



FEATURE ARTICLE

Spatio-temporal diet variability of the California sea lion *Zalophus californianus* in the southern California Current Ecosystem

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ABSTRACT: Characterizing predator diets is essential to understanding food web dynamics. We investigated the dietary breadth and variation of the California sea lion (CSL) *Zalophus californianus* at 3 of the California Channel Islands from 1981–2015. Prey species were identified from hard parts and soft-tissue remains of pyrosomes recovered from fecal samples, revealing a diverse diet of fish and cephalopods. Percent frequency of occurrence and percent split-sample frequency of occurrence were used to describe long-term trends, correlations between prey taxa, diet diversity, and diet similarity. The most common of 142 prey taxa identified to species were market squid *Doryteuthis opalescens*, northern anchovy *Engraulis mordax*, shortbelly rockfish *Sebastes jordani*, jack mackerel *Trachurus symmetricus*, Pacific sardine *Sardinops sagax*, Pacific hake *Merluccius productus*, and Pacific mackerel *Scomber japonicus*. Dietary differences were observed between male and female sea lions, and between animals from different islands and seasons. Intra-island diets at 2 locations were more similar than inter-island diets. Important inter-annual and decadal changes in diet were identified. CSL diet shifted from an anchovy-based diet in the 1980s to a market squid based-diet in the 1990s and 2000s, with other prey taxa being consumed more frequently when consumption of those 2 main prey declined. Prey-switching likely provides flexibility needed in the dynamic California Current Ecosystem, and may allow CSLs to adapt to changes in food supply and availability driven by climate change.

KEY WORDS: Foraging ecology · Marine mammal · Pinniped · Fecal analysis · Forage species



California sea lion rookery, San Nicolas Island, USA. Sea lion diet reveals changes in prey availability with climate.

Photo: NOAA Fisheries / Mark S. Lowry

1. INTRODUCTION

Spatially and temporally explicit information on predator–prey interactions is essential to understanding food web dynamics and assessing ecosystem function in marine systems (Koehn et al. 2016, 2017, Kaplan et al. 2017, Pethybridge et al. 2018). Predator diet datasets, an important source for identifying predator–prey interactions, are thus valuable to ecosystem-based fisheries management, as they can provide insights into the dietary requirements of top predators and their potential impact on commercial fish stocks. In marine systems, the complex linkages within pelagic food webs are complicated by the

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effects of environmental variability on multiple timescales. The California Current Ecosystem (CCE) is a productive eastern boundary upwelling ecosystem in the eastern North Pacific that experiences multidecadal variability (Ohman et al. 2013), inter-annual variability (McClatchie 2013), and strong seasonal upwelling (Garcia-Reyes & Largier 2012). The vertical transport of nutrients within this temperate marine ecosystem creates localized areas of high primary productivity, which support fisheries of northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and other pelagic species (Chavez et al. 2003, Checkley & Barth 2009). These forage species (small schooling pelagic fish), in turn serve as food for many birds, large fish, and marine mammals (Szoboszlai et al. 2015).

Inter-annual variability in the CCE is driven by the Eastern Pacific El Niño and Central Pacific El Niño Southern Oscillations which are known to have profound impacts on primary and secondary production that can directly affect successive trophic levels (Barber & Chavez 1983, Chavez et al. 2002, McClatchie 2013, Schmidt et al. 2014, Capotondi & Sardeshmukh 2015), underscoring the importance of determining trophic structure over various timescales that can serve to better predict climate impacts on marine communities. In particular, El Niño and other warm water events affect upwelling, thermocline depth, salinity, water temperature, and current flow in the CCE (McClatchie 2013). These changes subsequently affect the abundance and distribution of forage fishes and squid (McClatchie 2013), which alters the foraging behavior and diet of marine predators, such as large pelagic fishes, seabirds, and pinnipeds (Melin et al. 2008, Weise & Harvey 2008, Glaser 2011, Robinson et al. 2018, Warzybok et al. 2018).

The California sea lion (CSL) *Zalophus californianus* is an abundant pinniped and apex predator of the CCE, ranging from Baja California, Mexico to British Columbia, Canada (Allen et al. 2011). The CSL population discussed in this paper is the US population that primarily breeds at the California Channel Islands in Southern California (Fig. 1). Studies on CSL over the past several decades have highlighted the importance of these predators in the CCE and their utility as ecosystem indicators (Lowry et al. 1991, Weise & Harvey 2008, Orr et al. 2011, Melin et al. 2012, Laake et al. 2018), particularly given their abundance and potential to interact with commercial fisheries. The maximum estimated population growth rate of this population was 7.0% yr⁻¹ during 1975–2014, increasing from 96 997 individuals in 1981 to 306 220 individuals in 2012, before declining to

approximately 257 606 in 2014 (Laake et al. 2018). Recent population surveys have shown that 99.7% of pups are produced at 4 Channel Island rookeries: San Nicolas Island (SNI), San Miguel Island (SMI), Santa Barbara Island (SBI), and San Clemente Island (SCI) (Lowry et al. 2017a; Fig. 1).

A CSL non-pup population of about 250 000 was estimated to consume about 446 000 t of forage per year (McClatchie et al. 2018), and commercial species of fish and squid, including northern anchovy, Pacific sardine, jack mackerel *Trachurus symmetricus*, Pacific mackerel *Scomber japonicus*, Pacific hake *Merluccius productus*, salmonids *Oncorhynchus* spp., and market squid *Doryteuthis opalescens* are important components of the diet (Lowry et al. 1990, 1991, Weise & Harvey 2008, Melin et al. 2010). CSLs have also been reported as bycatch in commercial fisheries (Carretta et al. 2017). Given the high abundance of CSLs and their consumption of commercially important species, understanding CSL foraging patterns over space and time is significant to assessing their impacts on forage communities and managing the subsequent effects of the environment and fishing on the CSL population.

A number of studies on CSL diet conducted over the past century at various haulout sites and rookeries in Mexico and the USA demonstrated variability in the diet, as well as spatial and temporal trends in foraging patterns (Jameson & Kenyon 1977, Everitt et al. 1981, Garcia-Rodriguez & Aurióles-Gamboa 2004, Mellink 2005, Melin et al. 2012, Robinson et al. 2018). Notably, variation in CSL diet has led some researchers to describe them as either being opportunistic feeders (Antonelis et al. 1984) that take advantage of available prey, or as plastic specialist feeders that switch between a limited number of schooling or aggregating species (Lowry et al. 1990, 1991, Weise & Harvey 2008). Prey movement and life history characteristics of prey can influence CSL seasonal consumption (Weise & Harvey 2008), while climate variability has been linked to inter-annual and longer-term prey switching by CSLs (Lowry & Carretta 1999, Weise & Harvey 2008, Robinson et al. 2018).

