

THE INFLUENCE OF DIET QUALITY ON THE DIVERGENT POPULATION TRENDS OF
CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*) IN THE CHANNEL ISLANDS
AND THE GULF OF CALIFORNIA

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Abstract

The global population of California sea lions (*Zalophus californianus*) has declined in the Gulf of California (Mexico), while numbers have increased along the California coastline (U.S.). It is unclear what is behind the divergent population trends, but differences in diets likely play a role. I used diet data to investigate whether the changes in sea lion population numbers that occurred in sea lion numbers from 1980–2020 could be explained by differences or shifts in diet quality — specifically energy density and diet diversity. I also explored whether diet quality in the Gulf of California was affected by increased sea surface temperatures that occurred in 2014. I considered rookeries in California (Channel Islands) to be a single ecological Zone and divided the Gulf of California breeding islands into nine Zones based on geographic proximities and similarities in population trajectories. Years with matching population and diet data within all these Zones were used to test for relationships between measures of diet quality and population changes. My results showed that diet variability and composition differed between the Channel Islands and the Zones within the Gulf of California. In general, sea lions breeding in the Gulf of California consumed a large variety of mostly benthic species and schooling fish, whereas sea lions at the Channel Islands primarily consumed schooling fish and squid. Contrary to expectations, no significant relationships were found between population changes and measures of diet quality across all Zones and times. However, the average energy density of sea lion diets in certain Zones within the Gulf of California declined as sea surface temperatures increased. While my results did not reveal a direct relationship between population changes and diet quality, they demonstrate the significance of considering the influence of environmental heterogeneity on regional population dynamics. My results also highlight the importance of better understanding the ecosystem dynamics of the Gulf of California at small regional scales. Such findings may be key to fully understanding the interplay between environmental changes, diets, and future population trajectories of California sea lions and other pinniped species in geographic locations throughout Mexico and the U.S.

Lay Summary

I explored why California sea lion populations have decreased in the last few decades (1980–2020) throughout the Gulf of California, while those in the Channel Islands increased. I hypothesized these differences could be linked to differences in diet quality, which I investigated by comparing diet quality (specifically energy density and species diversity) between the two divergent populations over time. I did not find any significant relationships between measures of diet quality and population trends but did find that some regions within the Gulf of California experienced a decline in diet quality associated with increased sea surface temperatures. This study highlights how the Gulf of California is subject to ecological complexities in different regions, and that the drivers of sea lion population growth cannot be generalized across this entire area but must be considered on a fine-scale basis.

Preface

The original research topic was of my choosing. The final study design was developed with guidance and support from my supervisor Dr. David Rosen, with feedback and suggestions from committee members Dr. Andrew Trites and Dr. Claudia Hernández Camacho. I gathered all data used in this study from existing published literature, and some unpublished data provided by Dr. Hernández Camacho. Dr. Tony Orr provided additional initial guidance and Dr. Miram Gleiber provided essential prey species energy density data that was unpublished at the time. I compiled and manipulated data, conducted analyses, interpreted, and summarized findings in this thesis with guidance from Dr. Rosen. I incorporated feedback and suggestions from Dr. Trites and Dr. Hernández Camacho throughout the analysis and writing processes.

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In reflection, what originally inspired my research topic was the appreciation for the ocean I developed while diving in the Gulf of California, Mexico – my home country. I'd like to emphasize the importance of being able to experience and value healthy ecosystems, because it can fuel motivation and action towards ocean conservation like it has for my career.

To all minorities in the field of science

Chapter 1: General Introduction

Identifying population drivers is key for understanding past changes and predicting future trajectories of populations of marine mammals that might be declining or at risk. Such insight also paves the way for designing efficient conservation management strategies. Various threats and drivers have been identified among marine mammal species, but those related to changing environmental conditions are thought to be the most likely contributors to population trajectories. In pinnipeds, many of these drivers operate through changes in diet; environmental conditions can affect the composition of prey species available to predators and may lead to changes in the ‘quality’ of their diet. Changes in diet quality can ultimately impact population levels through decreases in the nutritional status of individuals, that can influence rates of reproduction, survival, disease, and predation (Rosen & Trites 2000; Trites & Donnelly, 2003).

California sea lion populations

California sea lions (*Zalophus californianus*, Lesson 1828) inhabit the Pacific coast of North America from British Columbia, Canada to the Gulf of California, Mexico. Around 80% of the species resides and breeds along the coast of southern California, United States (U.S.). The remaining 20% are found at breeding sites (rookeries) in Mexico, with 14% living on islands off the Pacific coast of the Baja California peninsula, and 6% in rookeries along the Gulf of California (Hernández-Camacho et al., 2021). Some California sea lions are also commonly found in Oregon, U.S., and Vancouver Island, Canada, but these sites are used mainly by adult and sub-adult males during the fall and winter as non-breeding haul-outs. Rare sightings have been reported as far north as the Aleutian Islands, Alaska (Maniscalco et al., 2004), and as far south as Costa Rica (Lenin Oviedo, pers. comm.). There are a total of five recognized subpopulations of California sea lions: the Temperate Pacific (U.S.), the Tropical Pacific (Mexican Pacific), and three within the Gulf of California: northern (Figure 1; rookeries e-g), central (rookeries h-n), and southern (rookeries o-q) populations (Hernández-Camacho et al., 2021; Schramm et al., 2009).

In recent decades, the global California sea lion population has increased and is slowly expanding geographically. It is currently considered as a species of ‘Least Concern’ according to the latest

IUCN assessment (Aurioles-Gamboa & Hernández-Camacho, 2015). However, this trend is mostly driven by the population in the U.S., where most of the species is found. In contrast, population trajectories of rookeries in Mexico have predominantly declined in recent decades with a few exceptions (Hernández-Camacho et al., 2021; Laake et al., 2018; Pelayo-González, González-Rodríguez, et al., 2021; Szteren et al., 2006; Ward et al., 2010).

The California sea lion population in the U.S. has experienced rapid growth since the 1970's — increasing from a total of ~75,000 individuals to an estimated 257,606 in 2014 (Laake et al., 2018; Lowry, Melin, et al., 2017). This growth was facilitated by passage of the Marine Mammal Protection Act (MMPA) in 1972 which protects marine mammal populations and is designed to prevent them from experiencing significant declines (Laake et al., 2018). Population growth models have predicted that the maximum estimated growth rate for the population in the U.S. was 7% per year (1975-2014) under a normal sea surface temperature regime without anomalies (Laake et al., 2018). It is believed that the U.S. population is approaching carrying capacity, given recent declines in pup production and survival (Laake et al., 2018).

The geographic site accounting for most of the growth of the U.S. California sea lion population are four rookeries that form part of the Channel Islands: San Miguel, San Nicolas, Santa Barbara, and San Clemente islands, where 99.7% of the species' breeding in the U.S. occurs (Laake et al., 2018). Of these four rookeries, San Miguel and San Nicolas islands have considerably larger populations of around 60,000 and 43,000 sea lions respectively and contain ~90% of the total number of pups in the Channel Islands (Lowry, Melin, et al., 2017). In contrast, Santa Barbara and San Clemente islands have much smaller populations of around 5,500 and 3,000 individuals respectively (Lowry et al., 2021). Collectively, the California sea lion populations of the Channel Island rookeries have grown by an average of 2.9% per year from 1964-2014 (Lowry, Melin, et al., 2017), to a total of 114,873 individuals according to the latest 2019 count (Lowry et al., 2021).

In contrast to U.S. breeding sites, California sea lion rookeries in Mexico vary considerably in their population trajectories. Abundance estimates for the populations occurring on 10 islands in the Mexican Pacific have declined from 75,000–87,000 individuals in 2000 (Lowry & Maravilla-Chávez, 2005) to 52,846–54,482 individuals in 2010 (Milanés Salinas, 2012).

Unlike the Channel Island rookeries which are contained within a relatively small geographic area (< 100 km from one another), populations within the Gulf of California are distributed along 13 rookeries spanning 823 km that make up the northern, central and southern Gulf regions (Figure 1). In total, there are around 18,642 California sea lions within the Gulf of California, but rookeries vary in population sizes (~400–7,500 individuals). While rookeries within the Gulf of California vary in their individual population trajectories, they have shown the fastest collective decline of around 2% annually since the 1980's compared to the Channel Islands. While most individual rookery populations in the Gulf of California are declining, the southernmost rookery of Los Islotes has the only stable and significantly increasing population of 751 individuals (as of 2021, Figure 2, Table 2). The largest rookery in terms of population is San Esteban, located in the central Gulf which has around 5,100 individuals and is the only other population showing a seemingly increasing trajectory. The smallest is the northernmost rookery of Rocas Consagradas, with a population of around 400 individuals (and an inconclusive trajectory due to lack of data). Most other rookeries in the Gulf of California have seemingly or significantly declining population trajectories since the 1980's (Figure 2).

Due to the collective decline of most rookeries in Mexico, California sea lions have been assigned the category of being under 'special protection' by the Mexican government under the NORMA Oficial Mexicana (NOM-059-SEMARNAT, 2010). This category designates the California sea lion populations in Mexico as being threatened or subject to possible risk of extinction. As a result, recovering or conserving their populations has been identified as a national conservation goal.

Given the starkly contrasting population trajectories of California sea lions in the U.S. and Mexico, my study will focus on the populations in the four Channel Island rookeries and the 13 rookeries in the Gulf of California to identify possible factors that may be driving their opposing population trajectories. More specifically, I will investigate the influence of diet quality on the long-term population trajectories from 1980–2020, when population and diet data were most available in a useful format. Unfortunately, I was unable to include populations from the Mexican Pacific due to a lack of sufficient relevant data.

Environmental and contextual differences of study areas

The environmental differences of the Channel Islands and throughout the Gulf of California are known to influence California sea lion populations. Sea lions within each region are subject to distinctive oceanographic conditions in their immediate environment, and also exhibit different foraging behaviours, philopatric behaviours, and genetic make-up (Schramm et al., 2009). The Gulf of California populations in the northern and central regions have been identified as being especially vulnerable to environmental changes or catastrophes compared to those in the south, due to their more extreme genetic and geographic isolation from the rest of the populations in the Gulf of California and the Pacific coast (Hernández-Camacho et al., 2021; Schramm et al., 2009).

The unique oceanographic dynamics of the Channel Islands and the Gulf of California influence the potential prey available at different rookeries. The Channel Islands in the Eastern Pacific Ocean are impacted by oceanographic dynamics such as the California Current (colder southwards nutrient-rich water), which persists year-round, and seasonal winds that cause upwellings, leading to increased primary productivity and the presence of important pelagic prey species (e.g., sardines, anchovies, squid) in spring and summer (Lowry & Carretta, 1999; Weise & Harvey, 2008). Rookeries in the Channel Islands are also impacted by increased sea surface temperatures during El Niño events, which modify the California Current characteristics and can cause a decrease in the availability of important prey (McClatchie et al., 2016). This, in turn, can cause increased pup and yearling mortality due to nutritional stress and dehydration (McClatchie et al., 2016). These effects were apparent during the 2013-2016 increased sea surface temperature event, also known as the “Blob”, which originated in Alaska and moved south to California and the Baja California peninsula (Tseng et al., 2017). During subsequent years, it also coincided with a strong El Niño event (2015-2016), which increased sea surface temperatures by 2-5 °C (NOAA, 2017). Although these oceanographic events can cause short-term California sea lion population declines in the Channel Islands, population totals typically return to previous counts in subsequent years once environmental conditions stabilize (Laake et al., 2018).

In contrast, populations in the Gulf of California do not seem to be affected by El Niño events to the same degree as those in the Channel Islands. This is because the Gulf of California has very unique oceanographic features, even compared to similar semi-enclosed seas of comparable latitudes and dimensions (Lavin & Marinone, 2003). Furthermore, the oceanographic conditions vary by region within the Gulf, influencing local ecosystem dynamics accordingly (Lavin & Marinone, 2003). In the north and central regions of the Gulf of California, wind-induced upwellings drive high productivity areas compared to the southern Gulf (Álvarez-Borrego, 2010). These seasonal winds also differ between the eastern vs. western parts of the Gulf, producing distinctive conditions in each of these two areas that do not affect the south (Álvarez-Borrego, 2010). In terms of macrofaunal composition (fish, invertebrates, and non-fish vertebrates), diversity is generally highest in the south and decreases towards the northern Gulf. Biodiversity hotspots have been identified in the northern end of the Ángel de la Guarda Island (site of Granito, Cantiles, and Machos rookeries) and in Rocas Consagradas (Brusca et al., 2005; Thomson & Gilligan, 1983).

Small-scale differences in oceanographic dynamics impact compositions of local California sea lion prey availability and abundance, and therefore likely influence the population trajectories of each rookery differently. Rookeries in each region are mainly populated by adult females that show highly philopatric behaviour to where they birth and nurse their pups year after year, and therefore are likely affected by the same local oceanography over their entire lives (Hernández-Camacho et al., 2021; Rayas-Estrada & Hernández-Camacho, 2019; Schramm et al., 2009). Furthermore, adult California sea lion females are estimated to have a foraging range of only around 60 km from their rookery (although longer foraging trips >100 km have been seen in other populations in the Mexican Pacific Molina-Chávez, 2022), suggesting a localized impact of prey availability on female nutrition.

In addition to natural oceanographic differences, the population trajectories of California sea lions within the study areas can be affected by anthropogenic activities. Both the Channel Islands and the Gulf of California are nationally protected areas in the U.S. and Mexico respectively. In general, this means specific rules and protection measures have been established to limit potentially harmful activities within these areas such as fishing or excessive tourism. The Channel

Islands National Park has laws and policies that prevent any disturbances or harm to park wildlife or plant life and has banned any fishing within this area.

The Gulf of California is recognized as an area of marine conservation significance where roughly one-third of the world's marine mammal species occur (Urbán, 2010). Both its marine and terrestrial ecosystems contain a high degree of endemic species unique to Mexico. In 2005 the Protected Areas and Islands of the Gulf of California were deemed a UNESCO World Heritage site due to having representative components of major oceanographic and biogeographically diverse zones considered to be of important conservation value.

The protection measures in the Gulf of California are not only important due to its economic and conservation value but are also necessary given the current human-wildlife conflicts in the upper Gulf region. Tensions continue to rise regarding illegal gillnet fishing practices and its effects on local marine life, stemming from poor fisheries management, lack of effective enforcement, corruption, and lack of viable economic alternatives (Sanjurjo-Rivera et al., 2021). Specifically, the gillnet fishery in the upper Gulf of California targets the endangered totoaba fish (*Totoaba macdonaldi*) for its highly valued gall bladder, which is sold to foreign black markets as an aphrodisiac (Rojas-Bracho et al., 2022; Sanjurjo-Rivera et al., 2021). This activity has accelerated the risk of extinction for the world's smallest cetacean endemic to the upper Gulf of California — the vaquita (*Phocoena sinus*). Although difficult to quantify, other illegal activities potentially harmful to marine life are thought to be likely happening in nearby regions of the upper Gulf, such as the use of California sea lion flesh for bait (Masper et al., 2019; Zavala-González & Mellink, 2000).

The effect of changes in prey availability on populations

The growth or decline of a California sea lion population depends on reproductive rates and the survival of newborn pups, as well as the mortality rates of adult and juvenile sea lions. The proximate mechanisms that lead to changes in demographic parameters vary and often depend on biological, oceanographic, and anthropogenic factors. Previous literature has identified various drivers of marine mammal populations that ultimately affect the survival, mortality, and

reproductive success of individuals. Several anthropogenic causes of mortality have been implicated as potential threats to California sea lions including noise or chemical pollution, entanglements in fishing gear, illegal shootings, disease (including bacterial infections and parasitism), biotoxins, increased ocean temperatures, and nutritional health. Migration may be considered a special case, as it leads to changes in population numbers without affecting survival or reproductive success of individuals.

Changes in prey base availability can occur over small or large temporal and geographic scales. Environmental changes often shift the availability and abundance of prey, which in turn can affect the nutritional state of individuals and therefore the reproductive success of females and the survival of pups, ultimately affecting the population growth. Numerous studies have documented the effect of prey availability on marine homeotherms, including seabirds (Velarde et al., 2015) and cetaceans (Jory et al., 2021).

Other studies have linked changes in prey availability to changes in the nutritional state of individual pinnipeds, as well as their population trends. In a study on Galápagos sea lions (*Zalophus wollebaeki*), Schwarz et al. (2022) found that as prey availability changed in response to increased temperatures, pupping probability and pup body condition generally decreased. Steller sea lion populations (*Eumetopias jubatus*) in the Gulf of Alaska declined by around 80% from 1970-1990 (National Research Council, 2003; Trites, 2021). Decreases in the body size of the sea lions, birth rates, and survival rates were thought to be associated with shifts to a lower energy-density diet that was hypothesized to cause nutritional stress in individual sea lions (Trites & Donnelly, 2003). Similarly, in San Miguel Island, changes in the relative abundance and quality of important prey species (sardine, anchovy, rockfish, squid), likely driven by environmental changes, were observed from 2004-2014 (McClatchie et al., 2016). These changes were, in turn, strongly associated with low birth weights of pups, suggesting that long-term shifts from high to poor quality forage fish for breeding females results in a sub-optimal pup condition at birth. Subsequent low quality food intake during growth can further jeopardize survival, which can ultimately affect their populations (McClatchie et al., 2016; Trites, 2021).

Harbour seal (*Phoca vitulina*) populations in the U.K. have declined over the last 20 years, specifically in regions where the availability of sandeels, an important component of their diet, had declined. Studies suggest the change in availability was therefore strongly linked to the decline of the population (Wilson & Hammond, 2019). Similarly, ringed seals (*Phoca hispida*) in Hudson Bay experienced a lower body condition as a result of a lower overall diet energy density subsequent to changes in availability of their main prey, sand lance (Chambellant et al., 2013). In addition to these observational studies in the wild, manipulative studies with captive Steller sea lions have also contributed to our understanding of the physiological mechanisms whereby diet changes can result in nutritional stress of individuals (Rosen, 2009). These studies can inform us about the short-term health impacts of diet changes (e.g., weight loss, reduction in body condition) and also provide insight into the possible long-term consequences of changes in diet quality on pinniped populations (Trites & Donnelly, 2003).

Measuring diet quality in marine mammals

If marine mammals are not able to meet their nutritional requirements from their food, then by definition their diet can be classified as being of “poor quality”. However, in practice “diet quality” is an exceedingly broad and poorly-defined term. The two most common diet characteristics used to assess diet quality are diet diversity and diet energy density. Both of these measures have been quantitatively associated with sea lion population trajectories (Merrick et al., 1997; Trites et al., 2007; Trites, 2021; Winship & Trites, 2003).

Diet energy density

Diet energy density is a measure of the energetic content, calculated either as an average of individual prey species in the diet or the estimated energy density of a reconstituted diet (accounting for both prey type and quantity). Either method yields a mean value of how energy-rich the prey species that compose the diet are, and is calculated by averaging the energy density values for each prey species (kilojoules per gram of wet weight; kJ/gww). Energy density values can be obtained through direct measurements using bomb calorimetry (Johnson et al., 2017), or calculated from measures of proximate composition of macronutrients. However, these values are

difficult to obtain since they require performing laboratory analyses on each prey species; therefore, using published values for the exact or similar species is often required. Nevertheless, measures of diet energy density provides quantitative estimates for the degree to which a diet can be considered “nutritionally adequate” (Fritz et al., 2019; Johnson et al., 2017; Rosen & Trites, 1999, 2000; Tollit et al., 2015). This is especially useful when comparing diet changes throughout time or comparing the diet of multiple populations since differences in average diet energy density can suggest shifts in diet quality either towards or away from the consumption of energy-rich and nutritionally adequate prey.

All other things being equal, a shift to lower energy density diets can present a challenge for obtaining adequate nutrition, based on the simple principle that animals will have to catch and consume a greater biomass of prey. For example, Winship & Trites (2003) incorporated diet energy density into a bioenergetics model of Steller sea lions to estimate food requirements (Winship & Trites, 2003). They found that estimated food requirements were highest in regions where Steller sea lions consumed higher proportions of low energy dense-prey, and experienced the highest population decline rates.

Diet diversity

Another aspect of diet quality accounts for the number and abundance of prey species that compose the diet — that is, the diet diversity. Quantifying diet diversity can show differences in both the “breadth” and homogeneity of diets. It can also be combined with measures of diet energy density to illustrate the contribution of different prey species to the total diet energy density. While some sea lion populations may rely on one main prey species and others rely on a high diversity of prey options to meet their energetic requirements, neither strategy is necessarily intrinsically “better” in terms of diet quality. However, changes (or differences) in diet diversity may indicate shifts in available prey and associated foraging options, which may ultimately link to population health.

Multiple studies have used diet diversity as one measure to describe diet quality and investigated its role in population trajectories (Fritz et al., 2019; Tollit et al., 2015; Trites et al., 2007). For instance, Merrick et al., (1997) found a strong positive correlation between diet diversity and the

level of population decline of Steller sea lions in six areas within the Aleutian Islands and the Gulf of Alaska from 1990-1993. Specifically, areas with lower diet diversity had greater rates of population declines. The authors therefore concluded that these sea lion populations thrived when there was a variety of prey available, perhaps because this allowed them to buffer significant changes in the availability or abundance of any single prey. Trites et al. (2007) later arrived at the same conclusion when including additional data from Southeast Alaska (1990-1994) — Steller sea lions that consumed the least diverse diets in turn experienced the greatest population declines, and these diets also happened to be those with the lowest energy content.

Fritz et al., (2019) later re-examined the relationship between diet diversity of prey groups and opposing population trends of Steller sea lions in the western and eastern Aleutian Islands (1990–2012) but found no significant differences in diet diversity. However, unlike previous studies they did not group prey species into categories, demonstrating how different data analyses can yield alternate conclusions that are not directly comparable.

Among the multiple ways to quantify diet diversity, the most straightforward is to tally the number of species present in the diet (species richness). Other measures include diversity indices that incorporate both species abundance (total number of species appearances) and species richness (number of different species regardless of their abundance). These indices include the Shannon Index and the Simpson's Index (Ricklefs & Miller, 2000; Simpson, 1949).

Shannon's Index of Diversity (H)

The Shannon Index was invented by Claude Shannon in 1949, a mathematician who originally developed this index in the context of communication theory. The original purpose was to quantify the ability to predict the next letter in a message, with the uncertainty expressed by the Shannon function 'H' (Spellerberg & Fedor, 2003). Ricklefs & Miller (2000) helped popularize this index in ecological studies, first as a measure of ecological diversity and later to define diet diversity evenness. In this context, the Shannon's Index of Diversity (H) is defined as a unitless value with no upper limit that expresses the (prey) species diversity by incorporating both species richness and relative species abundance (or evenness) (Berg, 1979; Moore, 2013).

Furthermore, the Shannon Index demonstrates the difference between two samples that have the same number of species, but in different relative abundances. For example, in two communities with equal species richness (same number of different species present), but different relative abundance (different number of representatives from each species), the diversity value would be higher for the community with a more even distribution of species abundance. In other words, this measure accounts for homogeneity in the diversity.

Simpson's Diversity Index

The Simpson's diversity index (Simpson 1949) can also be used to compare the diet diversity of prey species, where (unlike the Shannon Index) its maximum value is equal to the number of species present in the sample.

This index can be cumbersome when dealing with large numbers of potential prey species. However, by using this index after grouping prey species into a smaller number of species categories, it provides an easily interpretable picture of diet diversity. Specifically, the closer the diversity value (D) is to the total number of categories, the more evenly each category is represented in the diet.

Overview of diet quantifications from raw data

Calculating diet energy density and diet diversity obviously requires data on the diet of individuals within a study population. In general, accurately knowing the diet of marine mammal species is a challenge and usually relies on indirect methods to reconstruct the diet. Historically, these methods have commonly relied upon the identification of prey hard parts (otoliths or beaks) recovered from stomach contents, intestines, or scats (feces). Identifying hard parts is a means to determine what prey species were recently consumed by an individual. Data denoting the identity and how frequently each prey appears allows a picture to be formed of what the diet of a population might be composed of. However, it is important to note that this method only provides an estimate of the relative amount consumed of each species for a limited number of individuals, and that the composition and proportion of the diet for the entire population is only an approximation.

Building on the basic hard part remains identification technique, biomass reconstruction models are a more complex way of estimating the composition of diet. By incorporating more information about the prey species such as their size, they presumably result in more accurate diet estimates (Laake et al., 2002; Tollit et al., 2015). However, the greater data needs can be a disadvantage as it can be difficult to gather this additional prey information. Further, this method also requires the application of techniques to account for changes in size after digestion (such as appropriate allometric regressions and correction factors) (Laake et al., 2002; Tollit et al., 2010). As a result, few field studies attempt to use biomass reconstruction models using data from hard part structures. Increasingly, prey DNA signatures found in scat are combined with hard part remains to provide additional information on the diet prey composition (Tollit et al., 2017). Other methods using more advanced technology, such as stable isotope analysis or fatty acid signature analysis, have been developed to provide information on the relative abundance of prey species consumed over a longer time frame from chemical analyses of consumers' tissues, with the limitation of providing coarser diet information.

While all methods have different advantages and limitations, diet estimates using analysis of hard parts from scat is by far the most common technique used for pinnipeds (despite its biases and inaccuracies), in part because scats can be routinely obtained from haul-out sites with little to no impact on the animals (Lance et al., 2001; Tollit et al., 2010). Since it is the most commonly used standard technique, it also provides the longest record of historical, comparable data. As a result, indices of diet data based on hard part recovery are often the best option to use for long-term diet studies such as this one.

There are several ways to convert raw hard part data into an expression of “average diet”. Most studies, especially in the U.S., convert the raw data into the form of frequency of occurrence of each prey species (Lowry et al., 1991, 2022; Lowry & Carretta, 1999; Melin et al., 2010, 2012). Others, mostly in the Gulf of California, have used the index of importance to represent the relative abundance of prey species expressed using proportions (García-Rodríguez, 1999; García-Rodríguez & Aurióles-Gamboa, 2004; Morales, 2015; Porras-Peters, 2004; Porras-Peters et al., 2008; Zavaleta Romero, 2015).

Frequency of Occurrence Index

The frequency of occurrence (FO) index is a commonly used way to demonstrate the prey species found in the diet data from otoliths and beaks identified from collected scat samples. This index expresses the relative importance of each prey species based on the presence or absence of a particular species in a single scat sample (Orr et al., 2011; Tirasin & Jørgensen, 1999). It does not, however, account for how many times a species showed up in each individual scat sample, only the relative number of times each species was identified at least once in a scat, expressed as a proportion in relation to the total number of scat samples with identified otoliths (the total does not include scat samples without any identified otoliths). Although this cannot account for the number of times a prey appears in a scat (i.e., relative consumption rates in a meal), it has an advantage in terms of processing scats because not all structures have to be recovered from a sample (Orr et al., 2011), and it is a good measure to use when looking at population-wide diet habits (Tirasin & Jørgensen, 1999).

There are other ways to express diet diversity that use FO as their basis. For example, the modified frequency of occurrence (MFO) expresses FO of a specific prey species as a proportion relative to the FO of all prey, that allows for statistical comparisons of diet across sites and years by controlling for total number of species in the diet (Bigg, 1985; Tollit et al., 2007, 2015). Some studies have used an alternate index termed split sample frequency of occurrence (SSFO) which calculates the relative importance of prey by incorporating the total number of prey species in each scat. SSFO avoids the tendency of FO to overestimate the importance of prey consumed in small quantities (Olesiuk et al., 1990).

Index of Importance

Another method for describing data based on prey occurrence is the index of importance (IIMP). This index uses prey species occurrence, but also incorporates additional information about the relative abundance (and therefore importance) of each prey species in the diet (García-Rodríguez 1999).

The index of importance (IIMP), developed for scat analysis by Garcia-Rodriguez (1999), expresses the importance of a specific prey taxon, based on the probability of finding it in any given scat. It considers each scat as an independent collection measure and is based on the following two assumptions: a) prey species found and identified through otoliths in each scat represent 100% of the prey species consumed, and b) all scats have the same probability of being selected during collection, and therefore all sea lions in the collection site are represented in the analyzed scats (García-Rodríguez 1999).

IIMP values range from 0-1 and are usually expressed as a percentage ($\text{IIMP} \times 100$) (Porrás-Peters et al., 2008). In contrast to the FO index, the IIMP index accounts for the number of identified individuals of each prey item and provides the relative proportion of each prey species in scat collections from one rookery. However, like MFO it does not provide information on the importance of prey biomass.

If a scat contains only one prey species, the IIMP does not change regardless of how many individuals of that species are identified in that scat. This avoids the case of a scat containing multiple individuals of one prey species from dominating numerically. Instead, IIMP normalizes the effect of one prey's frequency within one scat by allowing each scat to contribute an *equal amount* of information (García-Rodríguez & Aurióles-Gamboa, 2004). It is also important to note that, as with any measure of relative abundance, IIMP also assumes a uniform prey distribution across scats.

IIMP is able to determine the relative importance of prey species, any temporal and spatial variation in the diet, estimate diversity of prey, and provides measures of diet similarity among rookeries (García-Rodríguez & Aurióles-Gamboa, 2004). The IIMP can be considered a more descriptive index than FO and was therefore included in this analysis when possible.

This research study

The California sea lion populations of the Channel Islands and in the Gulf of California was the focus of my thesis research to investigate my main research question: what is the influence of diet

quality in divergent population trajectories of California sea lions in the Channel Islands and the Gulf of California (1980-2020)? To answer this question, I analyzed the population trends of 17 rookeries over time, and calculated the population change over specific time periods with corresponding available diet data. The diet data was analyzed to calculate measures of diet quality by measuring diet diversity and diet energy density for each rookery over time.

Diet diversity was quantified using three methods: the Shannon Index which incorporates both species richness (number of prey species) and species diversity (frequency of each species present), the Simpson's Index which compared diet diversity before and after environmental changes using a limited number of prey species categories, and finally the raw number of total prey species in the diet (since these differences were masked by the Shannon Index' account for evenness in the diet). The energy density in the diet was calculated by combining prey occurrence diet data with energy density values for each prey species, to yield values of average diet energy density.

My analysis relied entirely on historical published and unpublished diet and population data for all rookeries from 1980–2020. Data were not continuous, but rather were patchy over time and between rookeries. As a result, diet data were gathered and analyzed using both frequency of occurrence and the importance index values when available to maximize the amount of diet data incorporated, particularly given the lack of continuous data in the Gulf of California.

In Chapter 2, I present the different population trajectories at each rookery from 1980–2020, and subsequently group rookeries into geographic Zones based on trajectory and geographic location for further diet analyses. I then demonstrate differences in the diet quality (diversity and energy density) between and within Zones and over time, and test relationships between measures of diet quality and population changes during certain periods. Finally, I analyze and discuss significant changes in diet quality in the Gulf of California before and after increased sea surface temperatures after 2014. The significance of my findings is discussed in Chapters 2 and is expanded upon in Chapter 3, which also includes management recommendations and ideas for future research.

Chapter 2: The Influence of Diet Quality on the Divergent Population Trends of California Sea Lions in the Channel Islands and the Gulf of California

Introduction

California sea lions (*Zalophus californianus*) are widely distributed along the Pacific coast of North America from British Columbia, Canada to the Gulf of California, Mexico — but only breed on a small number of islands (rookeries) in the Mexican Pacific, the Gulf of California, and along the southern coast of California, U.S. (Lowry & Maravilla-Chávez, 2005; Peterson & Bartholomew, 1967). Most of the species' population (80%) breeds in California where numbers have increased at an annual rate of 3% between 1964–2014 (Lowry, Melin, et al., 2017). The remainder of the population (20%) breeds in Mexico, where — with a few exceptions — most rookeries have experienced population declines. More specifically, populations in the Gulf of California experienced an overall decline of 2% per year between 1984–2015 (Hernández-Camacho et al., 2021).

Within California, breeding occurs almost exclusively at four rookeries that form part of the Channel Islands. This growing population numbered 111,713 sea lions in 2019, and is distributed among four rookeries that vary in size from around 3,000–60,000 animals (Lowry et al., 2021). In contrast, populations breeding in the Gulf of California, Mexico, are distributed among 13 rookeries that vary from around 400–6,000 individuals per island (Lowry & Maravilla-Chávez, 2005; Peterson & Bartholomew, 1967). These Mexican rookeries are often divided into northern, central, and southern Gulf subpopulations that are associated with unique ecological and oceanographic regional dynamics (González-Suárez et al., 2009; Schramm et al., 2009). Only one rookery in the Gulf of California (Los Islotes, in the southern Gulf) is considered to have a healthy and growing population (Hernández-Camacho et al., 2021).

It is not known what is driving the divergent increases and decreases in population numbers of California sea lions in the different geographic areas. Possible contributing factors that affect marine mammal species include regional differences in prey availability, pollution (both chemical and noise), disease, biotoxins, fishing gear entanglements, anthropogenic mortality (disturbance, legal and illegal shooting), and migration (Loughlin & York, 2000; Read et al., 2006; Reeves et al., 2013; Stroud & Roffe, 1979). Of these possible explanations, regional differences in diets associated with environmental change have been identified in a number of species as the most likely contributor to population trajectories.

Previous studies have generally focused on the negative effects that reductions in prey *abundance* have on sea lion numbers at rookeries in the Channel Islands (Lowry et al., 1991; Lowry, Melin, et al., 2017; Melin et al., 2010), and the Gulf of California (Aurioles-Gamboa et al., 1984; Aurioles-Gamboa & Zavala-González, 1994; García-Rodríguez & Aurioles-Gamboa, 2004; Hernández-Camacho et al., 2021; Pelayo-González et al., 2021; Porras-Peters et al., 2008). Sharp declines in quantities of main prey available to sea lions are known to occur during El Niño events in California when warm water causes prey to remain at inaccessible depths (Melin et al., 2008). However, El Niño events do not appear to explain declines in sea lion numbers in the Gulf of California (Pelayo-González, González-Rodríguez, et al., 2021). This has led to the question of whether changes in the *quality* of prey rather than changes in the *quantity* of prey might better explain differences that have occurred in sea lion numbers over a longer timeframe (Lowry et al., 2022) as suggested for Steller sea lions (Fritz et al., 2019; Merrick et al., 1997; Rosen & Trites, 2000; Trites, 2021; Trites & Donnelly, 2003).

Diet quality can be assessed in many aspects, including in terms of diet energy density (i.e., an important aspect of the nutritional value of prey species) and diet diversity (i.e., the variety of species that compose the diet). These diet characteristics can change the nutritional status of individuals and their rates of reproduction, survival, disease, and predation (Rosen & Trites, 2000; Trites & Donnelly, 2003). In general, a simple diet dominated by energy-rich species would be expected to support a growing population — while a diverse diet of energy-poor species would be expected to cause population declines. Environmental conditions likely determine the diet composition and ‘quality’ of prey species available to predators. However, it is not known how

such differences or changes in diet quality influence the population dynamics of California sea lions at these rookeries.

