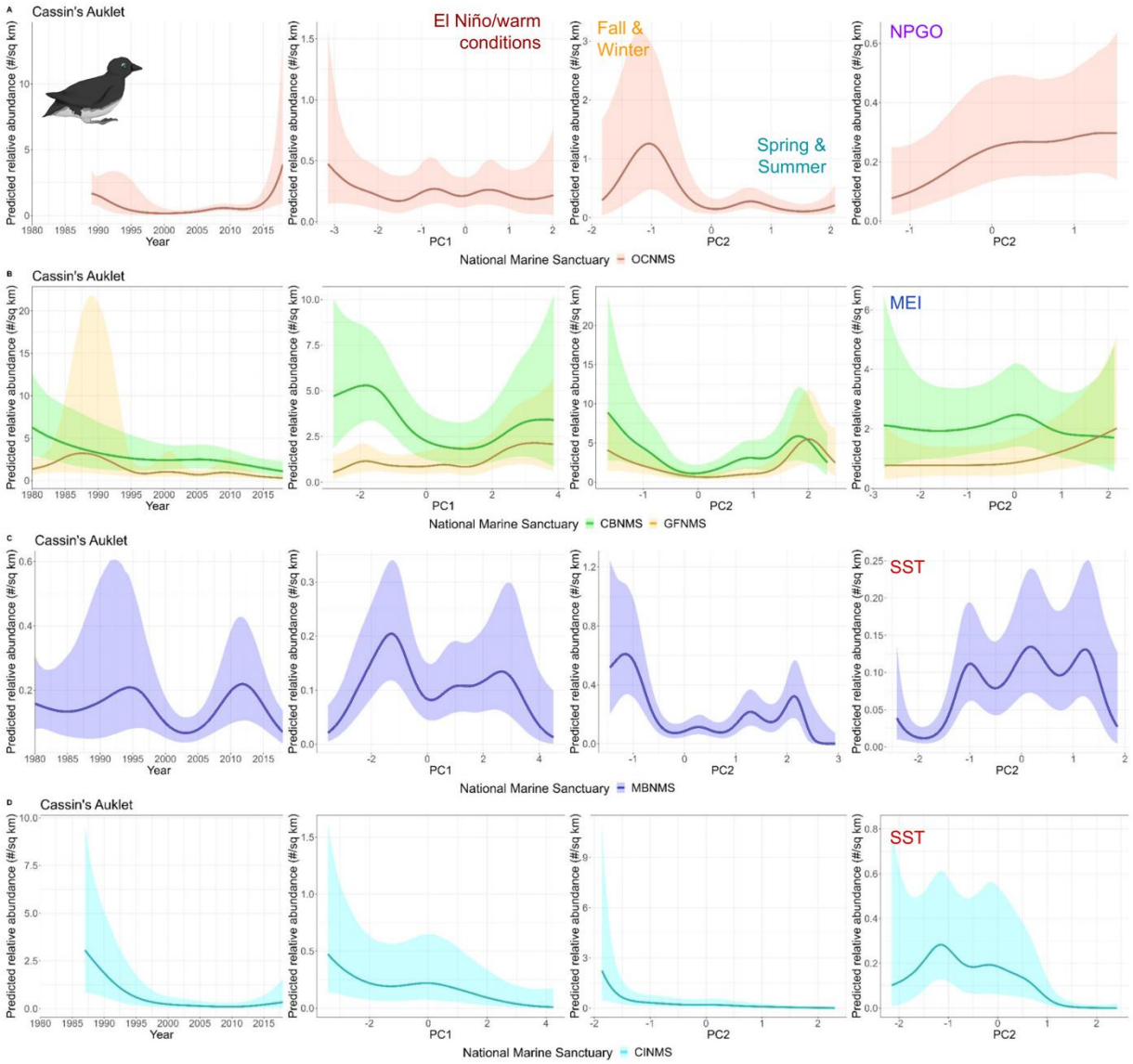


Figure 2.7. The results of the Bayesian hurdle, GAM using the relative abundance of Cassin's auklets within transects in the Olympic Coast National Marine Sanctuary (OCNMS), Greater Farallones NMS (GFNMS), Cordell Bank NMS (CBNMS), Monterey Bay NMS (MBNMS), and Channel Islands NMS (CINMS). Model covariates include PC1, PC2, and PC3 of the Principle Component Analysis of environmental variables within each NMS (bird illustrations by Freya Hammar).

Relationships with environmental variables

CCE-breeding species

Overall, there was high variability in seabird abundance trends with environmental conditions among and within NMSs, with no clear trend that defines the trends within the CCE. In OCNMS, the relative abundance of CCE-breeding species (Figure 3A) along with the longer-scale oceanic and atmospheric processes captured in PC1 (strongly positive with ONI and MEI, and weakly positive PDO) did not show a clear trend, although there is an uptick with high uncertainty at higher values (warm conditions). With PC2 (strongly positive with greater Bakun upwelling and positive with increased SST), we found higher abundance of these species during periods of higher SST and upwelling. The contrast here is that upwelling occurs here during times of warmer conditions overall. CCE-breeding species abundance also increased with PC3 (strongly positive with NPGO), although with high frequency oscillations. As NPGO reflects changes in wind stress curl and coastal upwelling, it correlates well with chlorophyll-a and nutrients, and also provides support for a positive relationship with these species abundances and upwelling conditions (Di Lorenzo et al., 2008). Within GFNMS and CBNMS, PC1 and PC2 varied similarly with the abundance of CCE-breeding species (Figure 3B). For PC1 (strongly positive with PDO and ONI), abundance peaked at low and high values, indicating that there are two processes that may affect the abundance of locally breeding species in these NMSs. We find similar patterns with PC2 (strongly positive with Bakun Index), with higher abundance during low and high values (i.e., weak and strong upwelling). For PC3 (strongly negative with MEI), there is no apparent relationship with abundance within CBNMS, while abundances within GFNMS are highest when MEI indicates upwelling. Within MBNMS, CCE-breeding species abundance increased along with increasing PC1 (strongly positive with MEI and ONI), and decreased with increasing PC2 (strongly positive Bakun Index; Figure 3C). Within MBNMS,

cycles and variations of abundance with environmental conditions were lacking, which was most apparent with the near-linear trend with PC3 (strongly positive with SST). In the south, CCE-breeding species within CINMS did not correlate well with the environmental conditions (Figure 3D). The seabird abundance was highly variable with PC1 (strongly positive with MEI and ONI) and PC3 (strongly positive with SST); while abundance was lower with PC2 (strongly positive with Bakun Index).

Non-CCE breeding species

Within OCNMS, non-CCE breeding species relative abundances overall tended to increase with PC1, PC2, and PC3 (Figure 4A). For both PC2 and PC3, there was a slightly positive relationship between relative abundance and increasing values. Within GFNMS and CBNMS, non-CCE breeding species abundance varied with PC1, with higher abundance at low, moderate and high values (Figure 4B). There was an overall positive relationship between non-CCE breeding species and PC2, especially within GFNMS. With PC3, there is no overall trend, although there are high frequency cycles of abundances within GFNMS. With MBNMS, there were near-opposite trends of the non-CCE breeding species compared with the CCE-breeding species (Figure 4C). Non-CCE breeding species relative abundance decreased with PC1 and increased with PC2. However, there was little relationship between non-CCE breeding species abundance and PC3. In CINMS, non-CCE breeding species showed slightly clearer relationships, although with high uncertainty, with environmental conditions than the CCE-breeding species (Figure 4D). Non-CCE breeding species abundance was highest with neutral and high PC1, although at large values, decreased with PC2, and was highly variable with PC3.

Indicator species

Within OCNMS, common murre abundance corresponded well with PC2 and PC3, and had higher abundance during upwelling and high NPGO conditions (Figure 5A). The relationship with ENSO conditions (PC1) were variable and murres were more abundant during neutral ENSO conditions and had high variability during El Niño conditions. Within GFNMS and CBNMS, common murres abundance had somewhat different relationships with environmental conditions between the two NMS (Figure 5B). Within GFNMS, there was high abundance during La Niña and El Niño, and high abundance during the breeding season. While within CBNMS, there was higher abundance during El Niño and no significant pattern in seasonality. Within MBNMS, the cycles of higher abundance were associated with increasing SST, and slightly higher abundance, however more variability, during El Niño (Figure 5C).

There was high variability between sooty shearwater abundance within OCNMS and environmental conditions, with higher abundance and variability during El Niño, spring, and low NPGO (Figure 6A). Within GFNMS and CBNMS, there is a higher sooty shearwater abundance during times of increased upwelling (PC2; Figure 6B). Within MBNMS, there was higher abundance during La Niña and neutral ENSO (PC1) conditions, higher upwelling during spring and summer (PC2), however only at temperatures above a threshold (PC3; Figure 6C). The 5-year abundance cycles of sooty shearwaters within CINMS only occurred during La Niña (PC1), upwelling season (PC2), and lower SST (PC3; Figure 6D).

Cassin's auklets were not abundant within OCNMS, but they tended to be present during fall (Figure 7A). The abundance of these auklets within these GFNMS and CBNMS did not show straightforward relationships with environmental conditions and was highly variable (Figure 7B). Within CBNMS, there was higher abundance during La Niña and El Niño conditions, while Cassin's auklets were more abundant only during El Niño within GFNMS.

Within MBNMS, there was high variability in their abundance with environmental conditions, with enhanced abundance during fall and winter, and during La Niña (Figure 7C). Cassin's auklets within CINMS were abundant during cool SST (PC3) and La Niña (PC1; Figure 7D).

Community Composition

Seabird communities varied among years within each of the NMS, but some tended to group during different SST conditions. Dendrograms based on the Bray-Curtis Dissimilarity Index revealed patterns of seabird communities among years with high, moderate, or low SST within OCNMS, MBNMS, and CINMS (Figure 8). By investigating patterns among species groups in each NMS during each SST classification, we further confirmed these patterns (Figure 9). For CCE-breeding seabird species, variation among SST conditions was stable, although there was a smaller proportion of Cassin's auklets in all NMS during warm conditions. For non-CCE breeding seabird species, the communities were highly variable during cool, neutral, and warm SST conditions, with greater variation in the north (OCNMS) and most southern (CINMS) NMS. There were more scoters during cool periods in OCNMS and CINMS, greater proportion of albatross during cool conditions in CBNMS and GFNMS, and a greater proportion of dark shearwaters in MBNMS, and non-dark shearwaters in CINMS during warm conditions.

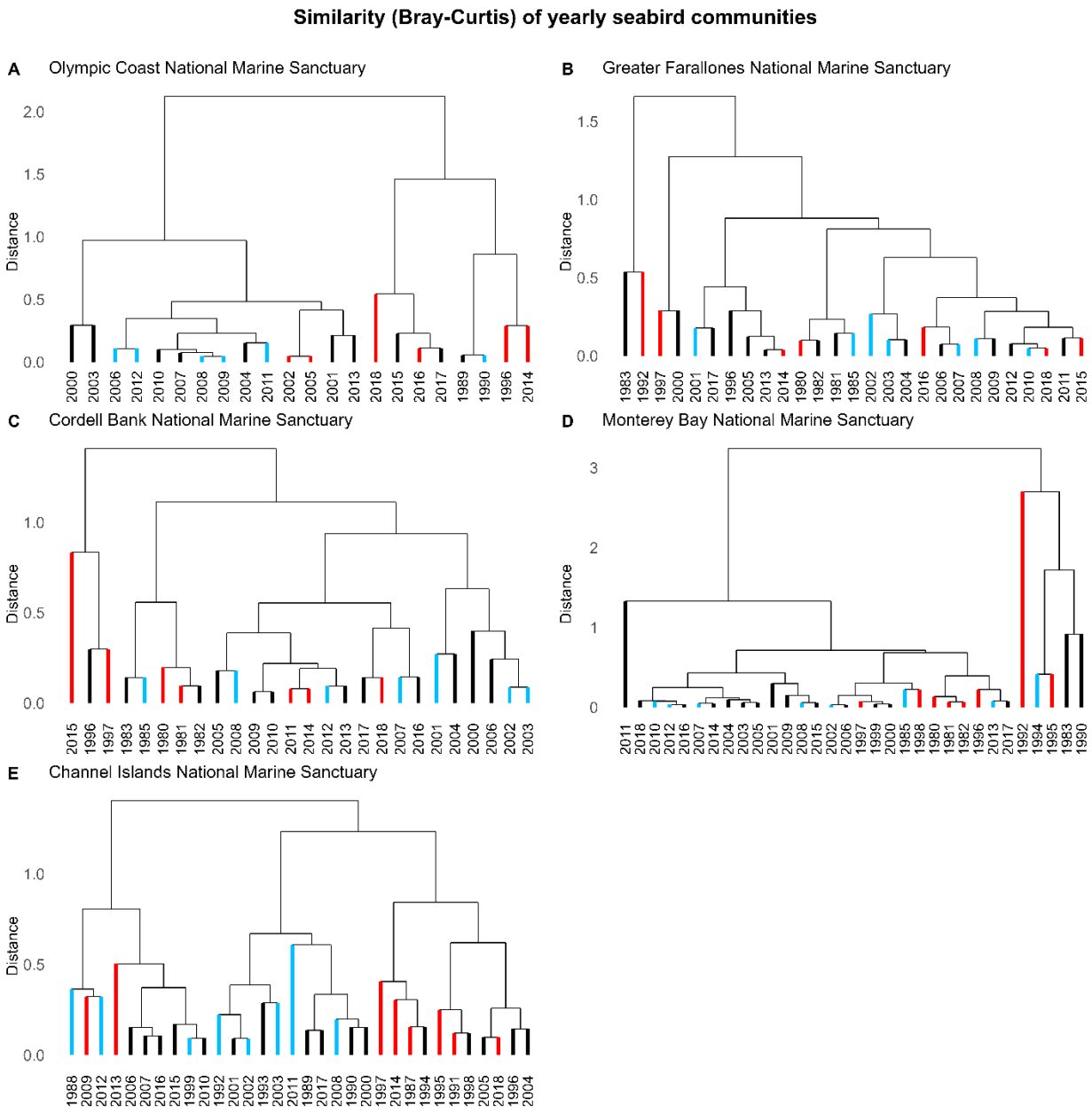


Figure 2.8: Dendrograms displaying the results of the clustering analysis on the Bray-Curtis Dissimilarity values between years of available data within each National Marine Sanctuary (NMS). The color of the dendrogram leaves reflect the mean sea surface temperature (SST) of that year. SST categories were classified using the 1st and 3rd quantiles for the cut-offs for low (blue), moderate (black) and high (red) classifications.

For OCNMS, the dendrogram showed two main groups of communities, a warm and a cool water community. The outlier within the warm cluster was 1990 (cool), and within the cool group were 2002 and 2005 (warm). Within CINMS, the warm cluster had no outliers, and within

the cool group the outliers were 2009 and 2013. Within the central NMS, there were no distinct clusters with SST conditions. Within CBNMS and GFNMS, the clusters reflected more interannual similarities rather than relationships with environmental conditions, perhaps a reflection of colony patterns of the dominant species in those regions. While within MBNMS, there were some clusters that appeared to reflect SST or interannual similarities.

Among SST conditions, the proportion of CCE-breeding species does not vary dramatically (Figure 9A). During cool periods, there is an increase in the proportion of Cassin's auklets within CBNMS, MBNMS, and CINMS. During warm periods, the proportion of CCE-breeding storm-petrels increase within CBNMS and MBNMS. During warm periods within CINMS, the proportion of brown pelicans increases and rhinoceros auklets are not present.

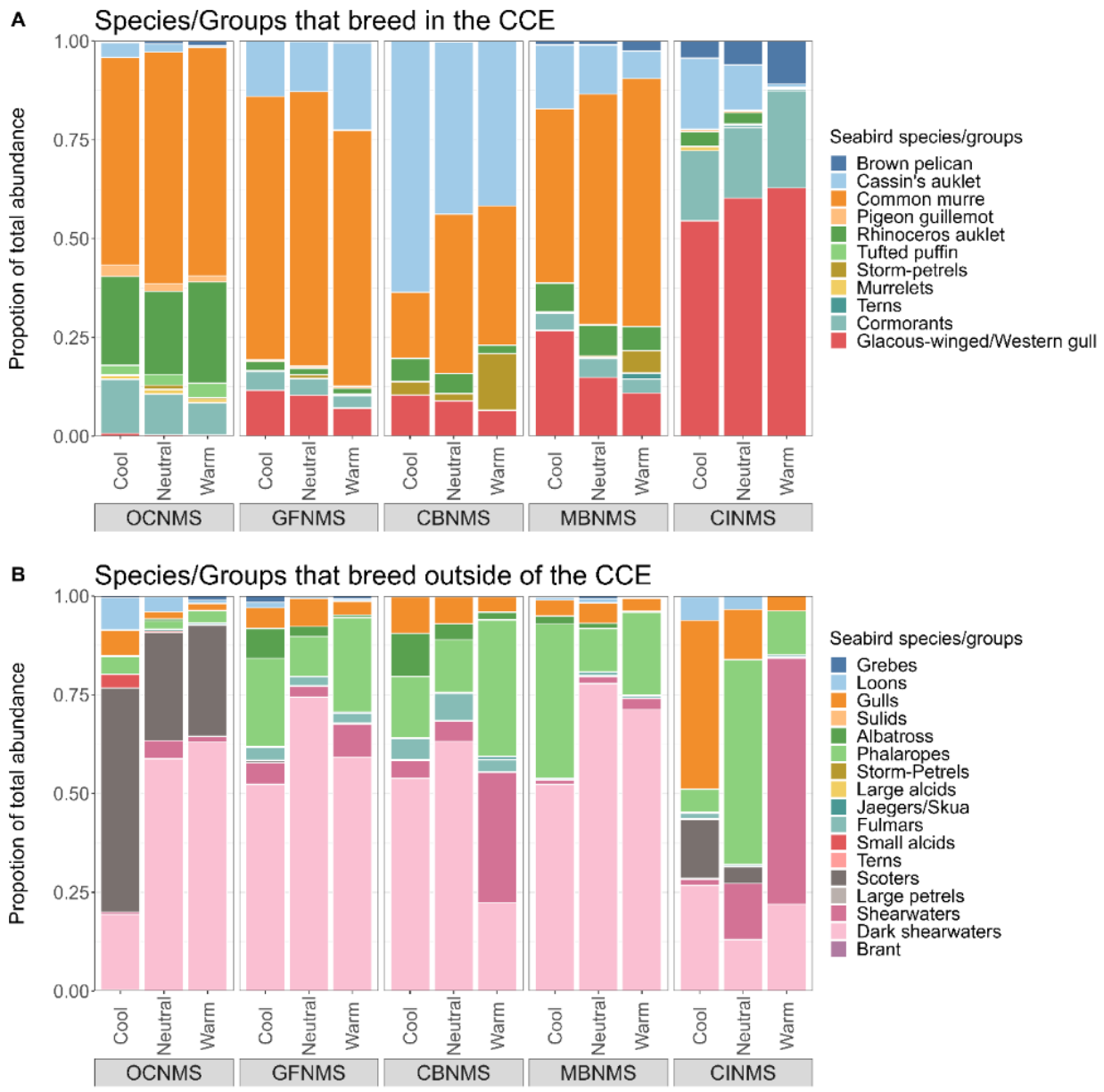


Figure 2.9: The proportion of species with different species groups during warm, neutral and cool periods (based on 1st and 3rd quartiles of local sea surface temperatures) within west coast National Marine Sanctuaries (1980-2018).

There was higher variability in the non-CCE breeding community within most of the NMS (Figure 9B). When it is cool, we see an increased proportion of scoters in OCNMS and CINMS, and a decreased proportion of all shearwaters in these two NMS. Inversely, when it is warm, we see an increase in other shearwaters (mostly pink-footed shearwaters, *Puffinus*

creatopus) within CBNMS, MBNMS, and CINMS. The central NMS communities remain relatively constant among the SST periods, supporting that these areas provide adequate habitat throughout varying conditions. An exception is an increased proportion of albatross during neutral and cool periods within GFNMS and CBNMS. When it is cool within CINMS, we also see an increased proportion of gull species, and when there are neutral conditions, an increased proportion of phalaropes.

DISCUSSION

Relative abundance

The abundance of avifauna within the NMS in the CCE has decreased since the 1980's, with greater declines in south. Decreases were largely due to a decline in non-CCE breeding species, which had decreased in abundance within all five NMS. Relationships between the abundance of seabirds with environmental conditions varied among the NMS, indicating that there are variable drivers within each of these regions.

Throughout all NMS, there were oscillations that occurred throughout our survey period. Such cycles of seabird abundance have been reported in other smaller scale studies (e.g., Central CA; Ainley and Hyrenbach, 2010). These oscillations may mask overall trends when analyses are conducted on smaller time scales. We detected oscillations that ranged between five and fifteen years, therefore confirming that time series of 30 years are needed to best evaluate long-term changes in abundance and sustained responses to climate change (Brito-Morales et al., 2018).

CCE-breeding species

CCE-breeding species have increased within the two NMS that capture the largest seabird breeding habitat (GFNMS and OCNMS). However, even within these two NMS, these locally

breeding species have been in decline since 2013. These CCE-breeding species have declined in the remaining three NMS, with the greatest declines in the south. Peak abundances of these species for all Central and Northern NMS occurred around 2010-2011, while peak abundance in the South occurred in the late 1980's.

Non-CCE breeding species

Non-CCE breeding species have declined within every NMS, with the greatest declines in the south and lowest in CBNMS, a known location of important foraging habitat for migratory species (Russell et al., 2023; Hyrenbach et al., 2006). In the North and Central there was a decrease in the proportion of zero sightings (i.e., decreased absence), meaning that within NMS where there were declines that there was a more even spread of seabirds, even though abundances were lower. These divergent patterns indicate that there may be underlying dynamics of changes in seabird patchiness; for instance, if birds are more evenly distributed during migration, foraging, resting, etc., this would result in decreased density but increased probability of seeing one. Such dynamics can reflect changes in seabird patchiness, which is a reflection of their marine prey (Fauchald & Erikstad 2002).