Fecal sample analysis has become the preferred method for pinniped diet studies because of the high taxonomic resolution of prey identifications and ease in collection and analysis. Prey taxa can be identified from fish otoliths, cephalopod beaks (i.e. mandibles), other hard parts, and soft tissue recovered from fecal samples. While stomach content analysis also provides high levels of taxonomic resolution, stomachs would have to be collected from killed animals (e.g. Fiscus & Baines 1966), from animals that died of nat-

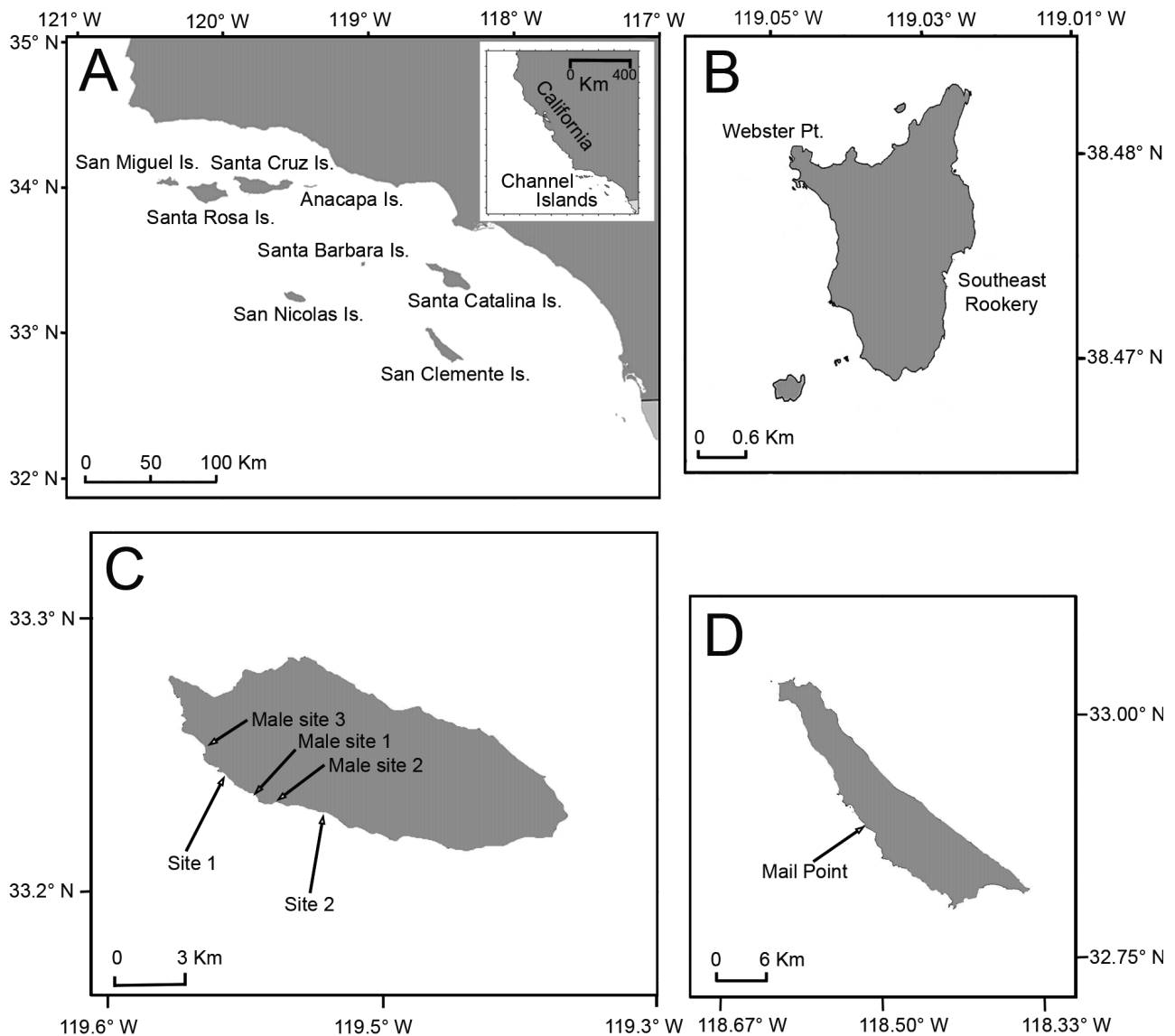


Fig. 1. (A) Location of the Channel Islands, where the California sea lion diet study was conducted during 1981–2015 at Santa Barbara, San Clemente, and San Nicolas Islands. Fecal collection sites are shown for (B) Santa Barbara Island, (C) San Nicolas Island, and (D) San Clemente Island

ural causes whose diet may have been compromised by illness prior to death (e.g. Dyché 1903, Lowry & Folk 1987), or by lavaging stomachs of immobilized live-caught animals (e.g. Antonelis et al. 1994). A number of recent approaches to estimating marine mammal diets, such as biochemical tracer techniques, vary in their taxonomic resolution and specific applications (Pethybridge et al. 2018).

Although the diet of CSLs in the CCE has been well-studied, current datasets do not include high resolution (e.g. seasonal) and long-term (e.g. multi-decadal) diet information on the population that is needed to understand the effects of environmental

variability on the population and the impact of the population on the ecosystem (Szoboszlai et al. 2015). In addition, little is known about the differences in foraging patterns between adult male and female CSLs—differences which could affect the interpretation of prey consumption by the population within regions of the CCE. One CSL diet study using stable isotope analysis found slight differences in stable isotope values between adult males and adult females, suggesting possible partitioning of resources (Orr et al. 2012), and significant diet differences have been observed between sexes of other pinniped species (Schwarz et al. 2018).

Here, we provide findings from the first multi-decadal study on CSLs in the southern CCE derived from an ongoing foraging ecology study at the Channel Islands that has been conducted since 1981. Our findings are summarized from 16 yr of summer sampling at SBI and 35 years of mostly continuous seasonal sampling at SCI and SNI during 1981–2015. Our objectives for this study were to examine the following: (1) prey species commonly consumed by CSLs, (2) seasonal and long-term CSL diet patterns, (3) inter- and intra-island differences in CSL diet, and (4) dietary differences between adult females and adult males.

2. MATERIALS AND METHODS

2.1. Sample collection

2.1.1. Detecting temporal diet patterns

CSL fecal samples were collected during summer at SBI in 1981–1996, year-round at SCI from autumn 1981 through 2015, and year-round at SNI from summer 1981 through 2015 (Fig. 1; Text S1 in the Supplement at www.int-res.com/articles/suppl/m692p001_supp.pdf). During the summer breeding and pupping season, all age-classes are present on the Channel Islands (Allen et al. 2011), while during the non-breeding season, the Channel Islands are mostly inhabited by adult females, pups, and juveniles. At SBI, samples were collected during June, July, and/or August during 1981–1983, and in July during 1984–1996. Samples were collected monthly during 1981–1985 at SCI and 1981–1990 at SNI, then pooled into winter (December, January, and February), spring (March, April, and May), summer (June, July, and August), and autumn (September, October, and November) for seasonal comparisons. Samples were then collected quarterly at SCI during 1986–2015 and at SNI during 1991–2015 in January (winter), late-March or April (spring), July or early August (summer), and October or early November (autumn). Not all months or seasons were sampled each year (Table S1). Henceforth, seasonally pooled monthly samples and quarterly collected samples will be denoted as sampling occasions.

Samples were collected at one site at SCI, 2 sites at SBI, and initially at various sites at SNI which were later narrowed to 2 sites beginning in summer 1991 (Fig. 1). Seasonal (i.e. quarterly) samples were collected during a 1–3 d period.

2.1.2. Sample sizes

After mid-1987 at SCI and 1990 at SNI, our target sample sizes were guided by power analysis conducted by Goodman (1987) on previously collected fecal sample data. This analysis showed that 47 seasonally collected samples were required to detect a percent frequency of occurrence value of $\geq 10\%$, which we use to denote prey species commonly consumed by CSLs (Lowry et al. 1990). Using this sample size allowed us to detect a 1 1/2-fold increase in the fraction occurrence of a prey taxa (indicating an event) and a 3-fold increase in the fraction occurrence of a prey taxa (indicating a major event), with a tolerance for false negatives at an alpha level of 0.05. Following this analysis, 50 samples were collected each season at SCI, and 50 samples were collected each season at Sites 1 and 2 at SNI (totaling 100 samples). Additionally, 50 samples were collected in July through August at Male Sites 1, 2, or 3 at SNI (Fig. 1). Occasionally, the target sample size was not reached during the 1980s and for a small proportion of subsequent visits when too few scats were collected. In these cases, we used 20 samples as a minimum because it allowed us to analyze more samples collected in the 1980s when the target sample size was unknown and many collections were made opportunistically. We recognize that the disparity in sample size between these collection events could bias the percent frequency of occurrence (%FO) index used to describe the diet of CSLs.