The goal of my research was to quantify *diet quality* using estimates of average diet energy density and three different measures of diet diversity to investigate how the quality of different diets may influence the divergent population trends (1980–2020) of California sea lions breeding on the Channel Islands and in the Gulf of California. Specifically, I quantified differences in diet composition and diet quality between the two regions over time. I also used data from all rookeries (either individually or grouped into Zones) to test for relationships between rates of population change and different measures of diet quality. Finally, I compared sea lion diets before and after a known climatic shift in the Gulf of California after 2014. Obtaining a better understanding of the interplay between environmental changes, diets, and population trajectories is needed to ensure the long-term conservation of California sea lions in Mexico and the USA.

Methods

Study areas

I focused my analysis on the four California sea lion rookeries in the Channel Islands and the 13 rookeries along the Gulf of California (Figure 1). California sea lion diets and populations have been studied for decades in the Channel Islands and the Gulf of California at various degrees of intensity.



Figure 1. Map of the California sea lion rookeries and designated Zones for this study. Study sites included the four rookeries in the Channel Islands (a–d: San Miguel, San Nicolas, Santa Barbara, San Clemente) designated as Zone 1, and the 13 rookeries along the Gulf of California (e–q), and their respective Zones (2–10). Red circles indicate rookeries within the indicated Zone. Rookery f (San Jorge) did not have diet data available and was omitted from further analysis. There are 823 km between the northernmost rookery of Rocas Consagradas (Zone 2), and the southernmost rookery of Los Islotes (Zone 10). Image adapted from NASA/GSFC.

Diet and population data

Population and diet data for California sea lion rookeries in the Channel Islands and the Gulf of California from 1980 to 2020 were obtained from published and unpublished data (Table 1). This included additional raw diet and population data for rookeries in the Gulf of California obtained from Dr. Claudia Hernández Camacho. These data also included total and pup-only sea lion population counts, and diet data summarized in various forms. Unfortunately diet data were too limited to include California sea lion populations along the west coast of the Baja California Peninsula.

For consistency, I only used population data collected during the breeding season (May–August) when pups are born and when the highest number of sea lions are at the rookeries. Similarly, I only used diet data from the breeding seasons to avoid the potential confounding effects that might be introduced by seasonal changes in diet.

All sea lion counts from 1980–2018 from the Gulf of California rookeries were obtained from Pelayo-González et al. (2021). Counts were made from boat surveys and included numbers for each age and sex class (i.e., adult males, adult females, subadult males, juveniles, pups, and unidentified). Population counts for the Channel Islands were sourced from Lowry et al. (2017a) for 1980–2014, from Lowry et al. (2017b) for 2015, and from Lowry et al. (2021) for 2016–2019 (Table 1). These counts were originally corrected for pups that were obscured from vision and for adult females that were foraging during the census. Whenever there was more than one source for population data for the same location and year, the source with the higher counts was used after confirming it was due to using a technique with greater accuracy (i.e., aerial photography counts vs. boat counts). For example, Lowry et al. (2017a) often reported multiple counts for the same rookery and year compiled from multiple publications. When available, population totals were used (i.e., included all sexes and age groups). Some data sources only reported pup counts for some years, which were later used to extrapolate population totals (see **Combining population and diet data:** *Estimating population totals*).

Table 1. Population and diet data sources used in analyses. Details include the rookery, data year and season, diet index or population estimate, and Table in source publication where relevant data is found. (FO; frequency of occurrence data, IIMP; index of importance data).

Source	Rookeries	Year(s) of data	Season	Data type/diet index	Table
Channel Islands					
Lowry et al. (2017a)	San Miguel	1971–1991 (pup counts) 1992–2014	July or August	Population (total live)	Table 2
	San Nicolas	1991–2008 2009, 2010 (pup counts) 2011–2014	July	Population (total live)	Table 2
	San Clemente	1981–2014	July or August	Population (total live)	Table 2
	Santa Barbara	1983–1985 (pup counts) 1986–2008 2009, 2010 (pup counts) 2011–2014	July	Population (total live)	Table 2
Lowry et al. (1991)	San Nicolas	1981–1986 (grouped)	June and August	FO	Table 1, 2
Lowry and Carretta (1999)	San Nicolas Santa Barbara San Clemente	1981–1995	Multiple months, summer (Santa Barbara)	FO	Table 3
Raw unpublished data from Alexandra (NOAA)	San Nicolas, San Clemente	1981–1986	Summer	FO	
Lowry et al. (2017b)	Channel Islands	2015	July	Population (total counts)	Table 3
Lowry et al. (2021)	Channel Islands	2016–2019	July or August	Population (total live)	Table 1
Orr et al. (2011)	San Miguel	2002–2006	March–July	FO	Table 3
S. R. Melin et al. (2012)	San Miguel	2000–2003, 2005, 2009–2011	June–Sept	FO	Table 5
S. R. Melin et al. (2010)	San Miguel	2000, 2001, 2002, 2004, 2005 and 2009	July–early August	FO	Table 1
Gulf of California					
Pelayo-González, González-Rodríguez, et al. (2021)	1–13 (not all rookeries have data for all years)	1980–2019	June or July	Population (total)	Raw data
García-Rodríguez (1995)	13	1990	February–September	FO	Table 4

Source	Rookeries	Year(s) of data	Season	Data type/diet index	Table
Gulf of California					
Raw unpublished data by Garcia-Rodriguez	5	1995	September	FO & IIMP	
Raw unpublished data by Garcia-Rodriguez and Cardenas-Palomo (2003)	3, 4, 6, 9, 10	1995	June	FO & IIMP	Cuadro 1, Anexo 3
	3, 4, 5, 8, 9, 10	1996	May		
	13	2000	May 2000–April 2001		
Porras-Peters (2004) and Porras-Peters et al. (2008)	1, 3, 5, 7–13	2002	Summer	IIMP	Figure 4 (Appendix II)
Pelayo-González et al., (2021)	13	2015	July	FO	
Raw unpublished data from Pelayo-González et al., (2021)	4	2016	October		
	5	2016	Unknown		
	6	2016	October	IIMP	
	8	2016	October	FO & IIMP	
	4	2018	August	FO	
	4	2018	July		
	5	2018	July		
13	2019	August			

Gulf of California rookeries: 1: Rocas Consagradas, 2: San Jorge (no data), 3: Isla Lobos, 4: Granito, 5: Cantiles, 6: Machos, 7: El Partido, 8: El Rasito, 9: San Esteban, 10: San Pedro Mártir, 11: San Pedro Nolasco, 12: Farallón de San Ignacio, 13: Los Islotes.

Establishing rookery Zones

I grouped rookeries into composite Zones (Figure 1) to prevent over-representing rookeries that could be considered common ecological units. Previous studies have partitioned the 13 Gulf of California rookeries into three areas based on factors such as environmental conditions, genetic structure, and diet (González-Suárez et al., 2009; Pelayo-González et al., 2021; Schramm et al., 2009; Szteren & Auriolles-Gamboa, 2011; Ward et al., 2010). However, because I sought to test whether there is a relationship between diet and population change across different geographic Zones, I chose the geographic Zones based on their population trajectories and geographic proximity to one another — and deliberately excluded any factors related to similarities or differences in diets.

Grouping individual rookeries into Zones entailed plotting available population data for each rookery over time (Figure 2) and determining their overall trend. Note that I only used reported population data for this analysis and did not use any of the estimated values used in later analyses to fill in years with missing population data. Population trajectories were designated as increasing, decreasing, or inconclusive by running a linear regression. I grouped rookeries into the same Zone if they occurred in a similar geographic area (<100 km away from each other) and had a similar positive or negative population trend over time (1980–2020). Following this methodology, I grouped all of the Channel Island rookeries into Zone 1 because they were all ~100 km or less from each other and each had increasing population trajectories from 1980–2020. Applying these principles to the Gulf of California rookeries resulted in 9 groupings (Zones 2–10; Figure 1, Table 2).

Diet data

I characterized diet quality in terms of diet diversity and energy density. Both diet characteristics incorporated data originally quantified as the frequency of occurrence index (FO) or the index of importance (IIMP) (see **Diet data indices**).

Diet data from the Channel Islands and the Gulf of California were reported in FO, while IIMP was only used to describe some diets from the Gulf of California. Whenever there was more than one published source for diet data for the same location and year, I used the source with the greatest number of samples. Some unpublished data sources reported raw diet data, which allowed me to calculate FO using occurrence values and total number of samples.

I calculated diet diversity and average diet energy density from the available FO and IIMP diet data. For the Channel Islands, data from FO was available from 1980–2011, although data availability varied by rookery (Figure S1). For the Gulf of California, FO data were available from 1990–2019 with most data available around 1995 or the late 2010's (Figure S2). Diet data from the Gulf of California in the form of IIMP was available from 1995–2020 — mostly around 1995, 2002, and the late 2010's (Figure S3). In some cases, diet data was reported as a single mean over a number of years (e.g., Santa Barbara Island 1981–1995; Figure S1).

Diet data indices

Diet data from published and unpublished literature (Table 1) was originally reported in the form of FO or IIMP.

Frequency of occurrence (*FO*) for each prey species (*i*) is calculated as:

$$FO_i = \frac{\sum_{k=1}^s O_{ik}}{s}$$

where O_{ik} = is the absence (0) or presence (1) of species *i* in scat sample *k*, and
s = total number of scat samples that contained identified prey species
(Lance et al., 2001).

The importance index (IIMP) for each prey species (*i*) is calculated as:

$$IIMP_i = \frac{1}{U} \sum_{j=1}^U \frac{x_{ij}}{x_j},$$

where x_{ij} = number of individuals of species *i* in scat *j*,
 x_j = total number of individuals from all species found in scat *j*, and
U = total number of scat samples with prey
(García-Rodríguez & Aurióles-Gamboa, 2004).

Only prey species with FO values $\geq 5\%$ were included in my dataset since this was the cut-off available from most of the data and it serves to highlight the main prey items. For this analysis, I also applied a $\geq 5\%$ cut-off to IIMP values to maintain consistency across the data (this is the same IIMP cut-off previously used by Porras-Peters 2008). Most literature uses a cut-off of IIMP values $\geq 10\%$ (García-Rodríguez & Aurióles-Gamboa, 2004). For my analysis a $\geq 5\%$ IIMP value cut-off could be applied since the raw (unpublished) diet data collected by García-Rodríguez (1995 and 1996) shared by Dr. Hernández-Camacho (which reported all IIMP values) was available.

To more accurately compare diet data between sites and years, I calculated modified frequency of occurrence (MFO; Bigg and Perez 1985) and modified importance index (MIIMP) values. The FO and IIMP values were transformed to sum to 1.0 (or 100%) within each year of data by dividing each reported value by the total FO or IIMP for that rookery and year (i.e., FO_i divided by the sum of FO values for all species present that year in that rookery). The MFO and MIIMP values were used from this point onwards to calculate diet diversity and energy density. In some instances, ‘non-identified’ species were reported in the IIMP data (Gulf of California data only). These were deemed not useful for this analysis and were therefore excluded from the total used for MIIMP.

Calculating diet diversity

One measure of diet diversity used in this study was to express it simply as the total number of species recorded in the diet. To better illustrate large-scale changes in the diet between areas and eras, I also assigned all prey species in the diet dataset into one of 9 categories based on broad ecological characteristics similar to previous studies (Trites et al., 2007). These categories included: benthic species (n=60 prey species), crustaceans (n=1), gadids (n=5), lanternfish (n=7), octopus (n=2), rockfish (n=5), schooling fish (n=21), squid (n=15), and miscellaneous (n=17) (Table S3).

A quantitative measure of relative diet diversity was calculated for each rookery and year where data was available by using the Shannon Index of Diversity (Shannon & Weaver, 1949):

$$H = -\sum_{i=1}^S p_i * \ln(p_i),$$

where p_i is the proportion of the total number of species (S) in the sample, calculated as MFO or MIIMP. The higher the H value, the higher the species diversity.

The Simpson’s Diversity Index (Simpson, 1949) was also used to compare the diet diversity of prey species categories (described previously):

$$D = \frac{1}{\sum(p_i^2)},$$

where p_i = the proportion of the species in sample.

The denominator is therefore the sum of all the squares of each species' proportion, and D can vary from 1 to the total number of species present in the sample. This index can be cumbersome when dealing with large numbers of potential prey species. However, in such cases other studies have used this index by grouping prey species into a smaller number of species categories. In this application, the closer the diversity value (D) is to the total number of categories, the more evenly each category is represented in the diet.

Calculating diet energy density

Energy density of each prey species was recorded as kilojoules per gram of wet weight (kJ/gww). This information was obtained from published and unpublished databases including Gleiber et al. (2022). If an energy density value was not available at the species level, I calculated an average energy density for that species' family. In a few cases where values were not available at the level of the species' family, I used a value from a closely related family to approximate energy density.

The average diet energy density for each rookery and year was calculated by averaging the energy density of all prey species present in the diet that year (Table S3). However, this measure treats all species equally, regardless of their relative consumption level. To account for how often (FO) or how important (IIMP) each prey species was in the diet, I calculated a *weighted* average diet energy density.

This weighted average diet energy density incorporates the MFO and MIIMP data to reflect the relative consumption of each prey species in the diet and their respective energy densities. Specifically, the weighted average diet energy density per year and rookery is calculated by multiplying the MFO by the respective energy density of that prey species (in kJ/gww). Summing these values gave an average weighted diet energy density for each rookery and year, which was used in subsequent analyses.

Combining population and diet data

To investigate the relationship between population change and diet quality, the available diet data were matched with a rate of population change value calculated to correspond to the specific year or group of consecutive years with available diet data (see *Calculating population change*). Ideally,

continuous data for all years and rookeries would have been available, and matching data groupings would have been strategically chosen. However, the reality was that the diet data were patchy, resulting in limited matching diet and population data between years and rookeries.

Another concern about the data available was that consecutive data points in time were not truly independent. I therefore grouped sequential data points into specific ‘year-rookery groupings’ — and used them in all subsequent analyses (Table S1). The temporal gaps between these year-rookery groupings meant they could be treated as independent data points.

Most rookeries in the Channel Islands had diet data available over consecutive years, which I grouped according to the continuity of the data. For example, San Miguel had continuous diet data for each year from 2000–2006, followed by data for 2009, 2010, 2011. In this case, I averaged diet data to form two groupings: San Miguel 2000–2006, and San Miguel 2009–2011. Several rookeries in the Channel Islands had diet data already averaged over several years (Table S1). In these instances, those year-rookery groupings were kept and used when calculating corresponding population changes.

In the Gulf of California, the available diet data were not continuous. Most years with diet data were single isolated years that varied by rookery (e.g., Los Islotes 1990, 2000, 2015 and 2019; Rasito 1996 and 2016, etc.). In cases where two consecutive years of diet data were available, I averaged the diet data, and grouped them to form one rookery-year grouping (e.g., San Esteban 1995–1996). In cases where non-continuous years with diet data were close in time such that their population change calculations overlapped (see *Calculating population change*), I also combined them to form a single rookery-year grouping (e.g., Los Islotes 2015, 2019).

Calculating population change

The overall rate of population change for a rookery was determined by fitting a linear regression to the annual total population counts. The average annual population change (percent) was calculated as the slope divided by the intercept (the predicted first year population) of the resulting equation. I used a regression line (instead of simply first and last year counts) to obtain a more accurate population change value by incorporating all relevant years with population counts, and

thereby buffered the errors associated with using only the first and last counts to estimate population change.

To obtain an estimate of the population change immediately associated with single or grouped years of diet data, a similar regression analysis was performed incorporating only population counts from a set number of years before and after the years surrounding the diet data. Since the range of years incorporated into each diet data point varied (e.g., San Miguel 2000–2006: 7 years vs. Los Islotes 1990: 1 year), a set of rules were established to define the number of years before and after the diet data span that were included in the calculation of population change, depending on how many years of diet data were included for that grouping.

In instances where a rookery had diet data for 3 or more continuous years, I incorporated population data from 1 year before to 1 year after the diet data years into the population change calculation. For example, an average value for diet data calculated from a sequence of diet data between 2000–2006 was matched with changes in population numbers calculated from data from 1999–2007. If the number of continuous years with diet data was less than 3 (e.g., just 1990), then I incorporated data from two years before until 2 years after the interval (or single year) of diet data into the population change calculation (i.e., 5 years total for 1 year of diet data and 6 years total for 2 years of diet data). This calculation yielded a single rate of population change over the matching diet data interval.

In practice, most of the Channel Islands data had 3 or more continuous years of diet data where the ± 1 year rule was used. As previously mentioned, some of the Channel Islands diet data came as multiple-year averages, so population changes were calculated the same way over the predefined interval.

For the Gulf of California, many rookeries had either 1 or 2 years of data only, so ± 2 years was mostly used in these instances. In a few cases, the calculated population change was extreme, i.e., there was a 43% population growth at Rasito over 5 years (2014–2018), which is an unrealistic growth rate under normal breeding conditions. Therefore, in the few cases where population changes using the standard ± 1 or ± 2 -year rule were calculated to be greater than $\pm 20\%$, I

incorporated 4 years on either side of the data into the calculation to obtain a more realistic rate of population change.

Estimating population totals

There were instances when a population change value associated with a specific set of diet data could not be calculated in the standard way because population totals were unavailable for years needed for the calculation. Most of the rookeries in the Channel Islands reported pup counts for years with missing population totals. I was therefore able to use pup counts to estimate total population for years with missing data. This was done by plotting pup counts against all years with total population counts available for each Channel Island rookery, and using an overall linear regression generated from the available data. The regression equation predicting total counts from pup counts was then used to estimate total counts for the year with the missing data.

There were no additional years with pup count data for the Gulf of California rookeries, so this method for estimating total counts could not be applied. Instead, I estimated population numbers by extrapolating from a linear regression performed on all available population data for that rookery. I then used the regression equation to estimate population numbers for years lacking counts, and the rate of population change over the period of interest calculated from this mixed data set. However, this extrapolation from the complete count database was not used in some cases.

Population estimates made by regression extrapolations were used if there were actual population data for years before and after the period requiring a population estimate; that is to say, estimates of missing counts were only made between intervals with actual counts. For example, diet data were available for Los Islotes 2019, but population data were only available up to 2019. Following the normal rule, to calculate the population change in Los Islotes associated with 2019 diet data, population totals from two years before and after 2019 (2017 to 2021) would be needed for the calculation. Since there is currently no population data available after 2019, only data from 2017 to 2019 were used to calculate population change. Extrapolating past 2019 would not be justified, and in fact, appeared to significantly alter the population change value in some cases (e.g., changing the estimate from 1% to 7%). This exception was incorporated to avoid population estimates that could suggest inaccurate population trends in the most recent years.

Finally, in cases where there were rookeries with one year of diet data where the associated population data range (when incorporating the ± 2 years rule for population change) overlapped with the population data range for another year of diet data, *and* one of those diet data years did not have +2 years of data after (due to it being the latest population year with data), I grouped those years of diet data. For example, diet data from Granito from 2016 and 2018 were combined into one grouping, and the years used to calculate population change were 2014–2018, with 2018 being the latest year with population data.

Grouping data by Zones and eras

The relationship between population changes and diet quality was also tested at the level of Zone-era groupings which were created by combining rookery-year groupings. These ‘Zone-era groupings’ data were created by averaging the population change of each year-rookery within the grouping as well as the respective diet quality (energy density and diversity) values *by era* to avoid averaging values across very different time periods. This created the following Zone-era groupings: Zone 1 (Channel Islands data) was averaged between two eras: 1981–1995 and 2000–2011. Zones 2–10 (Gulf of California data) were averaged over 2 eras: 1990–2000 and 2015–2019 for FO data and over three eras for IIMP data: 1995–1996, 2002, and 2015–2019 (Table S2). (Not all rookeries and therefore Zones had available data in both diet indices, so FO or IIMP estimates could not be estimated for all Zones).

Effects of environmental change

I explored changes in diet quality before and after the reported environmental shift in 2014. Specifically, I compared the change in average diet energy density and diet diversity in the Gulf of California before and after 2014. Diet data were not available for the Channel Islands beyond 2011, but diet quality was compared between the Gulf of California and the Channel Islands prior to 2014. In addition to the Shannon Index and the total number of prey species, I used the Simpson’s Index to compare changes in the diversity of prey species categories.

Statistical analysis

All energy density and diet diversity values derived from FO and IIMP data were tested for outliers using Grubb's and Dixon's outlier tests in Rstudio (version 2022.02.3) using the package "outliers", at the Zone-era grouping level. There were no statistically significant outliers found in the data.

To test relationships between population changes and diet quality, I fit linear regression models to the data in Rstudio. I also used simple linear models to test for relationships between diet diversity and energy density (using "The R Stats Package", version 3.6.2, and code "lm([population change] ~ [diversity/energy density])". The p-value and adjusted R-squared values were obtained from the linear model results. Since rookeries (and therefore Zones) were of varying population sizes, I weighted the regressions using Zone population size as the weighting factor. The median population value was used for each grouping (the population count in the middle year of the grouping, or the average of the middle two years; Table S2). The R-squared and p-values were noted for each regression.

Two-sample t-tests assuming unequal variances were conducted using FO data to compare diet diversity and energy density within the Gulf of California before and after 2014, and when comparing the Gulf of California and the Channel Islands before 2014.

Results

Population trajectories

Various individual rookeries of California sea lions breeding in the Channel Islands and the Gulf of California either increased or decreased in total population to various degrees over the four-decade study period (1980–2020), but overall growth rates varied between the two study areas (Figure 2, Table 2). Most notably, all four Channel Island rookeries (Zone 1) averaged 2–6% increases per year since 1980 while most of the rookeries within the Gulf of California tended to decline over time, with significant reductions of 1–2% per year in Zones 3, 4, and 8. The only exception was at Los Islotes (the southernmost breeding colony of California sea lions — Zone 10), which increased at an average rate of 2% per year from 1980–2020 (Figure 2).

Diet quality in the Channel Islands vs. the Gulf of California

California sea lions breeding in the Channel Islands (Zone 1) consumed only 23 prey species compared to 88 species in the Gulf of California diets (Zones 2–10; Figures 3, 4 and 5). Schooling fish (5 species; 36% of diet) and squids (7 species; 21% of diet) dominated sea lion diets in the Channel Islands from 1981–2011 — while benthic species (41 species; 47% of diet) and schooling fish (19 species; 22% of diet) dominated diets in the Gulf of California from 1990 to 2019 (Figures 5 and 6).

The mean Shannon Index of diet diversity from 1981–2019 was lower in the Channel Islands than in the Gulf of California (1.86 vs. 2.04; Table 3). Mean diversity was also much more variable among the Gulf of California rookeries (range: 0.79–3.26) than among the Channel Islands (Zone 1, range: 1.34–2.35). The lowest diet diversity (0.79) occurred in Zone 4 in 1996 (where just one species — largehead hairtail, *Trichiurus lepturus* — was consumed). Interestingly, the highest diversity recorded among all locations (3.26) occurred later in this same Zone in 2018, when sea lions consumed 31 species (Table 3).

In general, the overall average diet energy density across all Zones was highly variable (Figure 7). The mean diet energy density in the Channel Islands was 5.5 kJ/gww, with a surprisingly small overall variation considering that two data points had anomalously high or low energy densities

(7.25 kJ/gww in San Miguel, 2005 and 3.79 kJ/gww in San Clemente, 1982). The predominant species that mostly contributed the most to the average energy density in the diet belonged to the schooling fish category (Figure 8), and included jack mackerel, Pacific mackerel, and northern anchovy. San Miguel had years when diets had above-average energy densities, with a higher-than-normal contribution from Pacific sardine (2002–2005) and herring (2005) — both of which are schooling fish (Figure S19).

Much higher numbers of prey species were consumed in the Gulf of California (Zones 2–10) than in the Channel Islands (Zone 1). There was also greater variability between Zones and years in the Gulf of California in terms of which species contributed the most to the average diet energy densities. The highest diet energy density in any year occurred in Zone 3 (Isla Lobos, 1995, 6.13 kJ/gww), which mainly reflected the high energy density of Pacific anchoveta (a schooling fish) and largehead hairtail (miscellaneous fish) (Table 3 and Figure S20). Diets of sea lions inhabiting Zone 4 had the lowest mean energy density (4.90 kJ/gww) and included a high proportion of ‘other’ species beyond the top 17 for most years (1996, 2016, 2018) (Figure S20). In contrast, diets in Zone 6 (San Esteban) had the highest mean energy density (5.90 kJ/gww; 1995 and 1996). For both Zones 6 and 7, the overall energy density of the diet largely reflected a high contribution from lanternfish, followed by largehead hairtail, Californian anchovy, and chub mackerel (Figure S21). Interestingly, lanternfish was largely replaced in the diet in both Zones with other species in 1996, with little effect on the overall diet energy density.

Across both study regions, no significant relationships were found between diet diversity and energy density using either FO data ($p = 0.58$) (Figure S9), or IIMP data: ($p = 0.17$) (Figure S10). This was true whether the data was analyzed by Zones (all years averaged) or by individual year-rookery groupings (Figure S11).

Diet quality and population changes

Diet diversity calculated from MFO and MIIMP data did not correlate significantly with rate of population change within Zones ($p = 0.43$ and 0.62 , respectively; Figure 9 (left panels), and Figures S15 and S16). Nor were there significant relationships between rates of population change and energy densities of diets (as calculated from FO and IIMP data; $p = 0.80$ and $p = 0.12$, respectively;

Figure 9 (right panels), and Figures S17, and S18). The same was true when comparing individual rookeries within the Channel Islands (Figure S12) — as well as when using changes in pup counts instead of changes in total population for the same Zones-year groupings, and when using average energy density (instead of weighted; Figures S13 and S14).

The highest mean diet energy density of all Zones (including the Channel Islands) occurred in Zone 6 (San Esteban rookery) where the population showed a potentially increasing trend. However, the only significantly increasing population in the Gulf of California (Zone 10, Los Islotes rookery) had a mean diet energy density that was comparable to the median diet energy density for all Zones (Table 3).

Effect of environmental changes on diet quality in the Gulf of California

Average sea surface temperatures increased after 2014 in the Gulf of California compared to prior years (Figure 10). Comparing diets before and after the anomalously high sea surface temperatures of 2014–2016 using FO data showed similar mean diet energy densities at the Channel Islands (5.42 ± 0.36 kJ/gww) and the Gulf of California (5.22 ± 0.53 kJ/gww) prior to 2014 (two-tailed $p = 0.38$) — but a significant decrease in mean diet energy density within the Gulf of California following the temperature anomaly (dropping from 5.22 ± 0.53 kJ/gww to 4.69 ± 0.35 kJ/gww; two-tailed $p = 0.045$; Figure 11, bottom panel). However, the statistically significant decrease in energy density using the FO data was not consistent across all rookeries when examined on a finer scale (Figure S23). Also, there was a decrease in mean energy density between the two time periods within the Gulf of California using IIMP data, this difference was not statistically significant (Figure S22).

Diet diversity calculated using the Shannon Index showed no significant difference in mean values between eras before (1.92 ± 0.49) and after 2014 (2.30 ± 0.57 ; two-tailed $p = 0.24$; Figure 11, top panel). However, diet diversity by prey species category using the Simpson's Index decreased after 2014 which indicated that prey categories were consumed less evenly after 2014 (Table 4). Changes in the proportions of prey categories in the diet show an increase in benthic species (from 36% to 56%) after 2014, and a decrease in the proportions of schooling fish and squid (from 27% to 16%; and from 7% to 1% respectively; Figure 6). This shift from high energy schooling fish to

lower energy density benthic species decreased the overall average energy density of the diet in the Gulf of California.

The most notable change in the diet in the Gulf of California was an increase in the number of prey species consumed (from 51 to 65 species), and an overall increase in the average number of prey species consumed per rookery after 2014 (Figure S26). Within a rookery, sea lions consumed 9 prey species on average per rookery (range 5–15 species) before 2014 (data unavailable for Zones 8 and 9) — and 16 species on average per rookery (range 7–26 species) after 2014. Equally notable was that ~50% of the species consumed throughout the Gulf of California after 2014 were not present in the diet prior to this time (Figure S27). In other words, the sea lions did not simply add 14 more species to their diet, but rather made a fundamental shift in the species they consumed. Despite the overall dietary shifts in prey quality observed after 2014, there were no apparent differences in the rates of population changes between these two eras (two tailed $p = 0.98$).

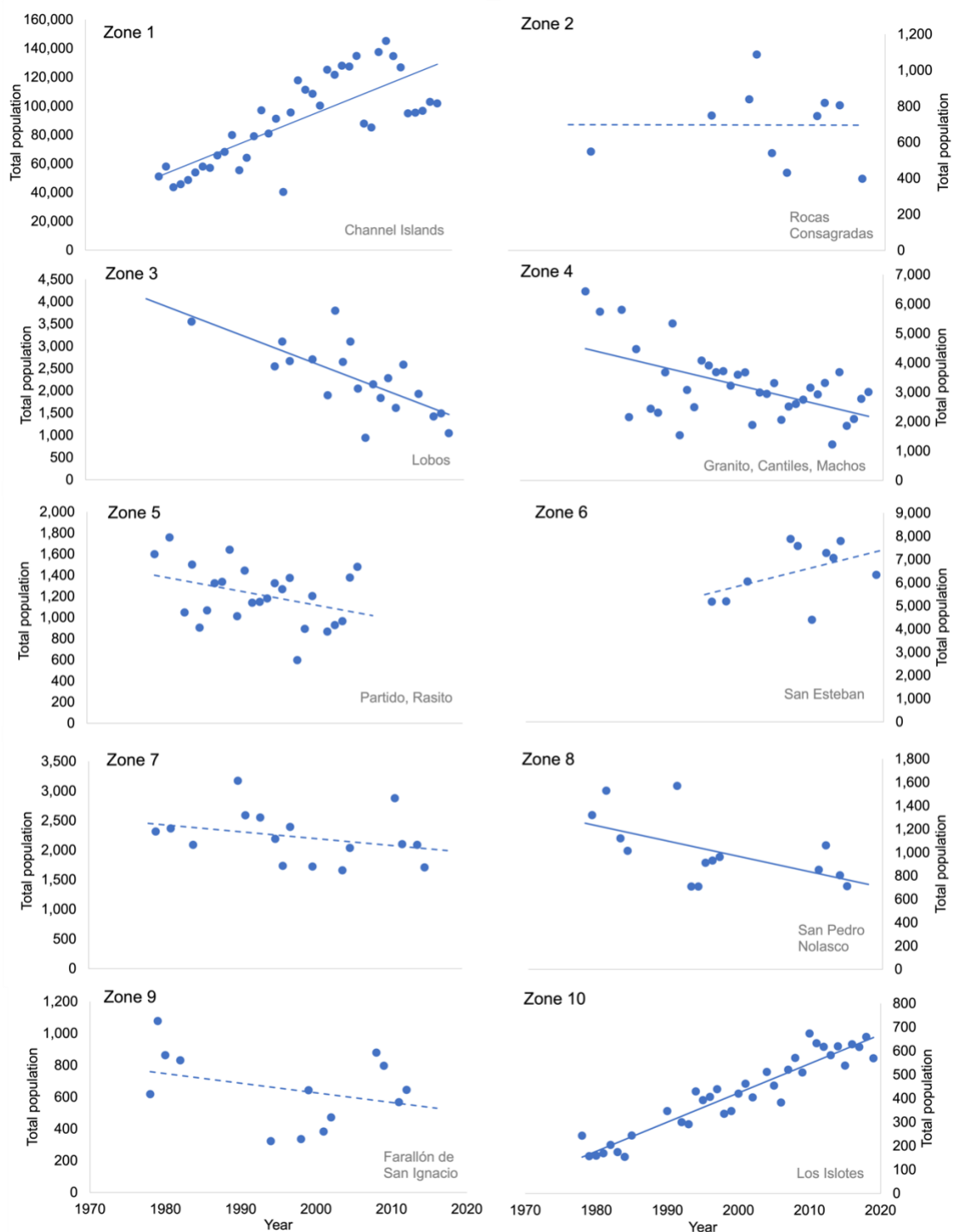


Figure 2. California sea lion population trends of Zones (1980–2020). Data shows total sea lion counts for each Zone with data from 1980–2020. Zones with multiple rookeries show the sum of the population totals in those rookeries. Solid lines represent statistically significant regression decreases and dotted lines represent regressions that were not statistically significant.

Table 2. List of Zones 1–10 and the respective rookeries, the population trend and population size of each Zone.