Beyond overall declines in non-CCE breeding species, the abundance trends within the NMS were highly variable. Peak abundance did shift later in time with increasing latitude, with peaks in abundance in CINMS in the late 1980's, MBNMS in the mid-1990's, CBNMS and GFNMS during 2002-3, OCNMS in 2016, and then again in CINMS in 2018. As these species tended to be more abundant during upwelling conditions in the north, the conditions across latitudes may drive their distribution and be responsible for variable patterns of abundance among the NMS. Further investigations into abundance and distribution outside of the NMS are needed to evaluate those mechanisms.

Indicator species in the NMS

The trends of our selected indicator species showed similar trends compared to overall trends in their corresponding groups (i.e., Cassin's auklets and CCE-breeding species). Common murres increased tremendously within OCNMS, likely affecting the similar overall increase in CCE-breeding species in this NMS. These common murres increased here until 2005-2010, when they leveled off and then began a steep decline until 2018. Within both NMS near/around the Farallon Islands (GFNMS and CBNMS), there has been an increase in common murres here until about 2014 and have been in decline since. Common murres on Southeast Farallon Island (SEFI) have increased since the early 1990's and show a continued long-term increase (Spears et al., 2022). There is a dip in their population in 2013 and dip in 2018-2019 before continuing to increase, which is similar to what was occurring at-sea. As these two data types display similar trends, it may be the case with more recent at-sea data that we see recoveries in these declines in at-sea common murre abundance.

Within all of the Central and South NMS, sooty shearwaters increased between the first and last 10 years, and decreased in the North. However, none of these estimates were robust indicating that there is high variability within their abundances and presence in NMS. This is further supported by our models, which showed abundance cycles of 5-15 years, except in MBNMS. Within Monterey Bay, sooty shearwaters increased through the 1980's and 1990's and have been declining since. MBNMS was previously highlighted as an important foraging location among west coast NMS, therefore trends here may best reflect broader trends and onshore-offshore movements (Adams et al., 2012).

Cassin's auklets declined in all NMS, with robust declines within OCNMS, CBNMS, and CINMS. The most drastic decreases in their abundance were within CINMS due to a

combination of an increase in the proportion of zeros, as well as a decrease in the mean relative abundance. Within the central NMS, there was very little change in the Cassin's auklets proportion of zeros, therefore trends were driven only by changes in the number of birds per sighting. However, within OCNMS, the abundance of Cassin's auklets within transect segments were low, therefore small changes in detections of this species may be overestimating these trends. The abundance trends of these auklets reflect the population trends on colonies within the CCE. On SEFI, within the GFNMS, there has been an overall decline, with periods of increased population size and breeding success. We detect these pulses in our data (pre-1998, between 2011-2004, and early 2010's; Spears et al., 2022) with increased 95% credible intervals during these periods.

Relative abundance and environmental conditions

CCE-breeding and non-CCE breeding species were abundant during different environmental and climatic periods, reflecting the breeding and migratory seasons and associated drivers. Within OCNMS, these species abundances were not driven by long time-scaled processes or conditions, but by seasonal upwelling conditions, with more birds during enhanced upwelling. This trend is further supported by higher abundances during enhanced NPGO, when there is higher wind stress curl and nutrient flux into this system. Within GFNMS and CBNMS, abundance was lower during neutral conditions, and higher during cool (La Niña) and warm (El Niño) conditions, and opposing upwelling seasons (during high and low Bakun). The abundance trends within MBNMS were strongly correlated with SST with higher abundances with higher SST. While the relationship between CCE-breeding species and longer scaled processes was complex, with high uncertainty during El Niño conditions, and was only slightly elevated during non-upwelling

seasons. In the south, CCE-breeding species abundance is highest during fall and winter when upwelling is reduced, and is highly variable with longer-scaled dynamics and with SST.

Within OCNMS, non-CCE breeding species relative abundance is highest during late summer/early fall, and without a strong relationship with broader spatial and temporal-scale dynamics or local, seasonally-scale environmental conditions. Within GFNMS and CBNMS, non-CCE breeding species were slightly elevated with upwelling, however highly variable patterns with ENSO. Non-CCE breeding species were at greatest abundances during La Niña and stronger upwelling conditions, although not dependent on SST. However, abundance within CINMS was variable with ENSO and SST conditions and higher during depressed upwelling conditions.

It is likely that every species has distinct environmental drivers, therefore, finer resolution on these dynamics can be gained by evaluating each species separately. These results do highlight how broad/fine scale environmental conditions may influence the abundance of these two species groups within CCE sanctuaries.

These trends are likely to increase as the ocean continues to warm and there is great intensity and variability in ENSO conditions. There are variable projections on how ENSO patterns will change along with climate change (Collins et al., 2010), but in scenarios that show there may be increased intensity and changing connections between atmospheric and oceanic processes (Cai et al., 2021), it is increasingly more important to monitor and update known trends and models on future changes in this complex current system. As SST continues to rise, it is also projected that the intensity and frequency of marine heatwaves is likely to increase (Athanase et al., 2024). Such heatwaves can have dramatic impacts on the marine food web, including mass mortality events of seabirds due to decreased availability and quality of prey (Piatt et al., 2020). Within all Central and Northern NMS, there was a declining trend of CCE-breeding species during the 2014-2016

heatwave (Gentemann et al., 2017), although the decline within MBNMS had begun before the start of these anomalously warm conditions. Within CINMS, there is a pulse of abundance during this time which may be driven by species moving south from off of Baja during those years. However, non-CCE breeding species increased in most of the NMS during this heatwave, even while overall trends were in decline. This may be due to species being constrained to coastal habitat due upwelling habitat compression. The cool, upwelled water habitat compresses because the California Current goes along the coast, and the warm water that upwelling displaces moves offshore. Therefore, during times of reduced upwelling, that warm water is closer to the shore, constraining the availability of upwelling habitat (and associated prey), but also moving warm water species closer to the coast (Ainley 1980; Santora et al., 2020).

For common murres, their abundance was linked with favorable foraging conditions (upwelling, high NPGO) in the north. However their abundance in the Central NMS was highly variable, with great abundances during El Niño, despite having more variability, and there was a stronger relationship with seasonality (PC2). This indicates that no matter the conditions in the Central region, common murres will be found there, while in the north, prime conditions may attract and retain murres from other regions and support increased abundance. Either scenario supports that these NMS play a crucial role during good and bad times for this species. However, during the marine heatwave 2014-2016, abundance in the Central NMS declined, but this is likely due to increased mortality rather than conditions that encourage them to forage elsewhere. During this marine heatwave, an estimated 1.2 million common murres died and there was widespread reproductive failure (Piatt et al. 2020).

Sooty shearwaters are a highly migratory species that travels to this region to forage in this upwelling ecosystem. Within Central and South NMS, sooty shearwaters are most abundant during

times of great upwelling. This species travels thousands of kilometers to forage here. They are efficient flyers and therefore they can easily travel to and select regions that will provide for them. Therefore, it makes sense that they are highest in abundance during times of high productivity. In contrast, they are found within OCNMS in the north during not poor El Niño conditions. This may be because the temperatures are less extreme in the north and even during times of El Niño or reduced upwelling, they are still productive.

Cassin's auklets had higher abundance in the Central NMS during warm water conditions. Their abundance was variable with environmental conditions within GFNMS and CBNMS, however show a tendency to be more abundant during El Niño, and were more abundant within MBNMS with warm water, low upwelling conditions. These patterns may be a result of these auklets moving northward during these warm water periods. Cassin's auklets are less abundant, or absent, from CINMS during warm water periods, and they have decreased substantially here. Some work has shown that these auklets will disperse offshore and further from colonies during warm conditions and that they avoided regions of high SST (Johns et al., 2020). Therefore, the more northern and offshore areas of NMS will become more essential for these species during these heightened conditions.

Community Composition

There were distinct patterns in the overall community composition within the NMS in the South and North in relation to SST conditions. In comparison, the North and South biogeographic regions experience disparate upwelling dynamics, local currents and eddies, and overall SST, in addition to different species breeding within the NMS in these regions. Between these two regions, when they experience anomalous ocean temperatures, they are impacted by seabirds coming from the North (OCNMS), or from the South (CINMS) resulting in shifting

communities. The seabirds that move between/near these regions, the Central biogeographic region, are more constant, as this is a transition zone between the two. Therefore, shifts in the communities are less extreme. The cluster analysis also showed that there was high interannual autocorrelation between the years, which may be tied to local conditions and breeding success between years.

When we investigate patterns among the communities of CCE-breeding and non-CCE breeding species, as expected, the proportions of locally breeding species are not variable during different SST. The availability of breeding habitat simplifies analysis and interpretation of at-sea data. The common assumption is that seabirds will be where their preferred prey/habitat are, however, if they are restricted to a colony, they may not have access to their prime foraging conditions (Ainley 1980). Therefore, we would expect these species to be within the NMS that are near where they breed no matter the oceanographic conditions so the presence is not a meaningful metric, unless it becomes an absence. We found within the models that we do detect differences in abundance and this may be tied to breeding success (i.e., they stay longer to raise a chick and therefore increase detectability). The exception to this was the proportion of Cassin's auklets during cool periods. These species depend on zooplankton, therefore are more sensitive to changes to nutrient availability and shifts at the base of the food web. With the increase in proportion of brown pelicans during warm periods is likely a result of more birds moving north to escape even warming conditions further south.

The communities of non-CCE breeding species were highly variable among SST conditions in the North and South. Scoters utilize both OCNMS and CINMS during the cool, productive conditions, while other shearwaters (mostly pink-footed shearwaters) increase in proportion during warm periods in OCNMS, CBNMS, and CINMS, which may be driven by the

habitat compression of upwelling habitat previously mentioned. Although there were minor fluctuations in some species (e.g., shearwaters during warm conditions in CBNMS, albatross during neutral and cool periods within GFNMS and CBNMS), the communities within the Central NMS remained stable among the different SST conditions. This finding further supports that this is a transition area between the North and South, a melting pot of various habitats between two extremes, and attracts a diversity of local breeders and migratory species with its productive habitat, even during warmer years.

NMS trends compared to other studies

Our results are in line with other studies, and show that monitoring seabirds within NMS can indicate long-term trends of birds within their corresponding biogeographic region. Previous studies, using smaller datasets and not only within NMS, found seabirds declining overall in the CCE (Veit et al., 1996) and within the Southern region (Mason et al., 2007, Sydeman et al., 2009, Sydeman et al., 2015). The abundance estimates in the South have shown severe declines, at 2% per year (Mason et al. 2007, Sydeman et al. 2009, Sydeman et al. 2015). We also found in the South large decreases in both CCE and non-CCE breeding species, and Cassin's auklets, however there was an increase in sooty shearwaters. Overall, we found non-CCE breeding species to be declining, and CCE-breeding species declining, except for the NMS with large colonies. In the North, previous work has detected an increase in total seabird density (Sydeman et al. 2009), however, we only see this trend within OCNMS with CCE-breeding species, while non-CCE breeding species and Cassin's auklets are decreasing here. Even CCE-breeding species may be on the decline, but further data and analysis will be needed to determine if the recent decline continues. Previous studies have detected large declines in dark shearwaters (sooty and short-tailed) during the 1980's and 1990's (Veit et al., 1996, Veit et al., 1997), and some

documented this decline and a following increase (Ainley & Hyrenbach, 2010). We found large fluctuations in their abundance within all five NMS, with sooty shearwaters increasing in all NMS but OCNMS. Perhaps our analysis within only the NMS is not able to capture larger, long-term shifts in abundance, but it also may be the case that these species fluctuate their use of the CCE and longer and broader spatial scale analyses are needed to fully disentangle their dynamics. The fact that our detected trends are not robust is likely due to these large fluctuations in their abundance; therefore, the real long term trend cannot be obtained without a long enough time series.

Implications for management

Within each NMS, there are monitoring programs on these marine ecosystem, and there are programs that collect data on seabirds at-sea within their boundaries (e.g., CalCOFI, ACCESS, Washington Department of Fish and Wildlife Northwest Forest Plan Marbled Murrelet surveys, etc.); although these are typically on different spatiotemporal scales and amounts of effort. Although there are currently limited protections throughout the entire NMS boundaries, these NMS provide a framework for further protections, and tools for implementing new conservation strategies. With the complex vulnerabilities of seabirds, and the apparent decline of several species and/or groups in all five west coast NMS, their continued monitoring is vital to understanding the dynamics of these marine ecosystems. Our understanding of how different species are changing in abundance and distribution can highlight underlying changes in the food web and overall ecosystem health, in addition to monitoring the health of these marine predators.

Limitations and future directions

Due to the wealth of data and species richness in the CCE, many investigations into these data remain. Our research is far from exhaustive and provides an overview of broad shifts and relationships of seabirds in NMS within the CCE using this newly available, comprehensive data. There are still gaps in our knowledge that would benefit from further studies, including updating species-specific distribution and abundance trends and spatiotemporal connections to environmental variables. Therefore, this work is a launching pad for further investigations, which would be enhanced with the addition of long-term data on prey to further disentangle these processes and trends.

The relationships between these species presence and abundance within NMS are complex, and while we detected some patterns with our analysis, processes affecting these dynamics may not be testable at these scales. For example, birds presence may be driven by fine-scale processes, such as tracking fronts and smaller scaled eddies. In addition, changes in the CCE-breeding and Non-CCE breeding species may be complicated by disparate trends of different species within these groups. For example, trends within non-CCE breeding species overall have declined, however, there is little change (even declines) in the proportion of zeros (absence). This may be due to changes in patchiness, which was previously mentioned, however, it might also be due to changes in species turnover within a system. As this ecosystem warms, new, more tropical species are moving northward (Velarde et al., 2015; Howard et al., *in press*). Alternatively, successes in breeding colony conservation and restoration (especially invasive species eradications), as well as an increased use of mitigation methods to decrease bycatch, have created success stories for threatened migratory species and may result in increased occurrence in the CCE. However, true detections of abundance changes may take time as a population recovers, therefore the first signs

may be of increased presence only. In addition, it should be stressed, that the failure to detect changes or clear trends in seabird abundance does not mean that no changes have happened, and we should strive to better our estimates, continue our data collection, and foster collaboration that allow these large-scale analyses to occur (Maclean et al., 2013). Continued long-term monitoring is essential for these investigations, as the longer we collect data, the more we can detect these fine-scale, yet critical changes in our CCE species and how they are using this dynamic habitat.

Chapter 2, in part is currently being prepared for submission for publication of the material. Russell, Tamara M.; Hinke, Jefferson T.; Jahncke, Jaime; Franks, Peter J. S.; Vernet, Maria; Ballance, Lisa T. The dissertation author was the primary researcher and author of this material.

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SUPPLEMENTAL MATERIALS

Table S2.1: Survey Data used in this study. Much of this was compiled by Leirness et al. (2021), with added years of CalCOFI, ACCESS, and the NOAA Southwest Fishery Science Center CCE data.

Survey Name	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	2005-2015
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

Table S2.1: Survey Data used in this study (continued)

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
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

Table S2.2: List of species that are California Current Ecosystem (CCE) breeding species and those that breed outside of the CCE. We only considered a species to be 'CCE-breeding if it was documented breeding within coastal/offshore regions during our survey period (1980-2018).

Group	Species
CCE-breeding	Ashy storm-petrel (*Oceanodroma homochroa*), black storm-petrel (*Chlidonias niger*), black skimmer (*Rynchops niger*), Brandt's cormorant (*Phalacrocorax penicillatus*), brown pelican (*Pelecanus occidentalis*), Cassin's auklet (*Ptychoramphus aleuticus*), Caspian tern (*Hydroprogne caspia*), common murre (*Uria aalge*), double-crested cormorant (*Phalacrocorax auritus*), elegant tern (*Thalasseus elegans*), fork-tailed storm-petrel (*Oceanodroma furcata*), glacous-winged gull (*Larus glaucescens*), Leach's storm-petrel (*Oceanodroma leucorhoa*), least tern (*Sternula antillarum*), marbled murrelets (*Brachyramphus marmoratus*), Xantus's murrelet (Guadalupe/Scripps; *Synthliboramphus* sp.), pelagic cormorant (*Phalacrocorax pelagicus*), pigeon guillemot (*Cepphus columba*), rhinoceros auklet (*Cerorhinca monocerata*), tufted puffin (*Fratercula cirrhata*), western gull (*Larus occidentalis*)
Non-CCE breeding	Ancient murrelets (*Synthliboramphus antiquus*), Arctic tern (*Sterna paradisaea*), black-footed albatross (*Phoebastria nigripes*), blue-footed booby (*Sula nebouxii*), black-legged kittiwake (*Rissa tridactyla*), black scoter (*Melanitta americana*), black tern (*Chlidonias niger*), Bonaparte's gull (*Chroicocephalus Philadelphia*), brown booby (*Sula leucogaster*), brown noddy (*Anous stolidus*), band-rumped storm petrel (*Oceanodroma castro*), Buller's shearwater (*Ardenna bulleri*), black-vented shearwater (*Puffinus opisthomelas*), California gull *(Larus californicus*), Clark's grebe (*Aechmophorus clarkia*), common loon (*Gavia immer*), Cook's petrel (*Pterodroma cookie*), common tern (*Sterna hirundo*), Craveri's murrelets (*Synthliboramphus craveri*), eared grebe *(Podiceps nigricollis*), flesh-footed shearwater (*Ardenna carneipes*), Forster's tern (*Sterna forsteri*), Franklin's gull (*Leucophaeus pipixcan*), glaucous gull (*Larus hyperboreus*), Hawaiian petrel (*Pterodroma sandwichensis*), Heermann's gull (*Larus heermanni*), herring gull (*Larus argentatus*), horned grebe (*Podiceps auritus*), horned puffin (*Fratercula corniculata*), Juan Fernandez petrel (*Pterodroma externa*), Kermadec petrel (*Pterodroma neglecta*), Laysan albatross (*Phoebastria immutabilis*), laughing gull (*Leucophaeus atricilla*), long-billed murrelets (*Brachyramphus perdix*), Least storm-petrel (*Oceanodroma microsoma*), long-tailed jaeger (*Stercorarius longicaudus*), Manx shearwater (*Puffinus puffinus*), mew/short-billed gull (*Larus canus*), mottled petrel (*Pterodroma inexpectata*), Murphy's petrel (*Pterodroma ultima*), northern fulmar (*Fulmarus glacialis*), parakeet auklet (*Aethia psittacula*), parasitic jaeger (*Stercorarius parasiticus*), Pacific loon (*Gavia pacifica*), Parkinson's/black petrel (*Procellaria parkinsoni*), Solander's/ providence petrel (*Pterodroma solandri*), pink-footed shearwater (*Ardenna creatopus*), Pomarine jaeger (*Stercorarius pomarinus*), ring-billed gull (*Larus delawarensis*), red-billed tropicbird (*Phaethon aethereus*), red phalarope (*Phalaropus fulicarius*), red-footed booby (*Sula sula*), ringed storm petrel (*Oceanodroma hornbyi*), red-necked grebe (*Podiceps grisegena*), red-necked phalarope (*Phalaropus lobatus*), royal tern (*Thalasseus maximus*), red-throated loon (*Gavia stellate*), red-tailed tropicbird (*Phaethon rubricauda*), Sabine's gull (*Xema sabini*), slaty-backed gull (*Larus schistisagus*), sooty shearwater (*Ardenna grisea*), south polar skua (*Stercorarius maccormicki*), short-tailed shearwater (*Ardenna tenuirostris*), short-tailed albatross (*Phoebastria albatrus*), Stejneger's petrel (*Pterodroma longirostris*), streaked shearwater (*Calonectris leucomelas*), surf scoter (*Melanitta perspicillata*), thick-billed murre (*Uria lomvia*), Thayer's gull (*Larus gaucoides thayeri*), wandering albatross (*Diomedea exulans*), western grebe (*Aechmophorus occidentalis*), Wilson's phalarope (*Phalaropus tricolor*), Wilson's storm petrel (*Oceanites oceanicus*), wedge-rumped storm petrel (*Oceanodroma Tethys*), wedge-tailed shearwater (*Ardenna pacifica*), white-winged scoter (*Melanitta fusca*), yellow-billed loon (*Gavia adamsii)*

Table S2.3: Comparisons between the first and last 10 years of data for three dominant species in the CCE; sooty shearwaters (SOSH; *Ardenna grisea*), common murres (COMU; *Uria aalge*), and Cassin's auklets (CAAU; *Ptychoramphus aleuticus*). It includes the years, the number of transect segments, the mean and the mean difference along with 95% confidence intervals, and the percentage difference between periods.