2.1.3. Detecting diet patterns between sexes

Generally, sub-adult and adult males increase in abundance during the May–July breeding season, and while some males may occupy reproductive areas (such as Sites 1 and 2 at SNI), most males segregate themselves into exclusively male haulout areas during that time period. In some years during the breeding season, fecal samples were collected at SNI from both male-dominated haulout sites and female-dominated reproductive areas to examine diet patterns between sexes. Male fecal samples were collected from 3 male haulout sites at SNI (Fig. 1) in 1991, 1993, 1995–1997, 1999–2001, and 2003 and compared to fecal samples from female-dominated reproductive Sites 1 and 2 for those years (Fig. 1). Knowing that males were present at female-dominated Sites 1 and 2, we used CSL count data from July aerial photo surveys to discern the proportion of adult females, juveniles, sub-adult males, and adult males present

at those collection sites, as such proportions could affect diet comparisons between sexes.

2.2. Sample processing

All fecal samples were frozen at -20°C until future processing. Prior to processing, samples were thawed for 24–48 h and soaked in water with a small amount of liquid dish soap. Fecal samples were then washed through nested sieves, with the smallest mesh size being 1.0 mm (1981 through March 1983 at SCI), 0.71 mm (April 1983–2005 at SCI and 1981–2005 at SNI and SBI), or 0.5 mm (2006–2015). We assumed that there were no differences in prey hard-part retrieval between the 3 sieve mesh sizes. Hard parts composed of fish sagittal otoliths, cephalopod beaks, shark and skate teeth, cartilaginous vertebrae, and crustacean fragments were collected from the samples for identifying prey-taxon consumed. Soft-tissue remains of pyrosomes were also collected when found in fecal samples during 2013–2015. Prey items were identified to the lowest possible taxonomic level (Text S1).

2.3. Consumption indices

FO and its derivative split sample FO (SSFO; Oleśniuk et al. 1990) were used to describe the presence–absence of prey categories in CSL fecal samples (Text S1). Certain analyses, such as the examination of diet similarity and diversity, require that diet indices sum to 100%. Therefore, we used %SSFO for these analyses because %FO values do not sum to 100%. The %FO index describes the percentage of fecal samples containing a specific prey category or group of prey, and %SSFO index provides a rough estimate of the percentage represented by each prey category in the diet. We recognize that each index is affected by prey size, variation in digestive effects on hard parts of prey, and proportion of different prey consumed. To date, no correction factors have been developed to adjust for these effects on %FO and %SSFO.

Prey taxa were aggregated into categories for various analyses. Common prey were defined as having a seasonal average %FO $\geq 10\%$ and being present in 80% or more of the total number of seasons sampled at each island-rookery (Lowry et al. 1990). Other groups of prey taxa were defined as non-common cephalopods, non-common fishes, and non-common cephalopods and/or fishes. Eschmeyer et al. (1983), Clarke (1986), Antonelis et al. (1994), and FishBase

(Froese & Pauly 2018) were used to identify marine environmental zones occupied by CSL prey taxa. Prey taxa were alternatively grouped (for different analyses) into 3 habitat categories: benthic–demersal, epipelagic, and epipelagic–mesopelagic prey taxa.

To aid with interpretation of patterns in %FO through time, a %FO anomaly index was calculated. The 1981–2015 means and SDs of sampling occasions for SCI and SNI were calculated for each prey category, and these long-term means were subtracted from the %FO value for each sampling occasion. A LOWESS smoother with 0.15 tension was fitted visually to seasonal %FO anomaly values (using Systat 64-bit v.13.00.05 statistical software). Values outside of 1 SD of the island %FO mean reflected anomalous foraging conditions.

2.4. Diet similarity

Various metrics have been used for examining diet similarity, or niche overlap, between 2 communities. The Morisita index of similarity described by Krebs (1999) and Magurran (2004) provides a numerical description of similarity between 2 communities. This index is negligibly affected by sample size and is considered to be one of the more accurate overall similarity indices (Wolda 1981, Krebs 1999). The Morisita index of similarity can compare seasonal dietary data between 2 different areas within the same island rookery, between 2 different island rookeries, or between male and female collection sites. The index varies between 0 (no similarity) to 1 (identical). %SSFO values were used to calculate similarity indices (Krebs 1999; Ecological Methodology, V. 7.2, available at <https://www.zoology.ubc.ca/~krebs/books.html>).

2.5. Diet diversity

The Shannon-Wiener Index (H') and species richness (S), were used to describe diversity in the diet of CSLs (Krebs 1999, Magurran 2004; Text S1). S gives equal weight to common and rare taxon, and enumerates the total number of taxon in a seasonal group of fecal samples. H' gives more weight to rare taxon, and characterizes species diversity in a community by accounting for both abundance and evenness of the species present. H' , which uses the %SSFO index, is sometimes expressed as number of species (N_1) from the exponent of H' ($N_1 = e^{H'}$), allowing direct comparisons to S . However, sample size must be standardized

because S and N_1 values increase with increased sample-size. A bootstrap procedure was then used to calculate S and N_1 diversity index values for each islands' seasonal samples by randomly choosing fifty sets of 30, 35, 40, or 45 samples with replacement.

2.6. Analysis

All samples with prey hard parts were used for analyses. Least-square regression analysis was fitted to %FO anomaly values (dependent variable) and year-season (independent variable) to determine whether the 1981–2015 slope of the trends was significant. Pearson correlation analysis on %FO values with Bonferroni significant test (using Systat 64-bit v.13.00.05 statistical software) was used to examine the association between common prey taxa and non-common prey categories appearing in the diet of CSLs from SCI and SNI. By labeling each prey taxa and category with the island it was associated with, it was possible to examine between-island and within-island correlations between prey categories.

A generalized linear mixed model (GLMM; using R v.3.4.0) was fitted by maximum likelihood (Laplace approximation) with binomial (logit) distribution and random effects on prey taxa data obtained from seasonally collected CSL fecal samples from SCI and SNI during 1981–2015 and from summer fecal samples collected at SBI, SCI, and SNI during 1981–1996. Fixed effects were season, island, with season \times island interaction, and year as a random effect. GLMM was also used on prey data obtained from seasonally collected CSL fecal samples from Sites 1 and 2 at SNI during 1991–2015 to test for intra-island differences in diet and on prey data obtained between male and female sites to test for differences in the diet between males and females. Fixed effects were season, site, with season \times site interaction and year as a random effect, or fixed effect was sex and year as a random effect.

A hierarchical linear mixed model (HLMM; using Systat 64-bit v.13.00.05 statistical software) was fitted to bootstrapped diversity indices S and N_1 , and separately to Morisita index of similarity values. For S and N_1 diversity measures, fixed effects were sample size, season, and island, with a season \times island interaction, and year as a random effect. For Morisita index of similarity, values were logit transformed (Warton & Hui 2011), season was the fixed effect, and year was a random effect. A paired t -test was also used to compare logit transformed Morisita values for the 2 male-female site comparisons to test for differences in sim-

ilarity values between males and Site 1 adult females with males and Site 2 adult females.

3. RESULTS

3.1. CSL fecal samples

From 269 sampling occasions between 1981 and 2015, a total of 19 023 fecal samples were collected at SBI ($n = 841$), SCI ($n = 6813$), and SNI ($n = 11\ 369$). Of these, there were 257 sampling occasions for which ≥ 20 fecal samples were collected, and these contained 17 182 fecal samples with hard parts for identifying prey taxa (Table S2). On average, 91.7% ($SD = 7.0\%$) of the fecal samples within a sampling occasion contained hard parts (Table S2).