Zone	Rookery	Population trend	Population size
1	Channel Islands: (a) San Miguel, (b) San Nicolas, (c) Santa Barbara, (d) San Clemente	Increasing	111,713
2	(e) Rocas Consagradas	Inconclusive	397
3	(g) Isla Lobos	Decreasing	1,044
4	(h) Granito, (i) Cantiles, (j) Machos	Decreasing	3,004
5	(k) Partido, (l) Rasito	Decreasing	1,478
6	(m) San Esteban	Increasing	5,093
7	(n) San Pedro Mártir	Decreasing	1,706
8	(o) San Pedro Nolasco	Decreasing	711
9	(p) Farallón de San Ignacio	Decreasing	644
10	(q) Los Islotes	Increasing	751
<i>Only population trends in bold were statistically significant. Population size is based on latest available counts which vary from 2015–2021. Note: San Jorge rookery (f) is not included in this study due to lack of available diet data, but its population in 2015 was of 3,814 individuals.</i>			

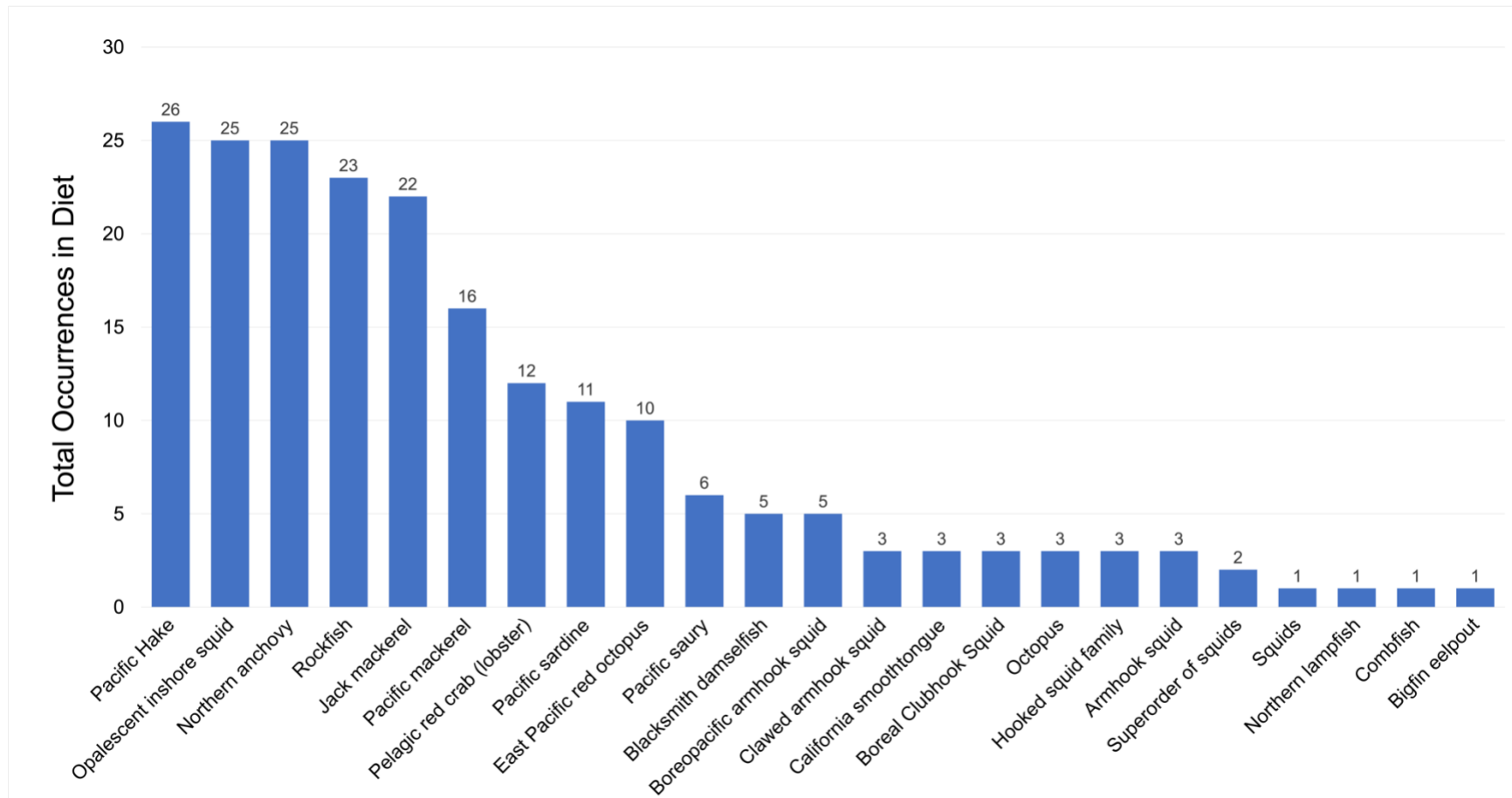


Figure 3. Prevalence of prey items for California sea lions in the Channel Islands (Zone 1). Bars represent the total number of occurrences (out of 41 possible occurrences) of each prey species from frequency of occurrence data from 1980–2011; that is, the total number of years where each prey species was present in the diet. All 23 species with $FO \geq 5\%$ are listed. The species' common name is listed when available, although some were originally reported only at the family or genus level. The top 5 species with over 20 occurrences were: Pacific hake, Opalescent inshore squid, Northern anchovy, rockfish species, and Jack mackerel.

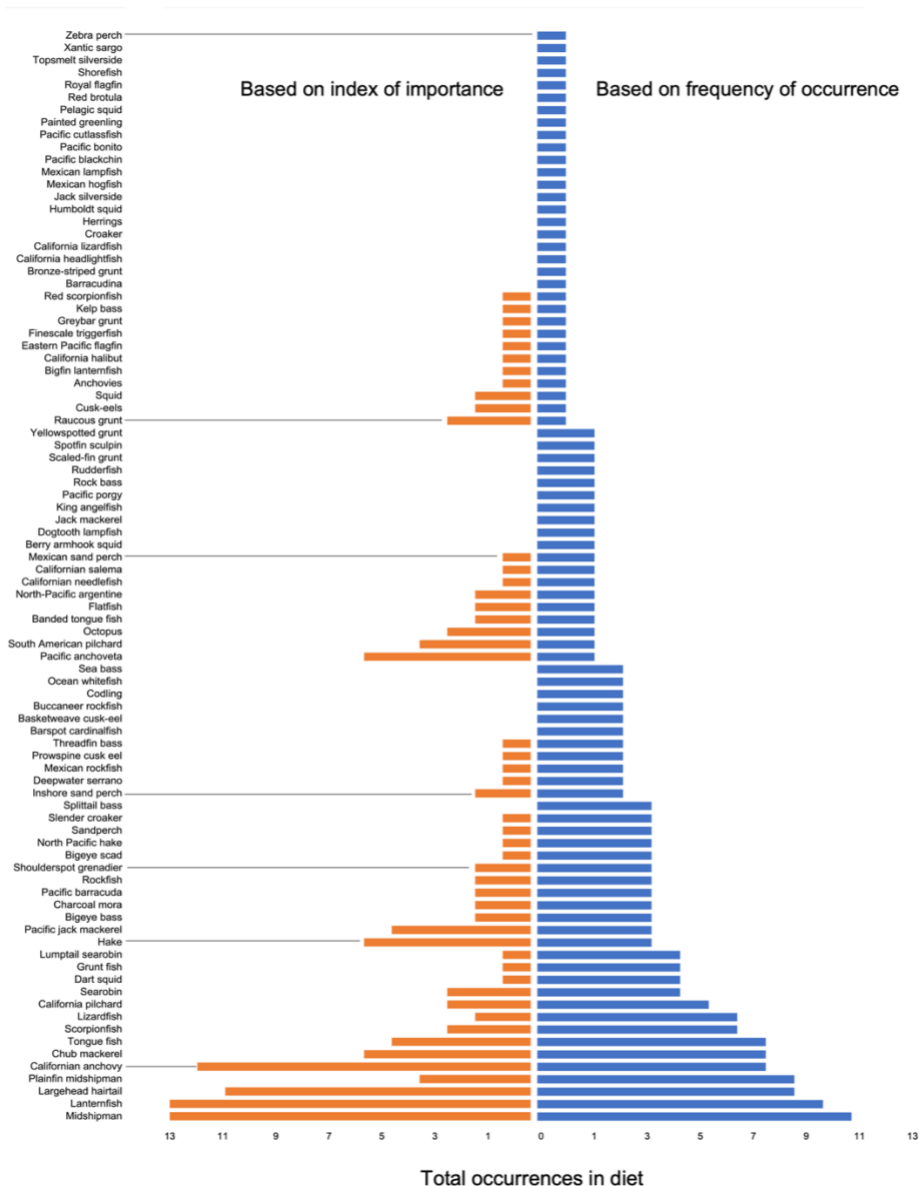
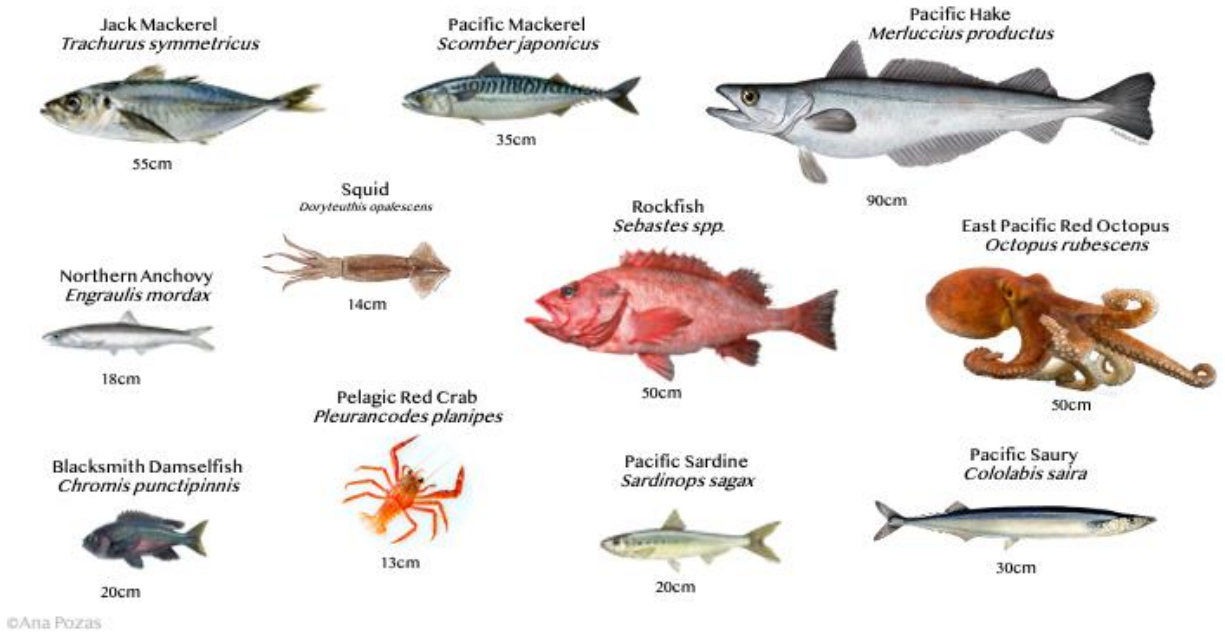


Figure 4. Prevalence of prey items of California sea lions in the Gulf of California. Bars represent total prey species occurrences in the diet (out of 21 possible occurrences using FO data and 30 using IIMP data) that is, the total number of years where each prey species was present in the diet. Data is from all Gulf of California rookeries (Zones 2–10) with available data from 1980–2019 based upon either frequency of occurrence (blue bars) or index of importance (orange bars). The common name of all 88 species (or species groups) is listed when available, although some were originally reported only at the family or genus level. The top four species with over 8 appearances were: midshipman, largehead hairtail, lanternfish, and plainfin midshipman, with Californian anchovy next with 8 appearances along with Chub mackerel and tonguefish.

Channel Islands – top prey species



Gulf of California – top prey species

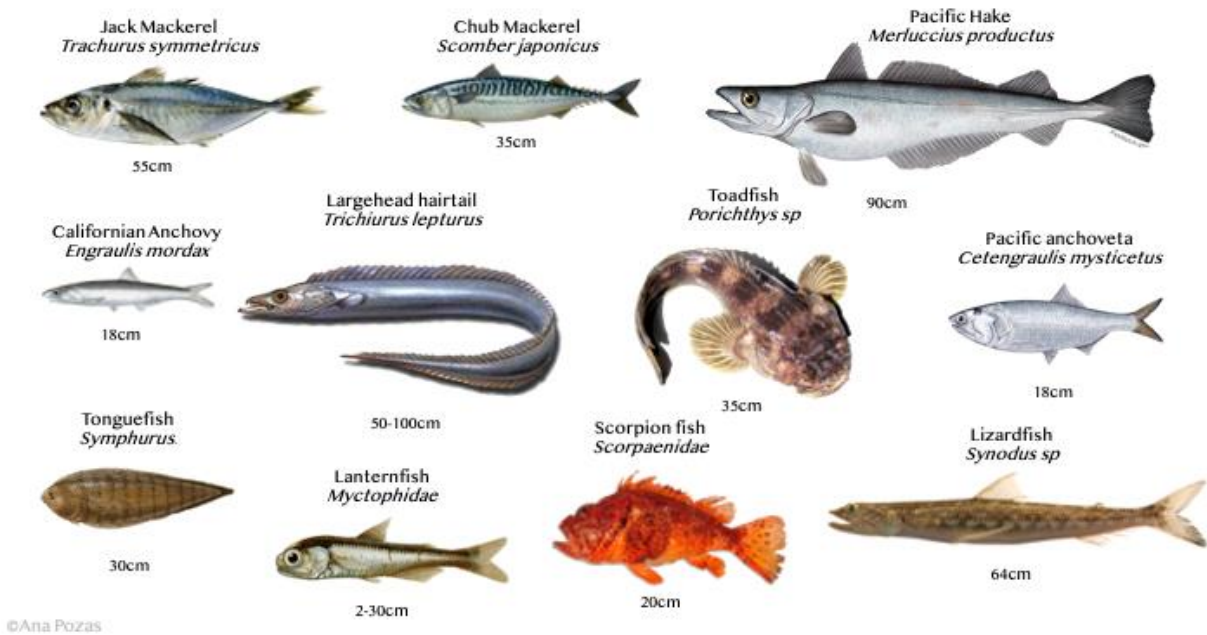


Figure 5. Visual representation of the top prey species in the Channel Islands (top panel) and the Gulf of California (bottom panel). Top species from the Channel Islands are from frequency of occurrence data, top species in Gulf of California are from IIMP data. Top name represents the common name and bottom name the scientific name. Average size of species is indicated below each illustration. Individual species illustrations were obtained from Google Images.

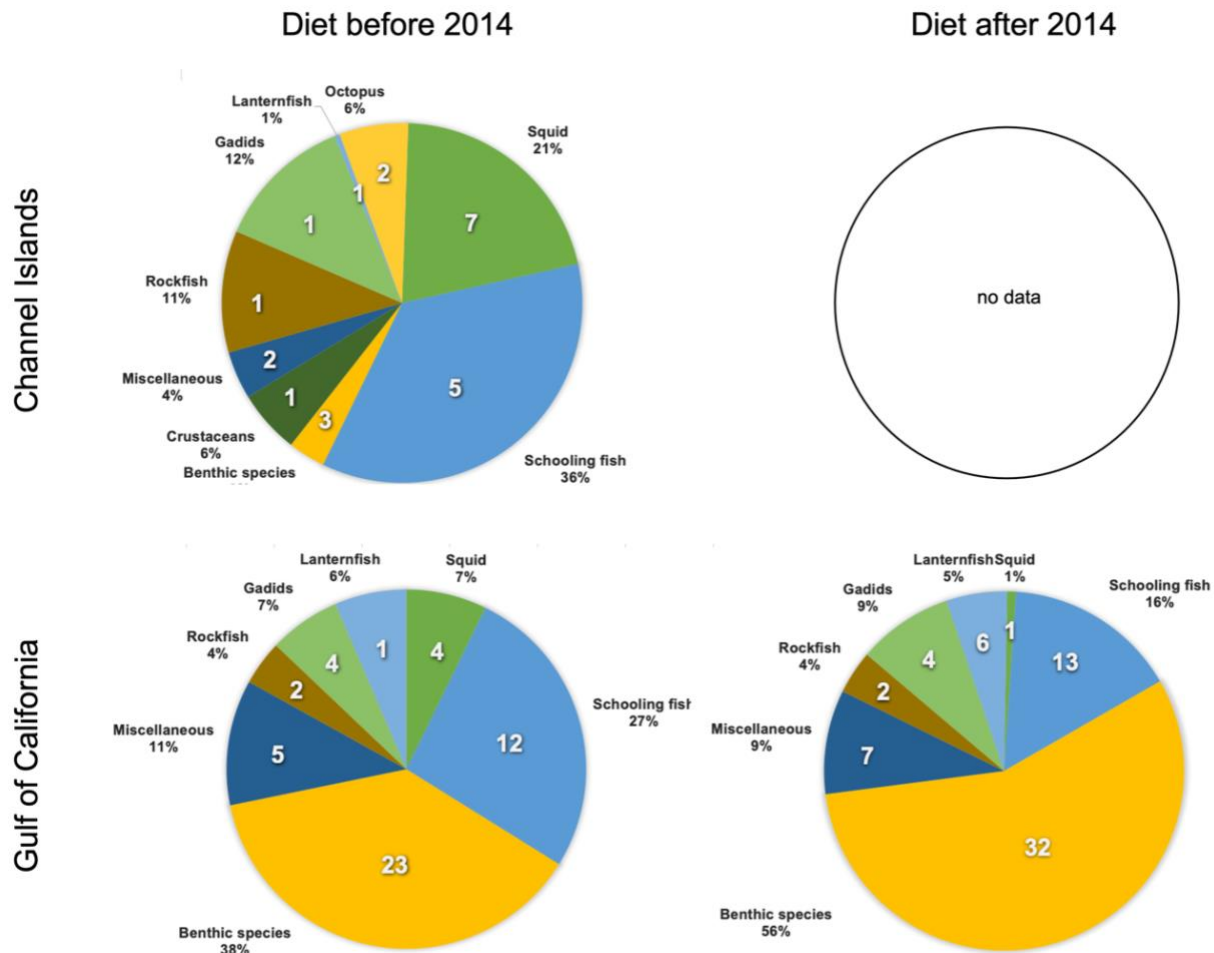


Figure 6. Diet composition by prey species categories before and after 2014. Pie chart slices represent the proportion of each species category. White numbers represent the number of species in the diet from each category. Diet composition data from the Channel Islands is from 1980–2011 (no diet data available after 2014). Diet composition data for the Gulf of California is from 1990–2000 for before 2014 and from 2015–2019 for after 2014.

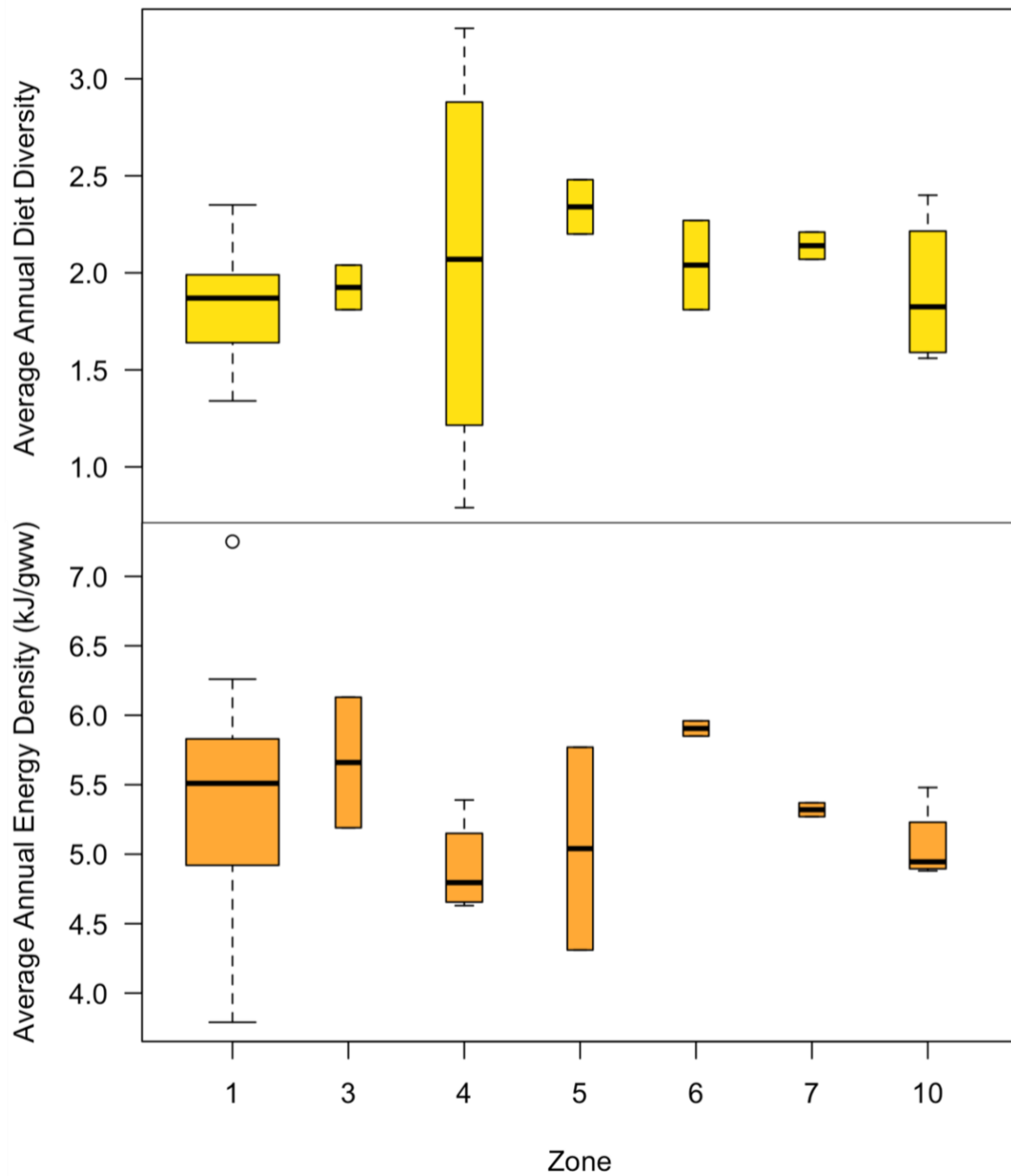


Figure 7. Average annual diet diversity and energy density by Zones. Diet diversity (top panel) and energy density (bottom panel) values were based on all available Zone and year groupings from FO (1981–2019; Zones 2, 8 & 9 are omitted due to lack of available FO data). Diet diversity values were calculated using the Shannon Index. Box limits represent the first, mean, and third quantile values, box whiskers represent the range of values. Bar widths are proportional to the number of data points in each Zone. The energy density value of 7.25 in Zone 1 (San Miguel, 2005) was considered an outlier according to Grubb’s test.

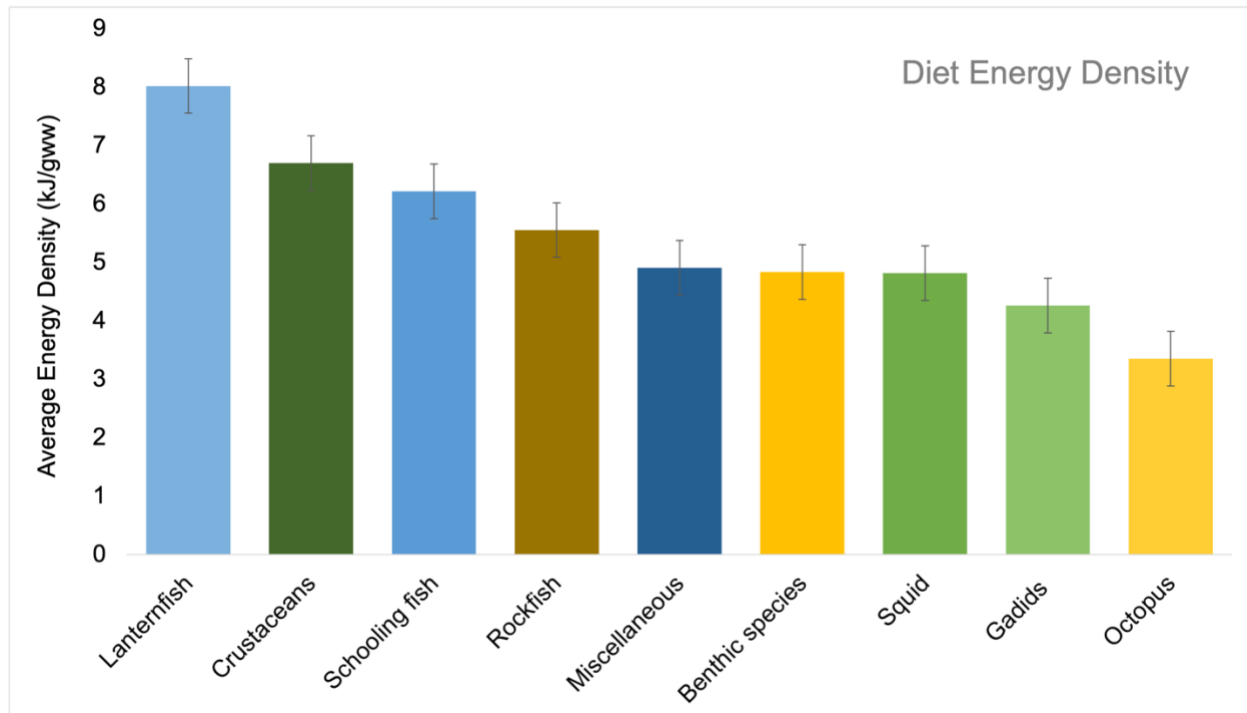


Figure 8. Average energy density of prey species categories. Colours correspond to species categories illustrated in Figure 6. Bars represent average energy densities (kJ/gww; mean value \pm standard error) from all species present in the diet data from each category ordered from highest (lanternfish) to lowest (octopus) values.

Table 3. Diet quality and population trajectory of each of the Gulf of California Zones and the Channel Islands. Mean (n and standard deviation) and range of annual weighted energy density (kJ/gww) and diet diversity (Shannon Index) for diets (incorporating individual prey species). Population trajectories in **bold** represent statistical significance.

Zone: rookery	Population trajectory	Energy density (kJ/gww)		Diet diversity		n
		Mean \pm SD	Range	Mean \pm SD	Range	
1: San Miguel	Increasing	5.43 \pm 0.94	4.14–7.25	1.79 \pm 0.94	1.34–2.35	10
1: San Nicolas	Increasing	5.63 \pm 0.22	5.26–5.94	1.75 \pm 0.23	1.46–1.96	8
1: San Clemente	Increasing	5.16 \pm 0.84	3.79–6.05	1.94 \pm 0.84	1.67–2.21	7
1: Santa Barbara	Increasing	5.48	N/A	1.87	N/A	1
1: Channel Islands average	Increasing	5.43 \pm0.2	3.79–7.27	1.82	1.34–2.35	4
3: Isla Lobos	Decreasing	5.66 \pm 0.66	5.19–6.13	1.93 \pm 0.66	1.81–2.04	2
4: Machos, Cantiles, Granito	Decreasing	4.90 \pm 0.35	4.63–5.39	2.05 \pm 0.35	0.79–3.26	4
5: Rasito	Decreasing	5.04 \pm 2.45	4.31–5.77	2.34 \pm 1.03	2.20–2.48	2
6: San Esteban	Increasing	5.90 \pm 2.83	5.85–5.96	2.04 \pm 0.08	1.81–2.27	2
7: San Pedro Mártir	Decreasing	5.32 \pm 2.50	5.27–5.37	2.14 \pm 0.07	2.07–2.21	2
10: Los Islotes	Increasing	5.06 \pm 2.17	4.88–5.48	1.90 \pm 0.28	1.56–2.40	4
2–10: Gulf of California average	Decreasing	5.32 \pm0.39	4.31–6.13	2.04	0.79–3.26	6

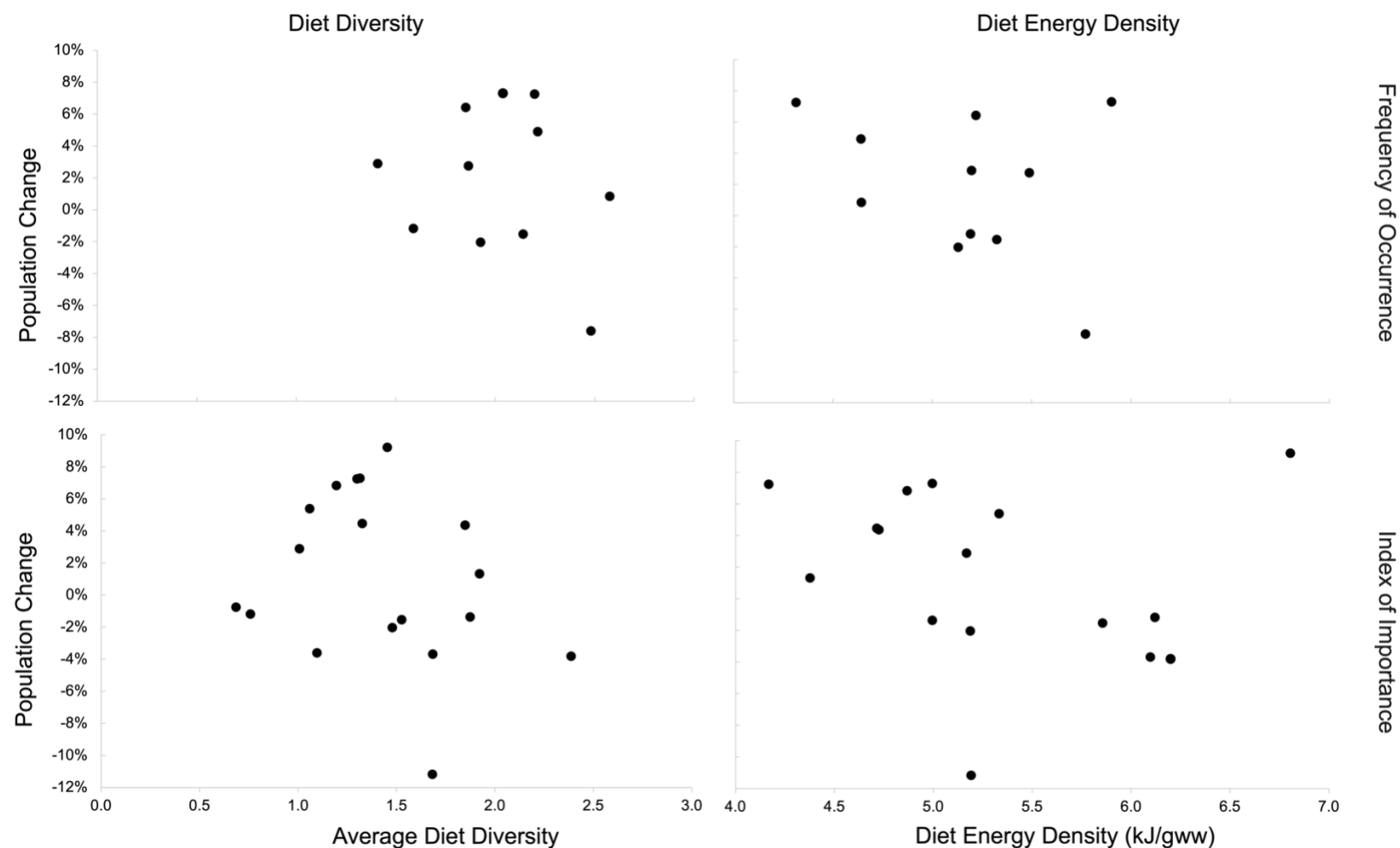


Figure 9. Population changes and diet quality from frequency of occurrence and index of importance data. Data presented represents values from Zone-era groupings. Diet diversity values were calculated using the Shannon Index from frequency of occurrence data (top-left panel) and index of importance data (bottom-left panel). Panels on the right include diet energy density values calculated using frequency of occurrence (top) and index of importance data (bottom). Regression analysis of data weighted by rookery population size indicated no statistical relationships.

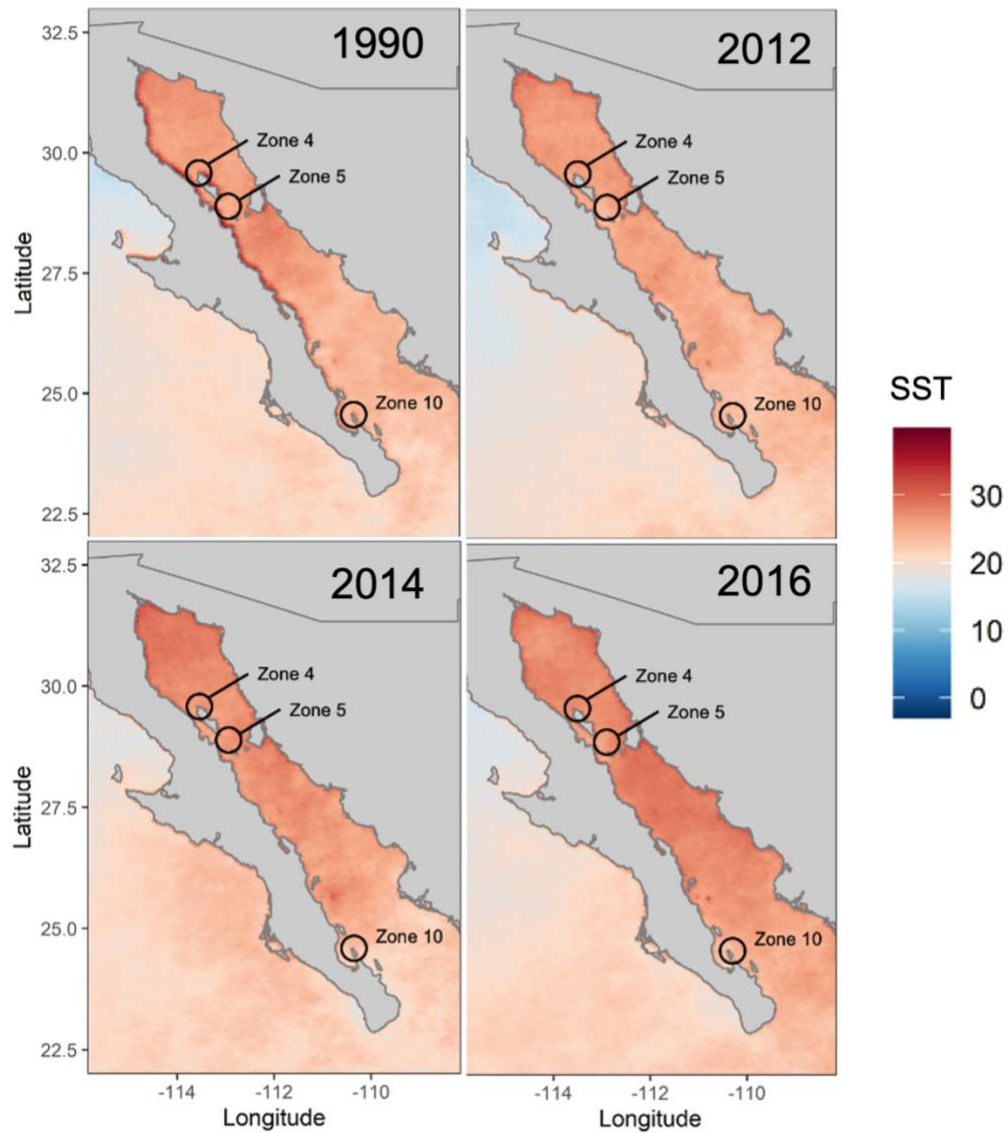


Figure 10. Average sea surface temperatures (SST, °C) from June–August in the Gulf of California. SST are an average of June, July, and August readings. Temperature data from 1990 and 2012 are prior to years with SST anomalies, whereas 2014 and especially 2016 show years with warmer average SST. The circles indicate the location of Zones 4, 5 and 10 from which diet data was analyzed before and after 2014. Colour legend shows SST (°C).