National Marine Sanctuary	Years	Species	% Zeros	Mean relative abundance (95% CI)	Mean difference (95% CI)	% Difference
Olympic Coast	1980-1996	SOSH	70.7	31.93 [0.22, 63.64]	-12.13 [-44.41, 20.15]	-38.0
	2009-2018		57.4	19.80 [14.04, 25.56]		
	1980-1996	COMU	71.6	10.14 [6.82, 13.47]	24.65 [17.80, 31.50]	243.0
	2009-2018		23.1	34.79 [28.81, 40.77]		
	1980-1996	CAAU	84.9	2.72 [1.89, 3.54]	-1.44 [-2.35, -0.53]	-53.0
	2009-2018		79.4	1.28 [0.89, 1.67]		
Greater Farallones	1980-1996	SOSH	84.9	6.96 [4.03, 9.88]	2.31 [-2.29, 6.92]	33.2
	2009-2018		66.7	9.27 [5.72, 12.82]		
	1980-1996	COMU	63.0	14.43 [10.92, 17.94]	9.38 [5.08, 13.68]	65.0
	2009-2018		28.2	23.81 [21.33, 26.29]		
	1980-1996	CAAU	75.1	7.41 [5.26, 9.56]	-2.23 [-4.59, 0.12]	-30.2
	2009-2018		75.7	5.18 [4.22, 6.14]		
Cordell Bank	1980-1996	SOSH	86.1	2.87 [0.75, 5.00]	1.19 [-1.52, 3.90]	41.5
	2009-2018		60.6	4.07 [2.39, 5.74]		
	1980-1996	COMU	77.8	5.61 [2.69, 8.54]	2.19 [-1.04, 5.41]	38.9
	2009-2018		49.3	7.80 [6.44, 9.16]		
	1980-1996	CAAU	67.8	11.41 [8.00, 14.81]	-5.35 [-9.19, -1.51]	-46.9
	2009-2018		70.8	6.06 [4.30, 7.82]		
Monterey Bay	1980-1996	SOSH	81.0	1.14 [7.99, 14.29]	4.21 [-3.50, 11.92]	37.8
	2009-2018		58.6	15.35 [8.32, 22.39]		
	1980-1996	COMU	78.6	8.09 [6.02, 10.16]	-3.10 [-5.26, -0.94]	-38.3
	2009-2018		59.7	4.99 [4.36, 5.63]		
	1980-1996	CAAU	88.5	1.96 [1.47, 2.44]	-0.54 [-1.13, 0.04]	-27.7
	2009-2018		89.0	1.41 [1.09, 1.74]		
Channel Islands	1987-1996	SOSH	81.9	2.58 [1.02, 4.13]	2.65 [-0.65, 5.95]	102.9
	2009-2018		73.4	5.23 [2.32, 8.14]		
	1987-1996	CAAU	79.0	3.13 [0.97, 5.30]	-2.86 [-5.03, -0.68]	-91.2
	2009-2018		93.3	0.28 [0.10, 0.45]		

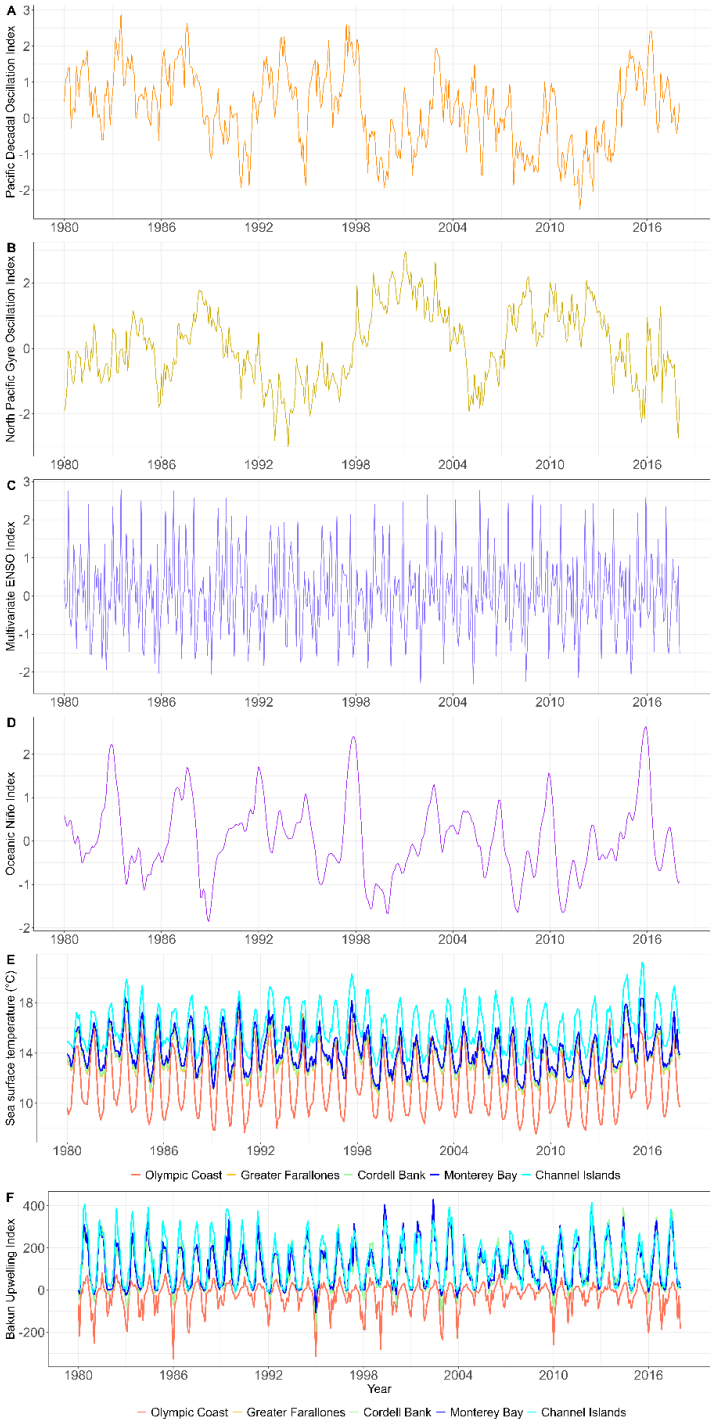


Figure S2.1: All environmental indices and variables used in the PCA. The Pacific Decadal Oscillation (A), North Pacific Gyre Oscillation (B), Multivariate El Nino Southern Oscillation Index (C), and the Oceanic Nino Index (D) are broad scale indices that are the same values throughout all National Marine Sanctuaries (NMS). Both sea surface temperature (E) and Bakun Upwelling Index (F) reflect more local conditions within or adjacent to the corresponding latitude and longitude of each NMS.

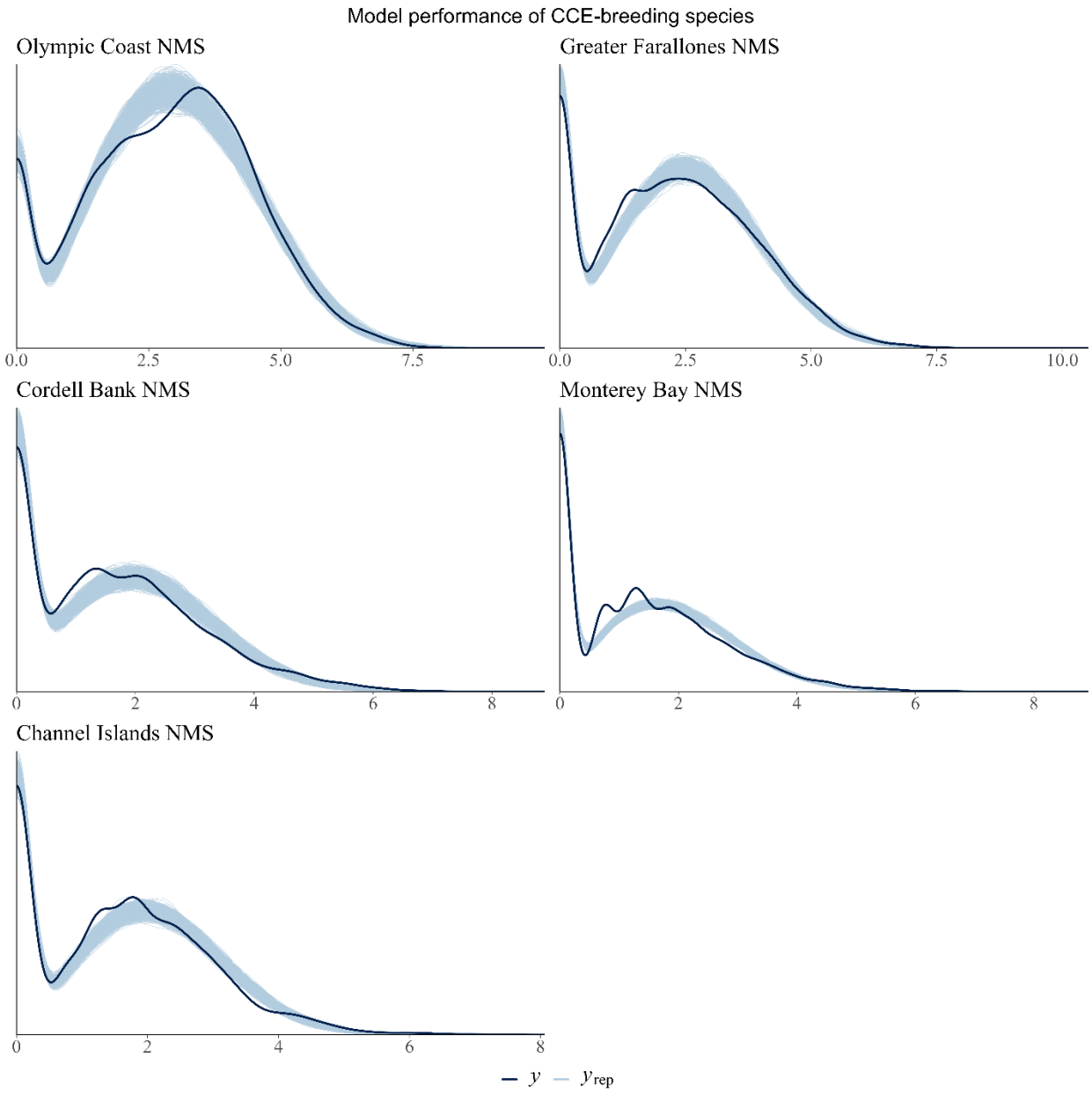


Figure S2.2: The fit of the Bayesian hurdle mixed model generalized additive models on CCE-breeding species over time in each of the National Marine Sanctuaries (NMS). These plots show the empirical distribution of the raw data to the distributions of 1,000 draws from the posterior predictive distribution

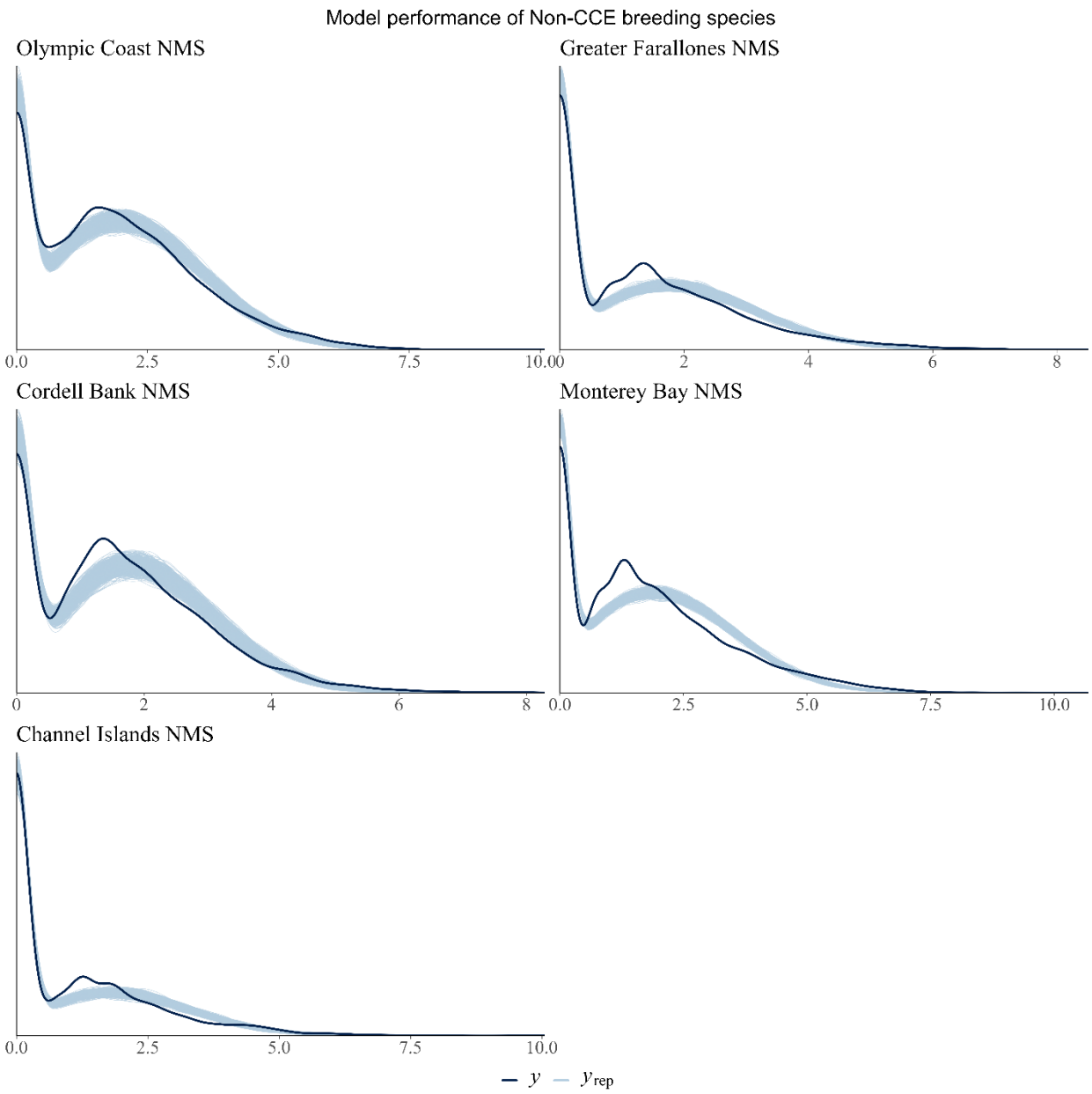


Figure S2.3: The fit of the Bayesian hurdle mixed model generalized additive models on non-CCE breeding species over time in each of the National Marine Sanctuaries (NMS). These plots show the empirical distribution of the raw data to the distributions of 1,000 draws from the posterior predictive distribution

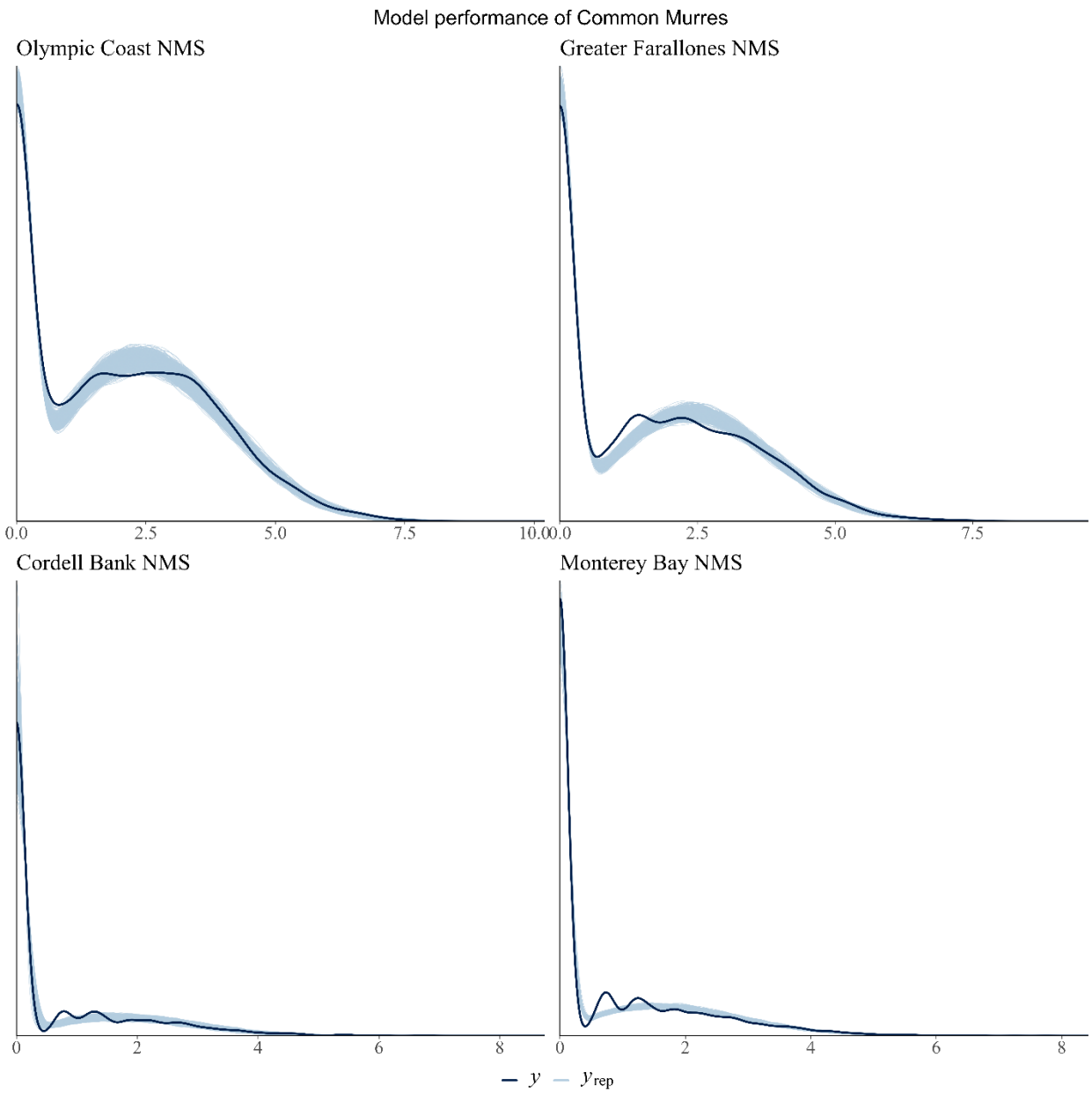


Figure S2.4: The fit of the Bayesian hurdle mixed model generalized additive models on common murres over time in each of the National Marine Sanctuaries (NMS). These plots show the empirical distribution of the raw data to the distributions of 1,000 draws from the posterior predictive distribution

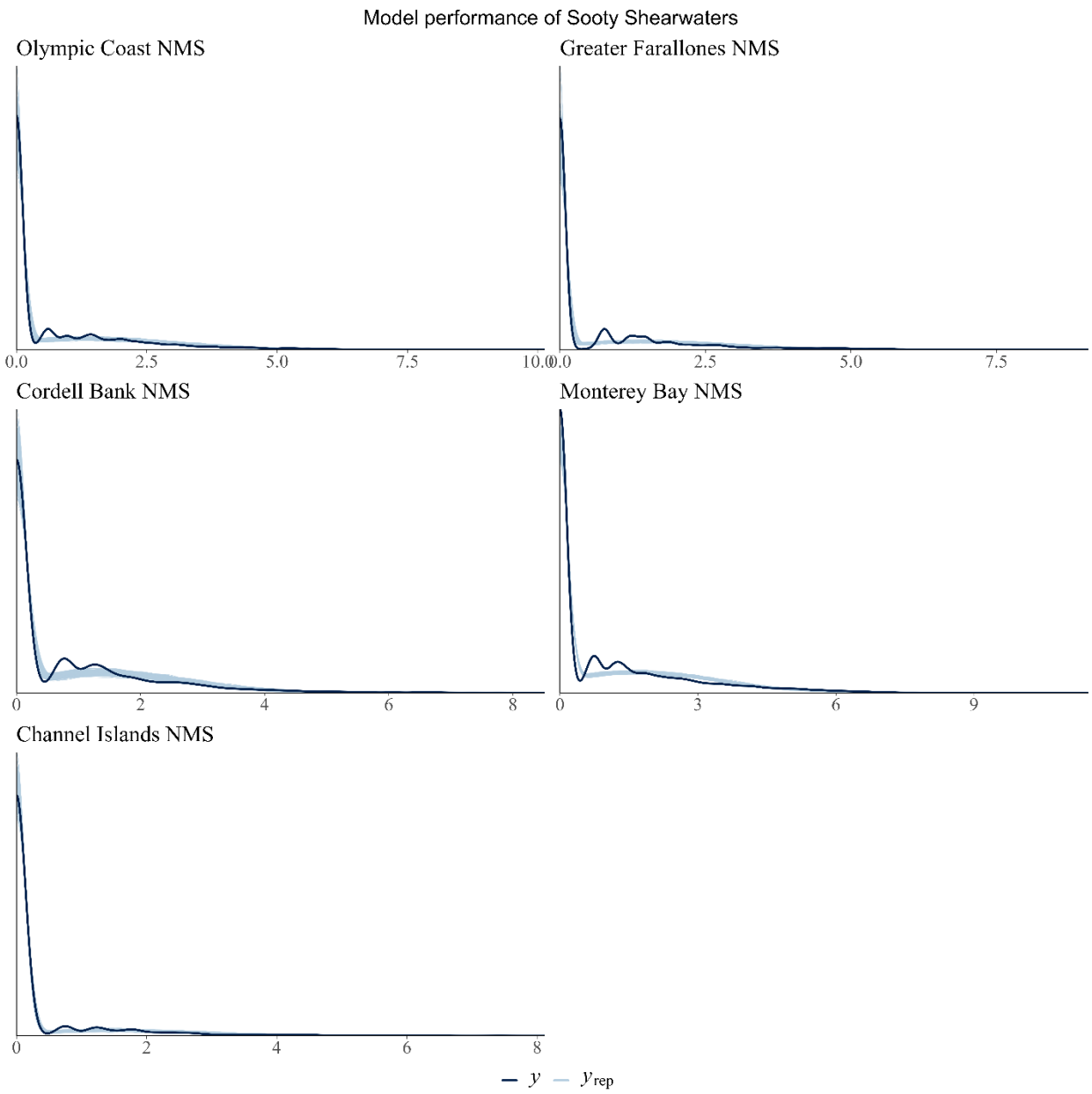


Figure S2.5: The fit of the Bayesian hurdle mixed model generalized additive models on sooty shearwaters over time in each of the National Marine Sanctuaries (NMS). These plots show the empirical distribution of the raw data to the distributions of 1,000 draws from the posterior predictive distribution