3.2. Prey species of CSLs

A total of 141 species (108 teleost [bony fish], 25 cephalopods [squid and octopus], 5 selachians [sharks], 1 cyclostome [hagfish], 1 pyrosome, and 1 crustacean) were identified to species level in CSL fecal samples collected at SBI, SCI, and SNI during 1981–2015 (Table S3). Other prey taxa were identified to genus, family, or order (Table S3). At SCI and SNI, market squid, northern anchovy, Pacific hake, jack mackerel, Pacific mackerel, and shortbelly rockfish each had a seasonal mean %FO index value $\geq 10\%$ in 80% or more of the seasonal collections. These prey were therefore considered to be 'common prey taxa' (Table 1, Table S3). Similar prey taxa were commonly consumed at SBI in summer, except for Pacific mackerel and Pacific sardine. Though Pacific sardine was present in $<80\%$ of sampling occasions since 1981, it was treated as a common prey taxon in our analysis because it occurred in $>80\%$ of sampling occasions after 1990, and fewer occurrences in the diet prior to then can be attributed to low sardine biomass in the 1960s–1980s (Wolf 1992, Szoboszlai et al. 2015). In addition, Pacific sardine is an important fishery stock with many stakeholders (e.g. fisheries) interested in its consumption by CSLs.

3.3. Oceanic habitats of CSL prey species

CSLs foraged within a broad array of habitats, mostly consuming epipelagic, epipelagic–mesopelagic, and benthic-demersal species (Table S3). Epipelagic species primarily consisted of northern anchovy,

Table 1. Summary of hard part detections across various prey categories derived from (A) seasonal collections at San Clemente and San Nicolas Islands (1981–2015) and (B) summer collections at San Clemente, San Nicolas, and Santa Barbara Islands (1981–1996). Number and percentage of seasons with hard parts present and corresponding mean \pm SD of percent frequency of occurrence (%FO) index values are shown. %FO values are based on seasonal means of California sea lion fecal samples containing ≥ 20 samples. For a complete list of prey taxa see Table S3

| Prey category | San Clemente Island | | | San Nicolas Island | | | Santa Barbara Island | | |
|--|---------------------|-------------------|----|--------------------|-------------------|----|----------------------|-------------------|----|
| | Seasons present % | Seasonal %FO Mean | SD | Seasons present % | Seasonal %FO Mean | SD | Seasons present % | Seasonal %FO Mean | SD |
| A) All seasons 1981–2015 | | | | | | | | | |
| Market squid | 98 | 55 | 28 | 99 | 54 | 32 | | | |
| Northern anchovy | 88 | 29 | 30 | 93 | 25 | 27 | | | |
| Shortbelly rockfish | 95 | 19 | 15 | 100 | 29 | 14 | | | |
| Jack mackerel | 98 | 24 | 17 | 98 | 18 | 16 | | | |
| Pacific sardine ^a | 75 ^a | 21 | 23 | 76 ^a | 21 | 23 | | | |
| Pacific hake | 91 | 17 | 16 | 100 | 25 | 16 | | | |
| Pacific mackerel | 90 | 13 | 12 | 86 | 11 | 12 | | | |
| Non-common fishes | 99 | 26 | 12 | 99 | 17 | 13 | | | |
| Non-common cephalopods | 94 | 13 | 10 | 99 | 17 | 14 | | | |
| Non-common cephalopods and/or fishes | 99 | 33 | 15 | 100 | 30 | 16 | | | |
| B) Summer 1981–1996 | | | | | | | | | |
| Market squid | 100 | 32 | 16 | 100 | 32 | 19 | 94 | 43 | 20 |
| Northern anchovy | 80 | 44 | 31 | 100 | 33 | 29 | 100 | 49 | 25 |
| Shortbelly rockfish | 100 | 18 | 17 | 100 | 28 | 17 | 100 | 29 | 14 |
| Jack mackerel | 100 | 21 | 16 | 100 | 29 | 23 | 100 | 21 | 14 |
| Pacific sardine ^a | 40 | 13 | 6 | 60 | 22 | 20 | 63 | 19 | 14 |
| Pacific hake | 100 | 34 | 18 | 100 | 35 | 15 | 100 | 40 | 17 |
| Pacific mackerel | 93 | 12 | 8 | 93 | 20 | 14 | 75 | 10 | 11 |
| Non-common cephalopods | 100 | 21 | 13 | 100 | 21 | 10 | 100 | 22 | 16 |
| Non-common fishes | 100 | 25 | 10 | 100 | 15 | 6 | 100 | 19 | 8 |
| Non-common cephalopods and/or fishes | 100 | 41 | 16 | 100 | 31 | 11 | 100 | 35 | 17 |
| ^a During 1990–2015, Pacific sardine was found in >10% of seasonal samples and was present in 90.7 and 89.5% of seasonal collections at San Clemente and San Nicolas Islands, respectively, making it a common prey taxon during that period | | | | | | | | | |

Pacific sardine, jack mackerel, Pacific mackerel, and Pacific hake. Market squid was the main epipelagic–mesopelagic species. Shortbelly rockfish was the main benthic–demersal species. Epipelagic–mesopelagic prey and benthic–demersal prey increased during the course of the study, whereas epipelagic prey decreased (Fig. 2, Table S4). Consumption of benthic–demersal prey peaked during 1992–1993 at SCI, 1991–1993 at SNI, and 2013–2015 at SCI and SNI (Fig. 2).

3.4. Seasonal and annual variability in CSL diet

All common prey taxa were consumed throughout the year, but some exhibited seasonal and

annual variability (Fig. 3, Table 2). Market squid was mainly consumed in autumn and winter. Northern anchovy was consumed most often in spring and was consumed least often in autumn. Pacific sardine was consumed most during spring. More Pacific mackerel, jack mackerel, and non-common fishes were consumed during autumn than other seasons. Pacific hake was consumed more frequently in summer. There was a seasonal difference in consumption for the combination of non-common cephalopods and/or fishes (Table 2). Greater annual variation (i.e. high SD relative to SDs of other prey categories) was found in the consumption of market squid, northern anchovy, and Pacific sardine than for all other species (Table 2).