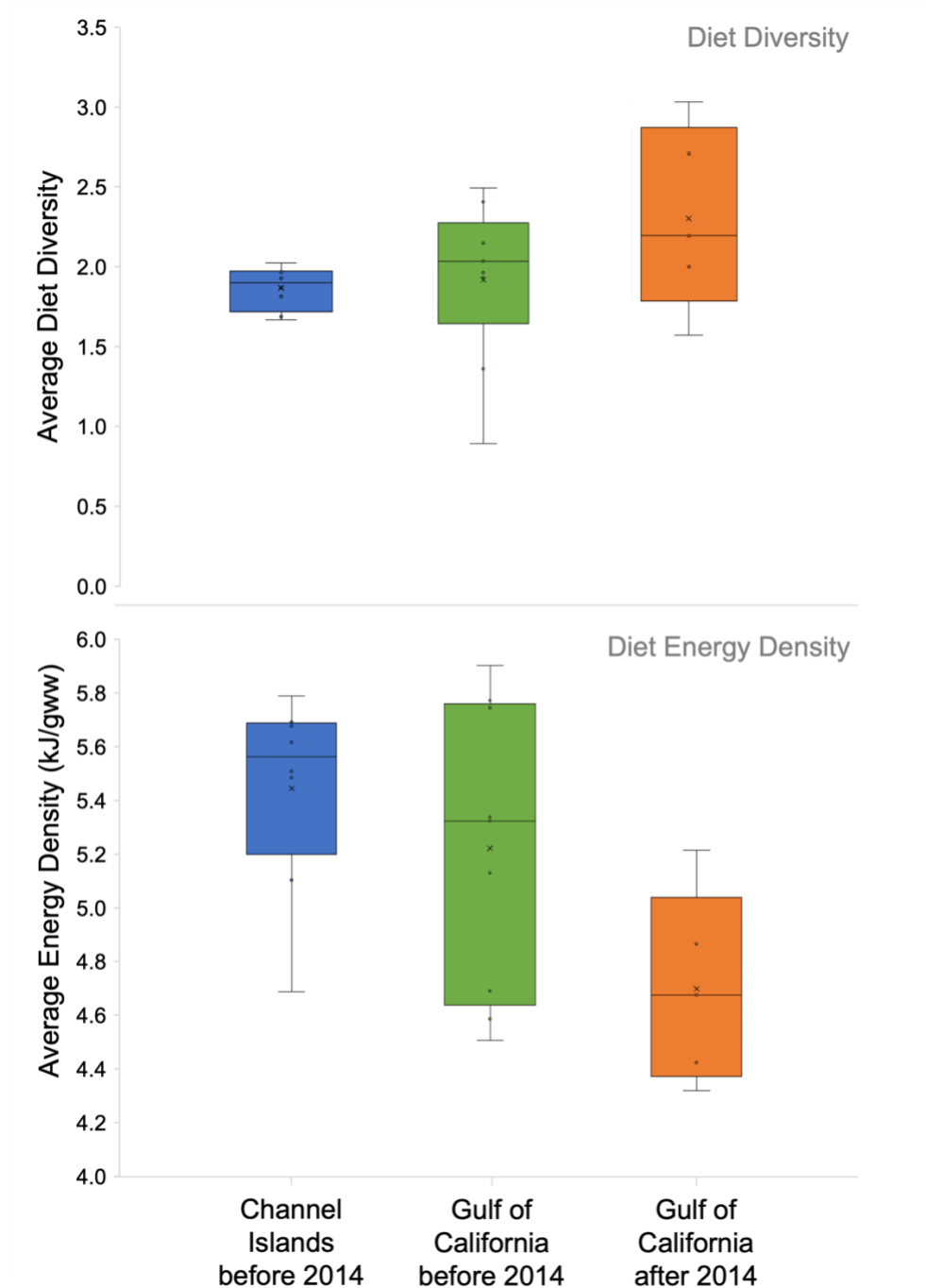


Figure 11. Average diet diversity from the Shannon Index (top panel) and average energy density (bottom panel) from frequency of occurrence data before and after 2014. Box limits represent averaged data (first, median and third quartiles \pm standard error, 'x' represents mean value) from all Channel Island and Gulf of California groupings before and after 2014 (no data for Channel Islands after 2014). Diet data is based on rookery-year groupings. No significant differences were found between mean diversity values between geographic areas before 2014, nor in the Gulf of California between eras. There was a statistically significant decrease in the average energy density in the Gulf of California after 2014.

Table 4. Diet quality by geographic area and era. Total number of prey species, diet diversity values using the Simpson's Index on the 9 prey species categories, and the Shannon Index and mean weighted diet energy density incorporating individual prey species.

Geographic area & era	Number of prey species in diet	Simpson's diversity Index (by category)	Shannon's diversity Index (mean \pmSD)	Energy density (kJ/gww; mean \pmSD)
Channel Islands before 2014	23	5.57	1.86 \pm 0.12	5.42 \pm 0.36
Gulf of California before 2014	51	3.54	1.92 \pm 0.49	5.22 \pm 0.53
Gulf of California after 2014	65	3.25	2.30 \pm 0.57	4.69 \pm 0.35

Discussion

Previous dietary studies on California sea lions in the Gulf of California have tended to focus on differences in the main prey species consumed at different rookeries, or have investigated feeding behaviours between rookeries (García-Rodríguez & Aurióles-Gamboa, 2004; Porras-Peters et al., 2008). Only one study has indirectly explored the relationship between population and diet, but found no significant relationships between these variables (Pelayo-González et al., 2021). My study not only explored the relationship between diet quality and populations within the Gulf of California, but it is the first to compare diet quality between these populations, and those increasing in the Channel Islands.

I found substantial differences in the types of prey species available to sea lions in Mexico and the U.S. but did not find any significant relationships between measures of diet quality (diet energy density or diet diversity) and rates of population changes. I also found that sea lions in central regions of the Gulf of California consumed prey with lower energy densities following the significant increase in sea surface temperatures that occurred in 2014. These findings underscore the importance of considering the environmental heterogeneity of different regions, which can heavily influence population dynamics on local levels. They also highlight the importance of better understanding the fine-scale ecosystem dynamics of the various populations of California sea lions throughout the Gulf of California. Overall, my findings suggest that the population drivers in the Gulf of California are likely more complex and differ at local scales compared to the more uniform and stable population trends in the Channel Islands.

The role of diet diversity

An ideal diet for California sea lions should allow them to meet their nutritional needs to grow and reproduce by feeding on sufficiently available prey species. However, this seems to vary depending on the characteristics of the ecosystem. Generally, in less biodiverse ecosystems, foraging on fewer, energy-rich prey species might suffice (low diversity, high energy density) — whereas in more diverse ecosystems, foraging on a greater combination of species of different sizes and energy densities might provide an adequate mix (high diversity, lower energy density). Exploring the changes in diversity and energy density within populations can allow changes in diet

quality to be assessed. In many species of marine mammals, increases in diet diversity are often accompanied by declines in energy density, suggesting higher diversity yields a lower diet quality (Jory et al., 2021; Lowry et al., 1991; Páez-Rosas et al., 2020).

Using the total number of prey species as a measure of diet diversity revealed a striking difference in diets between regions. The sea lions at Channel Islands consistently ate 23 primary prey species during summer (1981–2011, Figures 3 and S19) while sea lions in the Gulf of California targeted 88 primary prey species (1990–2019; Figure 4) that varied between Zones (Figures S20 and S21). These differences may mean that the ideal prey species were not consistently available for sea lions in the Gulf, or it may alternatively illustrate that there were more prey options available to facilitate diet adaptability (but only for some rookeries given that in the Gulf of California the number of species consumed per rookery ranged from 5–26 species between Zones and over time; Figure S28). Overall, the Shannon Index and the total number of species illustrate that the diet has been consistent over time in the Channel Islands compared to the variable diet composition between the different rookeries in the Gulf of California (Figure 7, Table 3).

The role of diet energy density

Energy density is an important characteristic of diets to consider beyond simply identifying prey species or available biomass. While the diet of a California sea lion population may be composed of prey available in sufficient amounts, it may not necessarily result in the energy-rich diet required for individuals to grow and reproduce. Each prey species differs in macronutrient composition and therefore in energy density (kJ/gww), meaning that some prey species are more energy-rich. Such a diet can be considered to be of “higher quality” as the higher energy density is more likely to meet the nutritional requirements of individuals, allowing populations to grow. Measuring diet energy density can provide important insight into the nutritional status of a population and the drivers of population change.

Contrary to expectations, I found that regions and periods when the diet had the highest energy density were not necessarily associated with years of greatest population growth within Zones. Alternate analyses — at a finer rookery-year scale or using changes in pup numbers as a more immediate indicator of changes in population demographics — also failed to reveal relationships.

Instead, my results showed that diets with the highest energy densities were associated with both increasing and decreasing population trajectories, which may explain the lack of an overall simple relationship between diets and populations.

While there is strong evidence from other studies to support the hypothesized link between diet energy density and population growth, it is possible that the changes in diet quality I observed were not great enough to be the primary population drivers in these regions, or that the effects were only apparent in cases with extremely low-quality diets. Other possible reasons for a lack of overall relationships between population changes and diet quality include the lack of continuous data over time, possibly masking long-term diet-population associations in some rookeries, or more subtle changes in diet that were associated with shorter-scale population changes, especially if these changes occurred after a ‘lag’ of a couple of years as has been documented for other pinniped species (Gibbens & Arnould, 2009).

Another factor complicating the relationship between population and diet quality could be that the two regions of comparison (the Channel Islands and the Gulf of California) are fundamentally different oceanographic systems with different population and diet dynamics. In the Channel Islands, most of the diet energy density comes from schooling fish (Figure S19), in contrast to the considerable variability in space and time in which prey species contribute the most to the total diet energy density in the Gulf of California (Figures S20 and S21). Sea lions in the Gulf of California rely on a large diversity of benthic prey species (~50% of their diets), and lesser amounts of schooling fish (~20%). Hence, while schooling fish are an important part of the diet similar to the Channel Islands, they are not the main contributor to diets in the Gulf of California. Instead, sea lions in the Gulf of California seem to rely on a plethora of benthic species (41 different benthic species in total) for their main source of energy from food, even though this prey category has a lower energy density than schooling fish (Figure 8).

This could explain the consistency in the mean energy density of diets consumed (and population dynamics) over time by sea lions breeding in the Channel Islands — when compared to the high variability in mean energy density of diets consumed by sea lions in the Gulf of California.

The heterogeneity of diet energy density across Zones and eras within the Gulf of California makes the relationship between diet quality and population trajectories in these Zones less straightforward to understand compared to the Channel Islands. Such heterogeneity raises questions about the specific trade-offs that result in unique diets and possibly foraging strategies among sea lions breeding on the different Gulf of California rookeries. In the Galápagos Islands, individual foraging strategies of Galápagos sea lions (*Zalophus wolfebaeki*) influence the coping abilities of their population (Schwarz et al., 2022) — and there are indications that some foraging strategies may be more advantageous than others under environmental change (Schwarz et al., 2022). In contrast to pelagic foragers, benthic foraging Galápagos sea lions appear to be less affected by increased water temperatures, despite consuming prey that was lower in energy density. Such environmentally dependent fitness trade-offs could also be at play in the Gulf of California populations, although further research on individual foraging strategies would be required.

The effects of environmental changes on diet quality

In 2014, a large-scale phenomenon of increased sea surface temperatures known as “The Blob” was documented in Alaska and traveled south along the Eastern Pacific in subsequent years. In 2015–2016, the Blob coincided with a strong El Niño event, further intensifying the effect of increased water temperatures (Tseng et al., 2017). In the Channel Islands, El Niño events are known to cause population declines, and are associated with a decrease in consumption of energy-rich schooling fish (Melin et al., 2010). Therefore, increased temperatures in the Gulf of California may also jeopardize a sea lion’s ability to obtain energy rich prey, affecting both the diet diversity and energy density.

Overall, although there was an increase after 2014 in the mean and range of diet diversity (expressed using the Shannon Index) within the Gulf, this change was not significant (Figure 11, top panel). However, an increase in the total number of species present in the diet did indicate an increase in diet diversity (from 51 to 65 species: Figure 6). In addition, there was a change in the proportions of species categories (Figure 6, Table 4), and species identity (i.e., ~50% of the species present after 2014 were not previously consumed and consisted mostly of benthic and lanternfish species; Figures 6 and S27). This change in diversity was accompanied by a significant decrease in the average diet energy density (Figure 11, bottom panel) driven by central rookeries (Figure

S23) that seemed to be mainly due to a decrease in the proportion of energy-rich schooling fish after 2014 (Figure 6). There was also an increase after 2014 in the overall number of lanternfish species in the diet (from 1 to 6 species; Figures 6 and S29), which were the highest energy density prey category, but without a large change in their proportion (5% vs. 6%). This could suggest sea lions are attempting to continue to meet their total energy requirements by increasing the diversity of energy-rich lanternfish species in their diet.

However, this pattern was not consistent across all rookeries in the Gulf of California. The largest decrease in energy density after 2014 was seen in Rasito (Zone 5), which had a lack of energy-rich lanternfish and Jack mackerel in 2016 compared to 1996 (Figure S20). Also, in Zone 10, lanternfish made up the largest energetic contributor to the diet in 2019, which likely resulted in the overall *increase* in diet energy density after 2014 (Figure S23). The variation in the average energy density in the diet across Zones could be due to a different availability of prey species in the different regions in the Gulf. This could necessitate the need for California sea lions in some regions to adopt different diets resulting in changes in the total calories to meet their energetic demands. For example, the unusual proportion of ‘other’ species making up most of the energy density in the diet in Los Islotes in 2015 may reflect a loss of ideal primary prey due to increased water temperatures (Figure S21). In this case, the adaptation strategy of sea lions at Los Islotes might have resulted in them consuming a higher number of prey species (Figure S28) to obtain their required amount of energy from prey, similar to other years (~5kJ/gww).

Previous studies have demonstrated how acute environmental changes and subsequent prey availability shifts can affect marine mammal population growth. For example, ringed seals (*Phoca hispida*) in western Hudson Bay switched to a more diverse diet that had a lower energy density due to decreases in the availability of their main prey (sand lance) triggered by changes in the seasonal breaking up of sea ice (Chambellant et al., 2013). As a result, body condition of individual seals was greatly reduced, and population declines ensued.

In the Channel Islands, models predict that every 1°C increase in surface temperature could decrease the population growth rate of California sea lions in the U.S. by 7% (Laake et al., 2018). A similar phenomenon appears to be occurring in the northern and central regions of the Gulf of California where California sea lion pup birth rates declined as sea surface temperature anomalies

exceeded 1°C (Pelayo-González et al., 2021). Furthermore, a positive relationship was found between sardine catches and the number of births in the central Gulf of California, suggesting a possible relationship between prey availability and reproductive success in this area. In contrast, population growth was not affected by increased sea surface temperatures in the southern Gulf (Molina-Chávez, 2022). However, pup abundance and body condition did decrease during 2014 and 2015, and adult females at Los Islotes were away from the rookery for longer periods than normal (Cruz-Vallejo, 2020). It appears that lactating females had to forage further away from the rookery, costing them more time and energy. Thus, the warmer sea surface temperatures affected the diet and foraging behaviour of California sea lions in the south (Zone 10), which may have affected pups during the lactation period.

Environmental heterogeneity and its implications for species management

Differences in diet and population trends detailed in my study suggest that sea lions at the different breeding colonies within the Gulf of California cannot be viewed nor managed as a homogeneous group. The Gulf of California is known to have considerable environmental heterogeneity (Álvarez-Borrego, 2010; Brusca et al., 2005; Lavin & Marinone, 2003; Thomson & Gilligan, 1983), which may influence both the quality of sea lion diets and, ultimately, predator-prey dynamics. It has been suggested, for example, that the greater diversity of prey species present in southern Gulf compared to the northern and central regions buffer the southern rookeries (e.g., Zone 10) against detrimental environmental changes (Álvarez-Borrego, 2010; Durán-Campos et al., 2022). Having access to a greater diversity of prey species would allow sea lions to compensate for prey that are no longer available.

Prey availability and abundance in the Gulf of California varies by Zone and is not as consistent or as predictable as in the California Current System. Such variability may mask the ability to identify simple relationships between diet and population growth, such as those shown in other Eastern Pacific ecosystems, such as the Channel Islands or Alaska (Lowry, Nehasil, et al., 2017; Rosen & Trites, 2000; Trites et al., 2007). Such regional variability may also underly differences noted by others in terms of genetic differences between California sea lions, their foraging areas, and the oceanographic conditions they experience (Adame et al., 2020; Pelayo-González et al., 2021; Schramm et al., 2009).

The high variation in the diets, population trajectories, rookery sizes, and oceanographic dynamics within the Gulf of California suggests that each rookery population faces different sets of challenges that impact their reproduction and survival rates in different ways. Management strategies for these populations need to account for the contextual and environmental conditions that occur at local scales. Conservation strategies should also prioritize monitoring and data collection of less accessible rookeries because they cannot be assumed to be similar to the better studied rookeries. Current management and surveillance programs in the central regions do not seem sufficient to monitor and assess how sea lion numbers are affected not only by changes in prey species, but also by other factors such as entanglements in fishing gear, shootings, contaminants, etc. (Hernández-Camacho et al., 2020). Such anthropogenic factors may also contribute to the lack of a direct relationship between diet and population trends in the northern and central Gulf (Pelayo-González et al., 2021). Understanding the unique challenges that each population faces is essential to effectively ensure their conservation.

Conclusions

Diet quality can be affected by sea surface temperatures and oceanographic conditions and can vary between Zones and eras as seen at sea lion rookeries along the Gulf of California. Differences in diet quality have undoubtedly played a role in the population trajectories of California sea lions. However, it was not possible to establish simple linkages between the two — possibly due to the confounding influence of other factors such as environmental heterogeneity. Further research is needed to better understand the differences at play between the different California sea lion rookeries within the Gulf of California so that it can guide and support efficient and relevant management practices for the species.

The Mexican government deems California sea lion populations in the Gulf of California in need of special protection — and recognizes the need to recover and conserve their populations (NOM-059-SEMARNAT-2010). However, efficient management of the populations within the Gulf of California is in part hampered by limited understanding of the population dynamics and the factors that drive population change at each rookery. Addressing this shortcoming will require robust data on sea lion diets, foraging strategies, and localized oceanographic changes.

Chapter 3: Overall Conclusions

In this study, I investigated the role of diet quality in influencing divergent population trends of California sea lions in the Channel Islands and the Gulf of California. My initial hypothesis predicted that there would be a relationship between diet quality and population changes, expecting to see a lower diet quality — specifically a diet with a lower energy density and a higher diversity associated with declining populations. Contrary to expectations, I found there were no direct relationships between these two factors at this geographically broad, long-term scale. However, I did identify the predicted decrease in diet energy density within regions of the Gulf of California in association with short-term environmental changes. Overall, my results highlighted the variation in diet quality between regions and over time — and emphasized the relevance of considering environmental heterogeneity to better understand the complex population dynamics throughout the Gulf of California.

Strengths and limitations of this study

One of the main research challenges I faced was the lack of continuous diet and population data available over the study period from 1980 to 2020, especially for multiple rookeries in the Gulf of California (Figures S1-S3). This has been recognized as a limitation by other researchers, impeding rigorous analyses of long-term trends in these rookeries. However, I implemented various methodological techniques to navigate this challenge.

To incorporate all available existing diet data, two diet data indices were incorporated in the analysis: frequency of occurrence (FO) and index of importance (IIMP). Most of the data were in the form of FO, including all Channel Islands diet data and much of the Gulf of California data. Additionally, including the IIMP data allowed me to confirm results obtained from analyses using FO data regarding the lack of overall relationships between diet quality and population changes. Perhaps more importantly, inclusion of IIMP data was the only way to calculate diet quality to compare with population trends at certain rookeries in the Gulf of California (Figures S4 – S8). For example, some rookeries only had FO data from 1995 and 1996, so additional IIMP data for years after 2000 allowed me to identify an increase in diet energy density over time in Zone 6

(with a growing population), and a large decrease in Zone 7 (with a decreasing population; Figure S25).

Another way to overcome the lack of continuous data was by combining patchy data from individual rookeries into Zone and era-specific groups, (which also addressed the issues of independent sampling). Using all available data assembled into rookery-year (or Zone-era) groupings enabled a long-term analysis of diet quality and population changes of matched diet and population data (Figure S1). In the process, I discovered that population change calculations over the shorter time frame associated with these groupings were sensitive to the methodology used. The number of years included in the calculation did, in some cases, radically change the apparent rate of population change. However, implementing a set of rules provided a standardized, repeatable methodology that provided the most realistic calculated rates of population change. Overall, the Channel Islands had more continuous population counts over time compared to the Gulf of California rookeries, but both regions lacked continuity. Fortunately, I was able to devise methods to objectively estimate total population counts for some missing years.

More continuous diet data throughout the study years could have allowed for a more direct comparison between diet and population over time, especially before and after environmental changes. This would have also allowed for the exploration of the effect of possible temporal lags in the effects of environmental changes and would have facilitated the investigation of subtle changes in diet quality and population growth. However, I am confident that my study included most available data, and there is no reasonable expectation of more historical diet data becoming available in the future.

I encountered some challenges when calculating diet diversity and diet energy density to assess diet quality. One of the main challenges with evaluating the effect of diet diversity on populations is choosing adequate ways to quantify the former, since different options may paint a different picture. The Shannon Index was the main measure used to describe differences in diet diversity between the Channel Islands and the Gulf of California. However, the Shannon Index gives information about the content of a community — in this case diet composition — rather than the number of species present (Moore et al., 2013). Since this index emphasizes evenness in prey species, it tends to mask insightful differences in the total number of prey species. Therefore, in

addition to using the Shannon Index, diet diversity was also expressed as the number of prey species present in the diet as well as by calculating the Simpson's Index (using prey species categories). Using multiple measures to quantify and describe diet diversity allowed me to better identify changes between Zones and over time at different levels of detail.

Gathering energy density values for the 114 prey species in the data was also quite challenging since values are not known for many species. Most of the values were obtained from the Gleiber et al. (2022) database (unpublished at the time), but many had to be estimated based on closely related species or species' families, thereby introducing an additional level of uncertainty in the data or potentially masking important differences. Despite all these challenges, my results demonstrated how changes in diet quality can be associated to short-term environmental changes and illustrated the contrasting difference between the diet variation and composition when comparing the Channel Islands and the northern, central, and southern regions of the Gulf of California.

Significance of study findings

My study showed that population dynamics in the Gulf of California vary by region and cannot be generalized. Therefore, to avoid inappropriate generalizations, the conclusions from my study should be discussed within the context of the specific geographic locations and oceanographic conditions in the regions, the historical population trajectory of the rookeries, and the relative changes in diet quality. For example, when sea surface temperatures were anomalously high throughout the Gulf of California, rookeries in the central Gulf experienced a significant decrease in average diet energy density, while the opposite trend was observed for rookeries in the southern Gulf. In addition, rookeries in the central Gulf showed declining population trends, whereas Los Islotes in the south had the only growing population. While these population trends did, in some cases, show an association with long-term diet energy density, non-continuous diet data did not allow for rigorous conclusions. Since additional historical diet data are not likely to become available, a concerted effort to acquire consistent data is required going forward to explore fine-scale relationships between diet quality and populations throughout different regions in the Gulf of California.

It is possible, however, to turn to previous studies on California sea lions in different ecosystems to infer what finer-scale population dynamics might be at play in certain populations throughout the Gulf of California in terms of possible adaptations or challenges in response to environmental changes. It has been previously shown that different environmental changes can have both short- and long-term effects on California sea lion populations in Eastern Pacific ecosystems. For example, El Niño events generally elicit short-term changes in main prey availability with corresponding short-term (1-3 years) population declines and recoveries (Aurioles-Gamboa & Le Boeuf, 1991; McClatchie et al., 2016; Melin et al., 2012). Studies have documented how ocean warming events like the 2014-2016 Blob and El Niño caused reductions in the availability and abundance of California sea lions' main prey, requiring them to perform longer and deeper foraging dives to find sufficient food (Hernández-Camacho et al., 2021; Melin et al., 2008; Weise & Harvey, 2005). Sea lions that are unable to adapt to a reduced quality or quantity of prey items risk losing body mass, which can have consequential impacts on adult health, reproductive success, and ultimately, pup health and survival.

The results of my study contribute to being better able to predict the consequences of environmental effects on sea lion populations in Eastern Pacific ecosystems like the Channel Islands. My results showed that the diet of California sea lions in the Channel Islands was composed of a consistent selection of prey (low variation over time) with a large proportion of energetically dense species, such as Jack mackerel, Pacific mackerel, and northern anchovy, providing an average diet energy density of 5.5 kJ/gww. There was a surprisingly small variation overall within the Channel Islands, despite two rookeries with years of anomalously high or low energy densities. The first was San Miguel in 2005 with a high diet energy density (7.25 kJ/gww) resulting from a greater than average consumption of schooling fish, specifically Pacific sardine and herring (Figure S19). The lowest diet energy density (3.79 kJ/gww) was seen in San Clemente in 1982 — a year that clearly showed a lack of sufficient energy-rich prey such as Jack mackerel and anchovy, and smaller than normal proportions of other common prey such as rockfish and crab (Figure S19).

In the long term, this means that — despite short-term population declines associated with El Niño events — adult and pregnant females in the Channel Islands are dependably meeting their energetic demands, which in turn results in good pup health and survival (Rosen & Trites, 2000), thus

allowing the population to grow consistently over time. This would therefore lead me to predict that if there had been available diet data for this study from the Channel Islands during the period of increased sea surface temperatures (2014-2016; Figure 6), I would have likely seen a temporary decline in average energy density in the diet associated with the observed population declines after 2014. Subsequently, I would have also predicted that the observed population recovery by 2017 was associated with the sea lions again being able to find and consume energy-rich prey species.

In contrast to the diet and population dynamics in the Channel Islands, the results from my study showed that the diet in the Gulf of California largely varies between Zones and over time in both the identity of main prey items and the resultant average diet energy density. Following increased sea surface temperatures in 2014, the average diet energy density of the Gulf of California decreased significantly overall but was not uniform throughout the regions. Central Zones (4 and 5) showed a decline in diet energy density and show a declining population trajectory, whereas the opposite trend was observed in the southernmost rookery (Zone 10) with a growing population which instead, showed an increase in diet energy density. These results may suggest a relationship between long-term changes in diet energy density and population trends within these regions, however, this relationship is difficult to test quantitatively due to the patchiness of the data in time and space available for the Gulf of California rookeries.

Overall, the California sea lion diet composition and population dynamics in the Gulf of California are very different from those in the Channel Islands. Most rookeries have a smaller population size, face different oceanographic dynamics, and show varying population trends over time. This suggests that ultimately, these populations likely face different resiliency challenges when environmental shifts occur. Accounting for environmental heterogeneity may therefore be more relevant when interpreting associations between diet quality and population trends.

This research in relation to other studies

My study showed that increased sea surface temperatures significantly affected the diet quality of California sea lions specifically in the central regions of the Gulf of California, suggesting these changes could play a role in influencing regional population trends. Previous research has linked

similar environmental changes to shifts in the presence and availability of important prey, and ultimately to declines in marine mammal populations.

Diet energy density has known effects on pinniped populations. Lack of high-energy density prey can make it difficult for individual animals to meet their energy intake requirements, eventually affecting aspects of reproduction and survival. For example, at San Miguel Island, low pup birth weights from 2004–2014 were associated with decreases in the relative abundance of high energy density forage fish which affected the pupping success of breeding females over this entire period (McClatchie et al., 2016). Similarly, Steller sea lions (*Eumetopias jubatus*) in the Gulf of Alaska experienced population declines from 1970–1990 along with decreased body size, birth rates, and survival rates associated with chronic nutritional stress from a reduction in the abundance of important high-quality prey species and a resulting decrease in diet energy density (Trites & Donnelly, 2003).

In terms of diet diversity, many studies of marine mammals have shown that shifts to higher diversity are an indication of decreases in diet quality or changes in the environmental conditions (e.g., Jory et al., 2021). For example, Lowry et al., (1991) described how the number of prey species in the diet of California sea lions at San Nicolas Island was low when their preferred prey, northern anchovy, was abundant, and diet diversity was higher when northern anchovy was not available. Similarly, Páez-Rosas et al., (2020) observed a high diet diversity in Galápagos sea lions during warmer ocean temperatures due to El Niño events, and a low diversity during periods of cooler ocean temperatures.

The pattern of increased diet diversity as an indicator of foraging challenges is not universal. Some studies on Steller sea lion populations in Alaska have shown the opposite; a lower diet diversity was associated with higher rates of population declines as an indication of a lack of prey options leading to an inadequate diet (Merrick et al., 1997). While some studies have suggested that measures of diet diversity can only provide limited information on the relationship between diet and population trends (Fritz et al., 2019), others have identified the importance of diet prey diversity when interpreted in the context of the specific ecosystems (Sinclair & Zeppelin, 2002). Overall, energy density can be a more direct measure of diet quality, but different measures of diet diversity (as included in this study) can paint a fuller picture regarding changes in diet allowing

inferences to be made about what this might mean in different ecosystems, such as in the Gulf of California.

The complex ecosystem dynamics throughout the Gulf of California have been described as possible factors influencing the effect of changes in the presence of prey on population dynamics of California sea lions (Lavin & Marinone, 2003; Schramm et al., 2009). My study concurs with previous findings that recognized that the central regions of the Gulf of California seem to have different population dynamics compared to the south (Pelayo-González et al., 2021), therefore suggesting that sea lions in central regions may be less resilient to environmental changes associated with shifts in diet quality. Explanations for this dynamic have been proposed to be specifically related to a decrease in the size of sardines, an important prey (Adame et al., 2020). However, further research on more fine-scale dynamics in the Gulf of California would be required to draw reliable conclusions about the relationship between population trends and additional measures of diet quality such as prey size.

When exploring population dynamics, it is also important to consider that not all members of a population are equally affected by environmental changes, partly due to adaptability differences. For example, Schwarz et al. (2022) suggest individual-specific foraging strategies in sea lions could play a role in their pupping success and survival. They found environment-dependent fitness trade-offs between benthic and pelagic foragers of Galápagos sea lions (*Zalophus wolfebaeki*), where, under increased sea surface temperature conditions, pelagic foragers experienced lower pupping success, whereas benthic foragers did not.

It is well understood that the sea lion populations at the Channel Islands are affected by El Niño, mostly because the availability of their most consistent type of prey — pelagic schooling fish — changes. In contrast, as illustrated by my results, California sea lions in the Gulf of California rely more on benthic species and have much more diverse and variable diets. Therefore, understanding the individual-specific foraging tactics of California sea lions throughout the Gulf of California regions might help further understand the population drivers at each rookery.

Other factors are also worth considering when investigating population dynamics throughout the Gulf of California. California sea lions in the upper and central regions have a lower genetic

diversity compared to the south, which suggests that California sea lions from each region do not often interbreed, and instead are philopatric to their rookery (Schramm et al., 2009). These genetic differences can heavily influence the resilience of declining populations in the northern and central regions, particularly compared to the growing, and likely more resilient population at the Los Islotes (Zone 10) rookery in the south.

In addition, anthropogenic contextual differences in different regions of the Gulf of California should also be considered. The northern and central regions (Zones 2-7) make up a very large marine protected area (MPA) or Área Natural Protegida (ANP), as deemed by the Mexican government. The MPA's large size makes it difficult to monitor and, in some parts, also difficult to access by government officials of the CONANP (National Commission of Protected Natural Areas). As a result, surveillance efforts of potential conflicts with fisheries or entanglements in this region have not been as successful (Pelayo-González et al., 2021).

Furthermore, high political and social tensions exist in the upper Gulf of California stemming from complex political, socioeconomic, and ecological issues, that have threatened human well-being and resulted in a lack of fisheries management (Sanjurjo-Rivera et al., 2021). These tensions have given rise to various known and unknown illegal activities such as the totoaba fishery (*Totoaba macdonaldi*) which, through accidental gillnet entanglements, has caused the near-extinction of the vaquita porpoise (*Phocoena sinus*) (Rojas-Bracho et al., 2022). While local tensions rise between fishers, the authorities, and conservationists, it is difficult to document or measure other consequences that may be arising from these issues, in turn limiting the understanding of the potential threats to California sea lions and other marine life in that general region. In comparison to the northern and central regions, the Los Islotes rookery in the south (Zone 10), is found near La Paz, the capital city of the Baja California Sur state, and is located within the PNZMAES (Espíritu Santo Archipelago Marine National Park). The PNZMAES is a much smaller MPA that has more monitoring and enforcement compared to the northern and central regions of the Gulf of California. The sea lions at Los Islotes have been identified as an important core population with the potential to become a re-populating rookery if populations in the northern and central regions were to keep declining (Hernández-Camacho et al., 2021).

Conservation considerations

The results from my study provide evidence to support the need for California sea lion conservation management strategies throughout the Gulf of California that are personalized to each region's context and challenges. In other words — one size does not fit all. My findings highlight the need to better understand the anthropogenic and ecological dynamics throughout the Gulf of California, and cautions generalizations about population dynamics when considering different California sea lion sub-populations in these areas. This is part of a larger recommendation that, in order to conserve most pinniped species, regional sub-populations and their unique ecological dynamics must be considered, not simply the larger, overall population trend.

The California sea lion populations in the Gulf of California are important to Mexico. The species has been categorized as requiring 'special protection' by the Mexican government based on recognizing that their populations may be threatened or at risk of extinction (NOM-059-SEMARNAT, 2010). Cisneros-Montemayor et al. (2020) further quantified California sea lions as the most important species for nature-based marine tourism in the Gulf of California (as deemed by tourism operators themselves) due to their site reliability and wide public appeal, thus playing an important role in the local economy (Cisneros-Montemayor et al., 2020). This is especially valuable since the importance of this species has not always been appreciated. As opposed to other iconic species such as sharks, whales, and marlins, California sea lions have previously been perceived as a threat to commercial fisheries and culls had even been proposed (Zavala-González & Mellink, 2000). Given their current overall population trends and their now recognized economic importance, the conservation of this species merits more attention including stronger conservation measures limiting the impacts of threats to individuals, such as fishing gear entanglements, over-fishing of important prey, or potentially stressful tourism practices (Hernández-Camacho et al., 2020).

Well-designed and efficient management strategies, routine surveillance by government officials, and consistent data collection on the individual rookeries throughout the Gulf of California are required to protect these populations. The urgency for establishing and maintaining these plans is even more critical following the 75% budget reduction in 2020 to the National Commission for

Protected Natural Areas in charge of monitoring and conserving these areas (CONANP: Comisión Nacional de Áreas Naturales Protegidas). My study, along with substantial existing knowledge on the Gulf of California and its biological importance, can serve as yet another piece of evidence to support the need to prioritize funds and research towards conservation in this area.