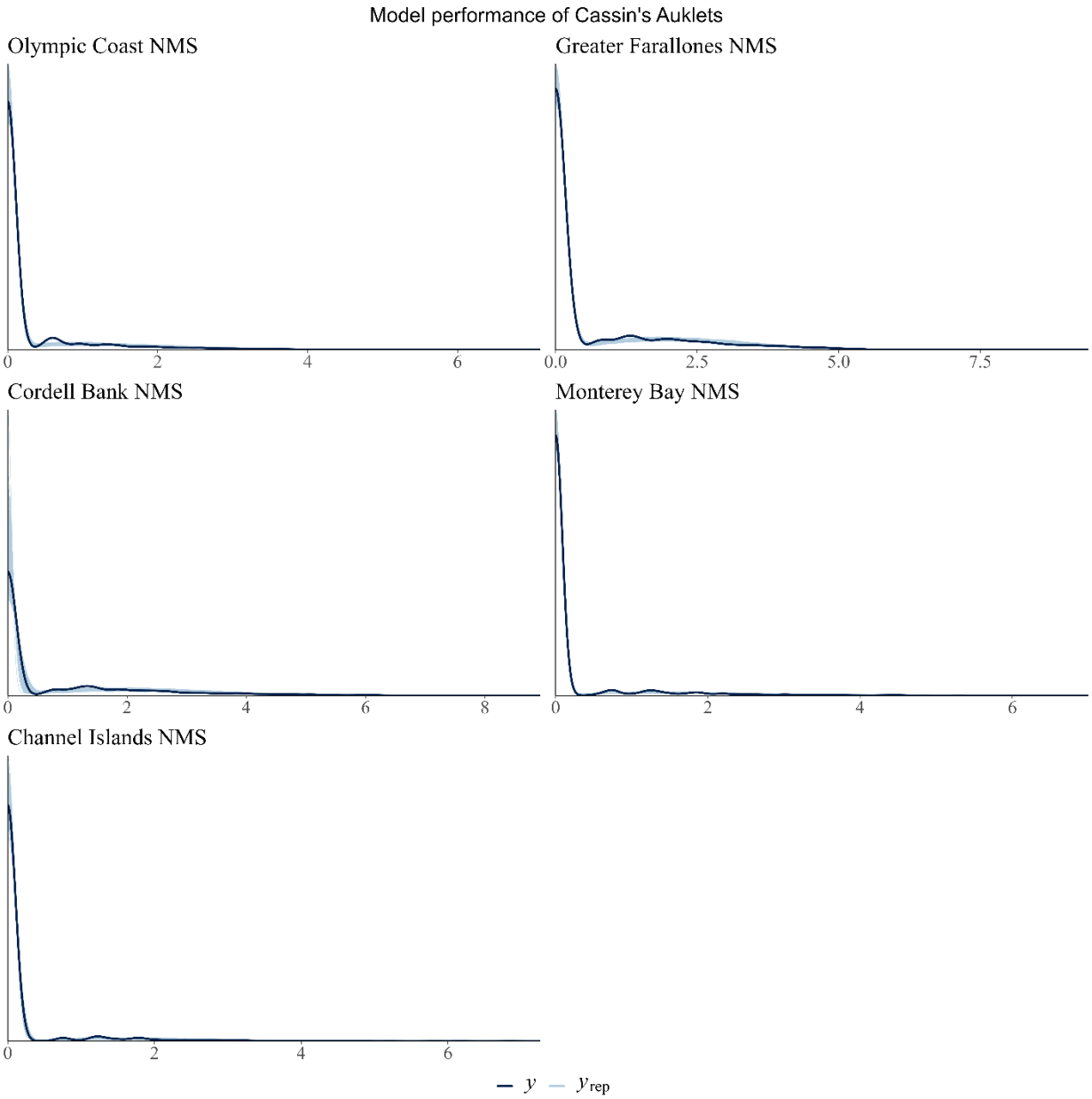


Figure S2.6: : The fit of the Bayesian hurdle mixed model generalized additive models on Cassin's auklets over time in each of the National Marine Sanctuaries (NMS). These plots show the empirical distribution of the raw data to the distributions of 1,000 draws from the posterior predictive distribution

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CHAPTER THREE

The increase of tropical seabirds (*Sulidae*) in the California Current Ecosystem with warmer ocean conditions

ABSTRACT

Climate change is impacting marine ecosystems in the California Current through physical changes (e.g., an increase in the frequency and intensity of marine heatwaves) that manifest themselves biologically at all trophic levels. We investigated range shifts in the California Current Ecosystem (CCE) and correlations with environmental conditions for tropical/sub-tropical Sulid seabirds. We assessed changes in the abundance (2002-2022) of five species (Brown, Blue-footed, Red-footed, Masked, and Nazca boobies) using four data sources (at-sea surveys (n=62 Sulid records), records from Southeast Farallon Island (n=130), the California Rare Birds Committee (n=795), and eBird (n= 28538)- a citizen science mobile application), and looked for relationships with the environmental, including El Niño Southern Oscillation, local upwelling conditions, and sea-surface temperature (SST). We also tested Sulid abundance with lagged air temperature and SST data from potential source locations around Baja and within the Gulf of California. All five species increased in abundance and all species with the exception of Blue-footed Boobies showed northward range shifts by as much as 10 degrees latitude and increased range area within the CCE (Brown, R2=0.57; Red-footed R2=0.49; Masked/Nazca, R2=0.57). Our models show that higher SST at potential source locations and local habitats of where these birds were reported explained much of variance in the abundance of Brown, Red-footed, Masked, and Nazca boobies, and all species had increased after the 2013 and 2014-2016 marine heatwaves (379-2508% increases in Sulid abundance between these periods). As marine heatwaves are projected to increase in frequency and intensity, in addition to long-

term warming, we hypothesize that these species will continue to expand their range northward in the CCE.

INTRODUCTION

Species distributions are changing rapidly in response to climate change (Pinsky et al., 2020). Such changes in species ranges may be periodic or long-term, and they may be directional shifts, contractions, or expansions of previous ranges. These distribution changes often reflect the direction of warming (moving poleward, deeper, etc.) or contract/expand as realized habitat availability changes (Pinsky et al., 2013; Wingfield et al. 2015; Pinsky et al., 2020). A species' range may change due to direct and indirect impacts from climate change, including physiological restraints of a changing habitat, changes in species interactions, prey availability/quality, reproductive habitat availability/quality (Pinsky et al., 2020). Species moving into or out of an ecosystem may have impacts on the ecosystem structure, such as food web efficiency, stability through diversity, and interspecies competition, as well as implications for conservation and fisheries management (Albouy et al., 2014; Bartley et al., 2019; Tekwa et al., 2022).

Seabirds are conspicuous marine predators, and their distribution and abundance patterns can provide information on the underlying marine food web (Fauchald 2009). Changes in seabird communities and distributions are of special concern for the management and conservation of seabirds and other marine life, as changing species distributions can signal that something unusual has occurred in the ecosystem or new species may become competitors for resources with resident species. Understanding drivers of shifting species distributions allows us to better predict how an ecosystem may continue to change with a warming climate and how these shifts may impact existing species in these regions.

The California Current Ecosystem (CCE) is a productive eastern boundary upwelling region. Within the southern sector of the CCE, the Southern California Bight (SCB) is a unique transition zone between cool and warm water ecosystems. The headland of Point Conception, California (Figure 1), is where cool water from the north meets warm subtropical waters in the south (Horn & Allen 1978, Hunt et al., 1980, Hendershott & Winant 1996), and is a location where the northern or southern extent of many species ranges end (Hayward & Venrick, 1998, Pitz et al., 2020, Sydeman et al., 2009, Horn & Allen 1978, Briggs & Bowen 2011). Strong upwelling occurs in the northern portion of the SCB, just off of Point Conception, and this cool, nutrient-rich water spreads southward (Sydeman et al., 2015).

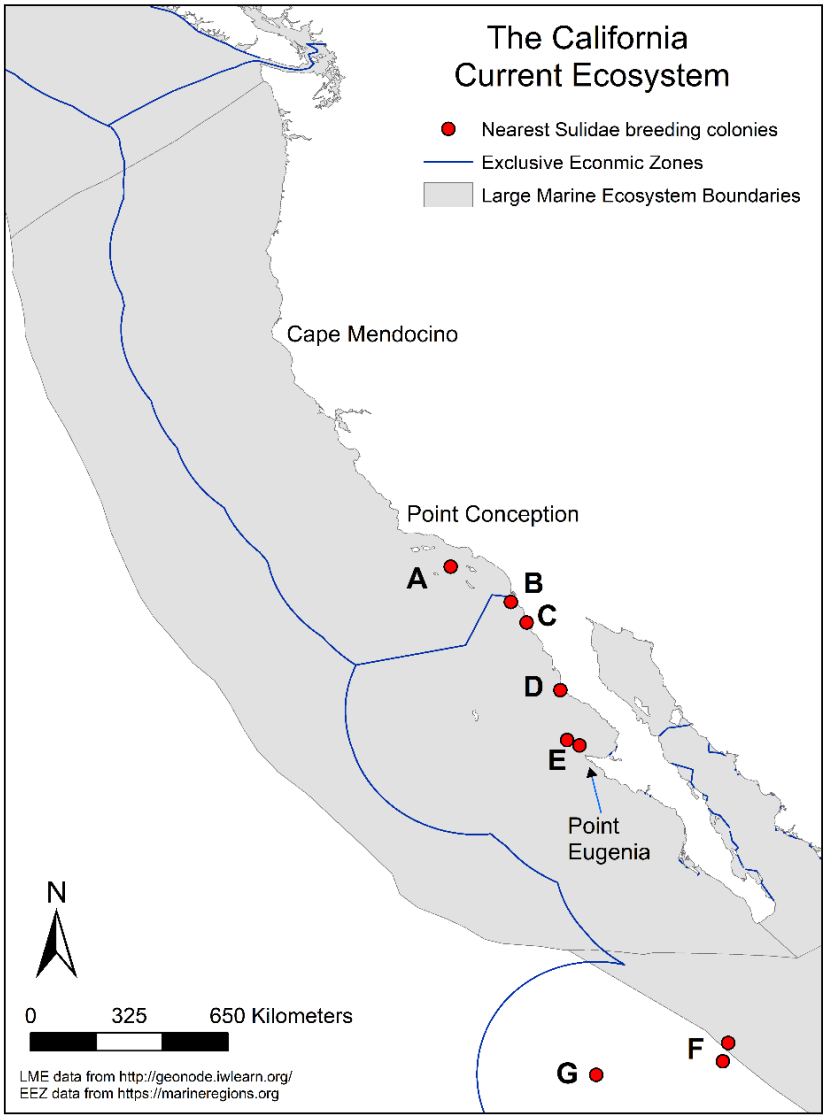


Figure 3.1: Map of the California Current Ecosystem. The north and central biogeographic regions are separated by Cape Mendocino, the central and south by Point Conception and the south extends down to Point Eugenia. The locations of breeding colonies of Sulidae in the Pacific are indicated in red and are as follows: (A) Sutil Rock, Santa Barbara Island, (B) Middle Rock, Coronado Islands, (C) Todos Santos Islands, (D) San Jerónimo Island, (E) San Benito and Cedros Islands, (F) San Benedicto and Socorro Islands (inner Revillagigedo Islands), and (G) Clarion Island (outer Revillagigedo Islands).

As the ocean temperatures have warmed, within the SCB, the cool-warm gradient has blurred, and subtropical species from warmer waters have moved north into the CCE (Rasmussen et al., 2020, Sagarin et al., 1999, Ainley 1980, Hyrenbach & Veit 2003). In addition

to long-term changes, the CCE has experienced an increase in frequency and intensity of marine heatwaves that may be expediting these changes in species distributions (Jacox et al., 2020). Such range shifts may be occurring in seabirds in the CCE, and while seabirds are central place foragers and are tied to feeding around where they breed, shifts in breeding locations have already occurred in the SCB region. Elegant terns that typically breed only within the Gulf of California have been shifting north to Southern California to breed during warm years when there is poor food availability in the Gulf of California (Velarde et al. 2015; Veit et al., 2021). In addition, both brown boobies (*Sula leucogaster brewsteri*) and blue-footed boobies (*S. nebouxii*) have recently (2017 and 2022, respectively) expanded their breeding range to Sutil Rock off Santa Barbara Island, California (Howard et al., 2024). Leading up to this breeding range expansion, brown boobies had expanded their breeding in 2005 to Middle Rock, off of the Islas Los Coronado in northern Baja California (Whitworth et al., 2007), and blue-footed boobies to San Jerónimo Island, off the west coast of Baja CA in 2016 (Bedolla-Guzman et al. 2019). Although these breeding expansions are now well-documented, the drivers of these expansions are unknown. In addition, sightings of all five Sulidae species found off Baja may be increasing in the CCE, which includes brown (BRBO), blue-footed (BFBO), red-footed (RFBO; *S. sula*), masked (MABO; *S. dactylatra*), and Nazca boobies (NABO; *S. granti*).

Species within the genus Sulidae are large, plunge-diving seabirds that are found in tropical and subtropical oceans and coastlines (Nelson 1978). Due to their size and flight-style, they have high energetic needs and require large amounts of food to sustain them (Ballance 1995, Nelson 1978). Of the five species that occur along western North America, four have pantropical distributions, while blue-footed boobies are constrained within coastal regions along the western coast of tropical/sub-tropical North, Central, and South America (Nelson 1978).

Prior to the expansion and colonization of Middle Rock, San Jerónimo Island, and Sutil Rock, the nearest Sulidae colonies were located off Southern Baja California, with other regional colonies located off Central Mexico and within the Gulf of California (Nelson 1978, Whitworth et al., 2007; Howard et al., 2024). Brown boobies are a common, medium-sized Sulid, that have well-established colonies near the CCE on Clipperton Atoll and Islas Revillagigedo (Schreiber and Norton 2020) off central Mexico and on Roca Consag and Isla San Jorge in the Gulf of California (Mellink 2000). The nearest breeding location of remaining pantropical species, red-footed, masked, and Nazca boobies, all occur on Islas Revillagigedo and/or Clipperton Atoll off central Mexico (Howell and Pyle 1997; Pitman and Jehl 1998). Red-footed boobies are the smallest and most abundant Sulidae with the most pelagic distribution (Nelson 1978). They have two distinct color morphs, a light and dark, which historically made identification difficult (Nelson 1978). Masked and Nazca boobies are a large Sulidae, with wingspans over 1.5 m (Nelson 1978). These Sulidae were once considered the same species, and are morphologically extremely similar. They were separated taxonomically in 2000, based on behavior, breeding, and distinct bill color; yellow in Masked Boobies and orange-pink in Nazca (Pitman and Jehl 1998). This recent split and their morphological similarities, have made historic and recent identification difficult. Additionally, on areas of sympatric breeding (Clipperton Atoll and the Islas Revillagigedo), hybridization does occur (Pitman and Ballance 2002). Blue-footed boobies are a medium-sized Sulidae with a coastal, patchy distribution along the western side of the tropical Americas (Nelson 1978). Although the largest breeding colonies of blue-footed boobies occur on the Galapagos Islands, prior to the colonization of San Jerónimo Island, the closest breeding locations were within the Gulf of California (Nelson 1978; Díaz and Gómez 2020). As these species mostly live in tropical, lower productivity regions, the impacts of warming

temperatures may have disproportionate effects on already low stocks of potential prey, and they may be experiencing high competitive pressures to venture further for resources.

Here, we document the northward range expansion of Sulidae into the CCE, and we test our hypothesis that their occurrence and trends relate to warmer ocean conditions. To evaluate these changes, we used a variety of data types to understand trends in the presence of these species, and their relationship to environmental conditions. Data on species of low frequency within a region, such as Sulidae within the CCE, are inherently lacking, therefore including all types of data available may increase our ability to detect abundance and distribution trends. In this study, we utilize data collected during structured surveys (at-sea strip transects and some of the field surveys on Southeast Farallon Island; SEFI) and semi-structured survey data (incidental sightings on SEFI & *eBird*; Sullivan et al. 2014). We then fill in potential gaps of observations with unstructured data (California Rare Birds Committee observations). Semi-structured data sources mean observations and records include information about the observation, such as duration and distance travelled during data collection, whether the observer recorded data on all species and other information that can provide rich metadata along with species observations. The integration of public-collected (i.e., 'citizen science'), semi-structured data with structured survey data has been shown to improve relative abundance estimations (Schindler et al., 2020) and population growth rates (Walker & Taylor 2017; Horns et al., 2018; Robinson et al., 2018).

METHODS

Survey Area

The CCE is a productive eastern boundary current that stretches roughly 2800 km from the North Pacific Current (~50◦N) down to Baja California, Mexico (23–25◦ N; Figure 1;

Checkley and Barth, 2009). Within the CCE are three biogeographic regions –North, Central, South– that have distinct upwelling patterns and biological communities (Ainley, 1976; Ainley et al., 2015; Schipper et al., 2016, Russell et al., 2023). The North and Central regions are separated by Cape Mendocino (40.438◦N), the Central and South by Point Conception (34.448◦N), and the South extends to Point Eugenia (27.848, -115.083; Checkley and Barth, 2009). As our aim is to test if Sulidae are increasing in abundance in the CCE and if their distributions are shifting north, we separated the southern CCE portion of our study area into the Southern California Bight and Northern Baja based on the northernmost location (pre-breeding expansion to the CCE) of brown and blue-footed booby breeding locations (Middle Rock, Coronado Islands and San Jerónimo Island). We then removed sightings at the Salton Sea, California (CA) and Gulf of CA, as these trends may have different drivers than trends for birds moving northward into the CCE.

Seabird data

All data processing and analyses were conducted in the R environment (version 4.0.3 R Core Team 2020). As vagrants are inherently rare, we used multiple data sources to investigate potential trends in Sulidae presence and potential environmental drivers (Figure S1 & S2). Vagrant species are defined as species that are rarely seen within a region due to it being outside of its typical range and not because the species is inherently rare (Stake 2012; Taylor et al., 1994; Mason et al., 2007).

a. At-sea data

Within the CCE, there are a wealth of data on the at-sea distributions of seabirds that has been collected through temporary or long-term systematic surveys over several decades. These data are collected using the ship, strip transect method (Tasker et al., 1984; Ballance, 2007) or

aerial strip survey method (Mason et al. 2007) and result in density estimates of all seabird species within the surveyed transect (Henkel et al., 2007). Data from 21 of these programs were compiled by Leirness et al. (2021) into a common format (1980-2017), and we added additional years from California Cooperative Oceanic Fisheries Investigations (CalCOFI), Applied California Current Ecosystem Studies (ACCESS), and NOAA's Southwest Fishery Science Centers California Current Ecosystem Survey (CCES) resulting in a dataset that spanned 43 years (1980-2021; Table 1S, Figure 1S.A). The species codes were standardized across the different datasets, and observations were subdivided into smaller transect segments (mean = 3.89 km) in order to calculate area surveyed (transect area) and assigned coordinates of each transect segment midpoint.

b. Southeast Farallon Island data

There has been avian monitoring at SEFI since 1967. During this period, researchers documented daily sightings of bird species, which were summarized in a monthly record of sightings spanning 56 years (1967-2022). These data include the species, number of individuals, and the date of first arrival for each individual (Figure 1S.B).

During the fall season (mid-Aug to early Dec), we conducted daily counts for Brown Pelican and Sulidae species from the lighthouse every morning when visibility allowed. These surveys were conducted from 0700 to 0900 when no part of the island was obscured by fog or clouds and it was not raining. During other seasons (Dec to mid-Aug), pelicans are less numerous and the counts were conducted haphazardly. Throughout the year, a 5-minute sea watch was conducted before 0900 with a 30x spotting scope from the houses facing southwest. Additionally, during the fall, a 30-minute sea watch was conducted from the east side of the island late in the afternoon. From 2005-2022, area searches were conducted twice daily during the fall season, one in the morning and one in the afternoon, except after mid-Nov when the

afternoon survey was dropped. Area searches consisted of a single person walking all the accessible parts of the island to search for land birds, but notes were recorded for non-land bird species such as Sulidae. Prior to 2005 and during non-fall seasons, area searches were not conducted.

The dates of arrival and counts were estimated by identification of the individual (age, sex, and plumage) within a one-month period. For brown boobies, an unknown individual (no age or sex information recorded) was assumed to be the same bird if it went undetected for up to 30 days. For blue-footed boobies, four juveniles showed up at SEFI in 2013 during a year when there was a large influx of juveniles into California waters (Rottenborn et al., 2016). Since there were very few birds in the CCE afterwards, the two blue-footed boobies that showed up as second-years in 2014, and then came back as adults to the same location each year (2015-2019) were considered two of the four juveniles from 2013. For red-footed, masked, and Nazca boobies, individual records were based on California Rare Birds Committee decisions.

c. California Rare Birds Committee

The California Rare Birds Committee (CRBC) is a volunteer committee that is part of the Western Field Ornithologists group. The public submits records of rare birds (which generally average four or fewer occurrences per year in the state; Hamilton et al., 2007) to the committee and the group evaluates, approves/declines observations, and manages an open access database on these records. We compiled data from the CRBC rare bird reports from (https://californiabirds.org; Benson et al., 2022). We only used accepted and verified reports in our analyses. From documentation, the committee also assesses whether new reports are new or recurring individuals, and if they are recurring, they record the date of their first arrival and date last reported. We used the date of first arrival in all analyses. The Sulidae records used in this

study from the CRBC included 502 records spanning 1946 to 2019, years where reports had been evaluated at the time of the data download (Figure 1S.C). By 2021, all species of Sulidae (brown =2007, blue-footed =2014, red-footed & Nazca=2019, masked=2021), were removed from the rare bird list and are no longer tracked by the CRBC.

d. eBird data

We used citizen science data from the highly used mobile application, *eBird,* which is hosted by Cornell Lab of Ornithology (Sullivan et al., 2014). Citizen science has the capabilities of covering larger spatiotemporal scales than what is economically possible for structured data programs (Conrad and Hilchey 2011; Walker and Taylor, 2017). On *eBird* you can record the location, survey effort and the number and species of birds seen. For birding trips that go out to sea, a specific pelagic protocol is used (https://support.ebird.org/). The use of *eBird* has been growing globally at exponential rates since it was launched in 2002 (Walker and Taylor 2017). This data is publicly available for download (www.ebird.org/science/download-ebird-dataproducts) and can be processed using the 'auk' R package (Strimas-Mackey, Miller, & Hochachka, 2017). The inherent concern with citizen science data is that the data is typically collected in an unstructured manner and is vulnerable to biases and variability due to observer skill, effort, detectability, and more (Isaac et al., 2014). However, *eBird* has several features that limit these effects. The observer can note method of data collection (e.g., stationary, travelling, incidental, or historic records), their survey effort (e.g., time and distance travelled)., and whether they recorded all species they could identify or if they were casually noting birds or interested in a particular species. Once lists are submitted, they are flagged if there are anomalous observations (e.g., species not regularly seen in that area or unusually high counts of

certain species), and regional volunteer reviewers contact the observer for more details and either accept or reject the observation.

We downloaded all *eBird* data for the five Sulidae species in our study, their hybrids, and Sulidae groups (those that could not be identified to species). This resulted in 204,577 individual records, spanning across all months, and from 1800 to 2023, which included many historical records (pre-2002 when *eBird* was established) that had been added into the *eBird* database.