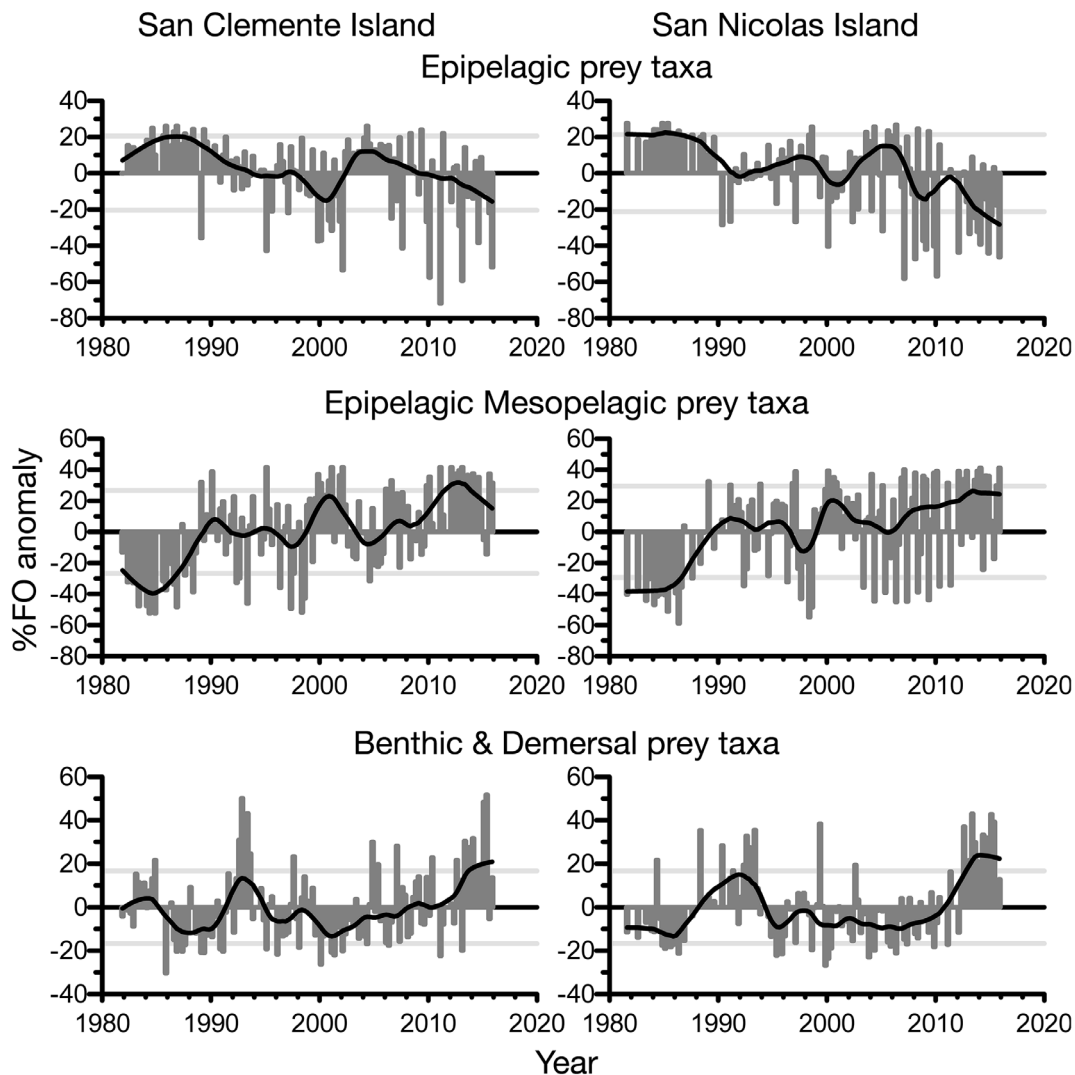


Fig. 2. LOWESS smoothing with 0.15 tension (black line) fitted to seasonal percent frequency of occurrence (%FO) anomaly values (gray bars) of 3 communities of prey taxa found in CSL fecal samples collected seasonally at San Clemente Island and San Nicolas Island during 1981–2015. Prey taxa were grouped into epipelagic, epipelagic–mesopelagic, and benthic and demersal taxa. Horizontal lines are ± 1 SD of the island 35 yr mean for each group of prey taxa

3.5. Correlations between prey taxa in CSL diet

With the exception of Pacific mackerel and jack mackerel, all common prey and non-common prey groups consumed by CSLs were correlated between SNI and SCI (Table S5). Anchovy was negatively correlated with market squid at SCI and at SNI, and with shortbelly rockfish at SCI. Shortbelly rockfish was positively correlated with Pacific hake at SNI, and was positively correlated with non-common fishes, non-common cephalopods, and non-common cephalopods and/or fishes at SCI and SNI. While Pacific mackerel and jack mackerel were not correlated to other common prey taxa, they were correlated to each other at SCI and SNI.

3.6. Inter-island comparisons

During 1981–2015, the most common prey taxon in the diet of CSLs at SNI and SCI was market squid (Table 1). Shortbelly rockfish was the second most common prey taxon for CSLs at SNI, while northern anchovy was the second most common taxon for CSLs at SCI. Throughout the study period, Pacific hake and shortbelly rockfish were consumed more at SNI than SCI, and jack mackerel and non-common fishes were consumed more at SCI than SNI (Table 2). In addition, summer collections during the first half of the study period (1981–1996) revealed that the most common prey taxon at SBI was northern anchovy, followed by market squid (Table 1).

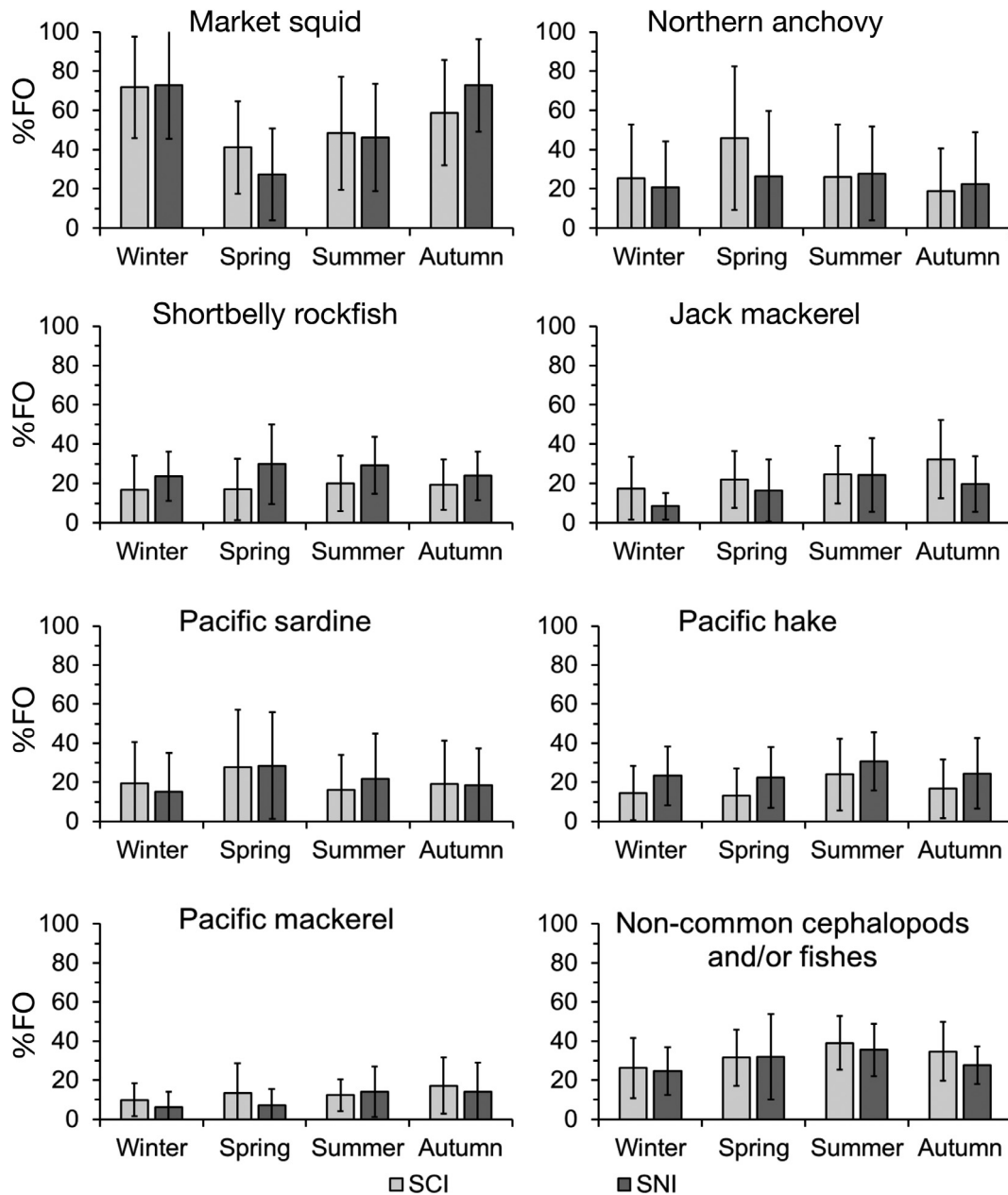


Fig. 3. Mean (± 1 SD) seasonal percent frequency of occurrence (%FO) values for common prey taxa and non-common cephalopods and/or fishes found in fecal samples collected at San Clemente Island (SCI) and San Nicolas Island (SNI) during 1981–2015