Future research

Future research should primarily be designed around the environmental heterogeneity of the Gulf of California, and other relevant anthropogenic contextual differences at each rookery. To gain a better understanding of the population drivers at each rookery, it is necessary to better define the ecological independence of each region. This would provide an important framework from which to subsequently explore the mechanisms driving population dynamics at each ecological region while accounting for environmental heterogeneity.

Such investigations should explore the different foraging locations of breeding California sea lion females at each region, which could provide a baseline idea of possible habitat overlap between rookeries and help establish the ecological independence of each breeding site. Understanding their foraging strategies could also provide insights about the resiliency of populations at different rookeries (or ecological regions once established) in terms of possible behavioural adaptations to environmental changes. Possible research topics include investigating what feeding strategies California sea lions rely on, their foraging trip length variations, if they switch between strategies during changing conditions, if multiple strategies exist within a rookery, and how this information may allow changes in population sizes in response to potential future environmental disturbance to be predicted.

In addition to information about their feeding behaviour, demographic studies could help pinpoint factors that may directly affect population growth such as adult female breeding and pregnancy successes, pup birth and survival rates, average adult mortality age, etc. Linking this information to data on the abundance and distribution of prey species could also contribute to painting a more complete picture of prey availability vs. consumption and ultimately, clarify population drivers throughout the rookeries in the Gulf of California. However, regardless of the specific focus, continuous and consistent population and diet data collection is crucial to continue to build on

existing knowledge about these populations and how they change or adapt over time. Monitoring different regions is also key for providing insights into other causes of mortality that may be at play in certain regions (such as incidental entanglements or illegal killings), as well as to evaluate current management strategies — and to design future ones that can establish the best protection measures for these populations.

Accelerating the implementation of effective management practices or the support for rigorous data collection often requires collective interest from government, scientists, and members of the local community. The California sea lions of Los Islotes are already recognized as a charismatic species that is appreciated by locals and tourists in La Paz, but the decline of most other rookery populations along the Gulf of California is not common knowledge. I propose that emotive science communication directed at emphasizing the importance of better understanding these California sea lion populations could mobilize and accelerate actions towards i) prioritizing research funding in the northern and central regions of the Gulf, ii) stronger protection measures against anthropogenic population threats (such as entanglements and pollution), and iii) increased education and communication between researchers and local community members (such as fishers, tourism operators, and NGO's).

Conclusion

It has been argued that the Gulf of California is a globally unique, biodiverse, ecologically complex region, earning the name “The Aquarium of the World” from Jacques Cousteau. Therefore, understanding the ecosystem dynamics and its effects on marine species here can be a fascinating challenge. In the case of California sea lions in the Gulf of California, my research demonstrated that pinpointing or isolating main population drivers can be challenging in comparison to other pinniped populations. Instead, my results suggest population dynamics are unique to each rookery's geographic location, direct environment, and anthropogenic contexts, thus highlighting the need to better understand the ecological independence of each region. California sea lions are a highly philopatric species that relies on the environmental and oceanographic characteristics of its habitat for survival. Therefore, management measures for populations within the Gulf of California require further understanding about each rookery's ecological dynamics to meet their conservation goals.

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Appendix: Supplementary Figures

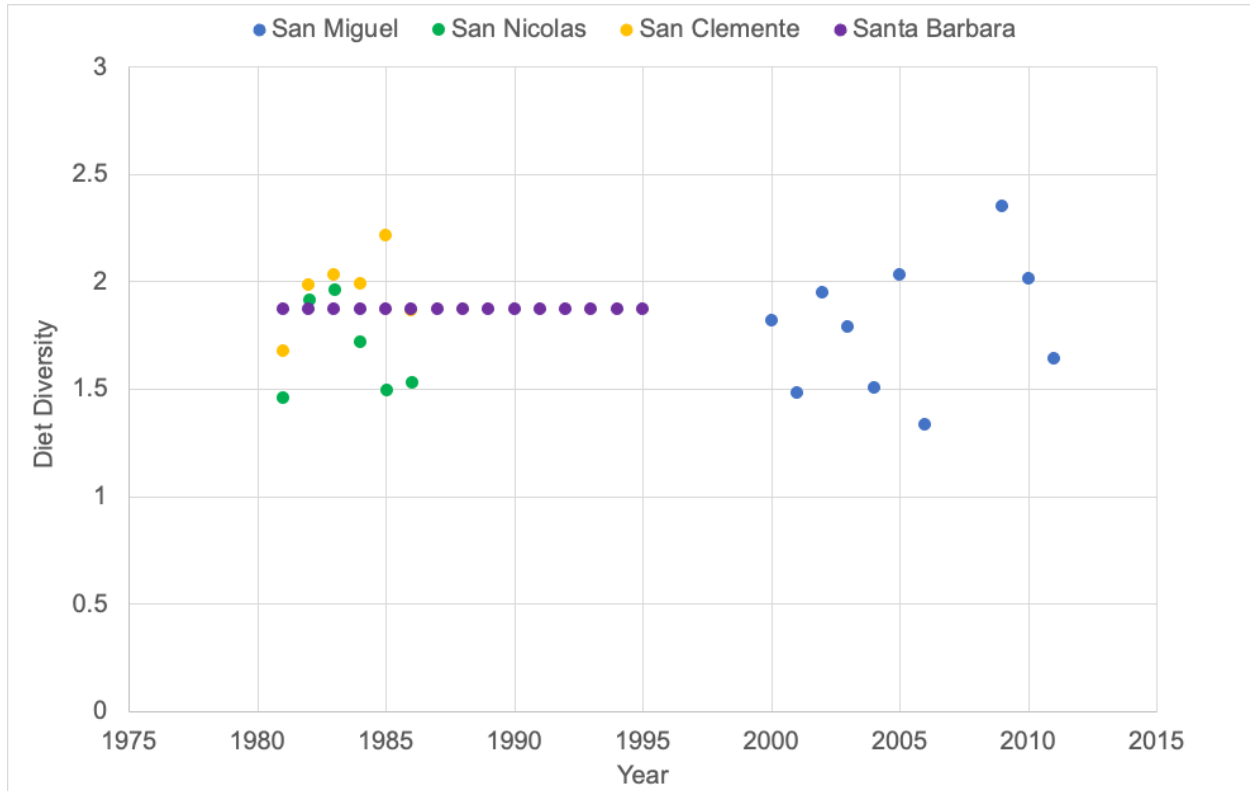


Figure S1. Diet diversity from frequency of occurrence data for the Channel Island rookeries. Data represents diet diversity values calculated from frequency of occurrence values from available data for each rookery and year 1980–2011. Data points for Santa Barbara are from grouped diet data from 1981–1995.

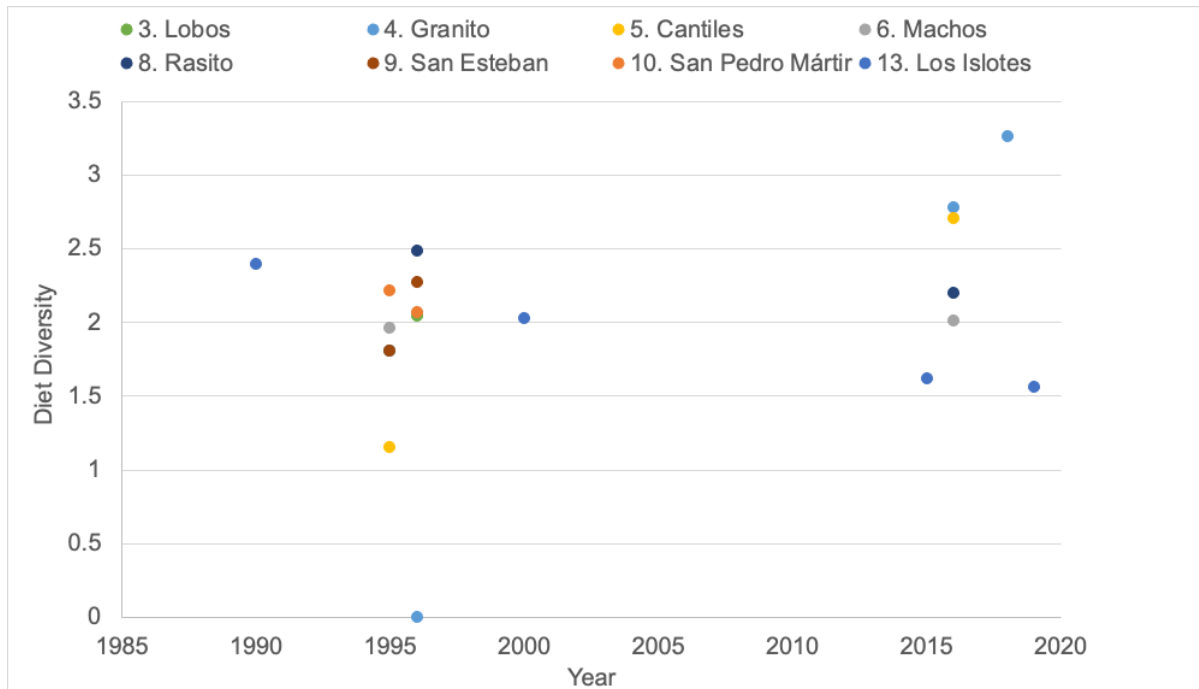


Figure S2. Diet diversity from frequency of occurrence data for the Gulf of California rookeries. Data represents diet diversity values calculated from frequency of occurrence values from available data for each rookery and year 1990–2019.

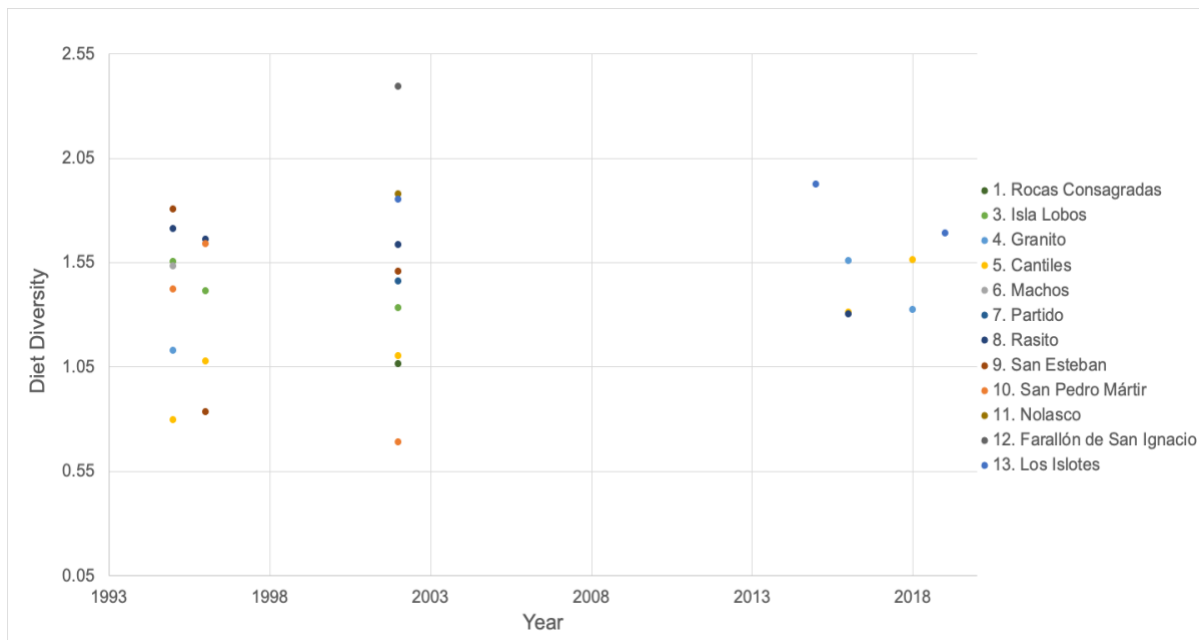


Figure S3. Diet diversity from index of importance data for the Gulf of California rookeries. Data represents diet diversity values calculated from index of importance values from available data for each rookery and year 1995–2020.

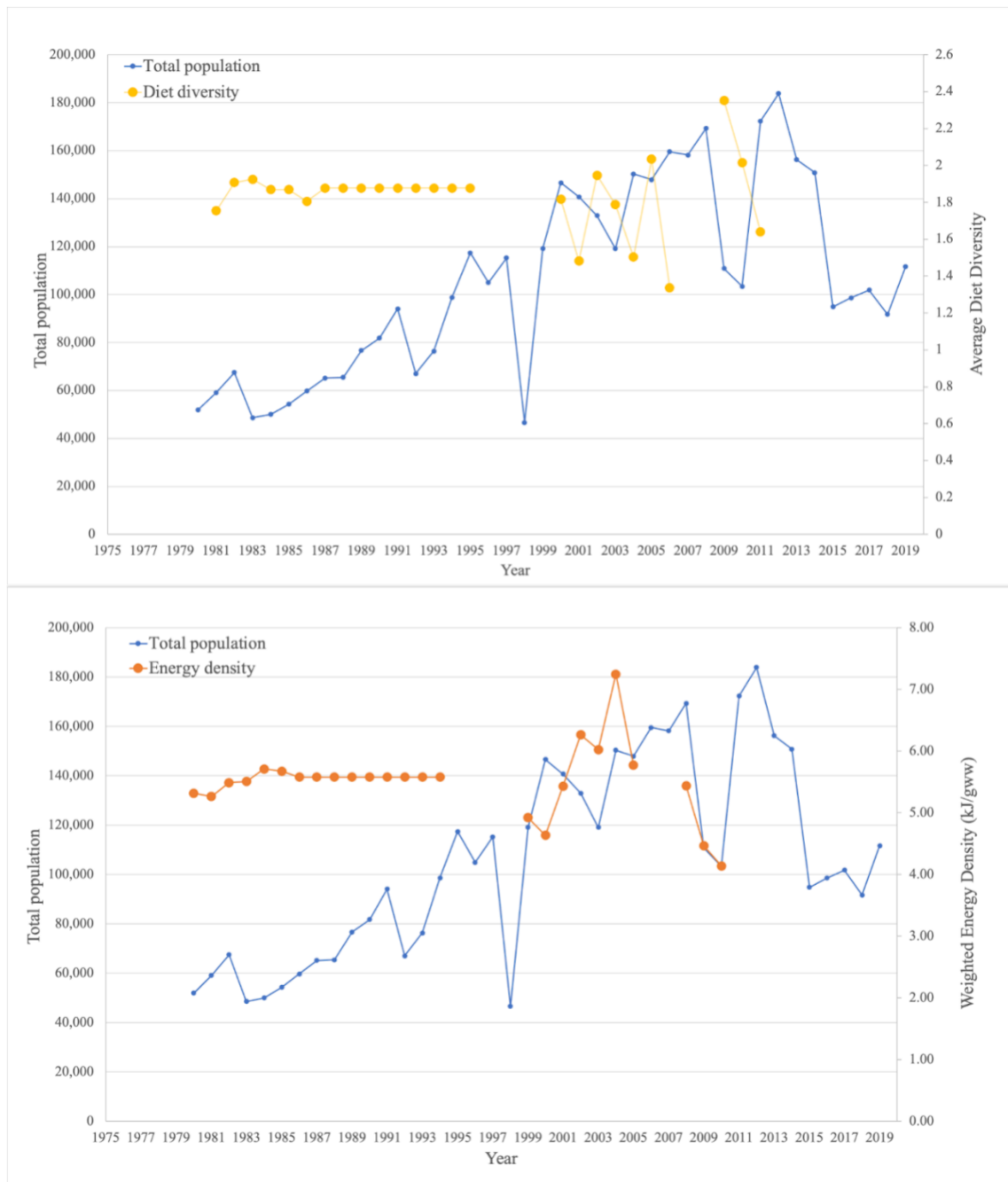


Figure S4. Total sea lion counts and average diet diversity (top panel), and energy density (bottom panel) over time from frequency of occurrence data for all rookeries in the Channel Islands (Zone 1). Data shows diet diversity and weighted energy density values calculated from available diet data from all four rookeries from 1980–2015. Diet diversity values from 1987–1995 represent the average diet diversity and energy density from grouped diet data values from San Nicolas, Santa Barbara, and San Clemente Islands for that time period. For years with missing population data, estimated population counts were used based on regressions from available pup count data.

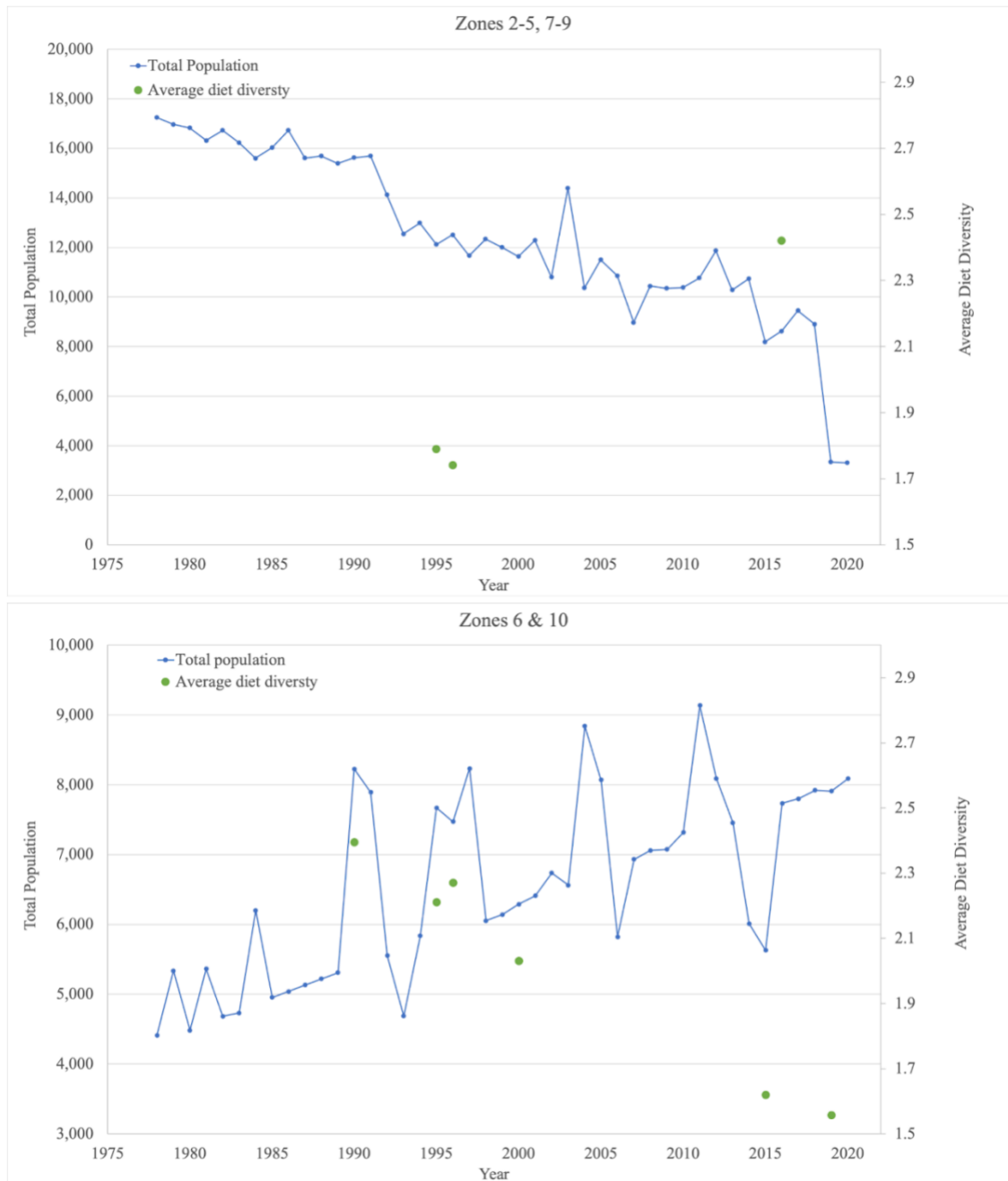


Figure S5. Total sea lion counts and average diet diversity over time from frequency of occurrence data for Gulf of California Zones with potentially decreasing (top panel) and increasing (bottom panel) populations. Diversity values represent the average diversity from rookeries in indicated Zones with available data that year. Note difference in scales of population axes. For years with missing population data, estimated population counts were used based on regressions from available data.

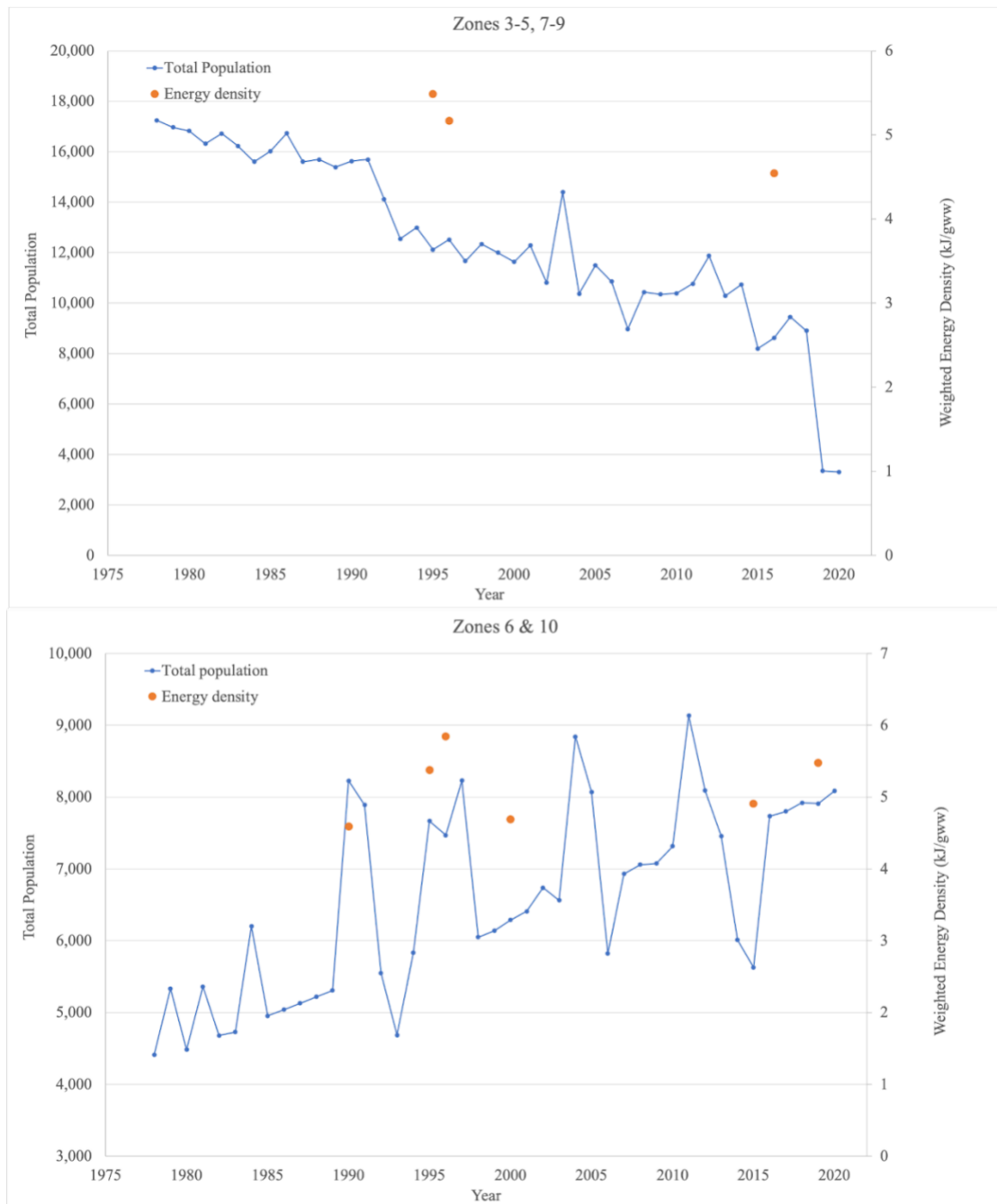


Figure S6. Total sea lion counts and energy density over time from frequency of occurrence data for Gulf of California Zones with potentially decreasing (top panel) and increasing (bottom panel) populations. Energy density values represent the average weighted energy density from rookeries in indicated Zones with available data that year. Note difference in scales of population axes. For years with missing population data, estimated population counts were used based on regressions from available data.

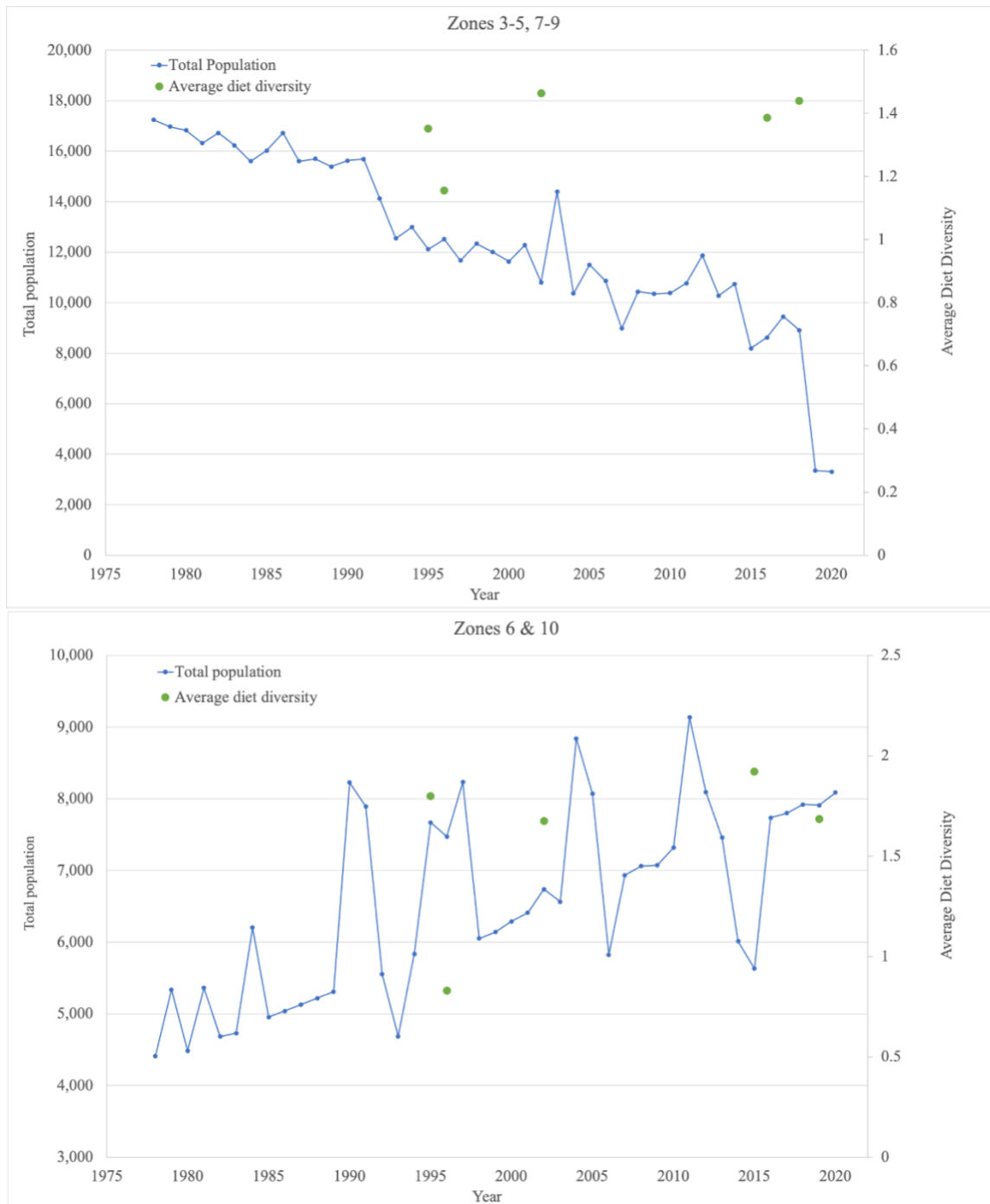


Figure S7. Total sea lion counts and average diet diversity over time from index of importance data for Gulf of California Zones with potentially decreasing (top panel) and increasing (bottom panel) populations. Diversity values represent the average diversity from rookeries in indicated Zones with available data that year. Note difference in scales of population axes. For years with missing population data, estimated population counts were used based on regressions from available data.

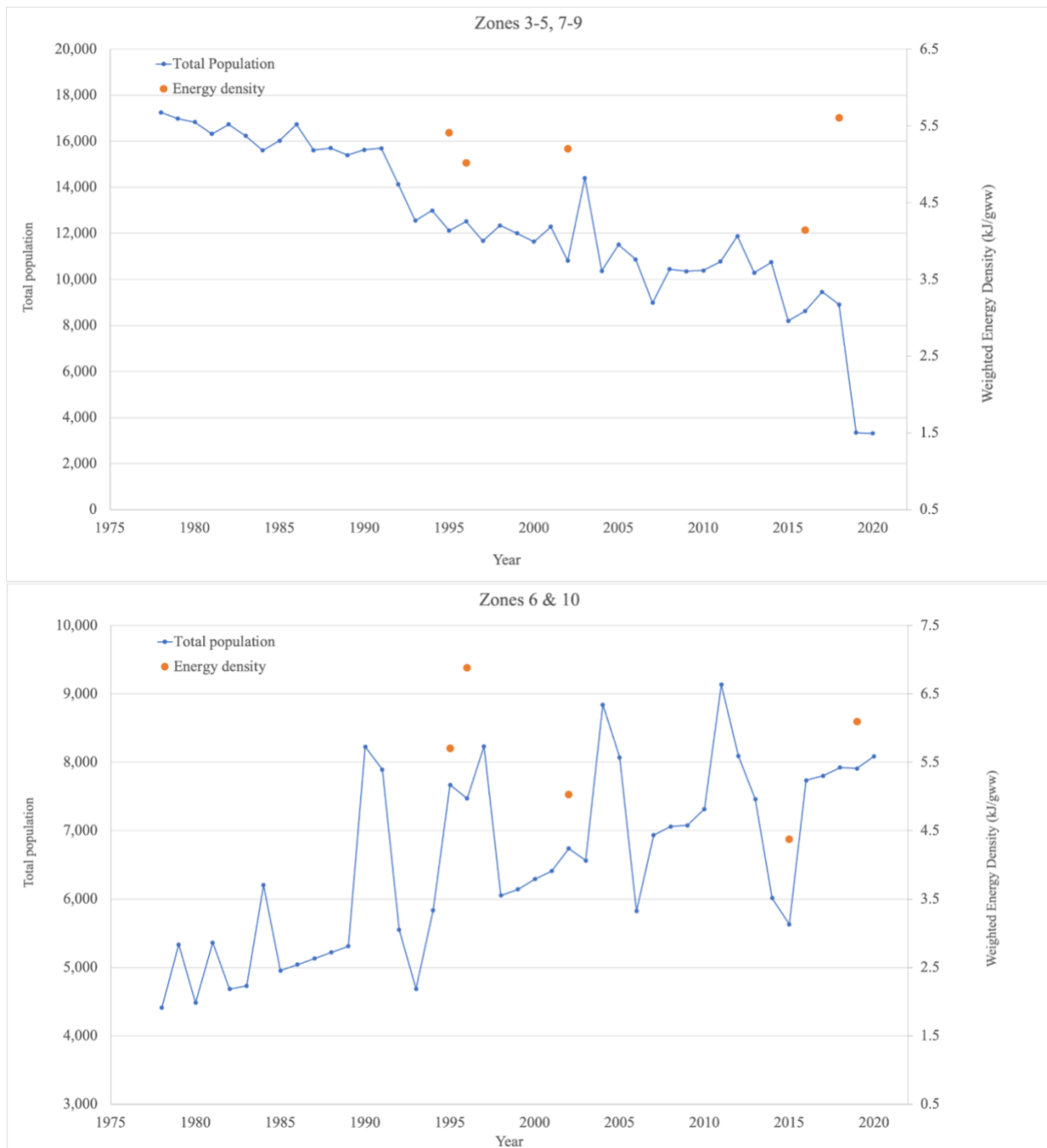


Figure S8. Total sea lion counts and energy density over time from index of importance data for Gulf of California Zones with potentially decreasing (top panel) and increasing (bottom panel) populations. Energy density values represent the average weighted energy density from rookeries in indicated Zones with available data that year. Note difference in scales of population axes. For years with missing population data, estimated population counts were used based on regressions from available data.

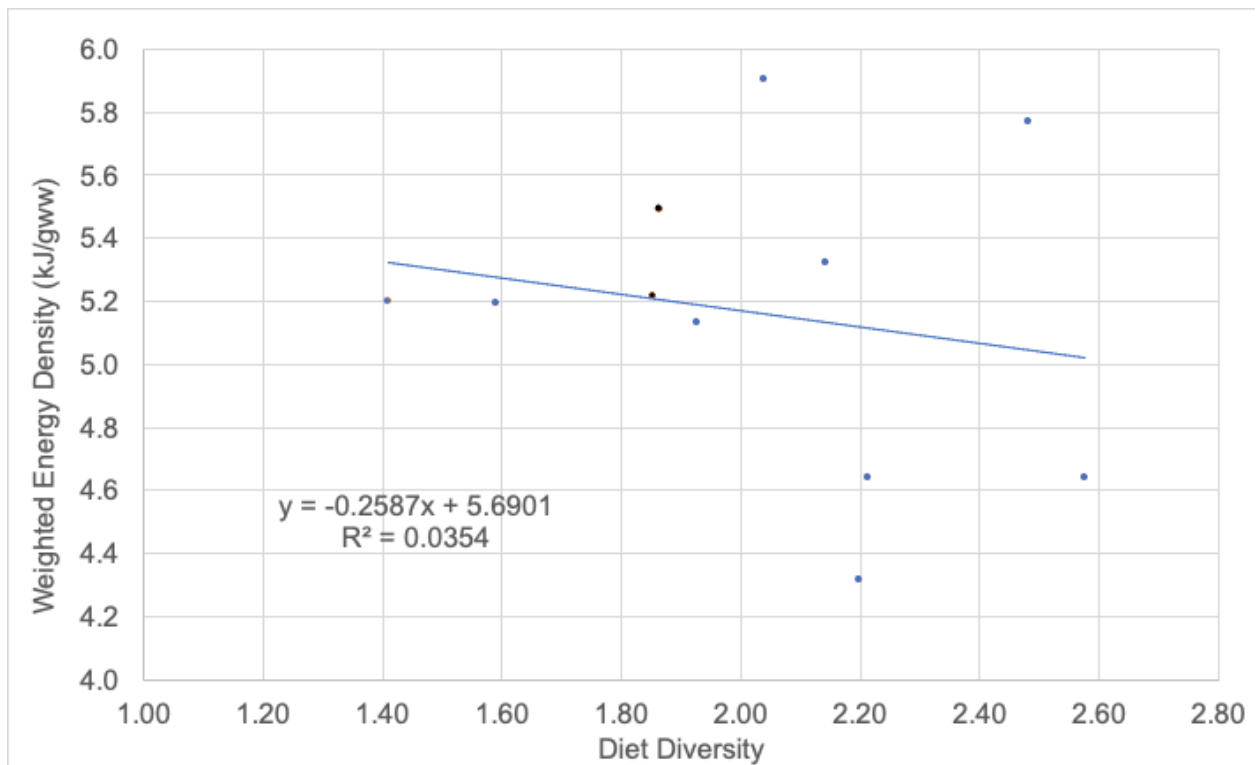


Figure S9. Relationship between weighted energy density and diet diversity from frequency of occurrence data. Data are presented for Zone-era groupings, black data points represent Zone 1 (Channel Islands), blue dots represent Zones 2–10 (Gulf of California). Linear regression analysis demonstrates no statistically significant negative relationship between energy density and diversity.