We only used *eBird* data that had been reviewed and accepted by regional *eBird* reviewers (see above). We extracted sightings within the CCE, from the southern end of British Columbia, Canada, down towards the end of Baja California, Mexico, and up to 1,000 miles offshore (Longitude: -143˚ to -113˚ W). We also included any observations north of the CCE for evidence of northward expansions along the west coast of North America and to the south and east to capture the Baja California Peninsula (Latitude 22-60˚ N, Longitude -143 to -110˚ W). This filtered the *eBird* data to 14,375 observation records, spanning from 1935 to 2022. We removed data prior to 2002 (the year *eBird* began) and removed 2023 from analysis, as there were still unverified reports that may have skewed results from not all of the confirmed observations being included; data then spanned from 2002-2022.

We connected *eBird* data to the sampling effort at each "hotspot", or unique survey location. We downloaded the sampling data and filtered it by year (2002-2022) within our bounding box (Latitude 22-60˚ N, Longitude -143 to -110˚ W) and kept only complete checklists. Most of our region of interest was along the U.S west coast; therefore, the sampling data were primarily from the U.S., which is where the majority of *eBird* reporting takes place (Johnston et al., 2019). We calculated the number of lists submitted per day at each hotspot and standardized any Sulidae observations with this number. This controlled for multiple reports on the same individual(s) at a

hotspot on the same day, and allowed us to compile all protocol types (Incidental, Stationary, Travelling) while accounting for observing effort.

We created subsets of data for different regions of interest by first extracting data within the CCE Large Marine Ecosystem (LME; downloaded from www.geonode.iwlearn.org) and the Gulf of CA (downloaded from ww.marineregions.org) each with a 20-km buffer to capture coastal observations, resulting in 10,401 and 6,161 lists submitted with a Sulidae recorded, respectively. The remaining data outside of the CCE and Gulf of CA (n=1,203) were grouped into areas not used in analyses but were compared with observations within the CCE. We classified these remaining data as the "Salton Sea" if hotspots were within California (CA) and south of 34˚N (n=367), "inland" if the location was within the remaining part of CA, Oregon, or Washington or anywhere within Arizona, Nevada, and Utah, and "north of CCE" for all observations north of the CCE. We classified the data within the CCE by latitude and biogeographic region- Baja and Southern CCE separated by Point Eugenia (27.8˚N), Southern CCE and Central CCE by Point Conception (34.4˚N), and Central CCE and Northern CCE by Cape Mendocino (40.4˚N). We calculated the maximum number of Sulidae observed at one time at each hotspot within these regions for each month and year. Some observations record the presence only of a species. We changed all of these 'presence-only' records to one, which conservatively estimates species records (Figure 2S).

Environmental data

To determine potential drivers of Sulidae in the CCE, we used a suite of environmental variables and indices as proxies for their source (southern location they came from) and CCE conditions. We used sea surface temperature (SST) and air temperature from southern Baja as a

metric for their source conditions. For CCE conditions, we used SST and the Bakun Upwelling Index within/nearest to the latitude of each Sulidae observation. For regional, broad-scale (3-4 year timescale) conditions, we used Oceanic Niño Index (ONI) for El Niño Southern Oscillation (ENSO) conditions.

For ocean temperatures, we used SST data from the Hadley Centre Global Sea Ice and Sea Surface Temperature (HadISST, source) obtained from National Center for Atmospheric Research (https://rda.ucar.edu/datasets/ds277.3). We used the 1° Monthly measurements calculated from a combination of in-situ and adjusted satellite-derived measurements (Rayner et al., 2003). The SST provides information on upwelling within a region, which affect ocean productivity and can support potential seabird prey (Thayer & Sydeman 2007). We extracted SST data within the bounding box that captured the region of our bird data (latitudes 0-60˚ N, longitude -157˚ to -98˚ W). We generated subsets of SST data by regions using shapefiles (Gulf of CA, marineregions.org; CCE Large Marine Ecosystem, http://geonode.iwlearn.org/). We then categorized data in the CCE region into North (>40˚N), Central (<40˚N and >34˚N), South (<34˚N and >27˚N), and Baja (<27˚N) subsets.

For temperatures on land, we used GHCN_CAMS Gridded 2 m Temperature (Land) data which contains monthly means of high resolution (0.5 x 0.5˚) analyzed global land surface temperatures (1948-2022; Fan and van den Dool, 2008). We extracted air temperatures from the southern sections of Baja (south of Point Eugenia) as a proxy of source conditions that may have influenced Sulidae to move northward.

We used ONI and Bakun as measurements of the upwelling conditions and broader regional patterns of productivity. The Bakun Upwelling Index calculates Ekman transport to estimate upwelling intensity, with positive values implying upwelling and negative values indicating

downwelling (Bakun 1973). We summarized the Bakun index into regions: North of CCE (>48˚N), Northern CCE (40˚-48˚N), Central CCE (34˚-40˚N), Southern CCE (27˚-34˚N), and central to southern Baja (21-27N), including only the two most western longitudes of data in our analysis (i.e., coastal upwelling zones). We downloaded ONI data using the data retrieval package, 'rsoi' (Albers 2023; version 0.5.5). The ONI is an indicator for ENSO climate pattern, that is calculated by a three- month running average of SST, where high values (>0.5) are El Niño, or warmer, conditions, conditions and (<-0.5) are La Niña, or cooler conditions (NOAA, 2023).

Data analysis

We used a combination of oceanographic variables to describe patterns and analyze trends in Sulidae abundance. We conducted analysis for each species separately, although we combined data on masked and Nazca boobies due to their difficulty in identification between them and their historic (until 2000) grouping as the same species; with Nazca's being a subspecies of masked boobies (Pyle 2020; Pitman and Jehl, 1998).

As all four data types had different coverage, methods of collection, effort across months and years, and acceptance protocols for approving records, we could not directly compile all data as-is. However, in pursuing our research objective of detecting if Sulidae had increased in abundance and northward range within the CCE, we took a conservative compilation approach. We first standardized all data to include the date, species, counts of individuals, coordinates of observation, assigned region (e.g., north CCE), and corresponding environmental data for that month and year, then we combined all data types. We then produced 50 km^2 grid cells over our study area (-144 ˚W to -109˚W 21 to 60˚N) and assigned all of our data with a grid ID using the 'sf' package (Pebesma 2018). We used 50 km, as typical foraging ranges of Sulidae are between

40-100 km (Lerma et al., 2020; Mendez et al, 2017; Weimerskirch et al., 2008). Although Sulidae are capable of travelling outside of this range within one day, it provides a way to limit the same individuals from being double-counted in the data compilation. To provide conservative estimates of Sulidae detected within the CCE, we used the max number of Sulidae species seen at one time within each grid cell for each month and year of the compiled data. This resulted in 911 grid cells and 140,164 Sulidae observed within 50 km^2 grids. We then summarized effort data for each data type, where available. For *eBird* we used number of lists submitted, for at-sea the area (km) surveyed, and SEFI the number of months per year within each grid cell. Although true "absence" within a grid cell cannot be obtained, we gave each grid cell a zero count during a month and year where there was any effort within the grid cell but no Sulidae detected. Lastly, each grid cell observation was connected with environmental data during that month and year for analysis and to provide a measurement of fine-scale conditions, while the SST data were extracted at each grid cell midpoint. Only grid cells that were surveyed within a month and year were included in analyses.

For analysis, we used only the gridded data within the CCE. This included 803 grid cells and 11,161 Sulidae observed within 50 km^2 grids. Because there were differences in years covered by each data type (*eBird* 2002-2022, CRBC 1946-2021, SEFI 1967-2022, At-sea 1980-2022), we could not analyze changes over time across the entire period. Therefore, we only analyzed years when there was overlap (2002-2002) in the compiled data.

To determine if the occurrence of each Sulid species was increasing the CCE, we used generalized additive models (GAM) to investigate non-linear relationships between Sulidae counts (abundance) and environmental conditions. We conducted GAMs using the 'mgcv' package (Woods 2017) and Restricted Maximum Likelihood (REML) smoothness estimation

was used in all models. To determine the variables to include in abundance models, we first ran models with just lagged variables and Sulidae species abundance and selected the month lag that best explained the variability in the data. We then checked for collinearity among variables using variance inflation factors (VIF). VIFs measure the amount of variance of a variable that is inflated by its correlation with another variable. We used a conservative threshold, with values less than 3 indicating no strong collinearity of the variable, and we excluded those with values greater than 3 from the overall model (Zuur, Saveliev, & Ieno 2012; Johnston et al., 2018). There was high collinearity between Baja SST, Gulf of CA SST, and air temperatures in S. Baja, therefore, we ran full models (with all other variables) for each conflicting variable. We ran these two GAMs for comparison, then removed any non-significant variables, and compared each to the initial models. Variables with effective degrees of freedom (EDF; i.e., the non-linearity of a curve) equal to 1 were then incorporated without smoothers. To select the model of best fit, we compared full and partial models using Akaike information criterion (AIC; Akaike 1973; Venables and Ripley 2002).

As our initial investigation of observations of Sulidae seemed to indicate they might be related to warm water events, we tested the impact of the 2013-2016 marine heatwave (MHW) on their abundance. We compared the mean counts of each species (max gridded counts) within the years before (2002-2012) to years during and after the MHW (2013-2022). We calculated the percentage difference between the means and conducted a student's t-test to compare them.

Range shift analysis

To test whether the ranges of these tropical species had significantly expanded north over this period, we conducted a variety of complimentary, conservative analyses. We first calculated the mean and maximum latitude of 50 km^2 gridded sightings of each species within the CCE per

year. We then conducted simple linear regression between the mean and maximum latitudes of a species observation within 50 km^2 grid cells per year. By consolidating observations into grid cells in this analysis, we limited the influence of differences in effort per latitude, account for potential double counts of the same individual, and take a conservative approach in changes in latitudinal range over time.

We tested for changes in the area of their range within the CCE by counting the number of 50 km^2 grids per year in which at least one individual was reported for each species. We controlled for different amounts of effort by dividing the number of grids with an observation by the number of grids that had any survey effort within our data. We used a generalized linear model with a gamma, log-linked distribution to evaluate changes overtime in range area for each species.

RESULTS

Changes in abundance

All Sulidae in this study have increased in abundance within the CCE within our survey period (2002-2022). Prior to 2002, all Sulidae were considered rare in the CCE, however our data show periodic observations and a pulse of blue-footed boobies (mostly inland) in 1973 (Figure 2). Only brown and blue-footed boobies are recorded within the Gulf of California, at the Salton Sea, and most of other inland reports. Within the CCE, blue-footed boobies were infrequently encountered in the north, with no observations north of the CCE. Within the northern CCE, and north of the CCE, most of the Sulidae recorded were brown boobies, along with few observations of Nazca and red-footed boobies. After 2002, an increase in brown boobies occurred throughout all biogeographic regions of the CCE, with a large increase in 2014

and 2015. Blue-footed boobies periodically had high abundance, with a large pulse in 2013 within the South and Central CCE. The increase in red-footed, masked and Nazca began around 2018, while numbers concurrently increased within the northern part of their historical range along Baja. For brown and blue-footed booby, there was not clear seasonality in their occurrences in the CCE or in other regions (Figure 3S). However, most of the red-footed, masked, and Nazca occurred in the CCE during late spring through to fall (June to November), although masked and Nazca boobies trends do not reflect seasonality along Baja. Observations of brown, red-footed, and Nazca boobies inland mostly occurred during summer and fall (July to November).

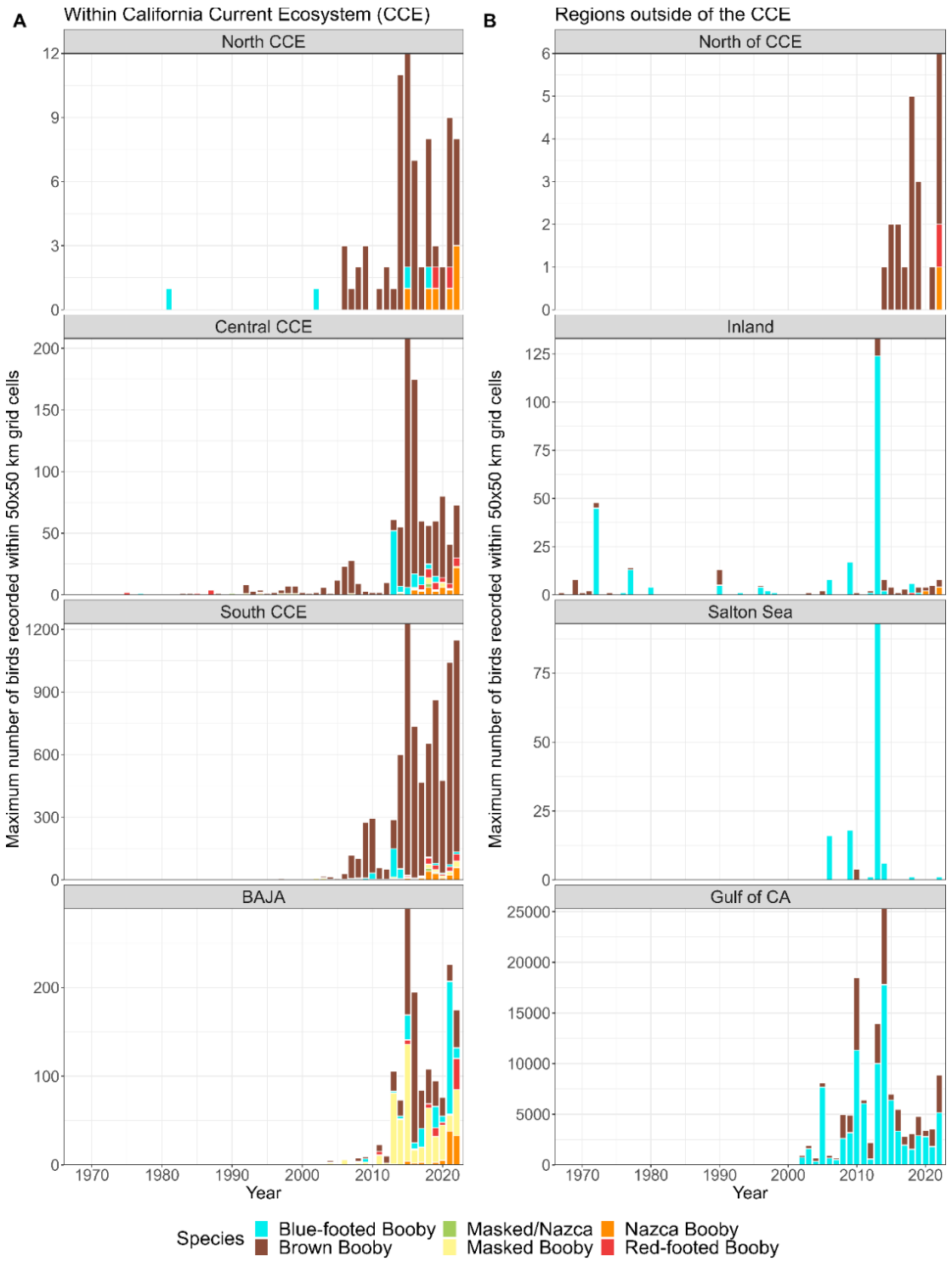


Figure 3.2: The maximum number of each Sulidae species recorded within a 50 km^2 grid cell for each year and region using all available data (19. (A) Regions within the California Current Ecosystem (CCE) and (B) regions outside of the CCE.

Conservatively using only the maximum number seen of each species within a 50 km^2 grid cell, our models detected increases in abundance for all five species (Figure 3A-6A). The increase in brown boobies was most apparent from 2002 to 2010, before their abundance stabilized until 2022 (Figure 3). A similar increase occurred in blue-footed boobies through this same period (2005-2010) before stabilizing in the CCE (Figure 4). Red-footed boobies had low abundance and high uncertainty from 2002-2013, representing the sparse observations during this period (Figure 5). Starting in 2014, red-footed booby abundance increased substantially, until stabilizing in 2020. There were moderate observations of masked and Nazca boobies during 2002 that declined to the abundance minima in 2006 before increasing throughout the rest of the survey period (Figure 6). Along this increase, there was an uptick in observations during 2013, and then a dip in observations during 2014 before continuing the upward trajectory through to 2022.

Changes with environmental conditions

We selected lagged variables that had the highest correlation with the abundance of each species (Figure S4). If there were two peaks in these correlations, we tested each lag in our models. The overall pattern of correlations with lagged data were similar for each species, although there were different months that had the highest correlation with their abundance. All species abundance had a positive relationship with recent conditions (0-2 month lags) and conditions 5-7 months prior. Although none of the correlations were strong (Spearman Correlation Coefficient >0.5), we selected lagged variables that had a correlation coefficient over 0.1.

The abundance of brown boobies in the CCE was negatively correlated with South Baja air temperatures at two-months and positively correlated with seven-month lags, positively correlated with Baja SST at one and five-month lags, and positively correlated with Gulf of CA SST at one and six-months. Blue-footed boobies were positively correlated with one and five-month lag of South Baja air temperatures, one and four-month lag with Baja SST, and one and five-month with Gulf of CA. Red-footed booby abundance was positively correlated with one and five-month lags of S. Baja air temperature, one and four-month lags of Baja and one and five-month lags with Gulf of CA SST. Masked/Nazca booby abundance was positively correlated with one and five-month lags of S. Baja air temperature, at zero and four-month lags of Baja and one and four-month lags with Gulf of CA SST.

There was high variability in the brown booby counts over time, and the model with environmental variables did a poor job capturing the variability in the data. The lagged Baja air temperatures, and SST along Southern Baja and within Gulf of California were similar (18.7%, 19%, 18.9%, respectively). After evaluating variables and model selection, the final model for brown boobies included Year, local Bakun upwelling index, local SST, ONI, and seven-month lagged S. Baja air temperature. Brown booby abundance in the CCE was associated with local SST being over 16˚C and when air temperatures are over 18˚C along Southern Baja seven months prior. The relationship between brown booby abundance and upwelling conditions in the CCE was complex, however, the highest abundance was during El Niño, high upwelling (Bakun) periods, with high uncertainty during low upwelling conditions. Our model did a poor job capturing their presence in the CCE though, suggesting that there are likely other factors driving this northward movement, or that their presence over this time has become steady, which may mask patterns.

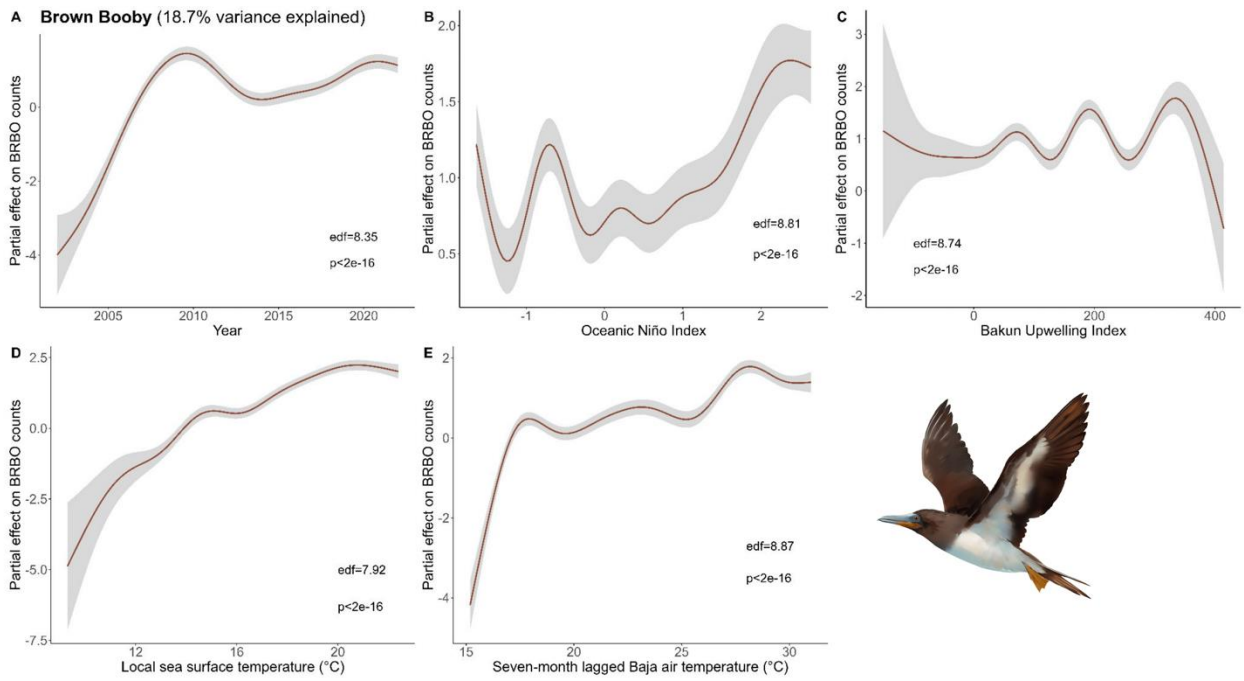


Figure 3.3: Results of generalized additive models (GAM) on Brown Booby (BRBO) counts across (A) years and with environmental variables: (B) Oceanic Niño Index, (C) Bakun Upwelling Index, (D) the SST of the coastal latitude of each observation, and (E) seven-month lagged air temperatures across Southern Baja. We used all data types to derive the maximum brown booby counts within a 50 km^2 grid cell and used these values as conservative estimates of bird abundance in our analysis (Bird illustrations by Freya Hammar).

For blue-footed boobies, the one-month lagged variables explained the highest variability in all three data types (Figure 4B, C, D). All lagged data (i.e., S. Baja air temperature, Baja, and Gulf of CA SST) had a similar effect on model performance (46.8%, 47.4%, 51.2 %, respectively), and the air temperature in the S. Baja was selected for our model based on AIC. In our initial models, the Bakun upwelling index was not a significant predictor and we removed it from the final model, based on AIC score with and without this variable. The final model included the variables Year, local SST, ONI, and one-month lagged S. Baja air temperature. Blue-footed boobies were abundant during diverse conditions in the CCE, such as during moderate La Niña and El Niño periods, with higher uncertainty during El Niño. We also detected

this bimodal pattern in the one-month lagged air temperature conditions in Baja. During cool, moderate, and warm air temperatures, there are pulses of blue-footed boobies. However, beyond changes overtime, local SST had the largest partial effect on this species' presence/abundance in the CCE, with greater abundance during warmer local SST.