3.7. Long-term trends and prey switching

During 1981–2015, CSL diet data revealed multi-year and multi-decadal variability in prey consumption. Consumption of market squid, Pacific sardine, and non-common fishes increased, while northern anchovy and Pacific hake decreased across all islands during the study period (Figs. 4 & 5, Table S4). Tem-

poral trends were also specific to each island from 1981–2015. Shortbelly rockfish increased at SCI, and jack mackerel and Pacific mackerel decreased at SNI (Table S4). Concurrent to these multidecadal trends, CSLs switched between different common prey taxa and non-common cephalopods and/or fishes multiple times throughout the study period (Figs. 4 & 5). Peaks in prey consumption for a given species lasted from

Table 2. Inter-island prey model coefficients from generalized linear mixed models (GLMMs) of prey categories found in California sea lion fecal samples collected (A) seasonally at San Clemente Island (SCI) and San Nicolas Island (SNI) during 1981–2015 and (B) in summer at SCI, SNI, and Santa Barbara Island (SBI) during 1981–1996. Year was included as a random effect in all models tested. Coefficients with p-values ≤ 0.05 are shown in **bold**

| Prey category | Fixed effects | | | | Random effects | | | | |
|---|---------------|--------------|--------------|----------------|----------------|--------------|--------------|--------------|-----------|
| | Intercept | Spring | Summer | Autumn | SNI | Spring × SNI | Summer × SNI | Autumn × SNI | Year (SD) |
| A) All seasons at SCI and SNI: 1981–2015 | | | | | | | | | |
| Market squid | 0.84 | -1.40 | -0.90 | -0.36 | 0.22 | -0.94 | -0.23 | 0.48 | 0.97 |
| Northern anchovy | -1.02 | 0.82 | -0.29 | -0.90 | -0.56 | -0.36 | 0.59 | 1.07 | 1.27 |
| Shortbelly rockfish | -1.67 | 0.02 | 0.23 | 0.21 | 0.39 | 0.25 | 0.20 | -0.16 | 0.44 |
| Jack mackerel | -1.52 | 0.21 | 0.38 | 0.79 | -0.79 | 0.49 | 0.69 | 0.13 | 0.43 |
| Pacific sardine | -2.16 | 0.69 | -0.01 | 0.29 | -0.38 | 0.38 | 0.80 | 0.04 | 1.53 |
| Pacific hake | -1.88 | -0.08 | 0.63 | 0.16 | 0.62 | 0.10 | -0.24 | -0.08 | 0.64 |
| Pacific mackerel | -2.30 | 0.30 | 0.27 | 0.74 | -0.46 | -0.18 | 0.56 | 0.20 | 0.55 |
| Non-common fishes | -1.32 | 0.16 | 0.29 | 0.41 | -0.35 | 0.12 | -0.08 | -0.52 | 0.37 |
| Non-common cephalopods | -2.70 | 0.57 | 1.11 | 0.57 | 0.53 | -0.06 | -0.14 | -0.15 | 0.42 |
| Non-common cephalopods and/or fishes | -1.16 | 0.35 | 0.66 | 0.54 | -0.04 | 0.00 | -0.08 | -0.37 | 0.42 |
| B) Summer at SCI, SNI, and SBI: 1981–1996 | | | | | | | | | |
| Prey category | Fixed effects | | | Random effects | | | | | |
| | Intercept | SCI | SNI | SNI | Year (SD) | Year (SD) | | | |
| Market squid | -0.37 | -0.50 | -0.33 | 0.77 | | | | | |
| Northern anchovy | -0.11 | -0.54 | -0.89 | 0.94 | | | | | |
| Shortbelly rockfish | -0.95 | -0.64 | 0.03 | 0.62 | | | | | |
| Jack mackerel | -1.36 | 0.08 | 0.22 | 0.47 | | | | | |
| Pacific sardine | -3.00 | -1.03 | 0.21 | 1.80 | | | | | |
| Pacific hake | -0.38 | -0.29 | -0.28 | 0.53 | | | | | |
| Pacific mackerel | -2.33 | 0.06 | 0.76 | 0.54 | | | | | |
| Non-common fishes | -1.47 | 0.30 | -0.24 | 0.30 | | | | | |
| Non-common cephalopods | -1.32 | -0.16 | -0.08 | 0.57 | | | | | |
| Non-common cephalopods and/or fishes | -0.64 | 0.19 | -0.16 | 0.45 | | | | | |

a single year to over a decade (Fig. 4). Market squid increased from below the 1981–2015 sampling occasion mean in the 1980s and 2000s (Fig. 4). Northern anchovy consumption peaked twice during the time series—once in the 1980s and again in the mid-2000s. Pacific sardine consumption also peaked twice in the time series—once during 1994–1998 and again in 2003–2012 (Fig. 4). Shortbelly rockfish was consumed most frequently in 1992–1993 and 2013–2015, which corresponded with the highest consumption of non-common cephalopods and/or non-common fishes (Figs. 4 & 5).

3.8. CSL diet diversity

S and N_1 diversity indices increased as fecal sample size increased (Table S6). N_1 diversity–sample curves flattened out after about 30 fecal samples, but S diversity–sample curves continued to increase. There was more diversity in the diet during summer than during other seasons (Table 3). Both diversity indices revealed dietary differences ($p < 0.05$) between islands and seasons (Table S7).

3.9. Diet similarity between islands and seasons

The Morisita Index of Similarity between SCI and SNI from 1981–2015 indicated that diets between the 2 islands were similar (mean = 0.784, SD = 0.151; median = 0.814; Table 4). Spring diets were less similar between islands (mean = 0.691, SD = 0.171; median = 0.720) than were summer and autumn diets (summer: mean = 0.837, SD = 0.114; median = 0.844; autumn: mean = 0.826, SD = 0.128; median = 0.854). These differences were significant