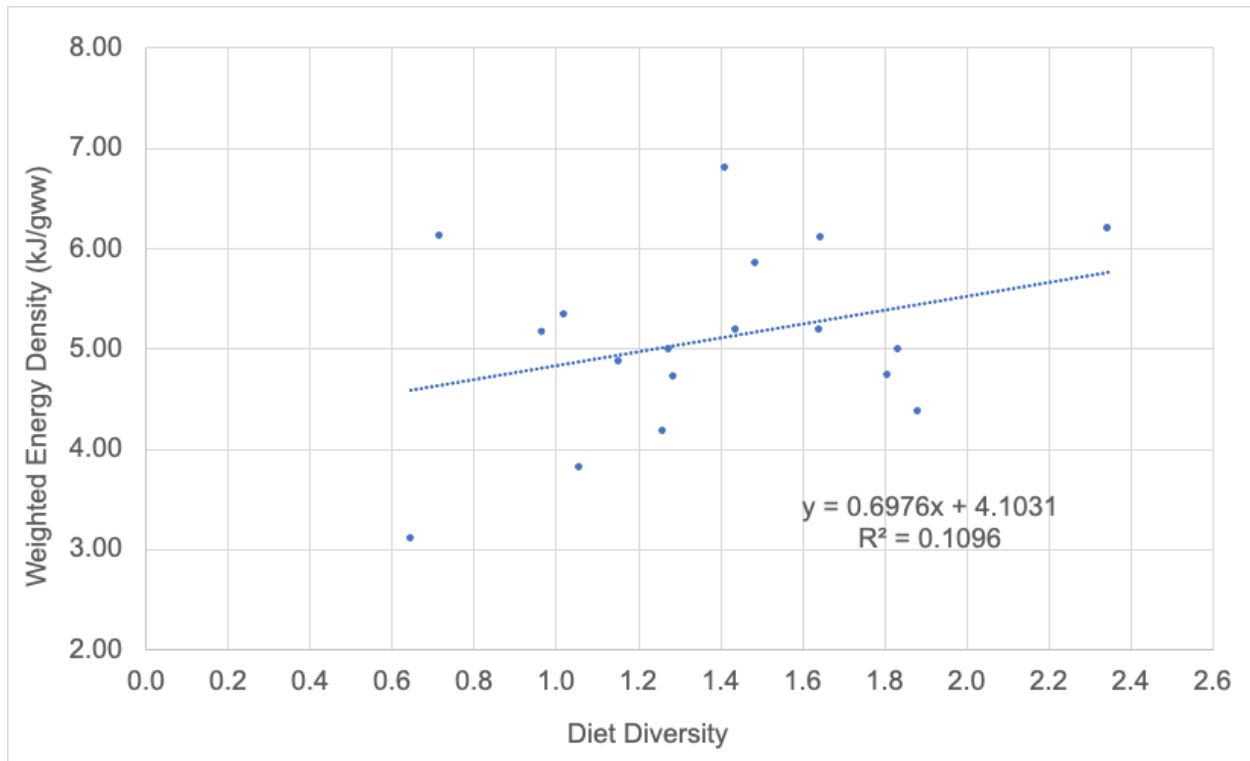


Figure S10. Relationship between weighted energy density and diet diversity from index of importance data. Data are presented for Zone-era groupings. Linear regression analysis demonstrates no statistically significant relationship between energy density and diet diversity.

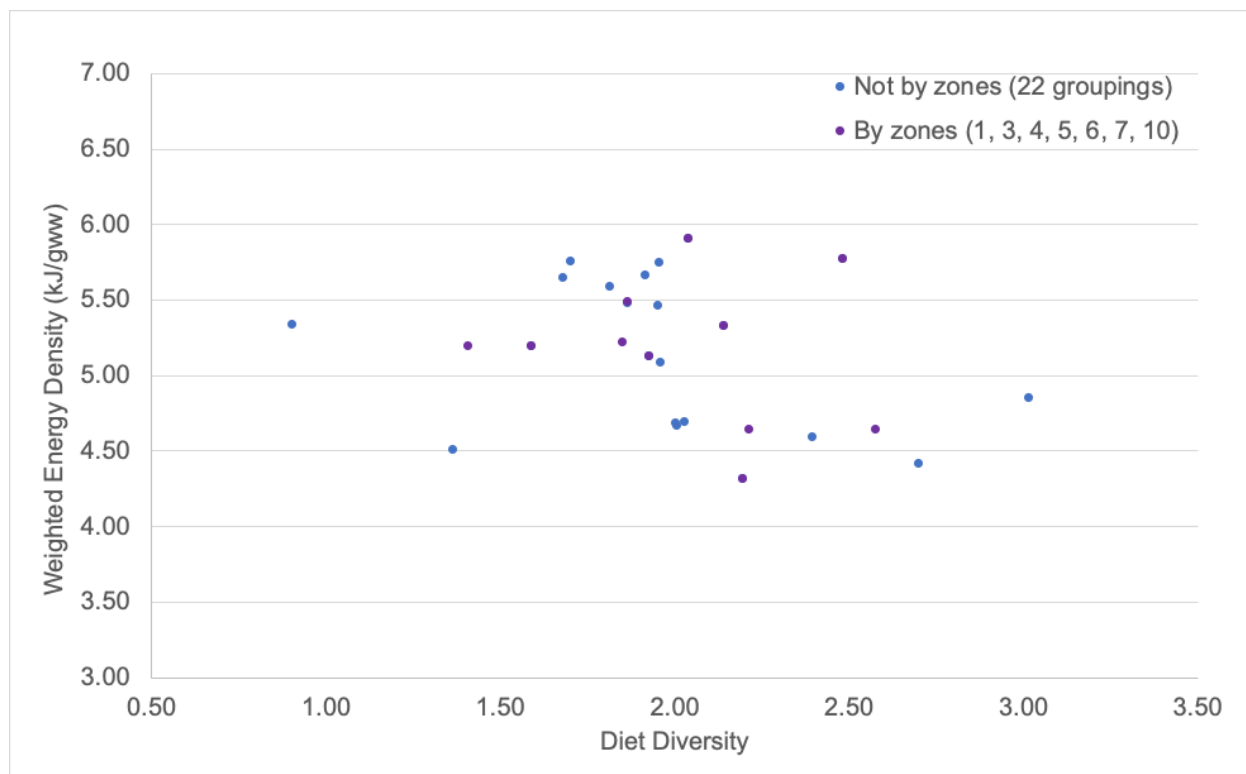


Figure S11. Relationship between weighted energy density and diet diversity. Data are presented for all rookeries with frequency of occurrence data. Data are shown both by individual year-rookery groupings (blue) and by Zones (purple).

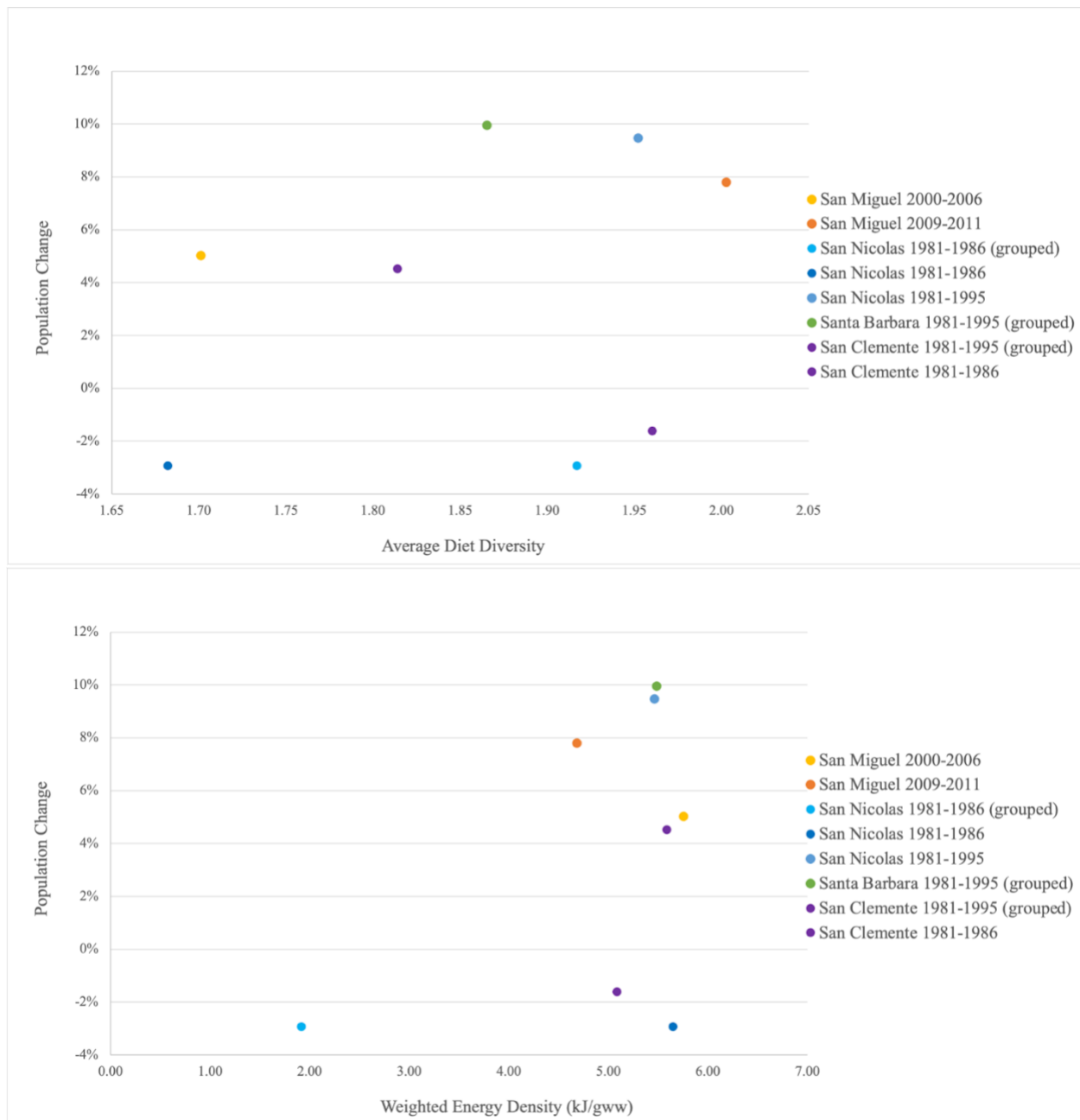


Figure S12. Population changes and diet diversity (top panel) and energy density (bottom panel) from frequency of occurrence data available for all Channel Island rookeries. Note that rookeries indicated as ‘(grouped)’ had grouped data for multiple years that was reported as a single average over those time periods in the literature.

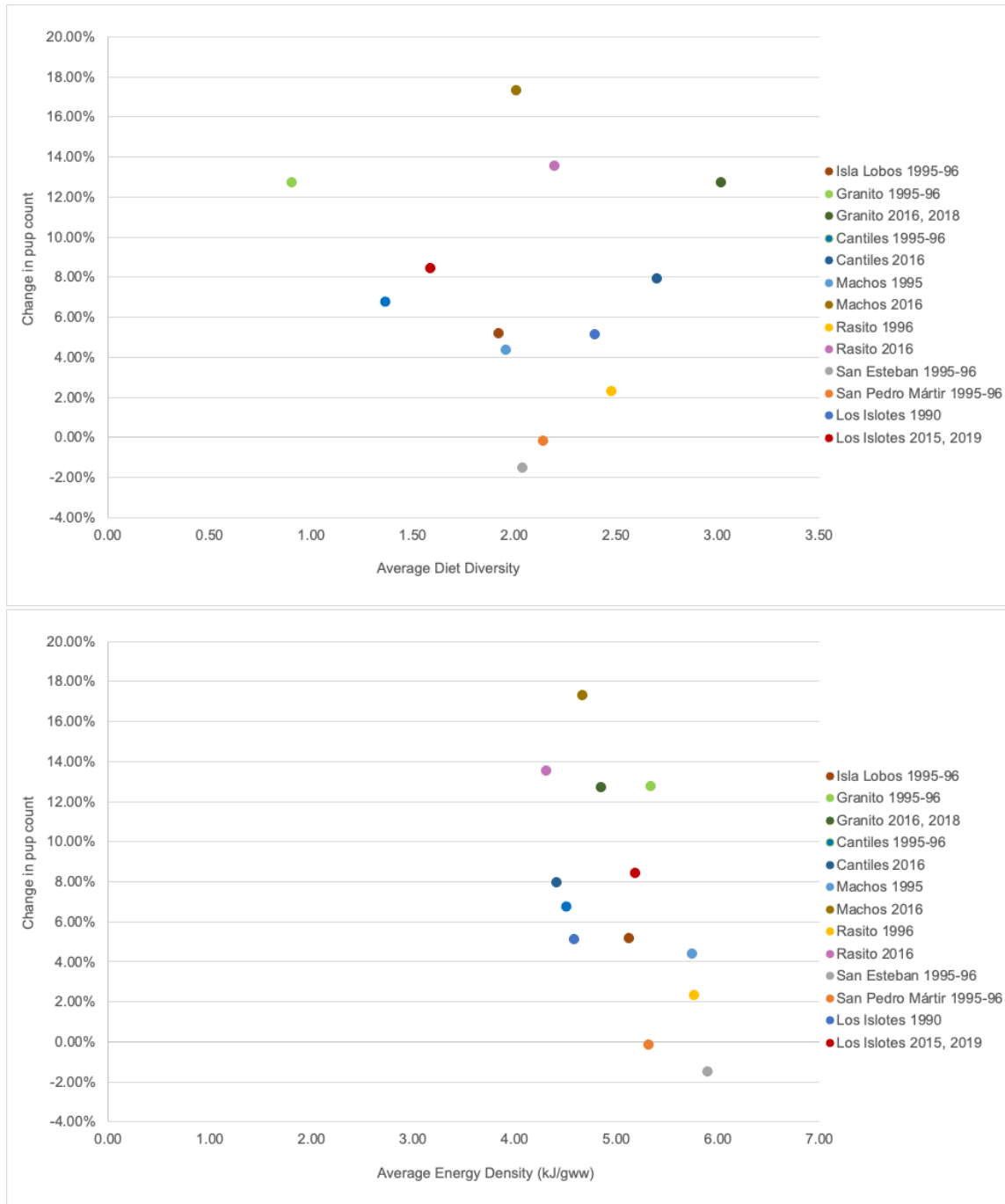


Figure S13. Diet diversity (top panel) and energy density (bottom panel) and change in total pup counts from frequency of occurrence data. No statistically significant relationship was found.

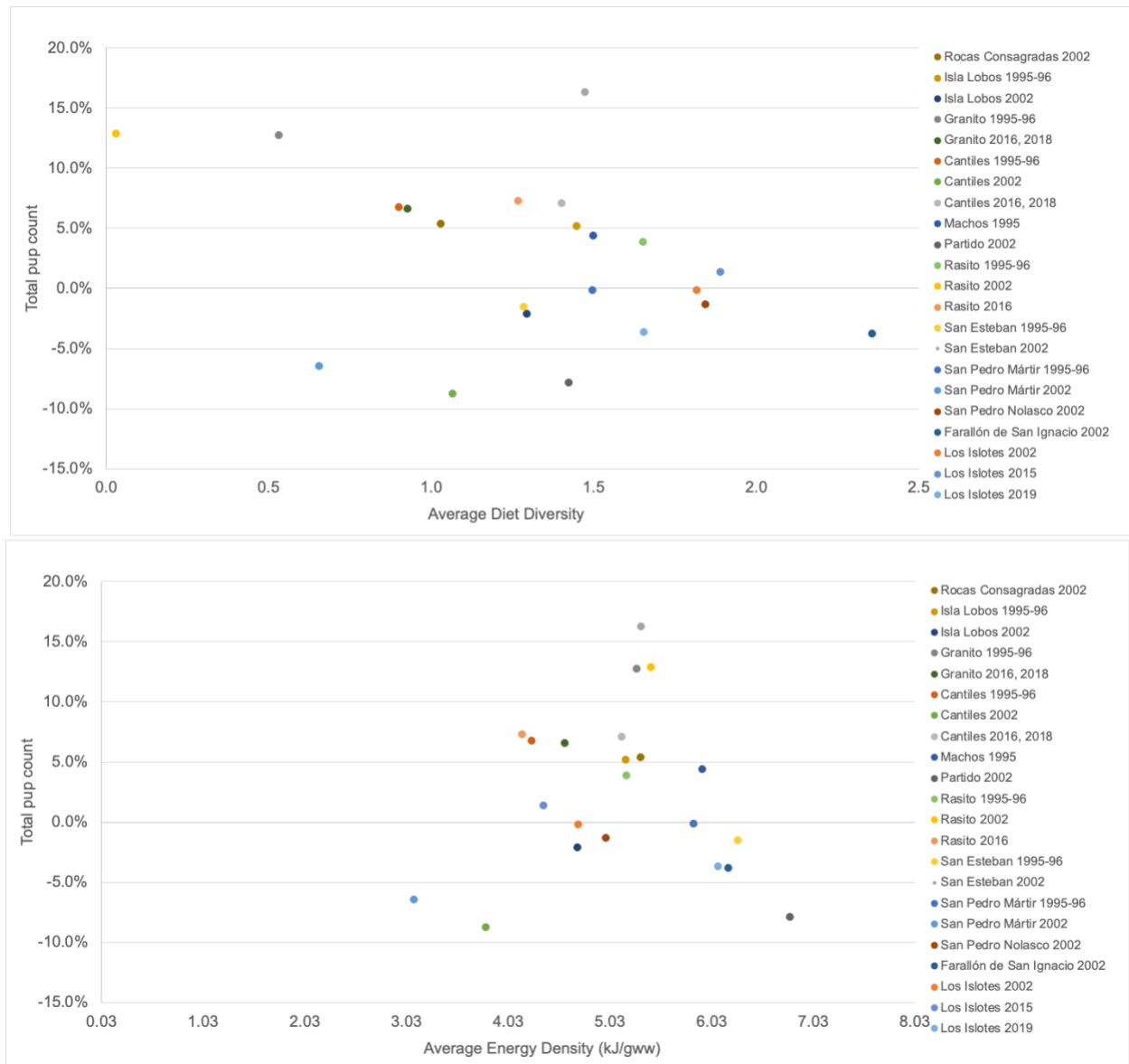


Figure S14. Diet diversity (top panel) and energy density (bottom panel) and change in pup counts from index of importance data. No statistically significant relationship was found.

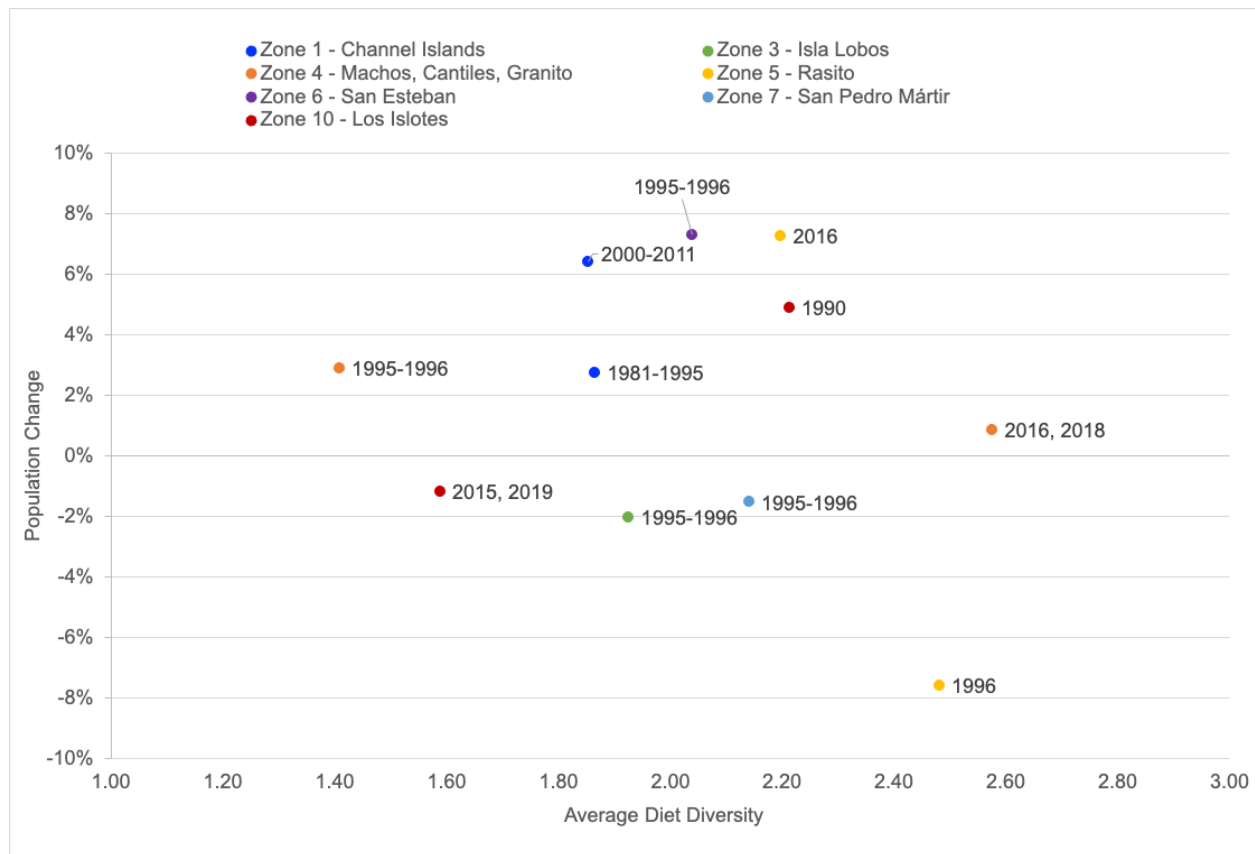


Figure S15. Population changes and diet diversity from frequency of occurrence data. Data are presented for Zone-era groupings from eras: 1990–2000 and 2015–2019. Regression analysis of data weighted by rookery population size indicated no statistical relationship.

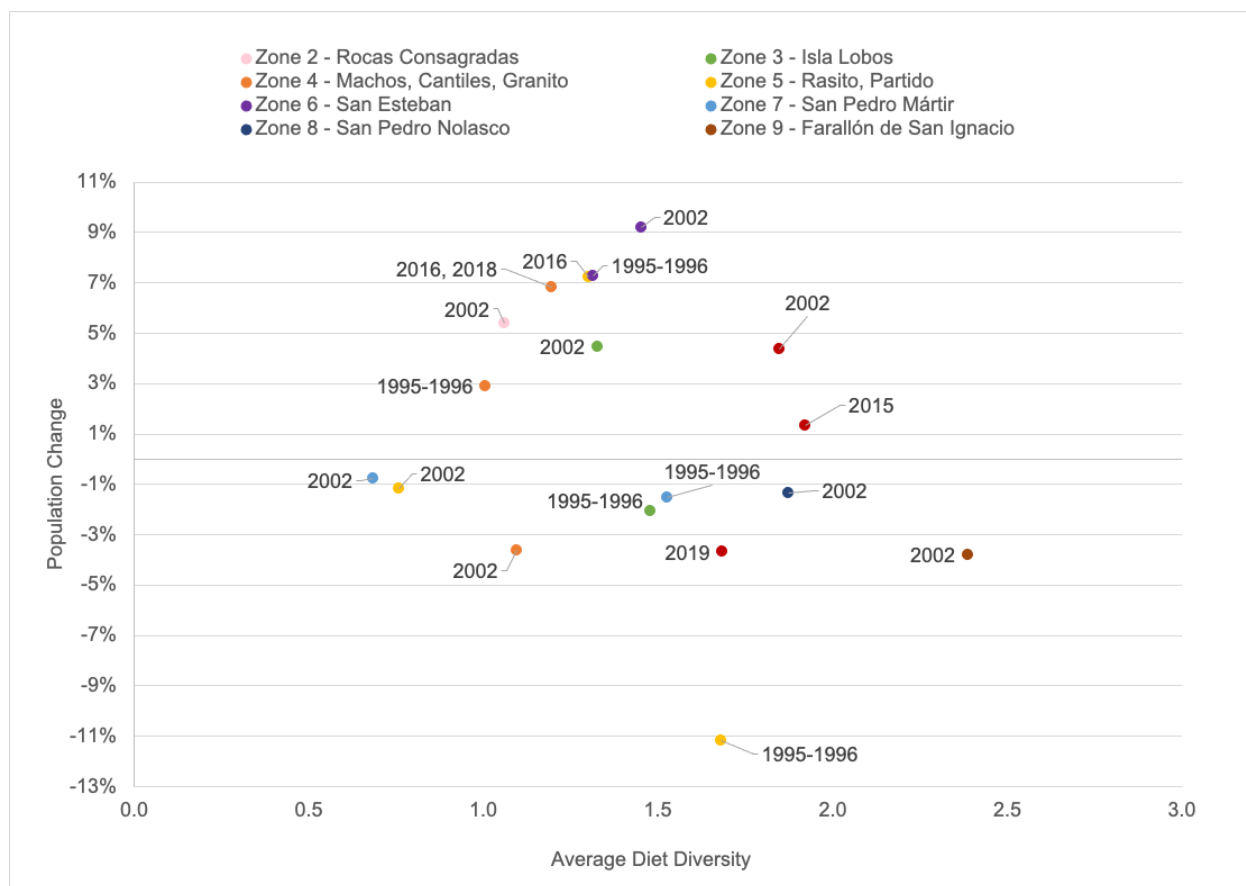


Figure S16. Population changes and diet diversity from index of importance data. Data are presented for Zone-era groupings from eras: 1995–1996, 2002, and 2015–2019. Regression analysis of data weighted by rookery population size demonstrated no significant relationship.

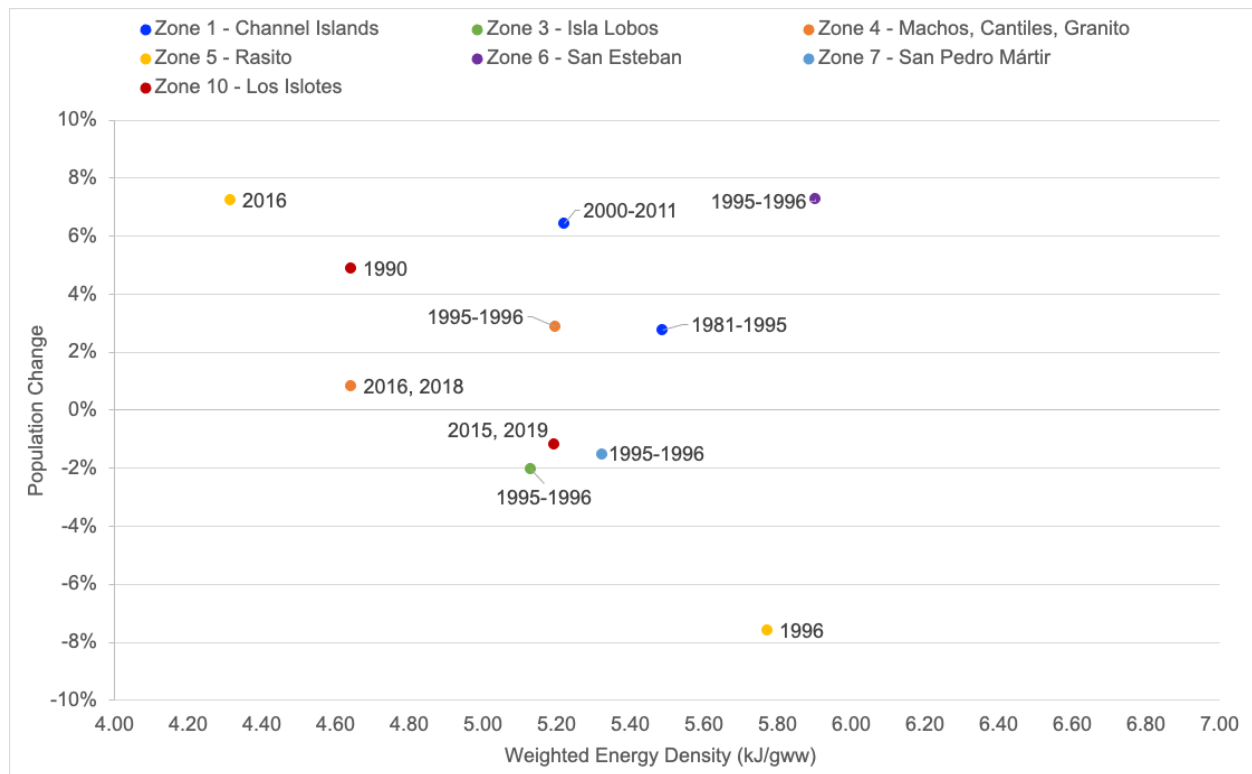


Figure S17. Population changes and energy density from frequency of occurrence data. Data are presented for Zone-era groupings from eras: 1990–2000 and 2015–2019. Regression analysis of data weighted by rookery population size demonstrated no significant relationship.

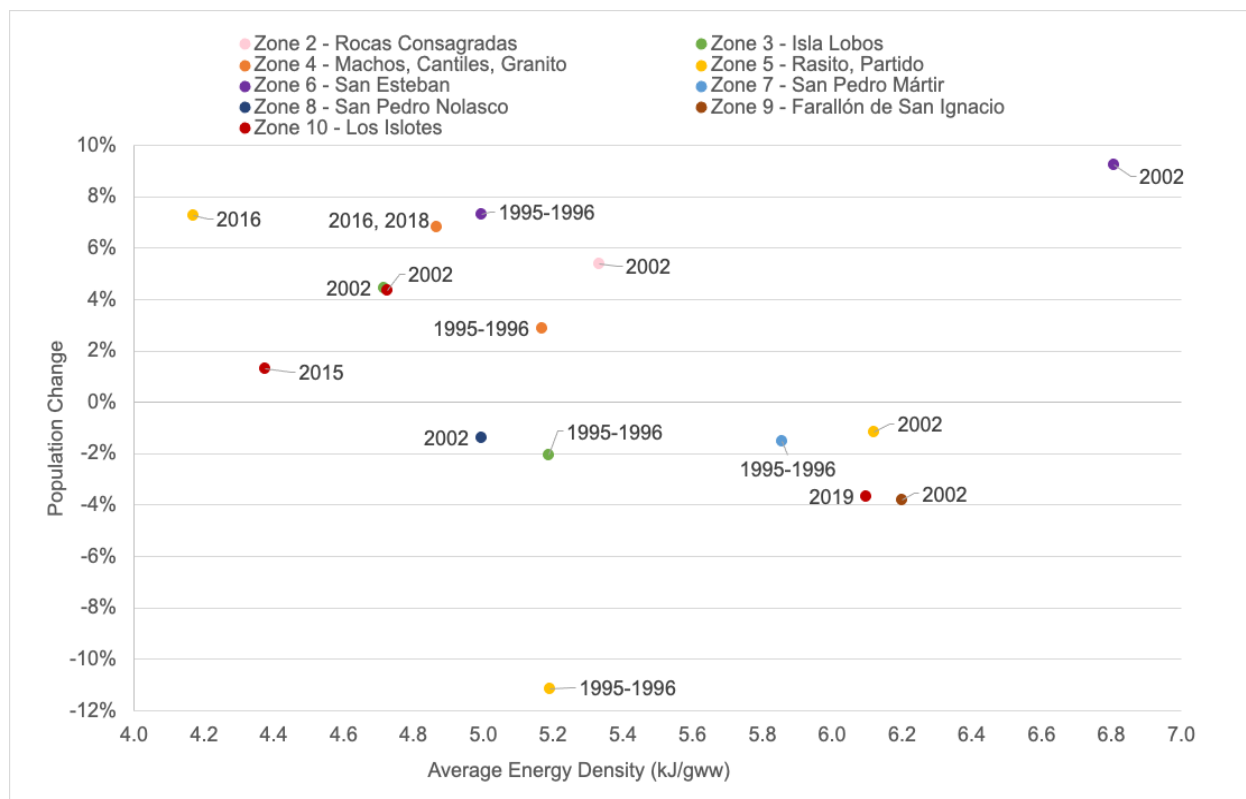
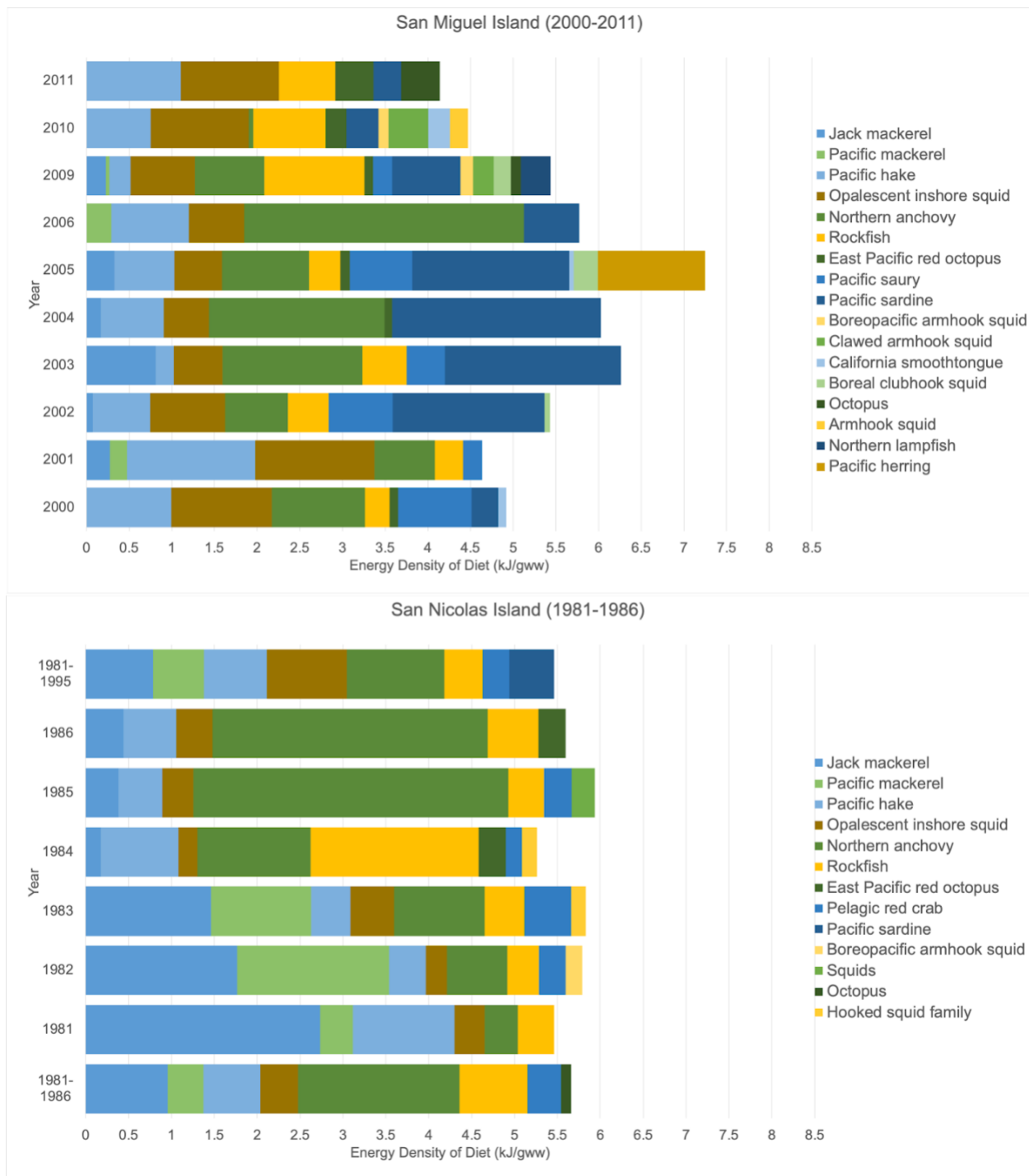


Figure S18. Population changes and energy density from index of importance data. Data are presented for Zone-era groupings from eras: 1995–1996, 2002, and 2015–2019. Regression analysis of data weighted by rookery population size demonstrated no significant relationship.