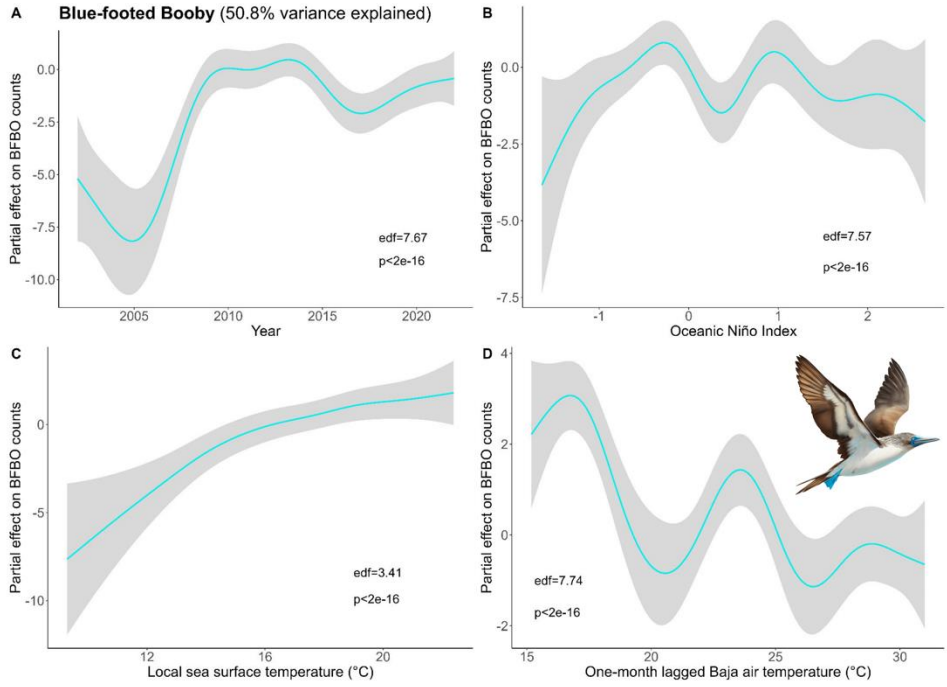


Figure 3.4: Results of generalized additive models (GAM) on Blue-Footed booby (BFBO) counts across (A) years and with environmental variables: (B) Oceanic Niño Index, (C) the SST of the coastal latitude of each observation, and (D) one-month lagged air temperature in Southern Baja. We used all data types to derive the maximum blue-footed booby counts within a 50 km^2 grid cell and used these values as conservative estimates of bird abundance in our analysis (Bird illustrations by Freya Hammar).

For red-footed boobies, conditions with one-month lag had better explanatory power for RFBO abundance than longer lagged data (Figure 5B, C, D). The one-month lagged SST within S. Baja explained more of the variability within Gulf of CA (91.8% and 91.1%, respectively). As red-footed boobies do not breed in the Gulf of CA and are rarely found there (*eBird* data), we used Baja SST in our final model. Both the Bakun upwelling index and the lagged Baja air

temperatures were not significant predicators and were removed, which slightly improved the explanatory value of our model (93.5%) which included Year, ONI, local SST, and one-month lagged Southern Baja SST. The abundance of red-footed boobies in the CCE was best explained by the year (increase), the local SST, and ONI, with higher abundances during warmer local conditions and during El Niño. There was a non-significant relationship with Baja SST and red-footed booby abundance.

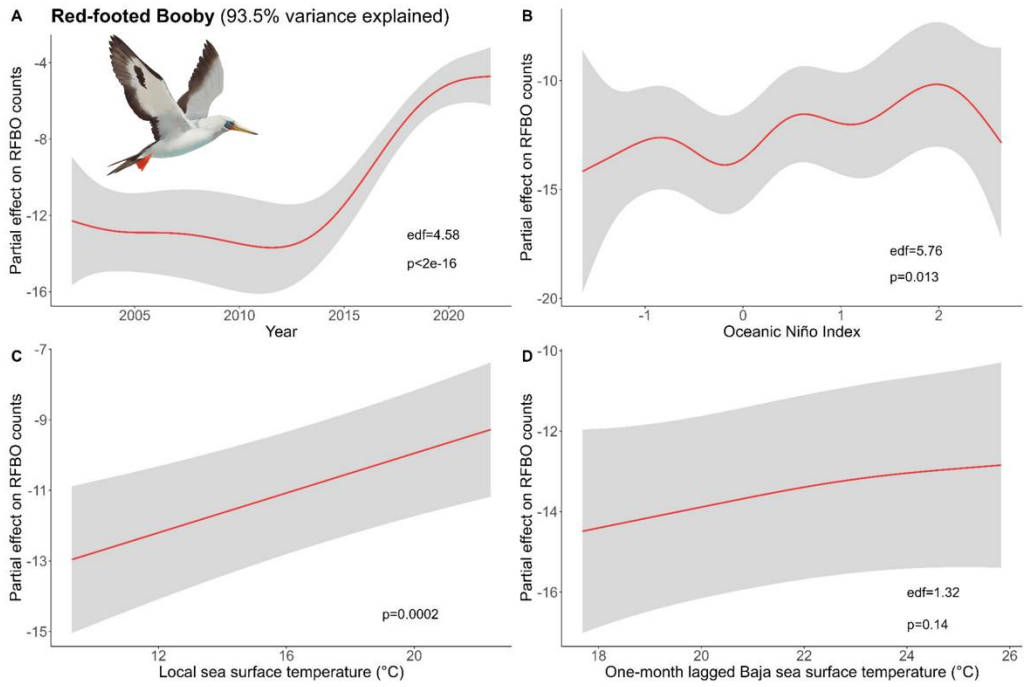


Figure 3.5: Results of generalized additive models (GAM) on Red-Footed booby (RFBO) counts across (A) years and with environmental variables: (B) Oceanic Niño Index, (C) the SST of the coastal latitude of each observation, and (D) one-month lagged SST along Baja. We used all data types to derive the maximum red-footed booby counts within a 50 km^2 grid cell and used these values as conservative estimates of bird abundance in our analysis (Bird illustrations by Freya Hammar).

For masked/Nazca boobies, the one-month lag Baja air temperature and longer-lagged SST (four-month Baja and Gulf of CA) were better explanatory variables (Figure 6B, C, D, E). The lagged SST within S. Baja and the Gulf of CA and the one-month lagged air temperature in

S. Baja had similar effects on model performance (85.5%, 84.9%, and 85.7%, respectively). Baja SST was used in the final model, along with Year, ONI, local Bakun and SST. Masked/Nazca booby abundances in the CCE were higher during warm water (local and four-month lagged Baja SST) conditions and during El Niño. There was a minor effect with Bakun upwelling index, with higher abundance during upwelling, which is likely driven by some occurrences during strong La Niña's, which we see in the relationship with ONI.

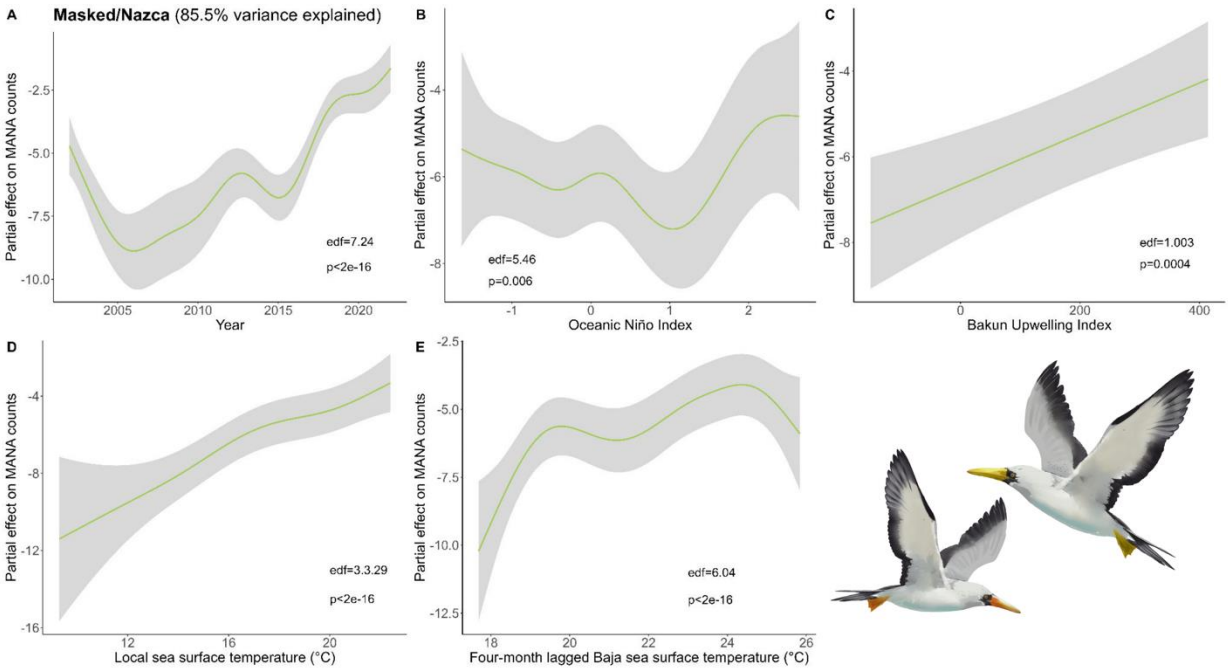


Figure 3.6: Results of generalized additive models (GAM) on Masked and Nazca (MANA) booby counts across (A) years and with environmental variables: (B) Oceanic Niño Index, (C) Bakun Upwelling Index, (D) the SST of the coastal latitude of each observation, and (E) four-month lagged SST in Baja. We used all data types to derive the maximum masked and Nazca booby counts within a 50 km^2 grid cell and used these values as conservative estimates of bird abundance in our analysis (Bird illustrations by Freya Hammar).

When we compared Sulidae abundance before and after the 2013-2016 MHW, we found that all species had significantly increased after this warm-water event (Table 1). For all species, the mean number of individuals, as well as the increased observation (lower proportion of zeros)

had both increased. The increase was greatest in red-footed and masked/Nazca boobies, and the lowest in blue-footed booby observations.

Table 3.1: Comparison between Sulidae observations before the 2013-2016 marine heatwave (2002-2012, n=4397) and the period during and after the heatwave (2013-2022, n=6040). Included are the proportion of zero observations per survey record as a measure of absence, the mean counts per period, the percentage change between the two periods, and t-test results from a comparison between these means.

Species	Period	% Zeros	Mean counts [95% CI]	% change	t test
Brown Booby	2002 to 2012	0.947	0.31 [0.22, 0.40]	769.9%	$t_{(6043.3)}$ = -11.30, p < 2.2e-16
	2013 to 2022	0.717	2.68 [2.28, 3.08]		
Blue-footed Booby	2002 to 2012	0.991	0.02 [0.008, 0.04]	379.0%	$t_{(9200)}$ = -6.36, p = 2.08e-10
	2013 to 2022	0.946	0.11 [0.09, 0.13]		
Red-footed Booby	2002 to 2012	0.998	0.002 [0.0009, 0.004]	2508.2%	$t_{(6011.3)}$ = -16.84, p < 2.2e-16
	2013 to 2022	0.942	0.06 [0.05, 0.07]		
Masked/ Nazca Booby	2002 to 2012	0.992	0.009 [0.006, 0.01]	1631.4%	$t_{(6098.9)}$ = -21.98, p < 2.2e-16
	2013 to 2022	0.872	0.15 [0.14, 0.16]		

Changes in range

All Sulidae species expanded their range northward into the CCE during our study period (Figure 7 & 8). However, this change was not significant for blue-footed boobies in change in mean or maximum latitude or area of their range in the CCE (Adj. R^2 =0.06, p=0.9; Adj. R^2=0.04, p=0.6; Adj. R^2=0.14, p=0.07, respectively). All other species increased their maximum latitude within the CCE, and increased the area of their range within the CCE (Table 2S). The range increase was most dramatic for brown boobies, which increased in range area (Adj. R^2 = 0.60, p=0.00002), mean latitude (Adj. R^2 = 0.17, p=0.036), and maximum latitude (Adj. R^2 = 0.59, p=0.00003) within the CCE. Both red-footed and masked/Nazca boobies increased in range area (Adj. R^2 = 0.51, p=0.0008 and Adj. R^2 = 0.53, p=0.0001, respectively) and maximum latitude (Adj. R^2 = 0.47, p=0.0034 and Adj. R^2 = 0.60, p=0.00006, respectively), but not in mean latitude (Adj. R^2 = 0.007, p=0.32 and Adj. R^2 = 0.07, p =0.14, respectively) within the CCE.

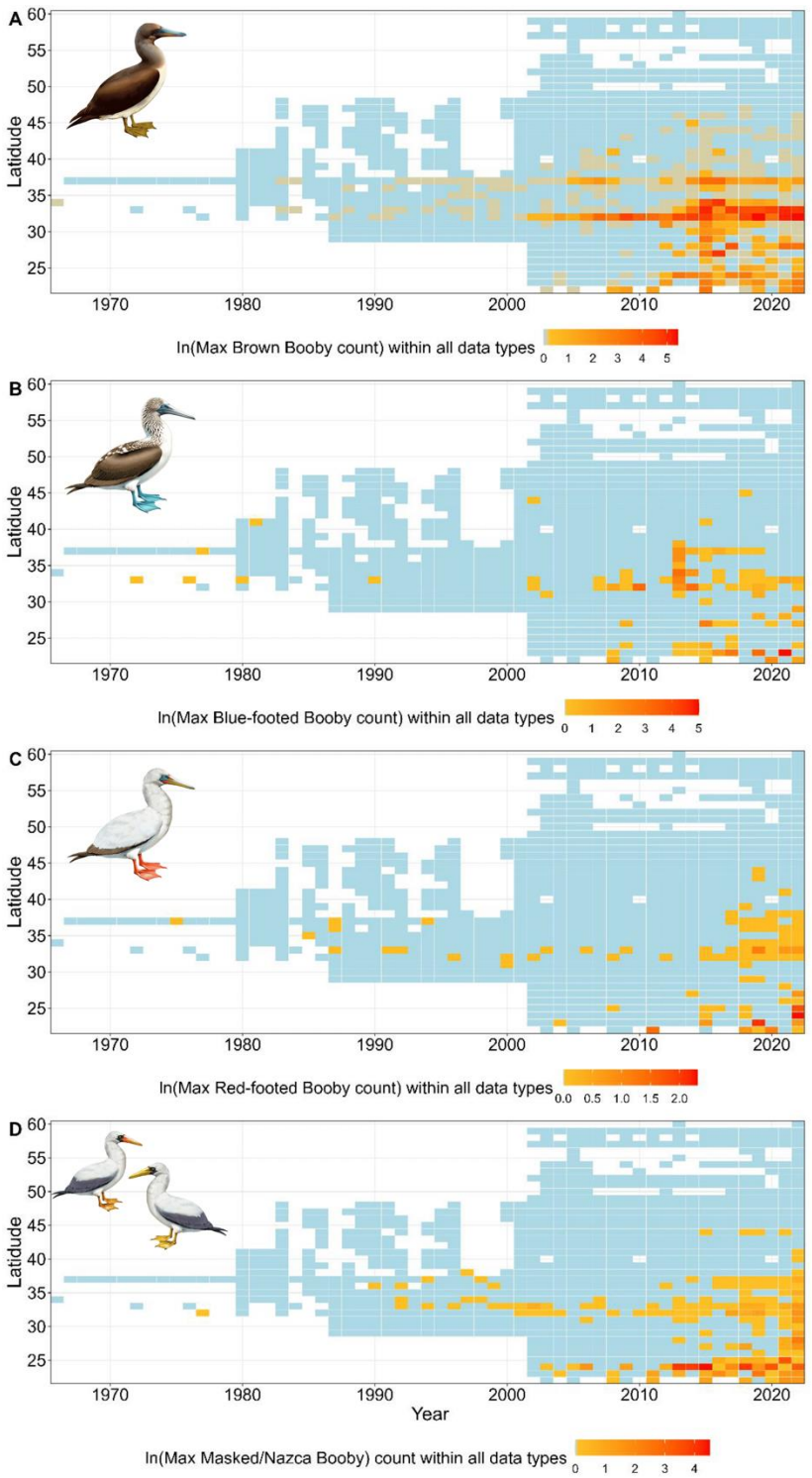


Figure 3.7: The maximum number of Sulidae species (A) Brown, (B) blue-footed, (C) red-footed, and (D) Masked/Nazca booby, observed within each latitude per year in the Northeastern Pacific Ocean. Boxes in blue indicate there was data collected within this latitude and year, but there were no Sulidae observations. As there are many single observations and some large values, we took the log of maximum counts and centered the color gradient on the mean in order to show smaller values (Bird illustrations by Freya Hammar).

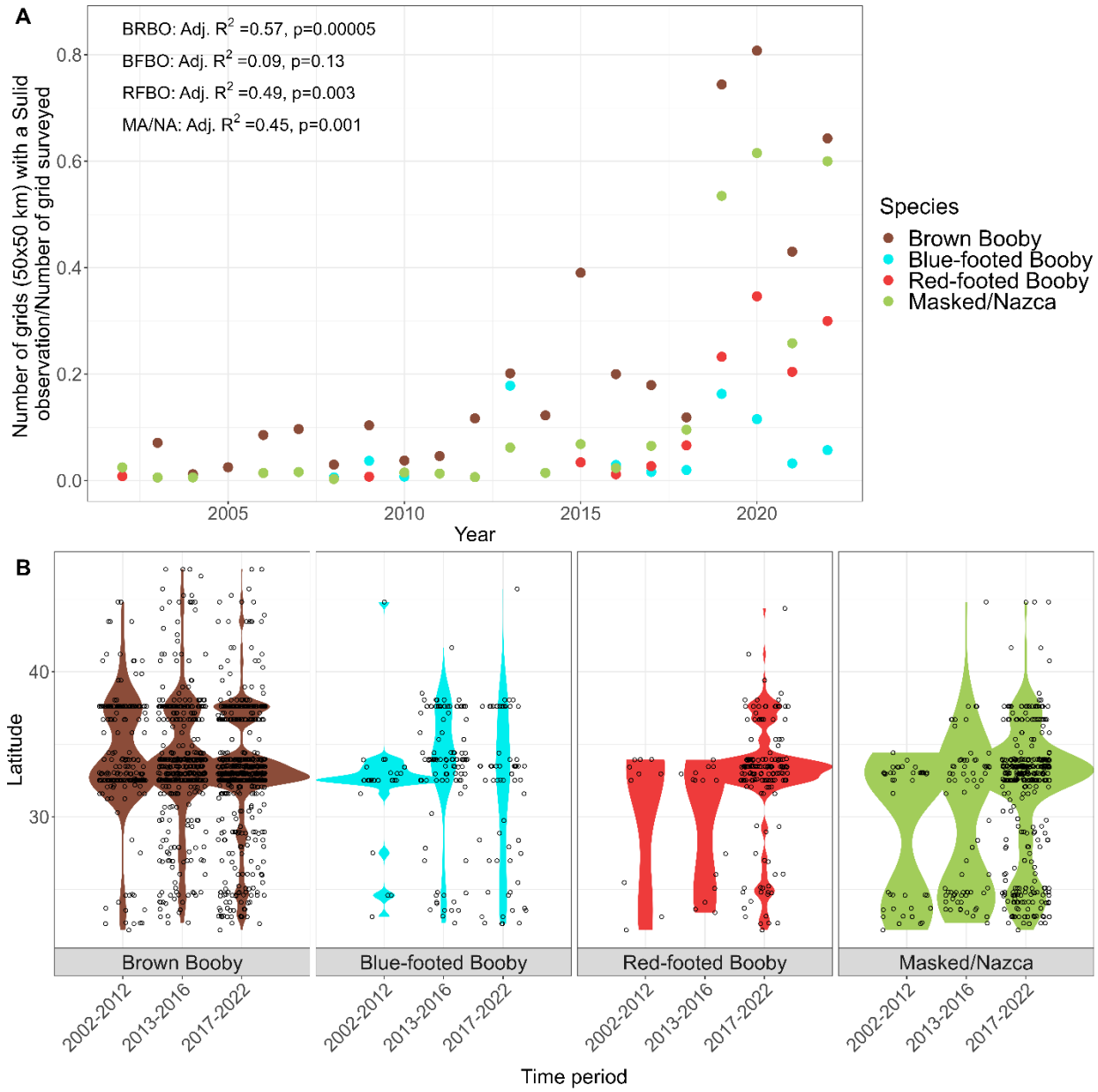


Figure 3.8: (A) The number of grid cells that a Sulidae species was observed divided by the total number of grid cells that had any survey effort within the CCE (North, Central and South only). In-plot statistics are the results of generalized linear models on the grids observed/grids surveyed per year for each species (BRBO=Brown, BFBO=blue-footed, RFBO=red-footed, and MA/NA= Masked/Nazca booby). (B) Violin plot with overlaid observations for the latitude of sighting per month and year for each species within each period (2002-2012, 2013-2016, 2017-2022). Only observations within the CCE were included, including those along Baja, South, Central, and North biogeographic regions.

The northward expansion of brown boobies in the CCE began in the late 2000's (Figure 7 & 8), however we see large increases in their range area during 2015, and in 2019, which has persisted since. During the 2013-2016 MHW, their abundance and latitudinal range increased in the CCE (Figure 8B) and has remained since. Blue-footed boobies expanded their range into the CCE during the initial parts of both strong MHW in our survey period (during 2013 and 2019). However, their range expansion into the CCE did not remain after these events. Prior to 2002, blue-footed boobies periodically moved northward, however the frequency or size of these pulses into the CCE are not changing linearly (Figure 7). Few red-footed boobies were observed within the CCE prior to 2002 (Figure 7), but since then, their abundance and range into the CCE have increased, especially during and after 2019 (Figure 8A). We did not find a difference between the period (2002-2012) before the 2013-2016 MHW and during this period, however since the MHW in 2019, they have increased in the CCE (Figure 8). Observations of masked/Nazca boobies occurred sporadically throughout the 1990's and 2000's, however their abundance increased in the CCE after 2012 (Figure 7). There was a slight uptick in their range area and northern latitude use during the 2013-2016 MHW, however this significantly increased during the 2019 MHW and has sustained this range since (Figure 8).