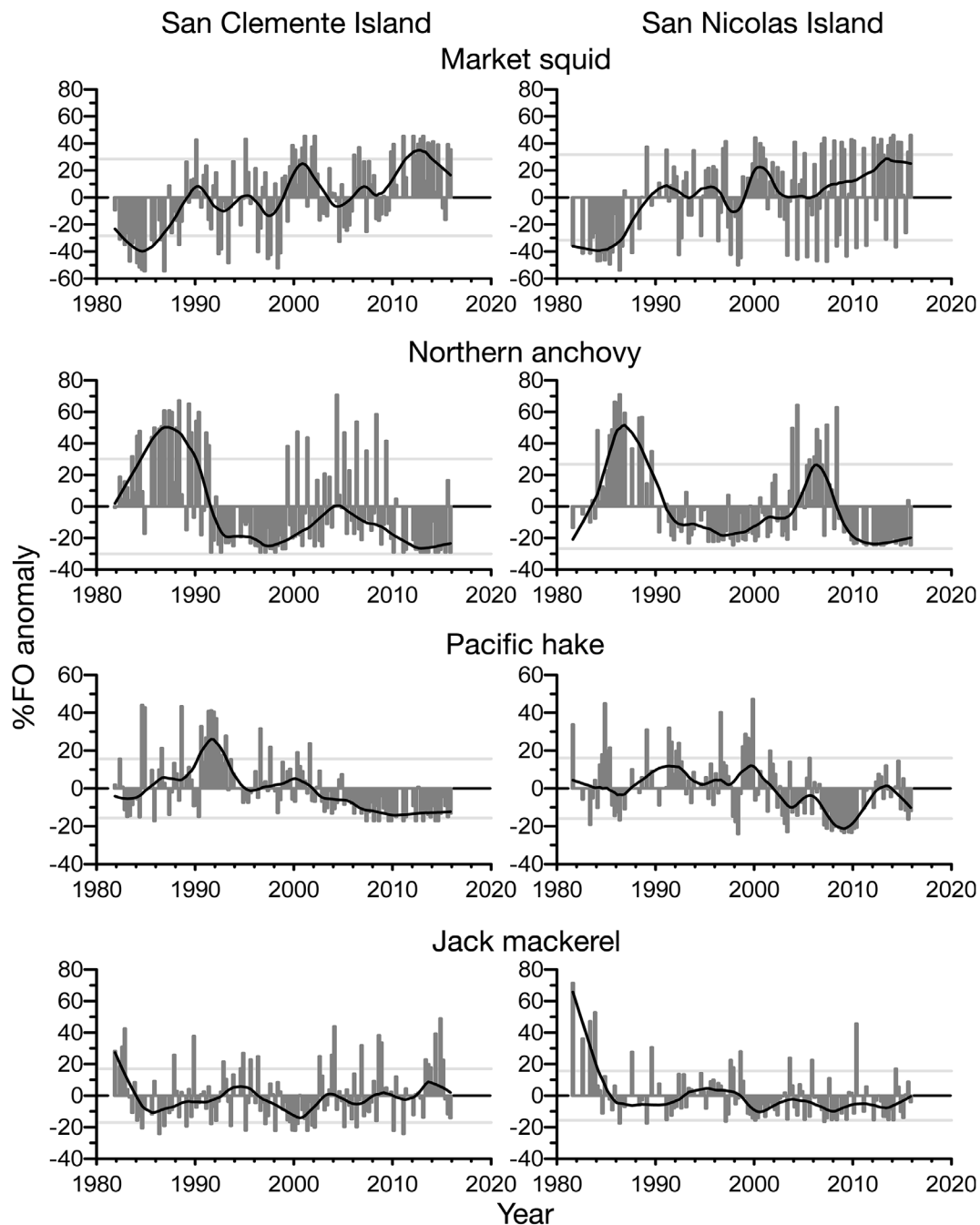


Fig. 4. LOWESS smoothing with 0.15 tension (black line) fitted to seasonal percent frequency of occurrence (%FO) anomaly values (gray bars) for prey-taxon found in CSL fecal samples collected seasonally at San Clemente Island (left panels) and San Nicolas Island (right panels) during 1981–2015. Horizontal lines are ± 1 SD of the island 35 year mean for each prey-taxon
(continued on next page)

(F -ratio = 5.997, p = 0.001). The Morisita index of similarity between SBI, SCI and SNI during summer 1981–1996 indicated that summer diets between the 3 islands were similar (mean = 0.751, SD = 0.176; median = 0.800; Table 4), and no significant island differences were found (F -ratio = 1.953, p = 0.155).

3.10. Intra-island comparisons

At 2 collection sites on SNI, fewer shortbelly rockfish, Pacific hake, and non-common cephalopods and/or fishes were consumed at Site 2 than were consumed at Site 1, but no differences were

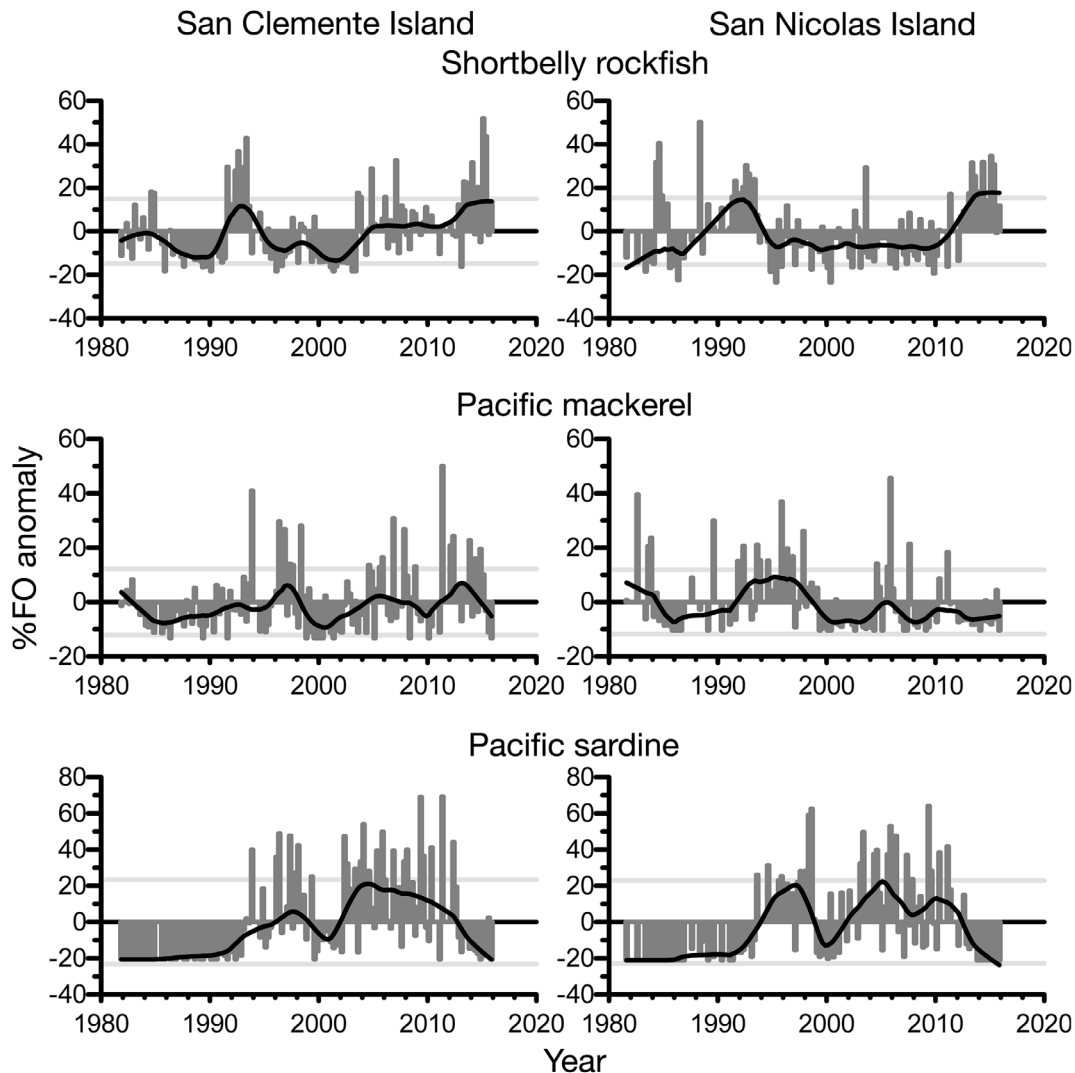


Fig. 4 (continued)

found for other prey categories (Table 5). A higher year effect (i.e. high year SD relative to SDs of other prey categories) was found for northern anchovy and Pacific sardine than for other prey categories at Sites 1 and 2 at SNI (Table 5). While differences were found in diversity indices for area and season between SNI Sites 1 and 2 ($p < 0.05$), there was no season \times area interaction effect for S ($p > 0.05$), but there was an season \times area interaction effect for N_1 ($p < 0.05$; Table S7). Diets of CSLs at the 2 sites on SNI were very similar (nearly identical) to each other (Morisita index of similarity mean = 0.898 [SD = 0.081] with the median = 0.919; Table 4). Seasonal differences were not found for Morisita index of similarity area comparisons (F-Ratio = 1.827, $p = 0.148$).