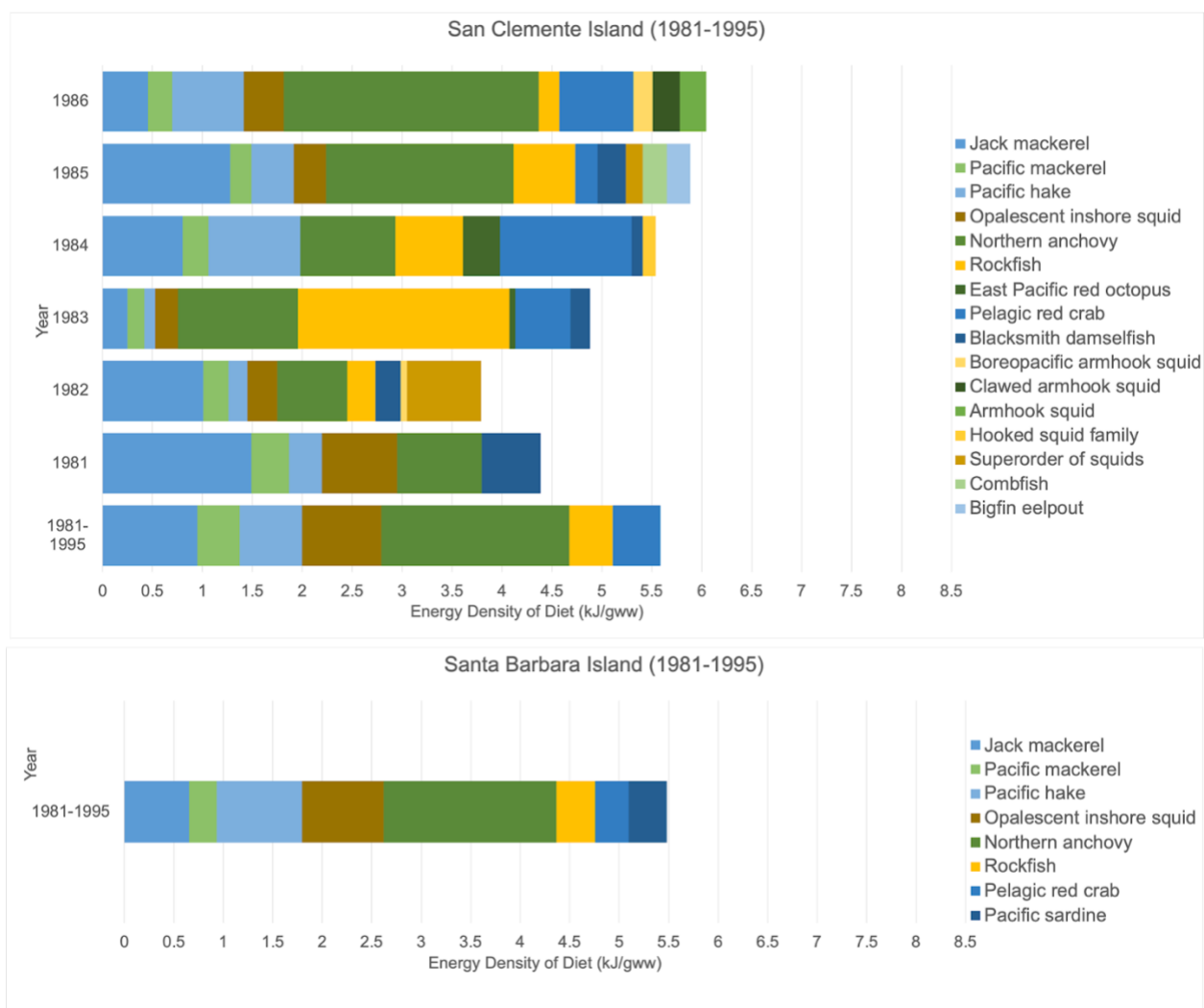
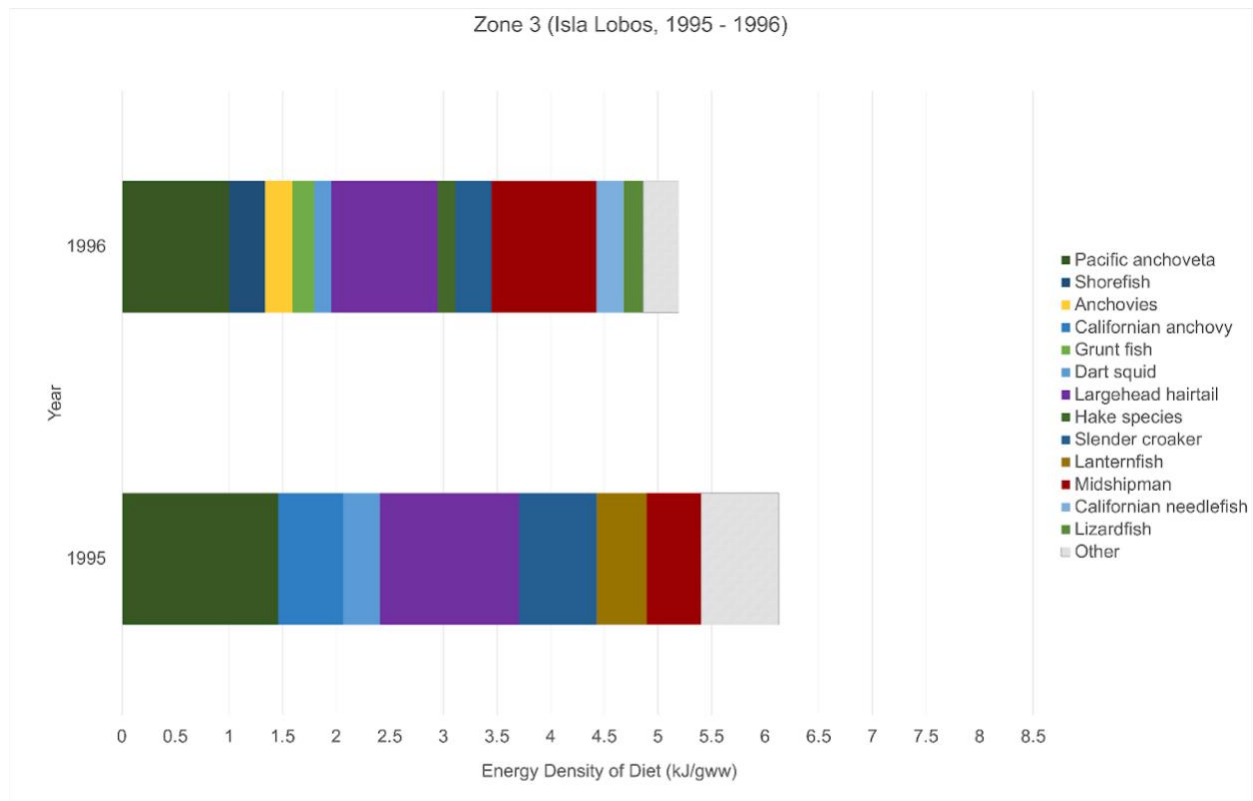


Figure S19. Energy density of diets of California sea lions in the Channel Islands (Zone 1). Average energy density and energetic content contributions (average weighted energy density) of the top 17 prey species to the total energetic content of the diet for each of the Channel Island rookeries from frequency of occurrence data. ‘Other’ category represents all other species in the diet beyond the top 17. Data availability differs between rookery: San Miguel Island 2000–2011, San Nicolas Island 1981–1986, San Clemente Island 1981–1995, and Santa Barbara Island 1981–1995.



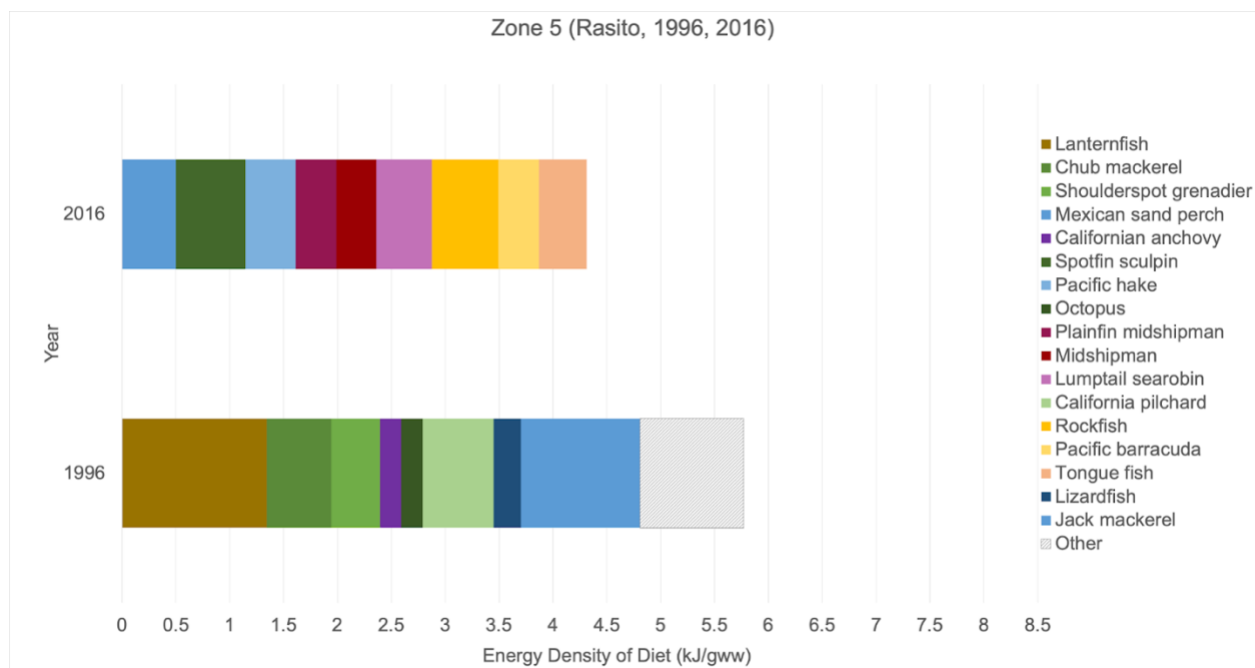
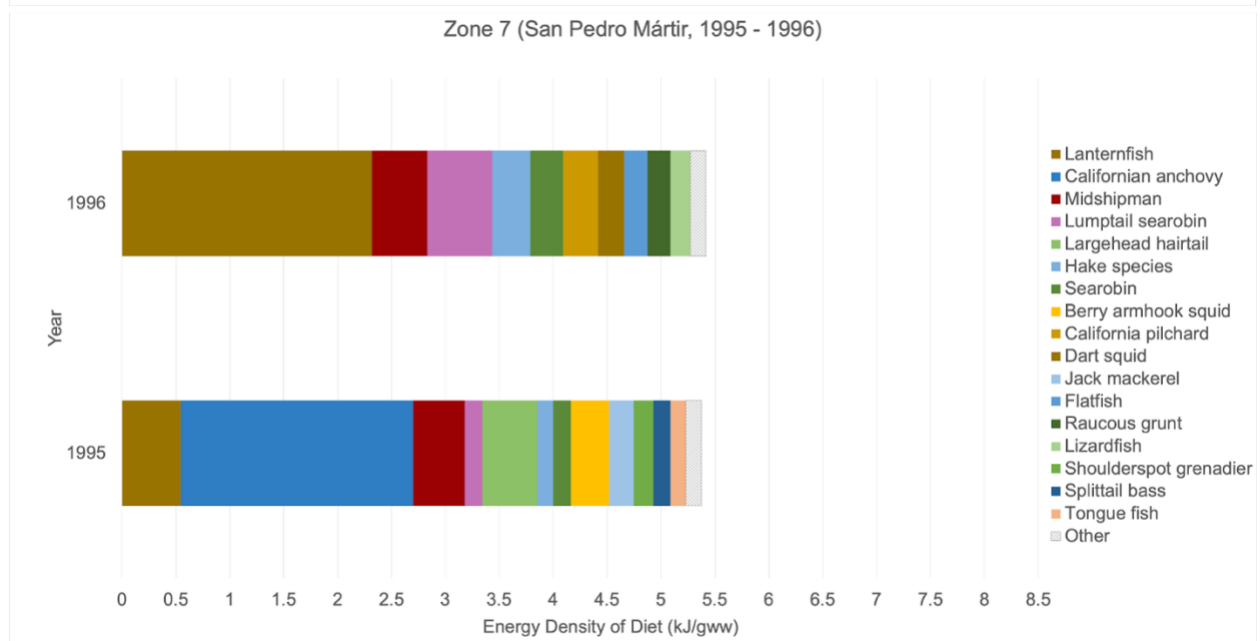
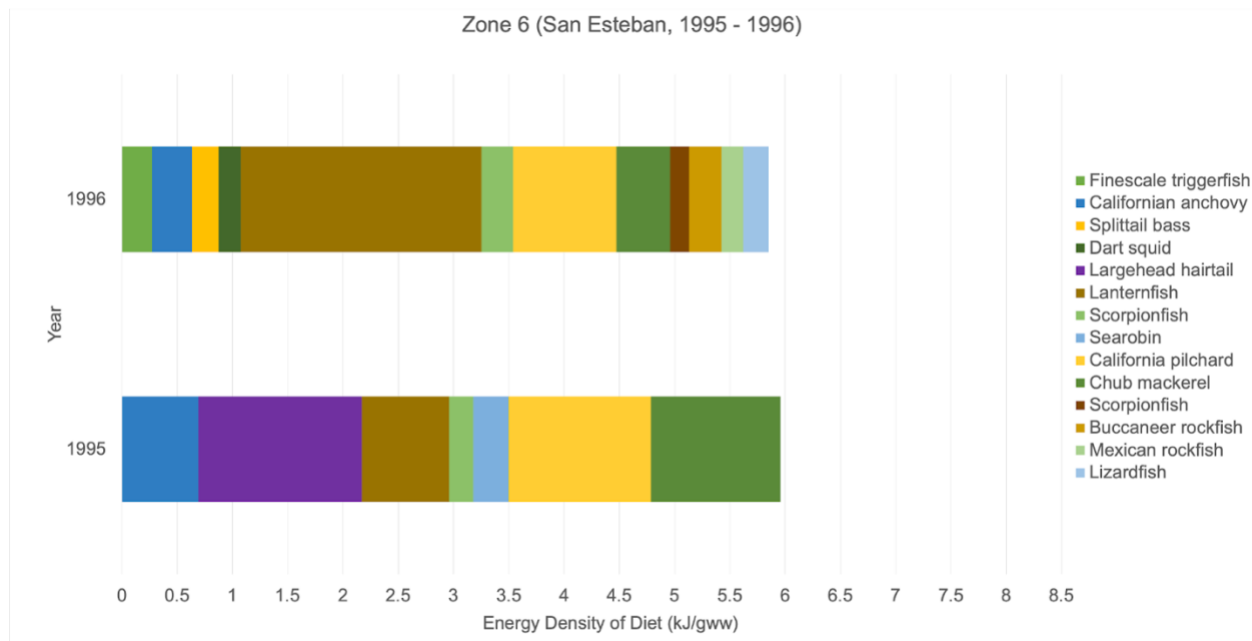


Figure S20. Energy density of diets of California sea lions in the Gulf of California (Zones 3–5). Average energy density and energetic content contributions (average weighted energy density) of the top 17 prey species to the total energetic content of the diet for rookeries in the Gulf of California from frequency of occurrence data (to maintain consistency with Figure 14 and allow for comparisons between the study areas). ‘Other’ category represents all other species in the diet beyond the top 17. Data availability differs between rookeries: Zone 3–Isla Lobos available diet data (1995–1996), Zone 4–Machos, Cantiles & Granito (1995–1996, 2016, 2018), Zone 5–Rasito (1995–1996).



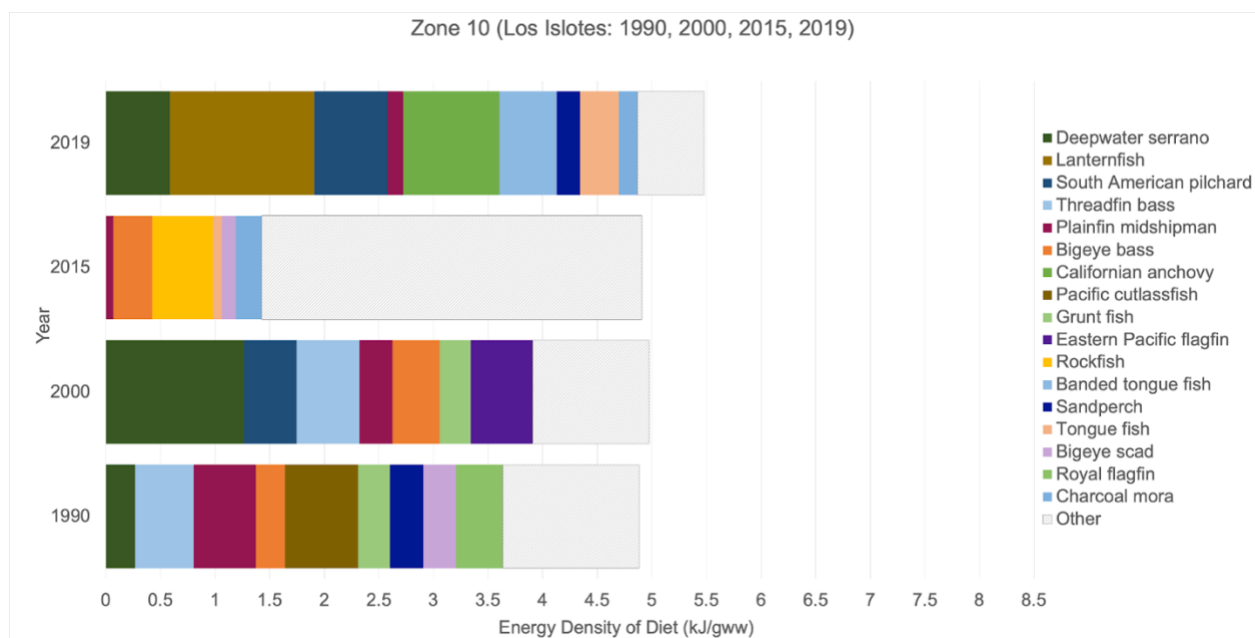


Figure S21. Energy density of diets of California sea lions in the Gulf of California (Zones 6, 7 & 10). Average energy density and energetic content contributions (average weighted energy density) of the top 17 prey species to the total energetic content of the diet for rookeries in the Gulf of California from frequency of occurrence data (to maintain consistency with Figure 14 and allow for comparisons between the study areas). ‘Other’ category represents all other species in the diet beyond the top 17. Data availability differs between rookeries: Zone 6–San Esteban available diet data (1995–1996), Zone 7–San Pedro Mártir (1995–1996), Zone 10–Los Islotes (1990, 2000, 2015, 2019).

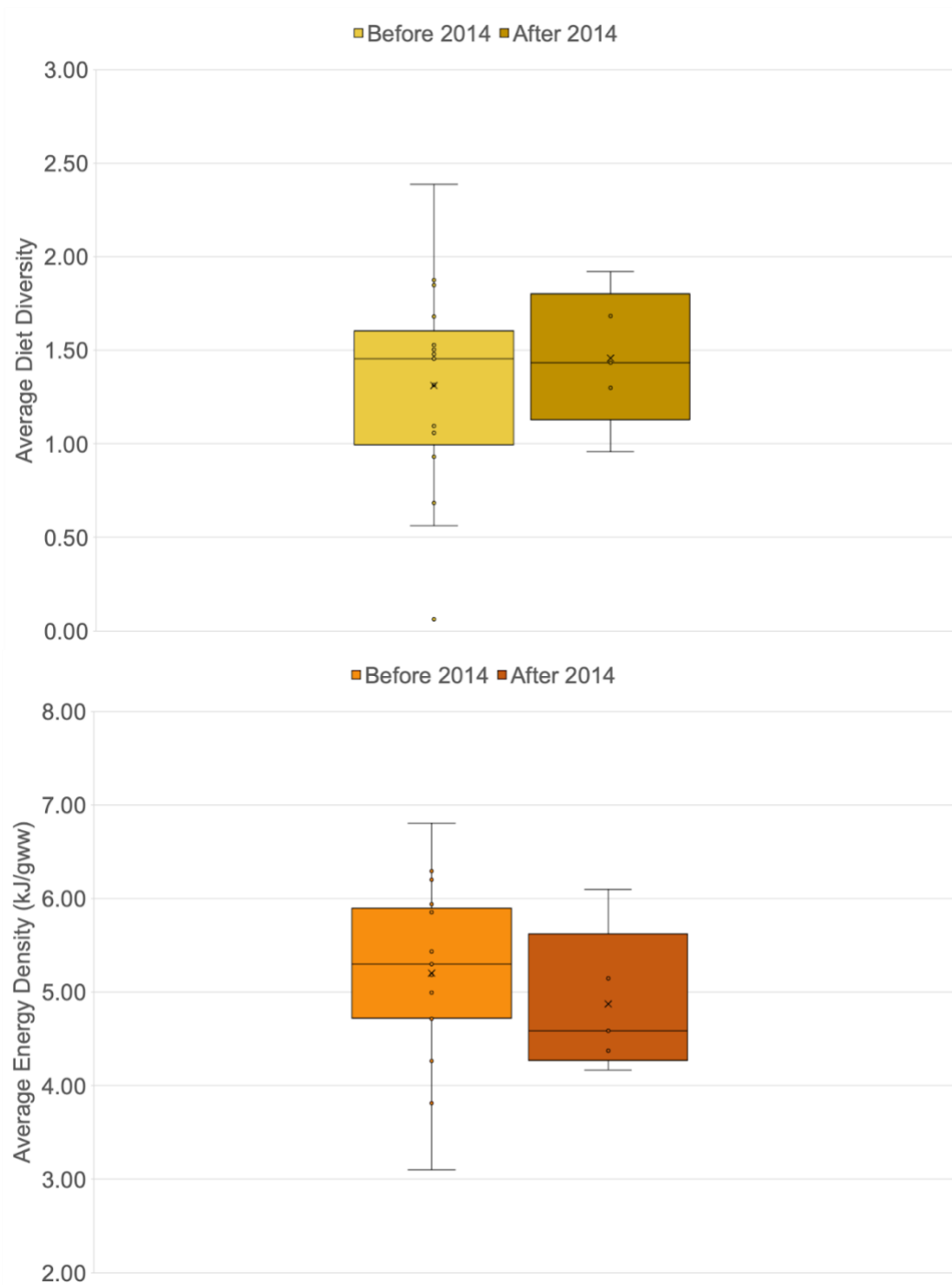


Figure S22. Average diet diversity (top panel) and average energy density (bottom panel) from index of importance data before and after 2014. Bars represent averaged data (mean value \pm standard error) from all Gulf of California groupings. Data represent the diversity and energy density values for each matching diet and population year grouping from available data at the level of the rookery. No significant differences were found between mean diversity values nor energy density between eras.

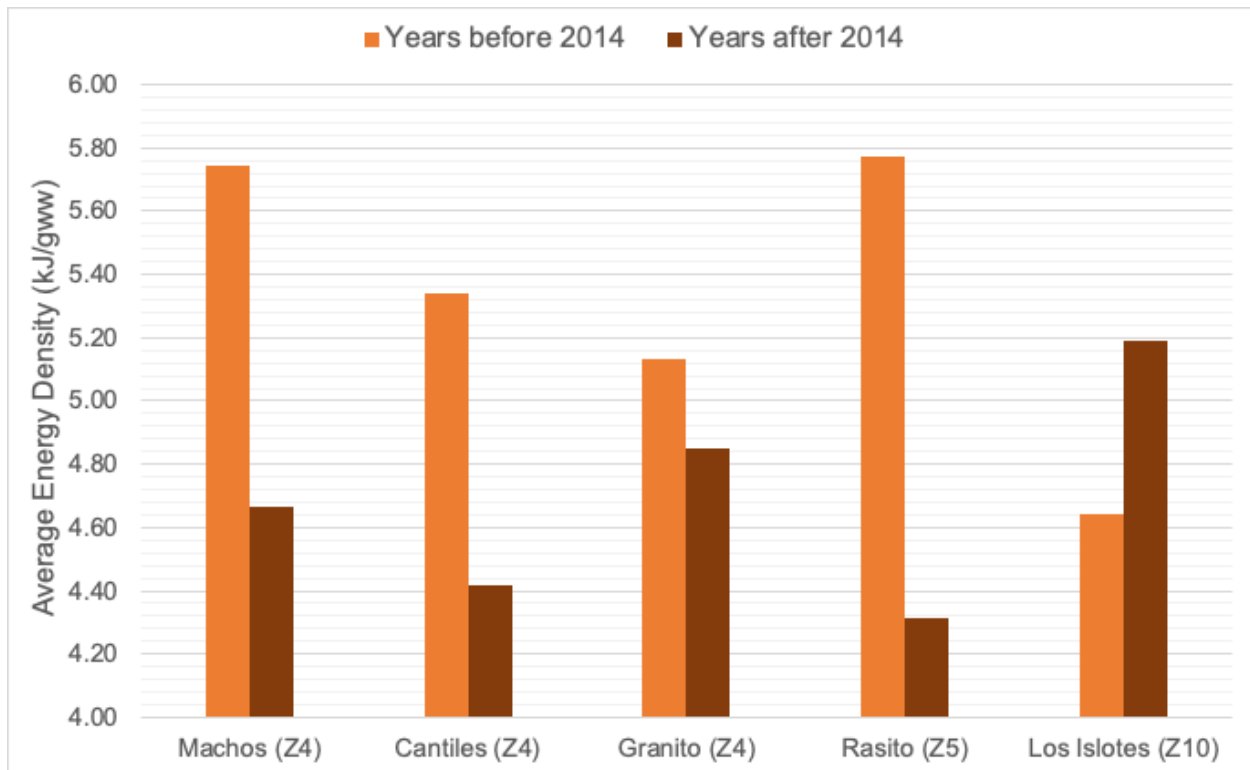


Figure S23. Average energy density from frequency of occurrence data from rookeries in Zones 4, 5, & 10 before and after 2014. Only rookeries within Zones with matched data before and after 2014 are included in this figure, their Zone number is shown in brackets. Zones that are not shown here lacked data after 2014 and were excluded from this figure.

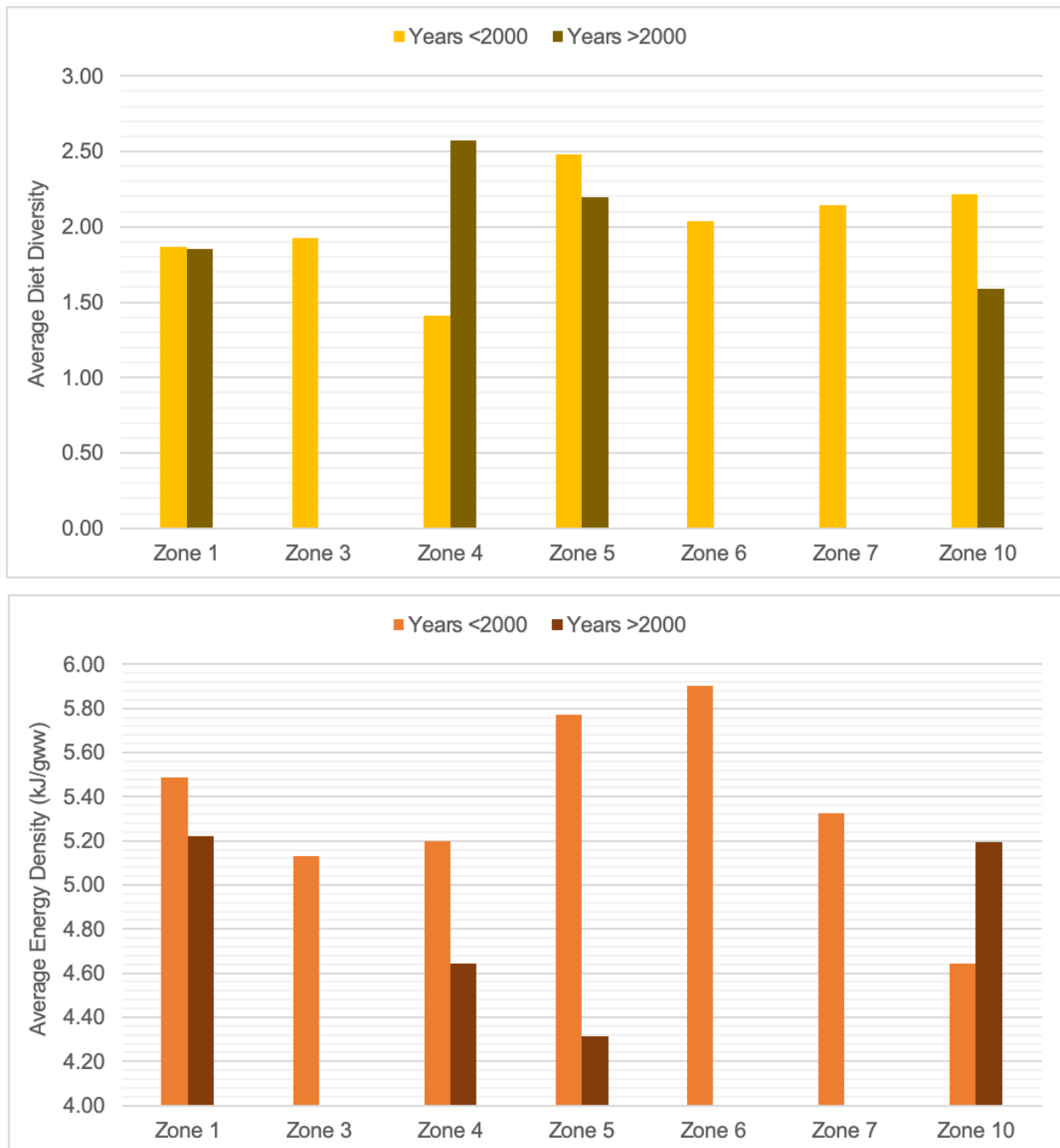


Figure S24. Average diet diversity (top panel) and energy density (bottom panel) by Zones from frequency of occurrence data. Zone numbers decrease in latitude from the Channel Islands (Zone 1) to the southernmost rookery in the Gulf of California, Los Islotes (Zone 10). Average diversity and energy density values were split by two eras: before and after the year 2000.