DISCUSSION

We found that all Sulidae species occurring in the CCE have increased in abundance, range area, and maximum latitude within this region over our study period (2002-2022), and overall, increases in their abundance correspond to warm water events. We also found that after large pulses in their abundance and range, for all species except blue-footed boobies, they did not contract back to their previous range and abundance in the CCE.

Changes in abundance over time

Brown boobies have a pantropical distribution and were recorded occasionally along the U.S. west coast. The first record in California, was in 1946 (McMurry 1948) in Imperial County, and since then they have shown up in small numbers until the 2000's (McCaskie 1970). This is now the most common species in the CCE, occurring in all months, with no apparent seasonality in their occurrence, establishing that they are now a permanent resident of the CCE. Since 2002, they have been increasing, but it was after 2013 when their abundance increased substantially within our data (Figure 2), although the models captured an increase beginning in 2010 (Figure 3). Our model failed to capture the increase in brown boobies during the 2014-2017 period that we see in our at-sea and SEFI data (Figure 1S). Because we took a conservative approach with our anlaysis and used the maximum counts within a 50 km^2 grid cell, we lost data that were collected near each other that may have been different individuals.

Blue-footed boobies are found within the Tropical Eastern Pacific and are more coastal in their distribution compared to other Sulidae (Nelson 1978). Although this species was not observed in the northern CCE, it is the most commonly observed inland in the U.S., with observations in Nevada, New Mexico, and Arizona (*eBird* data). This species was first recorded in California at the Salton Sea in 1929 (Clary 1930). North of the Galapagos, most of the breeding locations for blue-footed boobies are in the Gulf of CA, however they have expanded to San Jerónimo Island, and one pair has been breeding on Sutil Rock, off Santa Barbara Island since 2022 (Díaz and Gómez 2020; Howard et al., 2024). Beyond large pulses in their abundance that occurred in 1973 (inland only) and in 2013 (all regions but the north), this species has increased at a much slower rate than other Sulidae species. Additionally, this is the most

common and abundant Sulidae to find at inland water sources (e.g., rivers, lakes). This difference in distribution may be a result of birds moving north from Gulf of CA, or it may also be due to differences in finding prey, limitations on travel distances (e.g., energetics), or other causes. Blue-footed boobies are the most coastal of the Sulidae, which suggests limitations on their range and/or specific habitat preferences compared to other species.

Both red-footed and masked booby have a pantropical distribution, while Nazca boobies are found in the Eastern Tropical Pacific. All three of these species are pelagic and can be found far offshore, however, in this study, red-footed boobies are the smallest Sulidae, while masked and Nazca are the largest. These three species were observed in the CCE mostly between spring and the beginning of winter. Masked and Nazca boobies are seasonal breeding species. For example, masked boobies that breed on Clipperton Island begin laying eggs in November and chick-rearing can continue through February (Weimerskirch et al., 2008). With Nazca boobies that breed on the Galapagos, their breeding season spans from October to June (Tompkins & Anderson 2021). Therefore, most of the birds showing up in the CCE are arriving (May-Dec) during the non-breeding season. Conversely, red-footed booby are seasonal breeders at some locations (Weimerskirch et al., 2005), while not at others (Nelson 1969). Their seasonal occurrence may indicate that birds arriving in the CCE are from colonies with seasonality, and they are here during the non-breeding season, or that their presence is driven by environmental conditions. There was a very limited number of sightings of these three species during most of our study period. The first observation of red-footed booby in the CCE was at SEFI in 1975 (Figure 1S, Huber and Lewis 1980), the first masked booby in California was off of San Clemente Island in 1977 (Lewis and Tyler 1978), and the first confirmed Nazca booby was in 2001 on a ship in San Diego harbor (Benson et al., 2022). However, reports of these species

remained sparse until they trickled in during the 1990's before increasing in the mid-2000's, and substantially since 2018.

Changes with environmental conditions

As seabird distribution can reflect productive conditions for their marine prey, we evaluated which environmental conditions encouraged species to change their range. Connections between marine predators and the environment can be concurrent, or they may occur at different lagged time scales depending how the distribution, abundance, and quality of their prey are affected (Wakefield et al., 2009; Mendez et al., 2017A). We found that Sulidae responded to their 'source' conditions (SST and air temperatures) at scales of 0-2 months or 5-7 months, such that some species appear to respond rapidly to changing conditions, while others appeared to wait to head north until conditions worsened. Information on individual movements by different species are needed in this region to test these hypotheses to better understand the trends in these lags with the environment.

Our models did a good job characterizing the environmental conditions that may drive the presence and abundance of red-footed, masked and Nazca, however the trends with environment and brown and blue-footed boobies were not as straightforward. Generally, brown boobies were more abundant during warm water periods, but the disconnect between conditions and their abundance was likely due to their year-round presence in the CCE in recent years. Because they were present in the CCE every year, they will be difficult to correlate with environmental conditions in the CCE. Similarly, blue-footed boobies did not show a clear trend with the local or source conditions, or with ENSO conditions. Although pulses in abundance of this species occurred during warm periods (2013), they have persisted in the CCE since then, and like brown booby trends, this may be masking significant patterns between their distribution and

environmental conditions. Other studies have found that blue-footed boobies off South America forage over cold, productive waters to feed on their main prey, Peruvian anchovy, *Engraulis ringens* (Zavalaga et al., 2008). Their affinity towards cold, upwelled waters would support their abundance during La Niña and higher upwelling, but those were not the conditions during their influx into the CCE and inland, continental U.S. Their incursions happened during warm water periods however, the conditions may have been much cooler, more productive than further south, and may have retained recurrent visitors and the new breeding pair on Sutil Rock. Recurring blue-footed booby individuals were recorded on SEFI when two second-year birds showed up in 2014 and came back together to the same location each year (2015-2019).

For the highly-pelagic, wide-ranging red-footed booby, their abundance in the CCE increased during warm water periods and reduced upwelling conditions. As they do not breed along Baja or forage within the Gulf of CA, those environmental conditions were not good predictors of their occurrence farther north. Their increase from the mid-2010's to 2022 occurred during two MHW on top of long-term warming. However, further data are needed to determine if their abundance in the CCE continues to increase or if it has stabilized.

Masked and Nazca also do not breed along Baja or use the Gulf of CA, and their trends with environmental conditions reflected that. Their abundance in the CCE increased during La Niña (high upwelling) as well as El Niño (higher SST), however, it was highest during warm-water conditions. Tracking studies have shown that these large Sulids will expend the energy to travel far in search of productive conditions (Sommerfeld et al., 2015), therefore their occurrence during poor conditions is an indication that conditions in their typical range were likely even worse.

Changes in the range of Sulidae

All Sulidae species have increased their range into the CCE. As we are only evaluating these spatial changes at the northern edge of their range, we cannot say whether it is a range shift or expansion, but for the sake of brevity, we call it a northward expansion. Both the area and the mean latitude of their occurrences in the CCE have increased for most of these species. However, blue-footed boobies are outliers, and their presence in the CCE is limited except for periods of warm water incursions; the few individuals that remain afterwards show up as vagrants. This pattern may change now that they expanded their breeding range north in 2017 to San Jerónimo Island (Díaz & Gómez, 2011), then farther north when a hybrid blue-footed/brown pair nested on Sutil Rock from 2020; one blue-footed booby pair in 2022 also was seen at Sutil Rock (Howard et al., 2024). Similarly, brown boobies began attending Sutil in 2013, with the first confirmed breeding in 2017; they have steadily increased in attendance and nest numbers since (Howard et al., 2024). Prior to this northward breeding expansion, they had recently expanded their breeding range north to Middle Rock, Baja in 2005 (Whitworth et al., 2007). It is after this initial northward breeding expansion that brown booby numbers rapidly increased in the CCE, with their peak numbers being present during the initial years of attendance and breeding attempts at Sutil Rock.

For red-footed boobies, their northward expansion into the CCE did not occur until 2018. Red-footed boobies were observed sporadically before 2002, as lone individuals mostly within 31-33N, with one record at SEFI in 1975 (~37N). Starting in 2018, their range expanded northward, and they increased in area occupied within the CCE until 2020. The trends in our data show this increase may have plateaued, therefore future analysis will be needed to determine the continued trajectory of this species in the CCE.

Masked and Nazca boobies may have begun increasing in abundance during the mid-2000's, however they have been expanding their range northward into the CCE since 2013. The increase during this time was due to an uptick in observations of masked boobies (Figure S1 & S2). However, after 2018, their numbers, and the area of their range and maximum latitude within the CCE all increased and continue to increase. In the most recent year of our data (2022), there was a least one masked/Nazca booby detected within each degree of latitude between 22˚N and 37˚N.

Changes associated with marine heatwaves

Our main survey period (2002-2022) captured varying ENSO conditions, along with two intense marine heatwaves (MHW). MHWs are prolonged periods where there are anomalously warm waters (Hobday et al., 2016) due to a variety of dynamics, mostly atmospheric forcings that affect wind and pressure systems that reduce upwelling, therefore stratifying the water column and leading to overall warming (Di Lorenzo & Mantua 2016). Due to climate change, these MHW's have become more frequent and intense worldwide, and are projected to continue to increase (Oliver et al., 2018; 2019; Laufkötter, Zscheischler, & Frölicher 2020).

Beginning in the fall of 2013, warming of the waters in the North Pacific began, spread south, and soon became the largest, longest-lasting MHW globally within that decade; reaching temperatures three standard deviations above mean temperatures (Bond et al., 2015; Di Lorenzo & Mantua 2016; Suryan et al., 2021; Cavole et al., 2016). Anomalous warming began in the southern CCE in the spring 2014, and summer records of temperatures off Baja reached 4˚C above the mean (Robinson, 2016; Leising et al., 2015). This MHW peaked in 2015 and persistented into 2016 (Gentemann et al., 2017). In mid-2016, the MHW began to decline, however, there was still prominent warming along the equatorial northeastern Pacific that

overlapped with some of the breeding and foraging locations of the Sulidae in this study (Hobday et al., 2018).

The 2013-2016 MHW caused massive ecological changes in the North Pacific, including within the CCE. These changes included shifts in community composition and abundance of zooplankton (Brodeur et al., 2019), declines in fishes and/or decreased quality (von Biela et al., 2019; Arimitsu et al., 2021), changes in the ranges of lower and upper trophic level organisms (Sutherland et al., 2018; Lonhart et al., 2018; Tanaka et al., 2021; Welch et al., 2023; Osborne et al., 2020), mass mortality events of marine species (Jones et al., 2018; Piatt et al., 2020), and other ecological impacts (Cavole et al., 2016). Such changes have persisted in this ecosystem for at least 5 years (Suryan et al., 2021), and the impact of that MHW reached below the mixed layer, which remained through to 2018 (Scannell et al., 2020). In addition to these long-term effects from this MHW, there was little time for this ecosystem to recover before the next one in 2019. The 2019-2020 MHW began in summer of 2019 due to a weakening of the high-pressure system in the North Pacific and persisted through 2020 (Amaya et al., 2020; Chen et al. 2021; Welch et al., 2023). The warming during this MHW did not penetrate the water as deep as during the 2013-2016 MHW (Amaya et al., 2020).

The effect of both of these MHW are detected in our results, with Sulidae increasing in their abundance and range in the CCE during and/or after the 2013-2016 MHW (Figure S5). During this MHW, brown booby abundance peaked (Figure S1) and then stabilized (Figure 3). In addition to our results, the initiation of northern breeding colonies during this same period and continued use of this colony support that although they had been increasing in this region before the MHW, they stayed within the CCE afterwards. In contrast, blue-footed boobies increase into the CCE during initial warm conditions (September-December 2013), however they do not

remain in the CCE afterwards, with the exception of a few, likely recurring individuals. Masked and Nazca boobies began increasing in the CCE preceding the 2014-2016 MHW, however their abundance and range substantially increased during the MHW and after it concluded. Red-footed boobies remained rare vagrants in the CCE until 2018, when their abundance and range suddenly increased in the CCE. This increase in red-footed boobies preceded the 2019 MHW. This early arrival may be indicative of other drivers, or that they were exposed to conditions elsewhere in the Pacific that were linked to the shift in the North Pacific high-pressure system.

As MHW are projected to increase in frequency and intensity, in addition to long-term warming, we hypothesize that these species will continue to expand their range northward in the CCE (Jacox et al., 2020). Seabird prey are poikilothermic, therefore changes in the SST (along with subsequent changes in nutrients from depressed upwelling) directly influence the distribution and health of their prey (Sunday et al., 2012; Alfonso et al., 2021) and therefore the distribution of seabirds. Such changes in marine predator distributions can have consequences for pre-existing species in the CCE, such as increased competition for resources, including food and breeding habitat (Pinsky et al., 2020; Petalas et al., 2021; 2024).

Other drivers of Sulidae northward range expansion

We found that some of the trends in Sulidae in the CCE were explained well by environmental conditions, however some were not, and several questions remain. Although brown boobies increased during warm periods, what were the reasons for them to remain in the CCE? To determine this, investigations into potential 'thresholds' for their persistence are needed, such as environmental, foraging or migration distance constraints, or prey quality (at

their source or destination). In contrast, blue-footed boobies have large pulses into the CCE and inland continental U.S., however, they do not remain in the CCE in high numbers.

As we are using environmental variables as proxies for conditions that affect their prey, we cannot ignore what data are available on prey resources in this region. As was hypothesized in Howard et al., (2024), the combination of warm water conditions and prey availability likely played a substantial role in brown and blue-footed boobies. Coinciding with the 2013-2016 MHW was the collapse of the sardine fishery in the Gulf of CA (2013-2015; Velarde et al., 2013), while the anchovy biomass around the Channel Islands was at mean conditions (Gallo et al. 2019). These factors set up prime conditions for birds in the Gulf of CA to move northwest into the CCE.

In addition to prey availability in the Gulf of CA and southern CCE, there may also be impacts on brown and blue-footed abundance in the CCE due to successful conservation work in Baja. Many of the islands with Sulidae colonies within the Gulf of CA and offshore from Baja and Central Mexico have experienced successful eradication of their diverse invasive species (Aguirre-Muñoz et al., 2018). Invasive mammals can cause devastating harm to seabird eggs, chicks, and even adults (Spatz et al., 2023). The removals of invasive species and habitat restoration on many of these islands have had a positive impact on seabirds that breed there (Bedolla-Guzmán et al., 2019; Méndez Sánchez et al., 2022). A thorough investigation into how the timing of restoration and population trends relate to any long-term increases of Sulidae in the CCE would be useful. An increase in population size has been shown to increase vagrancy in other seabird species (Acosta Alamo et al., 2020; Zawadzki et al., 2021), therefore trends on these islands could play a role in their range expansion, especially for brown and blue-footed boobies.

However, the potential drivers for red-footed, masked, and Nazca boobies are complicated by thier breeding ranges being far removed from the CCE. We also do not have any indication as to what colonies these CCE visitors are travelling from. Increased biologging of individuals at colonies in the northeastern Pacific are needed to better determine foraging ranges during the non-breeding season.

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SUPPLEMENTAL MATERIALS

Table S3.1: Survey Data used in this study. Much of this was compiled by Leirness et al. (2021), with added years of CalCOFI, ACCESS, and the NOAA Southwest Fishery Science Center CCE data.

Survey Name	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	2005-2015
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

Table S3.1: Survey Data used in this study (continued)

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
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

Table S3.1: Survey Data used in this study (continued)

Wind to Whales	Donald Croll, James Harvey	UC Santa Cruz, Moss Landing Marine Laboratories	Ship	1997-2007

Table S3.2: Comparison between the range area of each Sulidae species before the 2013-2016 marine heatwave (2002-2012, n=4397) and the period during and after the heatwave (2013-2022, n=6040). We used the number of grids a Sulidae was recorded, divided by the number of grids surveyed as a proxy for range area. Included are the proportion of zero observations per survey record as a measure of absence, the mean counts per period, the percentage change between the two periods, and t-test results from a comparison between these means.

Species	Period	Mean # grid observed/ # grid surveyed [95% CI]	% change	t test
Brown Booby	2002 to 2012	0.053 [0.033, 0.074]	620.3%	$t_{(9.29)}$ = -3.93, p = 0.003
	2013 to 2022	0.384 [0.220, 0.547]		
Blue-footed Booby	2002 to 2012	0.384 [0.220, 0.547]	306.7%	$t_{(10.17)}$ = -2.44, p = 0.035
	2013 to 2022	0.066 [0.027, 0.105]		
Red-footed Booby	2002 to 2012	0.008 [0.004, 0.011]	1864.8%	$t_{(7.02)}$ = -3.06, p = 0.018
	2013 to 2022	0.153 [0.060, 0.246]		
Masked/ Nazca Booby	2002 to 2012	0.012 [0.007, 0.017]	1801.7%	$t_{(9.02)}$ = -2.79, p = 0.021
	2013 to 2022	0.234 [0.078, 0.389]		

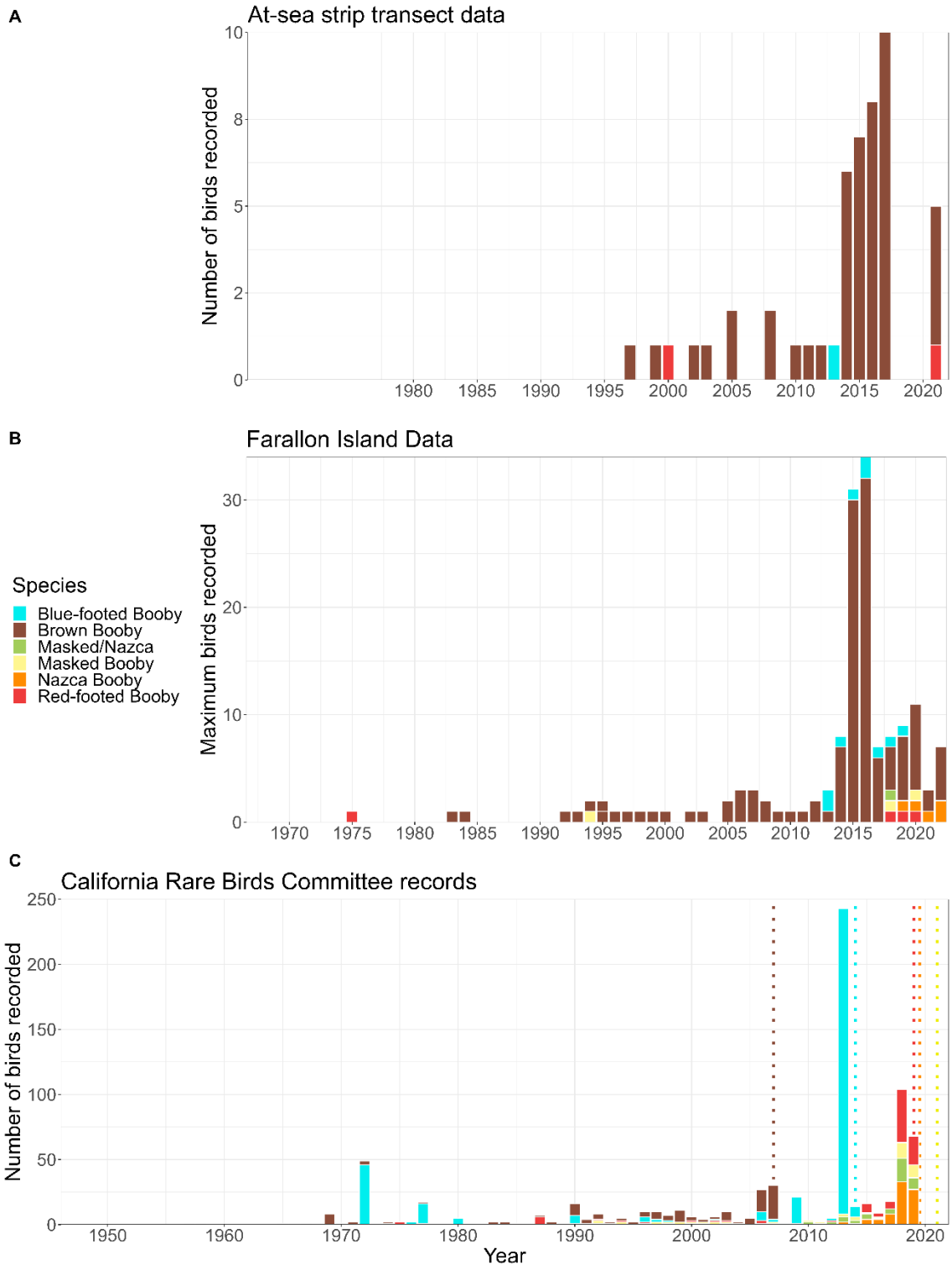


Figure S3.1: Observations of Sulidae species recorded in the (A) at-sea data, (B) the Farallon Island records, and (C) the California Rare Birds Committee records. The dotted lines on the CRBC plot indicate the years each corresponding colored species was removed from the rare birds list.