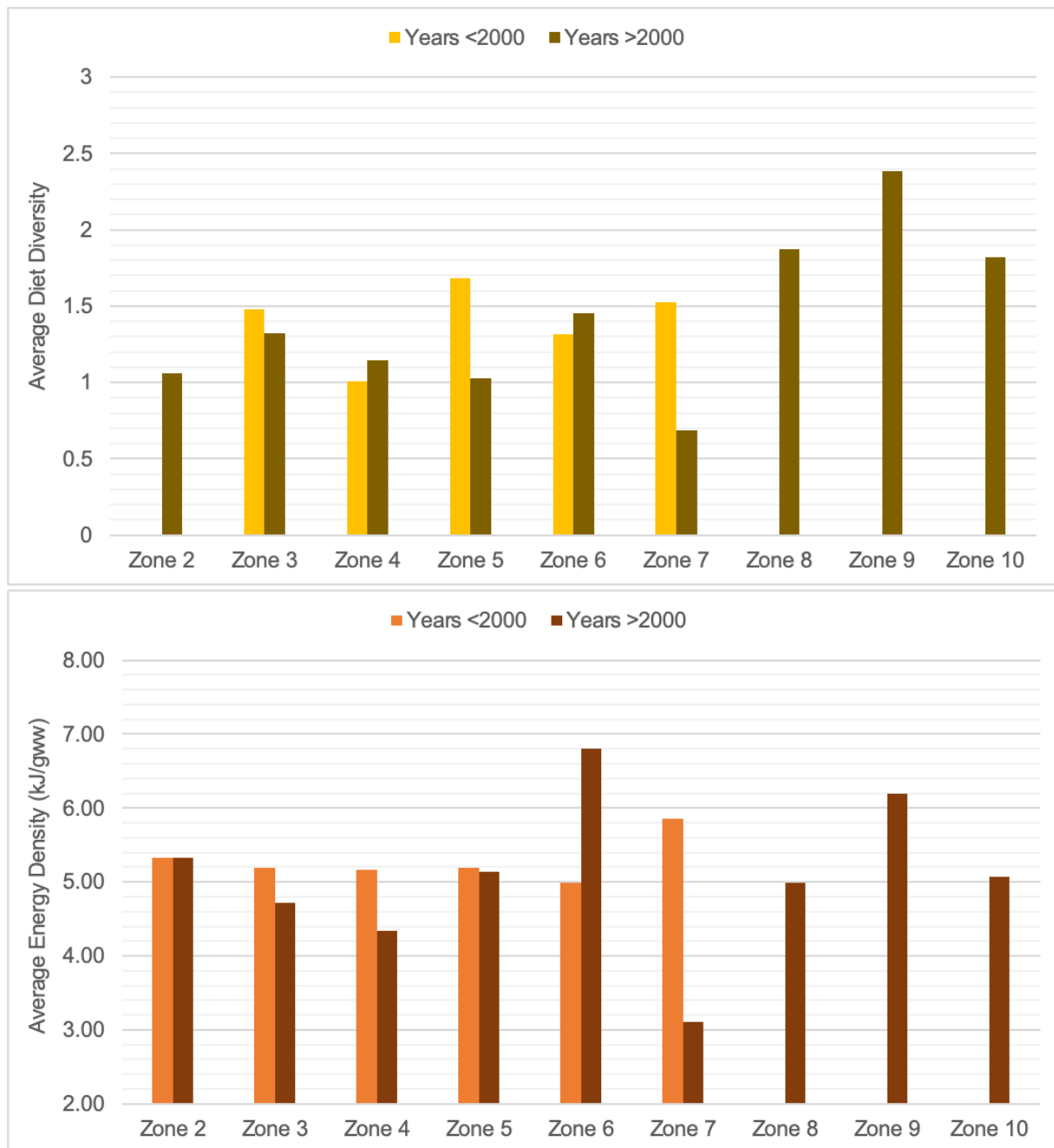


Figure S25. Average diet diversity (top panel) and energy density (bottom panel) by Zones from index of importance data. Zones include rookeries in the Gulf of California only, Zone numbers decrease in latitude from Rocas Consagradas (Zone 2) Islotes (Zone 10). Average diversity and energy density values were split by two eras: before and after the year 2000.

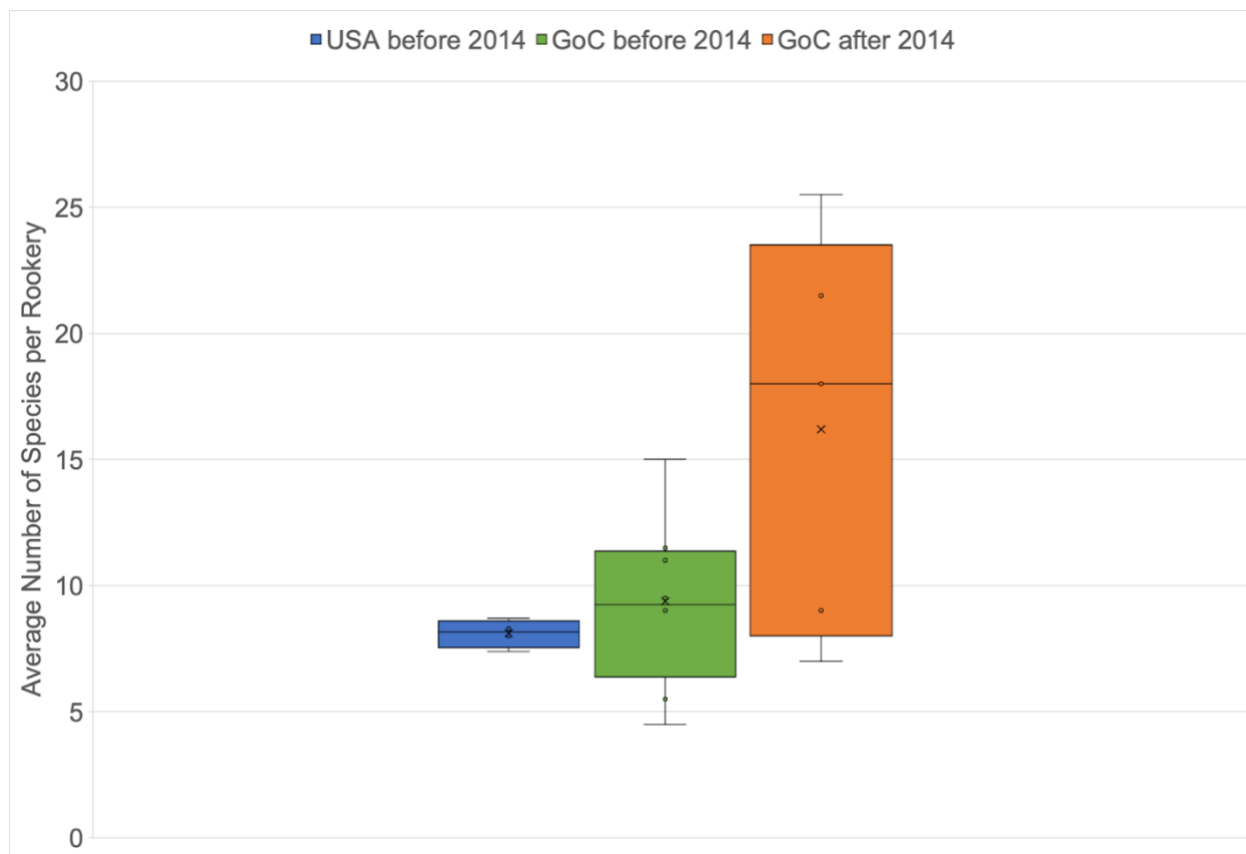


Figure S26. Average number of prey species per rookery before and after 2014. Bars represent averaged data (mean value \pm standard error). Average number of species is based on frequency of occurrence data. There was no data after 2014 available for the Channel Islands.

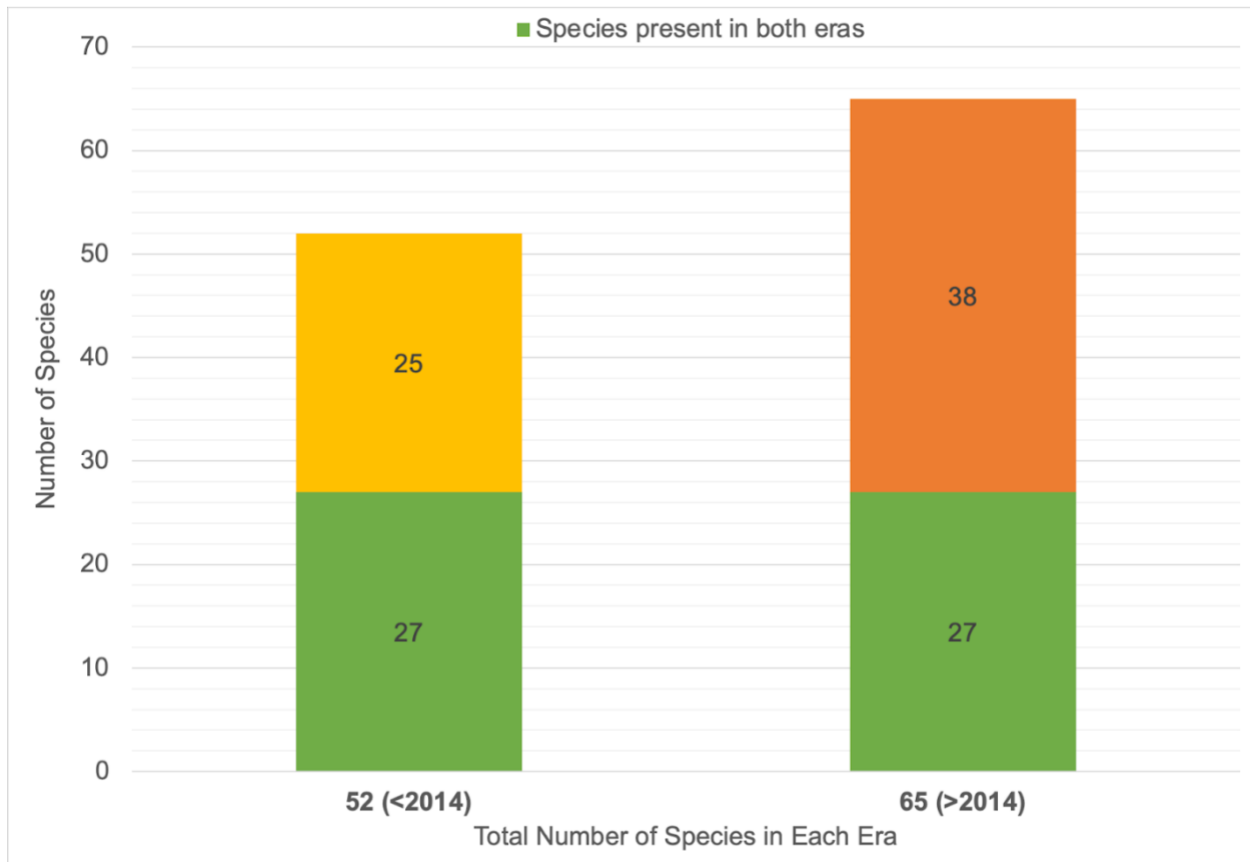


Figure S27. Total number of prey species in the Gulf of California before and after 2014 from frequency of occurrence diet. The bar on the left represents prey species before 2014, the bar on the right represents prey species after 2014. Green bars show number of species present in both eras, yellow bar shows species only present before 2014, and orange bar shows number of species present only after 2014.

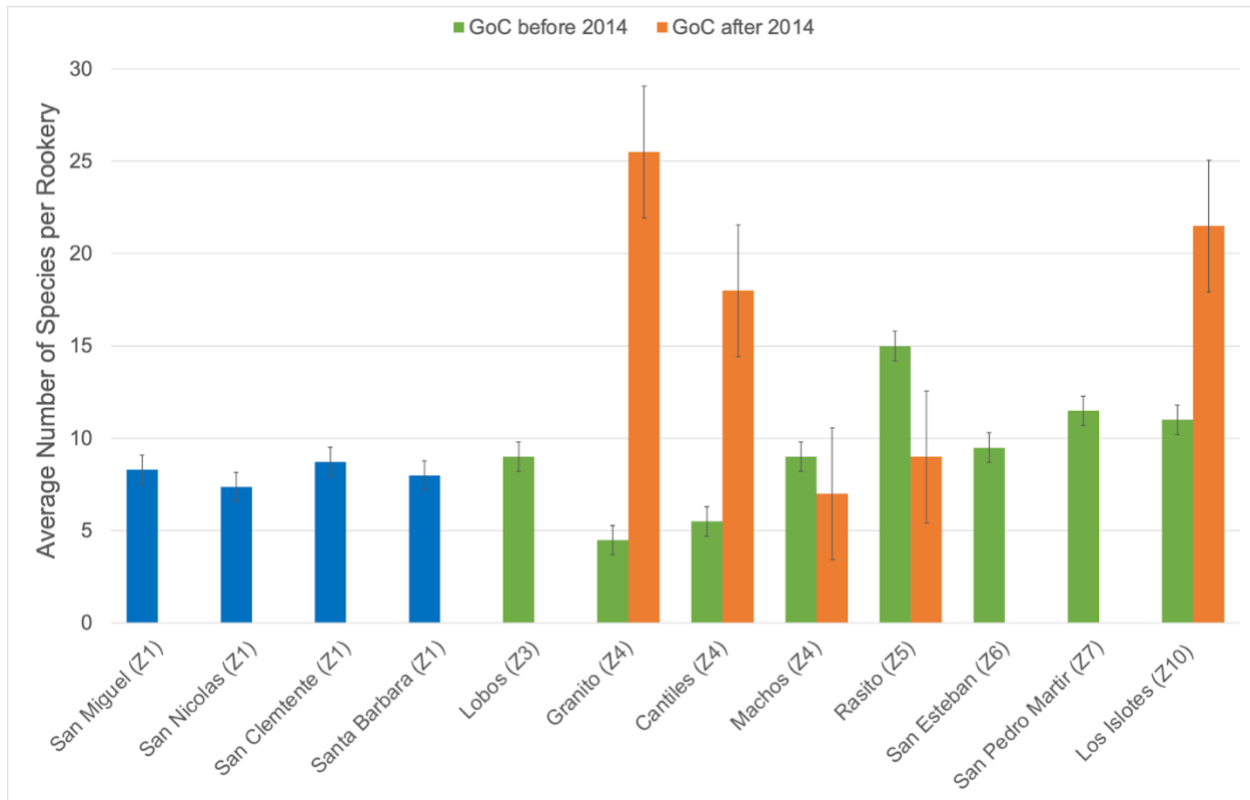


Figure S28. Average number of prey species per rookery before and after 2014 from frequency of occurrence data. Blue bars represent each of the Channel Islands before 2014, each rookery with available data in the Gulf of California is shown before 2014 (green bars) and after 2014 (orange bars). Zone number is shown in brackets.

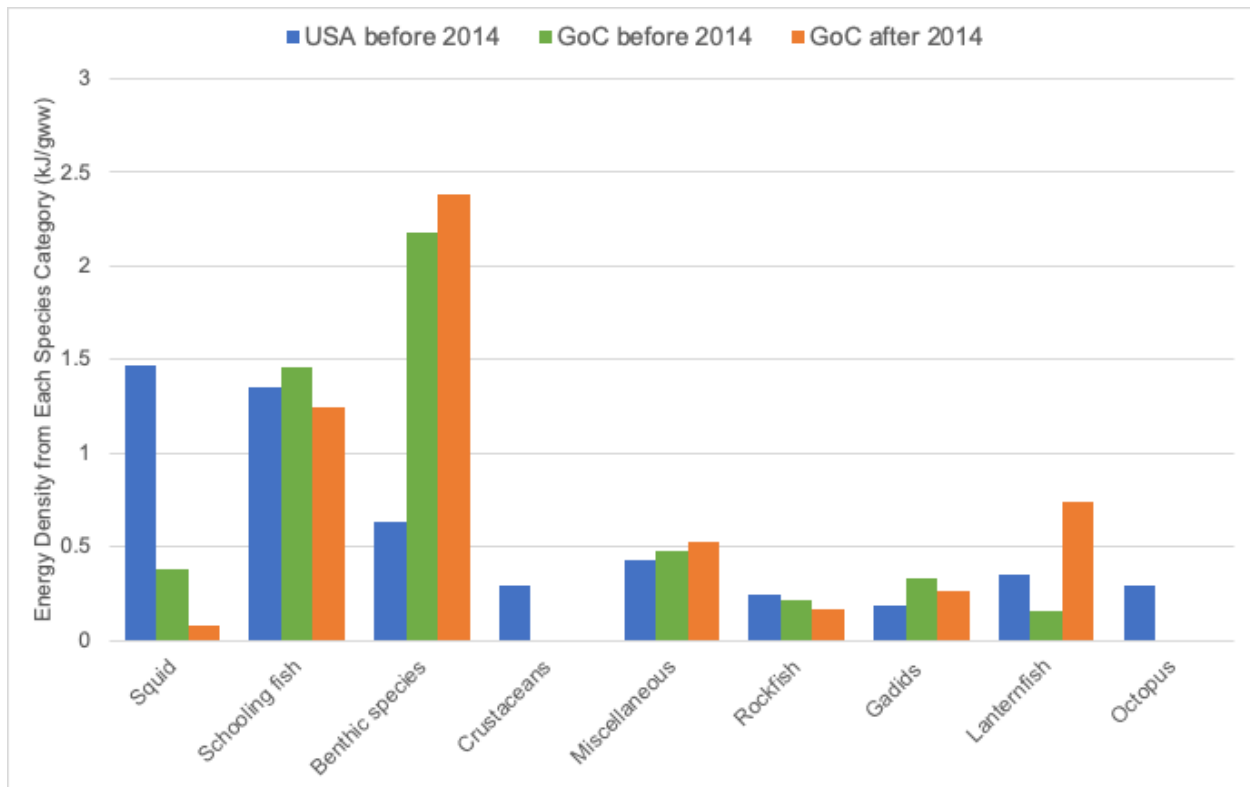


Figure S29. Average energy density from each prey species category in the Channel Islands, and the Gulf of California before and after 2014. Crustaceans and octopus were categories only found in the Channel Islands.

Table S1. Raw diet and population data from by rookery-year grouping.

Rookery-year groupings	Zone	Index	Average diet diversity	Weighted energy density (kJ/gww)	Population Change (%)	Average energy density	Pup change (%)
San Miguel 2000–2006	1	FO	1.70	5.76	5.03%	5.6	3.2%
San Miguel 2009–2011	1	FO	2.00	4.68	7.80%	5.1	11.6%
San Nicolas 1981–1986 (grouped)	1	FO	1.92	5.66	-2.92%	5.36	-4.8%
San Nicolas 1981–1986	1	FO	1.68	5.65	-2.92%	5.36	-4.8%
San Nicolas 1981–1995	1	FO	1.95	5.46	9.47%	5.85	32.0%
Santa Barbara 1981–1995 (grouped)	1	FO	1.87	5.48	9.95%	5.85	24.8%
San Clemente 1981–1995 (grouped)	1	FO	1.81	5.59	4.51%	5.74	7.7%
San Clemente 1981–1986	1	FO	1.96	5.09	-1.61%	5.50	-1.9%
Los Islotes 1990	10	FO	2.40	4.59	2.43%	4.7	5.12%
San Pedro Mártir 1995–96	7	FO	2.14	5.3	-1.53%	4.93	-0.18%
San Esteban 1995–96	6	FO	2.04	5.9	7.29%	5.08	-1.52%
Rasito 1996	5	FO	2.48	5.77	-7.60%	5.15	2.31%
Machos 1995	4	FO	1.96	5.74	-1.17%	5.29	4.37%
Cantiles 1995–96	4	FO	1.36	4.51	6.15%	5.05	6.76%
Granito 1995–96	4	FO	0.90	5.34	3.70%	5.15	12.74%
Isla Lobos 1995–96	3	FO	1.93	5.13	-2.03%	5.57	5.16%
Los Islotes 2000	10	FO	2.03	4.69	7.37%	5.00	3.26%

Rookery-year groupings	Zone	Index	Average diet diversity	Weighted energy density (kJ/gww)	Population Change (%)	Average energy density	Pup change (%)
Rasito 2016	5	FO	2.20	4.31	7.25%	4.31	13.52%
Machos 2016	4	FO	2.01	4.66	-11.65%	4.92	17.32%
Cantiles 2016	4	FO	2.70	4.42	7.09%	4.58	7.92%
Granito 2016, 2018	4	FO	3.02	4.85	7.09%	5.15	12.71%
Los Islotes 2015, 2019	10	FO	1.59	5.19	-1.18%	5.1	8.44%
San Pedro Mártir 1995–96	7	IIMP	1.526	5.86	-1.5%	5.58	-0.2%
San Esteban 1995–96	6	IIMP	1.315	6.29	7.3%	6.48	-1.5%
Rasito 1995–96	5	IIMP	1.682	5.19	-11.2%	5.50	3.9%
Machos 1995	4	IIMP	1.528	5.94	-1.2%	5.75	4.4%
Cantiles 1995–96	4	IIMP	0.931	4.27	6.1%	4.85	6.8%
Granito 1995–96	4	IIMP	0.561	5.30	3.7%	5.37	12.7%
Isla Lobos 1995–96	3	IIMP	1.479	5.19	-2.0%	4.47	5.2%
Los Islotes 2002	10	IIMP	1.848	4.7	4.4%	5.08	-0.2%
San Esteban 2002	6	IIMP	1.503	5.3	9.2%	5.42	16.3%
Rasito 2002	5	IIMP	0.062	5.43	5.5%	4.85	12.9%
San Pedro Mártir 2002	7	IIMP	0.685	3.10	-0.7%	4.98	-6.4%
Cantiles 2002	4	IIMP	1.096	3.81	-3.6%	3.81	-8.8%
Isla Lobos 2002	3	IIMP	1.326	4.71	4.5%	5.01	-2.1%
San Pedro Nolasco 2002	8	IIMP	1.874	4.99	-1.4%	5.11	-2.1%
Partido 2002	5	IIMP	1.454	6.81	-7.9%	5.29	-3.9%

Rookery-year groupings	Zone	Index	Average diet diversity	Weighted energy density (kJ/gww)	Population Change (%)	Average energy density	Pup change (%)
Rocas Consagradas 2002	2	IIMP	1.060	5.33	5.4%	4.63	5.4%
Farallón de San Ignacio 2002	9	IIMP	2.386	6.20	-3.8%	4.94	-5.2%
Los Islotes 2015	10	IIMP	0.957	4.38	1.3%	5.03	8.2%
Rasito 2016	5	IIMP	1.921	4.17	7.2%	4.31	13.5%
Granito 2016, 2018	4	IIMP	1.300	4.59	6.6%	4.84	12.7%
Cantiles 2016, 2018	4	IIMP	1.433	5.15	7.1%	4.90	7.9%
Los Islotes 2019	10	IIMP	1.684	6.10	-3.7%	5.09	8.6%

Table S2. Raw diet and population data by Zone-era grouping.

Zone	Year	Index	Average diet diversity	Population change (%)	Weighted average energy density (kJ/gww)	Average energy density	Median population
Zone 1 – Channel Islands	1981–1995	FO	1.87	2.7%	5.49	5.61	9,216
Zone 1 – Channel Islands	2000–2011	FO	1.85	6.4%	5.22	5.36	44,720
Zone 3 – Isla Lobos	1995–1996	FO	1.93	-2.0%	5.13	5.57	2,822
Zone 4 – Machos, Cantiles, Granito	1995–1996	FO	1.41	2.9%	5.20	5.16	1,355
Zone 4 – Machos, Cantiles, Granito	2016, 2018	FO	2.58	0.8%	4.64	4.88	696
Zone 5 – Rasito	1996	FO	2.48	-7.6%	5.77	5.15	362
Zone 5 – Rasito	2016	FO	2.20	7.2%	4.31	4.31	308
Zone 6 – San Esteban	1995–1996	FO	2.04	7.3%	5.90	5.08	7,171
Zone 7 – San Pedro Mártir	1995–1996	FO	2.14	-1.5%	5.32	4.93	1,963
Zone 10 – Los Islotes	1990	FO	2.21	4.9%	4.64	4.85	347
Zone 10 – Los Islotes	2015, 2019	FO	1.59	-1.2%	5.19	5.06	538
Zone 2 – Rocas Consagradas	2002	IIMP	1.06	5%	5.33	4.63	839
Zone 3 – Isla Lobos	1995–1996	IIMP	1.48	-2%	5.19	4.47	2,822

Zone	Year	Index	Average diet diversity	Population change (%)	Weighted average energy density (kJ/gww)	Average energy density	Median population
Zone 3 – Isla Lobos	2002	IIMP	1.33	4%	4.71	5.01	1,897
Zone 4 – Machos, Cantiles, Granito	1995–1996	IIMP	1.01	3%	5.17	5.32	1,355
Zone 4 – Machos, Cantiles, Granito	2002	IIMP	1.10	-4%	3.81	3.81	1,090
Zone 4 – Machos, Cantiles, Granito	2016, 2018	IIMP	1.20	7%	4.87	4.87	729
Zone 5 – Rasito, Partido	1995–1996	IIMP	1.68	-11%	5.19	5.50	366
Zone 5 – Rasito, Partido	2002	IIMP	0.76	-1%	6.12	5.07	507
Zone 5 – Rasito, Partido	2016	IIMP	1.30	7%	4.17	4.31	308
Zone 6 – San Esteban	1995–1996	IIMP	1.32	7%	4.99	5.11	7,171
Zone 6 – San Esteban	2002	IIMP	1.45	9%	6.81	5.29	6,334
Zone 7 – San Pedro Mártir	1995–1996	IIMP	1.53	-2%	5.86	5.58	7,171
Zone 7 – San Pedro Mártir	2002	IIMP	0.69	-1%	3.10	4.98	2,405

Zone	Year	Index	Average diet diversity	Population change (%)	Weighted average energy density (kJ/gww)	Average energy density	Median population
Zone 8 – San Pedro Nolasco	2002	IIMP	1.87	-1%	4.99	5.11	937
Zone 9 – Farallón de San Ignacio	2002	IIMP	2.39	-4%	6.20	4.94	643
Zone 10 – Los Islotes	2002	IIMP	1.85	4%	4.72	5.08	404
Zone 10 – Los Islotes	2015	IIMP	1.92	1%	4.38	5.03	538
Zone 10 – Los Islotes	2019	IIMP	1.68	-4%	6.10	5.09	659

Table S3. List of 114 diet prey species (scientific and common name) showing their average energy density, category assigned, and country where it appeared in the data. Some species had the same scientific name, but different common names depending on the region. Categories: B: benthic species, C: crustaceans, G: gadids, L: lanternfish, O: octopus, R: rockfish, SF: schooling fish, S: squid, M: miscellaneous.

Scientific name	Common name	Energy Density (kJ/gww)	Category	Country
<i>Abraliopsis affinis</i>	Squid	4.40	S	MEX
<i>Abraliopsis species</i>	Squids	4.40	S	USA
<i>Anisotremus davidsonii</i>	Xantic sargo	4.88	B	MEX
<i>Apogon retrosella</i>	Barspot cardinalfish	4.70	B	MEX
<i>Argentina sialis</i>	North-Pacific argentine	3.57	M	MEX
<i>Atherinops species</i>	Topsmelt silverside	6.20	SF	MEX
<i>Atherinopsis californiensis</i>	Jack silverside	6.20	M	MEX
<i>Aulopus</i>	Royal flagfin	4.43	B	MEX
<i>Aulopus bajacali</i>	Eastern Pacific flagfin	4.43	B	MEX
<i>Balistes polylepis</i>	Finescale triggerfish	3.84	B	MEX
<i>Bodianus diplotaenia</i>	Mexican hogfish	3.84	B	MEX
<i>Brommophycis marginata</i>	Red brotula	3.39	B	MEX
<i>Calamus brachysomus</i>	Pacific porgy	7.45	B	MEX
<i>Caulolatilus princeps</i>	Ocean whitefish	7.45	B	MEX
<i>Ceratoscopelus townsendi</i>	Dogtooth lampfish	7.16	L	MEX
<i>Cetengraulis mysticetus</i>	Pacific anchoveta	6.01	SF	MEX
<i>Chromis punctipinnis</i>	Blacksmith damselfish	4.68	B	USA
<i>Citharichthys species</i>	Flatfish	3.33	B	MEX
<i>Clupea pallasii</i>	Pacific herring	7.51	SF	USA
<i>Coelorinchus scaphopsis</i>	Shoulderspot grenadier	5.10	G	MEX
<i>Cololabis saira</i>	Pacific saury	7.50	M	USA
<i>Cynoscion reticulatus</i>	Shorefish	7.99	B	MEX
<i>Decapodiformes</i>	Superorder of squids	4.60	S	USA
<i>Diaphus theta</i>	California headlightfish	9.88	L	MEX
<i>Diplectrum macroposoma</i>	Mexican sand perch	4.50	B	MEX
<i>Diplectrum pacificum</i>	Inshore sand perch	4.03	B	MEX
<i>Diplectrum species</i>	Sandperch	5.02	B	MEX
<i>Doryteuthis opalescens</i>	Opalescent inshore squid	3.70	S	USA
<i>Dosidicus gigas</i>	Humboldt squid	5.39	S	MEX
<i>Engraulidae</i>	Anchovies	6.17	SF	MEX
<i>Engraulis mordax</i>	Californian anchovy	6.70	SF	MEX

Scientific name	Common name	Energy Density (kJ/gww)	Category	Country
<i>Engraulis mordax</i>	Northern anchovy	6.80	SF	USA
<i>Girella nigricans</i>	Rudderfish	4.40	M	MEX
<i>Gonatopsis borealis</i>	Boreopacific armhook squid	4.20	S	USA
<i>Gonatus berryi</i>	Berry armhook squid	5.02	S	MEX
<i>Gonatus onyx</i>	Clawed armhook squid	5.86	S	USA
<i>Gonatus species</i>	Armhook squid	5.90	S	USA
<i>Haemulidae species</i>	Grunt fish	4.88	B	MEX
<i>Haemulon californiensis</i>	Yellowspotted grunt	4.88	M	MEX
<i>Haemulon flaviguttatum</i>	Greybar grunt	4.88	M	MEX
<i>Haemulon sexfasciatum</i>	Scaled-fin grunt	4.88	SF	MEX
<i>Haemulon species</i>	Californian salema	4.88	SF	MEX
<i>Haemulopsis leuciscus</i>	Raucous grunt	4.88	B	MEX
<i>Haemulopsis species</i>	Grunt fish	4.88	B	MEX
<i>Hemanthias peruanus</i>	Splittail bass	4.50	SF	MEX
<i>Hemanthias species</i>	Sea bass	4.50	B	MEX
<i>Hermosilla azurea</i>	Zebra perch	4.40	SF	MEX
<i>Holacanthus passer</i>	King angelfish	7.45	B	MEX
<i>Icelinus tenuis</i>	Spotfin sculpin	5.82	B	MEX
<i>Lepophidium prorates</i>	Prowspine cusk eel	3.39	B	MEX
<i>Lestidiops species</i>	Barracudina	4.30	SF	MEX
<i>Leuroglossus stilbius</i>	California smoothtongue	3.90	M	USA
<i>Loliolopsis diomedae</i>	Dart squid	3.75	S	MEX
<i>Lycodes corteziensis</i>	Bigfin eelpout	7.60	B	USA
<i>Merluccius productus</i>	North Pacific hake	4.20	G	MEX
<i>Merluccius productus</i>	Pacific Hake	4.20	G	USA
<i>Merluccius species</i>	Hake	4.07	G	MEX
<i>Micropogonias ectenes</i>	Slender croaker	7.99	B	MEX
<i>Micropogonias species</i>	Croaker	7.99	B	MEX
<i>Myctophidae</i>	Lanternfish	7.62	L	MEX
<i>Nannobranchium species</i>	Lanternfish	7.63	L	MEX
<i>Octopus rubescens</i>	East Pacific red octopus	3.30	O	USA
<i>Octopus species</i>	Octopus	3.40	O	USA, MEX
<i>Oegopsida</i>	Pelagic squid	4.50	S	MEX
<i>Onychoteuthidae</i>	Hooked squid family	5.40	S	USA

Scientific name	Common name	Energy Density (kJ/gww)	Category	Country
<i>Onychoteuthis borealijaponicus</i>	Boreal Clubhook Squid	5.48	S	USA
<i>Ophidion scrippsae</i>	Basketweave cusk-eel	3.39	B	MEX
<i>Ophidion species</i>	Cusk-eels	3.39	B	MEX
<i>Ophistonema species</i>	Herrings	7.47	SF	MEX
<i>Orthopristis reddingi</i>	Bronze-striped grunt	4.88	SF	MEX
<i>Oxylebius pictus</i>	Painted greenling	4.44	B	MEX
<i>Paralabrax clathratus</i>	Kelp bass	4.45	M	MEX
<i>Paralabrax species</i>	Rock bass	4.45	B	MEX
<i>Paralichthys californicus</i>	California halibut	3.81	B	MEX
<i>Physiculus nematopus</i>	Charcoal mora	4.00	G	MEX
<i>Physiculus species</i>	Codling	4.00	G	MEX
<i>Pleuroncodes planipes</i>	Pelagic red crab (lobster)	6.70	C	USA
<i>Pontinus furcirhinus</i>	Red scorpionfish	3.19	B	MEX
<i>Pontinus species</i>	Scorpionfish	3.19	B	MEX
<i>Porichthys notatus</i>	Plainfin midshipman	3.36	B	MEX
<i>Porichthys species</i>	Midshipman	3.36	B	MEX
<i>Prionotus species</i>	Searobin	4.63	B	MEX
<i>Prionotus stephanophrys</i>	Lumptail searobin	4.63	B	MEX
<i>Pronotogrammus eos</i>	Bigeye bass	4.45	B	MEX
<i>Pronotogrammus multifasciatus</i>	Threadfin bass	4.45	B	MEX
<i>Sarda lineolata</i>	Pacific bonito	7.04	SF	MEX
<i>Sardinops caeruleus</i>	California pilchard	7.47	SF	MEX
<i>Sardinops sagax</i>	South American pilchard	7.50	SF	MEX
<i>Sardinops sagax</i>	Pacific sardine	7.50	SF	USA
<i>Scomber japonicus</i>	Chub mackerel	6.80	SF	MEX
<i>Scomber japonicus</i>	Pacific mackerel	6.80	SF	USA
<i>Scopelogadus unicolor</i>	Pacific blackchin	7.62	M	MEX
<i>Scorpaenidae</i>	Scorpionfish	3.19	M	MEX
<i>Sebastes exsul</i>	Buccaneer rockfish	5.51	R	MEX
<i>Sebastes jordani/species</i>	Rockfish	5.60	R	USA
<i>Sebastes macdonaldi</i>	Mexican rockfish	5.51	R	MEX
<i>Sebastes species</i>	Rockfish	5.60	R	MEX
<i>Selar crumenophthalmus</i>	Bigeye scad	6.27	SF	MEX
<i>Serranus aquidens/aequidens</i>	Deepwater serrano	4.45	B	MEX

Scientific name	Common name	Energy Density (kJ/gww)	Category	Country
<i>Specieshyaena argentea</i>	Pacific barracuda	3.36	M	MEX
<i>Stenobranchius leucopsarus</i>	Northern lampfish	9.70	L	USA
<i>Strongylura exilis</i>	Californian needlefish	6.20	SF	MEX
<i>Symbolophorus californiensis</i>	Bigfin lanternfish	7.07	L	MEX
<i>Symphurus fasciolaris</i>	Banded tongue fish	4.00	B	MEX
<i>Symphurus species</i>	Tongue fish	4.00	B	MEX
<i>Synodus lucioceps</i>	California lizardfish	4.43	B	MEX
<i>Synodus species</i>	Lizardfish	4.25	B	MEX
<i>Trachurus species</i>	Jack mackerel	6.30	SF	MEX
<i>Trachurus symmetricus</i>	Pacific jack mackerel	6.27	SF	MEX
<i>Trachurus symmetricus</i>	Jack mackerel	6.30	SF	USA
<i>Trichiurus lepturus</i>	Largehead hairtail	4.76	M	MEX
<i>Trichiurus nitens</i>	Pacific cutlassfish	5.05	M	MEX
<i>Triphoturus mexicanus</i>	Mexican lampfish	7.07	L	MEX
<i>Zaniolepis species</i>	Combfish	7.60	B	USA