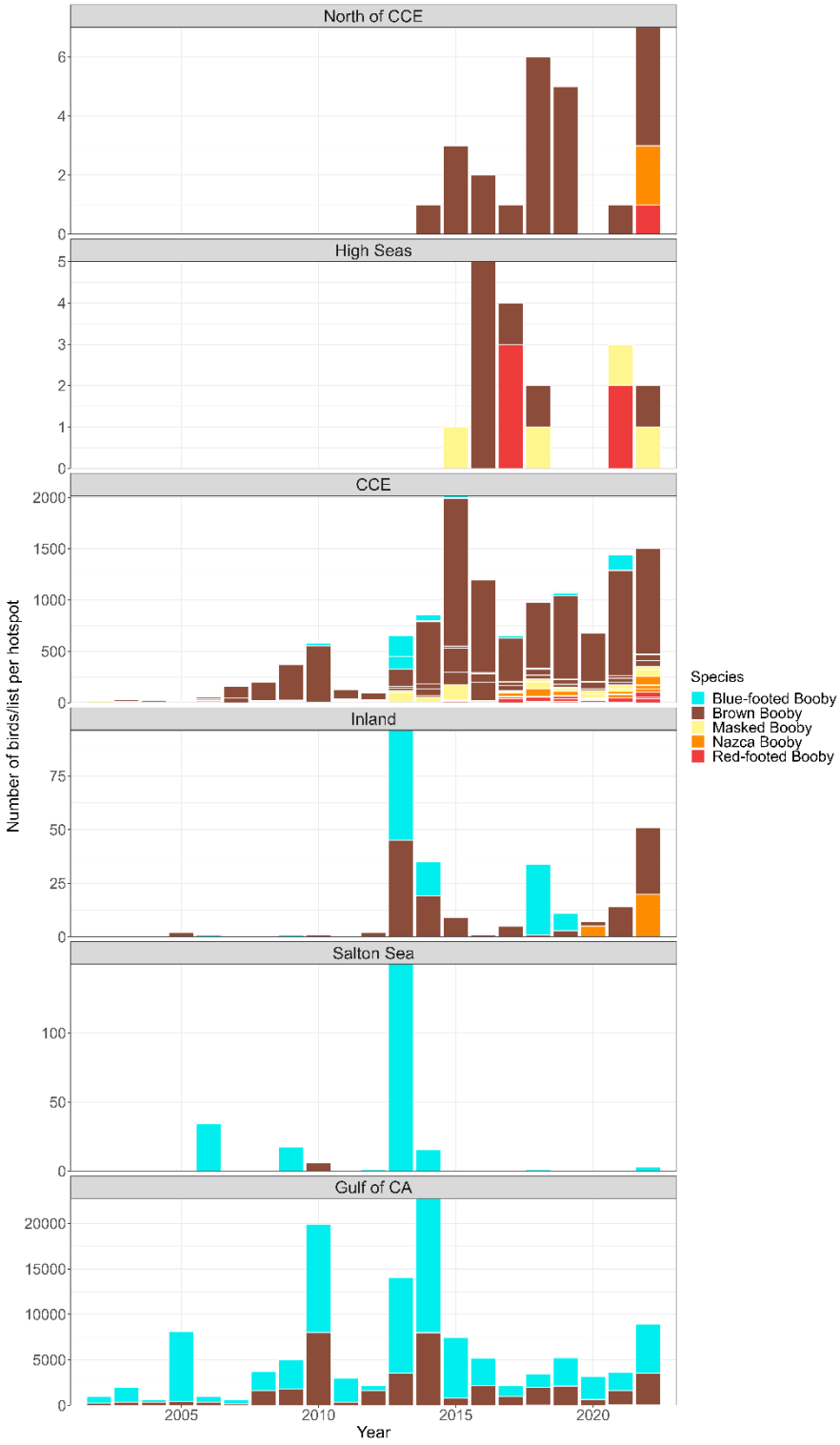


Figure S3.2: Observations of Sulidae recorded through eBird within the different regions of the CCE and surrounding regions.

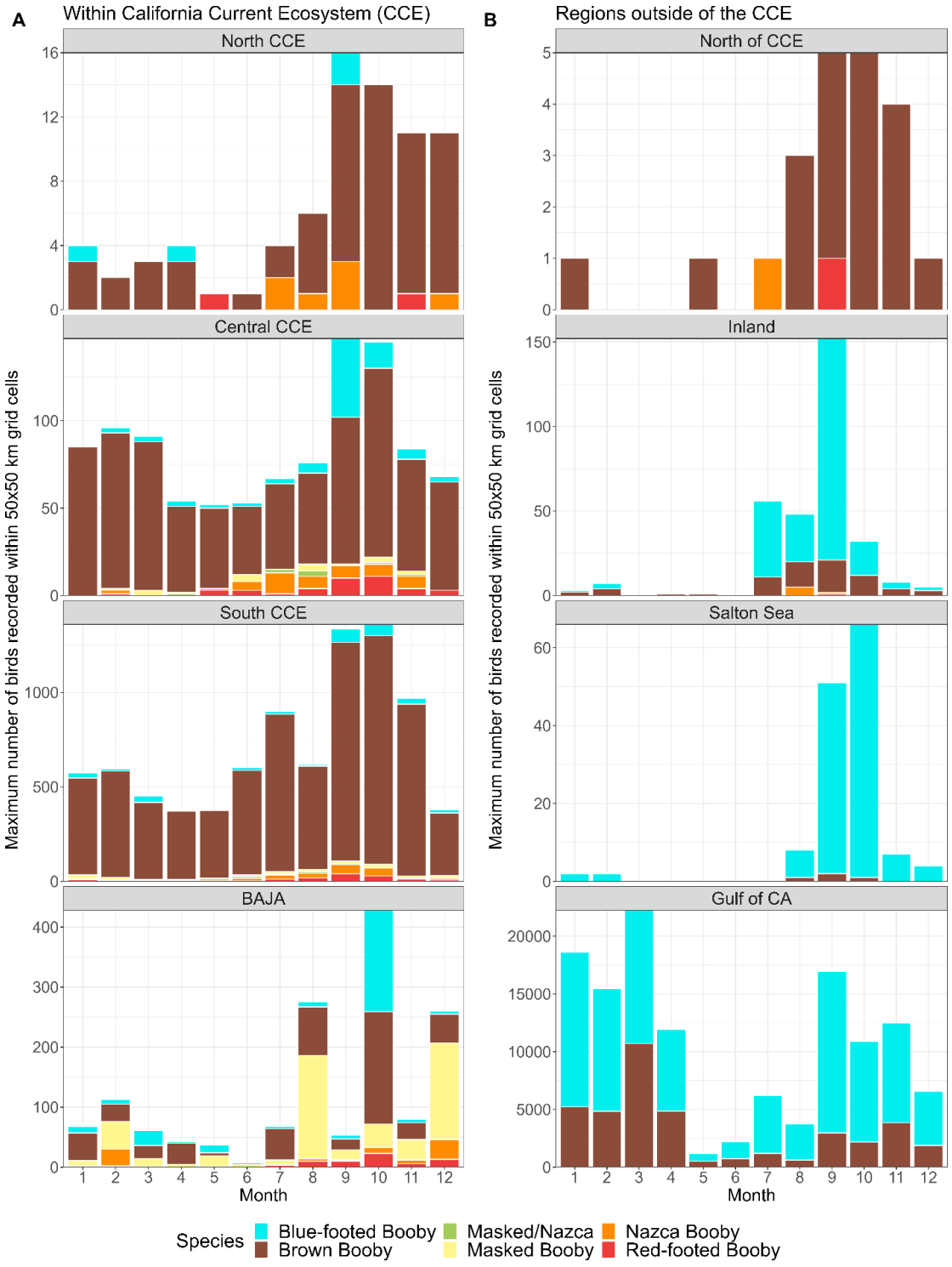


Figure S3.3: The maximum number of each Sulidae species recorded within a 50 km grid cell for each month and region using all available data (1965-2022). (A) Regions within the California Current Ecosystem (CCE) and (B) regions outside of the CCE.

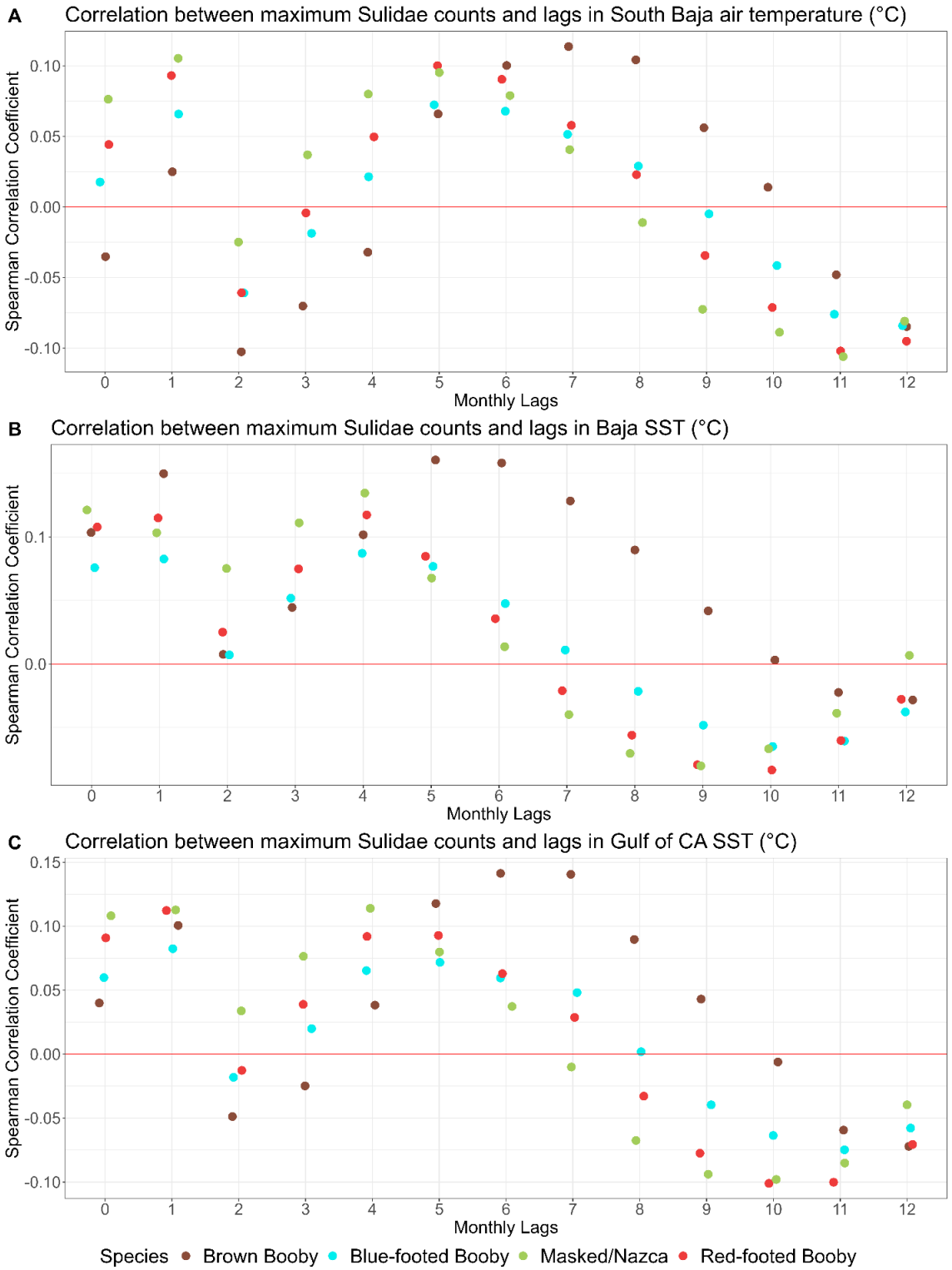


Figure S3.4: Correlations between environmental conditions around Baja California and Baja Sur, Mexico, with maximum counts of each species of Sulidae within the California Current Ecosystem. We compared lagged, monthly data for each variable (A) south Baja air temperature, (B) Baja sea surface temperature (SST), and (C) Gulf of California SST.

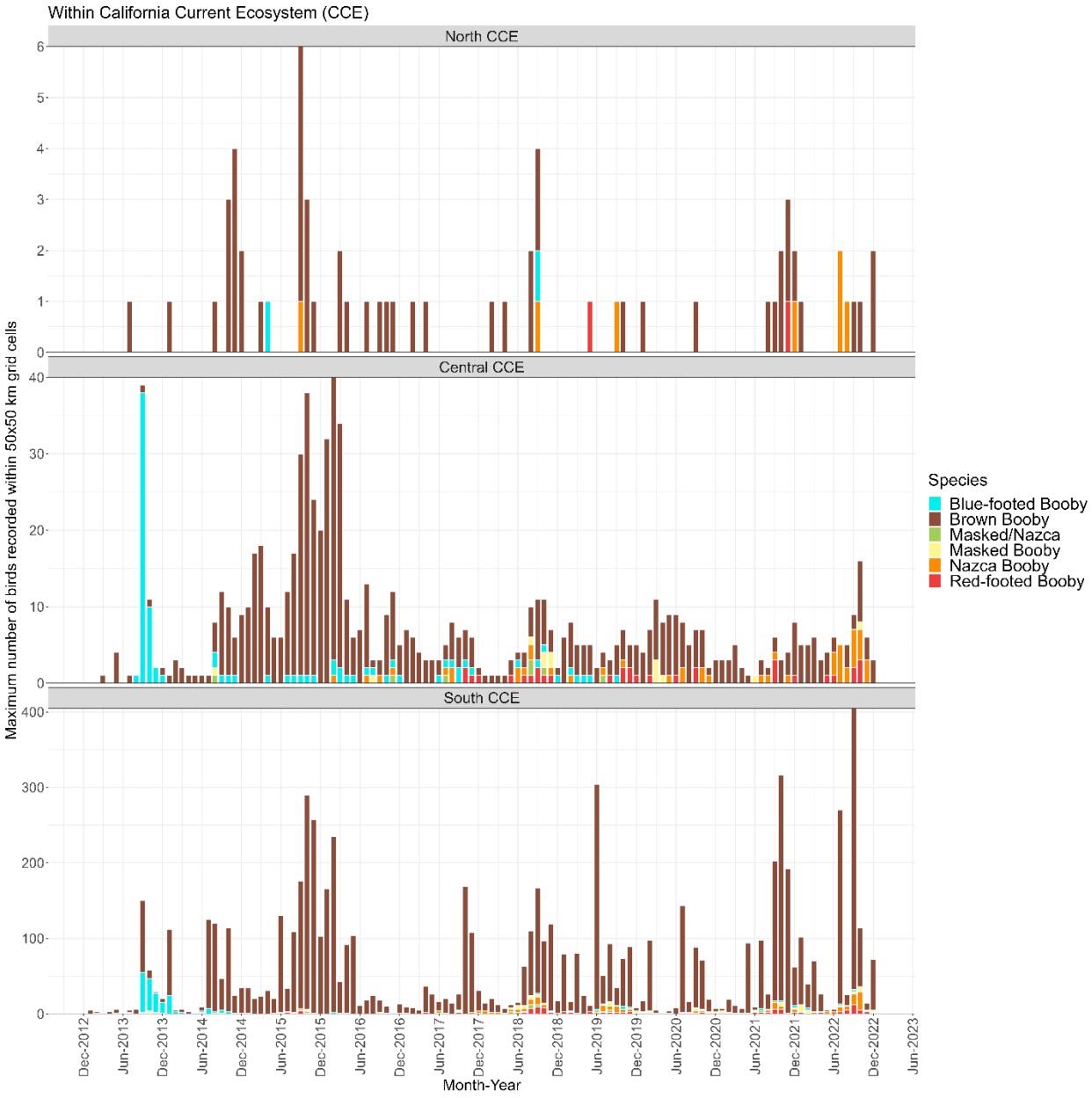


Figure S3.5: Sum of the maximum Sulidae observations per month and year for each region within the CCE over the period of two marine heatwaves (2013-2016 and 2019-2020).

CONCLUSIONS

This research used extensive compilations from diverse sources of seabird data collected in the CCE, by researchers and citizen scientists, alike, to inform the spatial and temporal patterns of seabirds in this region.

In my first chapter, I found that there is a positive, linear relationship between seabird abundance and diversity, with both being higher in more productive regions. This is contrary to what was is found with other organisms, which generally show enhanced diversity in low productivity regions (e.g., tropics). In order to investigate the relationship between seabird abundance and diversity, analyses using the functional groups and not species is needed to test whether it is functional or species diversity that correlates with their abundance. Next, research should be done to determine the realized niche overlap between species/groups with the same functional traits, and then we can start to understand the presence, dynamics, and the role of competitive exclusion among seabirds. In this chapter, I also determined that the biogeography in the CCE is reflected in the spatial patterns of seabird communities here, with the north and south being most distinct and the central region capturing a diverse, transition zone between the cool and warm regions in the CCE. As a result, research conducted across these regions, should first separate data into this biogeography before conducting analysis in order to better understand trends and disentangle relationships with the environment. In addition, I found that the NMS are reflective of their biogeographic region, in terms of latitudinal diversity and abundance trends, and that the placement of the NMS across the CCE complement each other and succeed in capturing diverse habitats. I noted, however, that there is an important area for seabirds that does not have a NMS, located along the coast of Oregon around the Columbia River mouth.

As U.S. west coast NMS capture similar patterns in seabird indices and communities within their corresponding biogeographic region, I used seabird data within their boundaries to describe and inform the long-term trends of abundance and community composition in the CCE. I found that the abundance of avifauna within the NMS in the CCE has decreased since the 1980's, with greater declines in south. Decreases were largely due to a decline in non-CCE breeding species, which had decreased in abundance within all five NMS. Relationships between the abundance of seabirds with environmental conditions varied among the NMS, indicating that there are distinct drivers within each of these regions. Further research is needed to determine if these are appropriate scales to use in analysis on seabird abundance trends, and if the trends we found are truly representative of what's going on in the overall, nearshore habitat of each biogeographic region.

From incidental sightings while bird watching, I noticed that Sulidae species were now becoming less of a rarity on my *eBird* account, thus I compiled many different data types on these species to investigate what was going on. Using a highly conservative approach because of the disparate data types, I found that, indeed, five of these species had increased in the CCE and their rise in abundance was linked with the two intense marine heatwaves that occurred in the 2010's. Although this was the overall result, there were difference in the trends among species. Even though both brown and blue-footed now breed within the southern CCE, the brown boobies slowly increased in occurrence, had a large pulse during the 2013-2016 marine heatwave, and then stayed in the CCE at enhanced abundances. In contrast, blue-footed boobies have had massive pulses in their abundance in the CCE and inland, continental U.S., just as marine heatwaves are ramping up; however, the high abundance is not sustained afterwards. With red-footed, masked, and Nazca boobies, these more tropical-restricted species had been incidentally

seen in the CCE before the heatwaves; however, all increased in abundance after 2019 and their occurrence at those abundances in the CCE have continued. As marine heatwaves are projected to increase in frequency and intensity, in addition to long-term warming, we hypothesize that these species will continue to expand their range northward in the CCE. Such changes in marine predator distributions can have consequences for pre-existing species in the CCE, such as increased competition for resources, including food and breeding habitat, which may result in the displacement of native species.

The NMS along the U.S. west coast capture a variety of marine habitats within each of the biogeographic regions in the CCE. During the spatial analysis, I found that the placement of the NMS is useful in that the abundance and diversity trends within the NMS not only are representative of the latitudinal patterns of each biogeographic region, but that they all capture areas of enhanced seabird indices relative to areas outside of their boundaries. These results validate the placement of these sanctuaries; however, my temporal analyses show that at the spatial scales of the NMS, determining linkages between seabird abundance and the physical environmental is difficult. Although the trends in abundance indicate overall declines, some species and groups within different NMS are increasing. Comparisons of these results at different resolutions and with trends outside of the NMS are needed. It is clear that seabirds patterns in the CCE and west coast NMS are changing, with shifts in abundance and species composition, including an influx of tropical species. Continued monitoring and more comparative analysis of inside vs. outside NMS boundaries are needed to further our understanding of the ecological importance of sanctuaries.

This research provides a foundation in spatial and temporal patterns of seabirds within the CCE and west coast NMS, and there are many questions left to pursue. With such an

extensive dataset now available, broad descriptive analyses are still needed, such as updated seasonal patterns of species and functional groups, persistent foraging hotspots, and finer spatial scale use over bathymetric features, such as seamounts, or oceanographic features, such as recurrent plumes. In addition, what are the temporal dynamics with those patterns? Determining how the phenology of seabird seasonality is changing in the CCE and NMS over time and during warm-water conditions, would provide insights into potential mismatches with prey availability, shifts in breeding phenology, and changes in seabird energetics. Although there are areas that are well known as persistent hotspots (e.g., the Columbia River mouth), temporal analysis is needed in order to determine if the locations of these areas are shifting and how their spatial extent changes during varying environmental conditions. Finally, by evaluating the use of areas with specific bathymetric or consistent oceanographic conditions, we can place a metric of importance to seabirds of these regions that could be useful in conservation management and planning. As data collection grows, these data compilations can grow richer and more informative, providing finer spatiotemporal coverage. With such extensive datasets, our knowledge on the ecology of these organisms and how they are responding to environmental variability and changes is improved, and ability to better mitigate damages and take care of these productive and diverse ecosystems. Seabirds are conspicuous and charismatic marine predators, whose role in biological oceanography is often overlooked (Ainley 1980; Ainley & Johns 2023), but they have the potential to inspire and inform scientists and the public alike (Appendix I).

REFERENCES

Ainley, D.G. 1980. Birds as marine organisms: A review. CalCOFI Rep., Vol. XXI.

Ainley, D.G., Johns. 2023. Opinion: A modest proposal—seabirds are marine organisms first, land-based marine predators second. Marine Ornithology, 51: 257–260.

APPENDIX I

Table 1: The number, set-up, and response of examples of how I have been inspired by my research on seabirds and experience with marine life in general during my time at Scripps Institution of Oceanography.

No.	Set-up	Response
1	Why did the albatross get lost?	Because it was wandering
2	Why didn't the seabird need to stop for gas?	Because it was a giant petrel
3	What does a leopard seals crave when its hungry?	Adélie
4	Why did the penguin recommend the krill for dinner?	Because it was *superba*
5	What do you call a car that runs on krill oil?	Toyota prion
6	Why did the ship head inshore?	They didn't want to deal with the Pterodrama
7	Why did the sea lice put on headphones?	It was going on a cormorant
8	What did the otter pack its pup for lunch?	Abalone sandwich
9	Why did the scientists cross the Drake Passage?	Because they also needed to dot their ice
10	Why did the scenery pose for the photographer?	It was an ecosystem model
11	What did the penguin do when it was getting too hot?	Turn on the ACC
12	Why weren't the scientists able to use their computer?	They couldn't find an auklet
13	Why was the shearwater telling the others that there was lots of food offshore?	It was all a front
14	Why didn't the diatom cross the Drake Passage?	It was just going with the flow
15	What was the scientists' response when they couldn't identify the bird?	"Sorry I'm still learning the phalaropes"
16	Why did the seabird keep complaining to the lifeguard?	It was a Peli-Karen
17	What did the tern say when a seabird flew up and said they found food?	Tell me murre!
18	A shearwater landed near a tern, and asked its friend why it looked so mad?	"Don't worry, it's naturally *Sterna"*
19	Did you hear that seabirds were voted the number one most popular group of marine animals?	You're so gull-ible
20	What is the one thing missing from this Appendix?	A porpoise