3.11. Male–female comparisons

Fecal samples collected in summer from male haulout sites in 2000 and 2001 could not be used due to sample size limitation (i.e. < 20 samples collected), leaving 7 yr for male–female diet comparisons. For those years, the mean age composition (with 95% CI) of non-pup age/sex classes at Site 1 was $77 \pm 4\%$ adult females, $12 \pm 3\%$ juveniles, $5 \pm 1\%$ sub-adult males, and $6 \pm 2\%$ adult males, and at Site 2 it was $84 \pm 4\%$ adult females, $8 \pm 4\%$ juveniles, $1 \pm 0\%$ sub-adult males, and $7 \pm 2\%$ adult males (Table 5). Fecal samples collected from male haulout sites were from sub-adults and adults, but the composition of each were unknown. The mean Morisita index

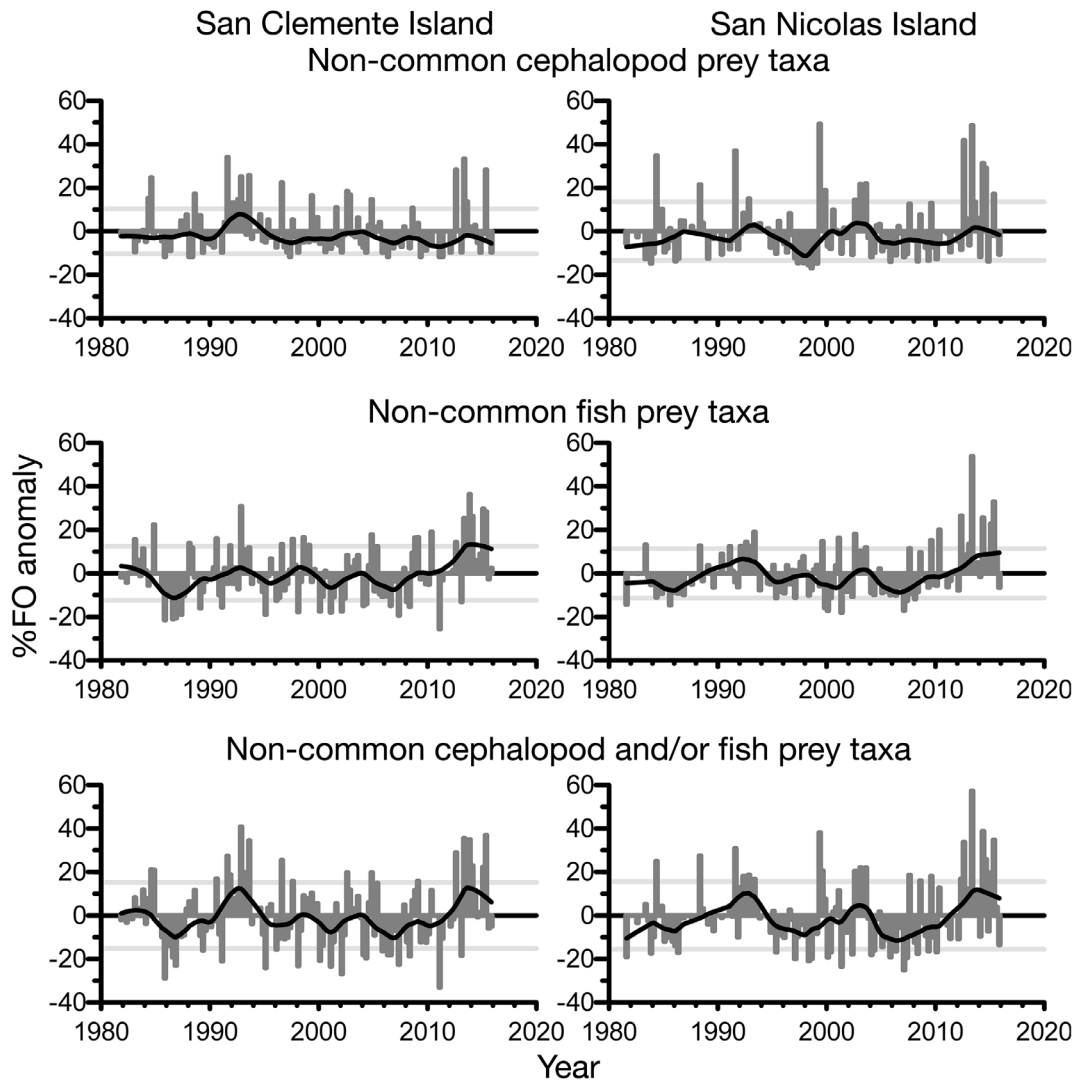


Fig. 5. LOWESS smoothing with 0.15 tension (black line) fitted to seasonal percent frequency of occurrence (%FO) anomaly values (gray bars) of non-common prey taxa found in California sea lion fecal samples collected seasonally at San Clemente Island (left panels) and San Nicolas Island (right panels) during 1981–2015. Horizontal lines are ± 1 SD of the island 35 year mean for each group of prey taxa

value between the diets of males and Site 1 adult females was 0.826 (SD = 0.128), and between males and Site 2 adult females was 0.763 (SD = 0.159; Table 4). No significant difference ($p \geq 0.05$) was found between Morisita index values for males and Site 1 adult females with males and Site 2 adult females. In addition, no significant differences between males and adult females were found in the consumption of market squid, shortbelly rockfish, Pacific hake, and Pacific mackerel, but males consumed significantly less ($p \leq 0.05$) anchovy, sardine, and jack mackerel and significantly more ($p \leq 0.05$) non-common cephalopods and non-common fishes (Table 5).

4. DISCUSSION

Our study revealed that CSL diet in the southern CCE is highly diverse and variable over time, and to a lesser extent, across space. H' , or its derivative N_1 , has been the most common metric used to describe diversity in the diet of pinnipeds (Merrick et al. 1997, Garcia-Rodriguez & Auriolles-Gamboa 2004, Trites & Calkins 2008, Geiger et al. 2013). Although diversity indices S and N_1 values differed, both indicated that CSL diet at the Channel Islands has a high degree of spatial (i.e. inter-island) and temporal variability.

Of the 4 Channel Islands rookeries, SCI and SBI are the smallest in terms of CSL pup production (4

Table 3. Species richness (S) and Shannon-Wiener (N_1) diversity indices of fecal samples collected seasonally from Santa Barbara Island (SBI), San Clemente Island (SCI), and San Nicolas Island (SNI) during summer 1981–1996 and from SCI and SNI during 1981–2015. Mean and SD for 50 random samplings of sample size 40 were derived from each set

| Years | Season | Island | Fecal sample samplings | Species richness (S) | | Shannon-Wiener (N_1) | |
|-----------|--------|---------------|------------------------|--------------------------|-----|--------------------------|-----|
| | | | | Mean | SD | Mean | SD |
| 1981–1996 | Summer | SBI | 650 | 21.4 | 6.3 | 9.1 | 3.3 |
| | | SCI | 600 | 20.8 | 5.1 | 8.9 | 3.4 |
| | | SNI | 650 | 19.6 | 4.6 | 8.8 | 2.3 |
| 1981–2015 | Winter | SBI, SCI, SNI | 1900 | 20.6 | 5.4 | 8.9 | 3.1 |
| | | SCI | 1350 | 18.9 | 9.2 | 6.6 | 3.7 |
| | | SNI | 1300 | 16.8 | 5.6 | 6.0 | 2.8 |
| | | SCI, SNI | 2650 | 17.8 | 7.7 | 6.3 | 3.3 |
| | | SCI | 1450 | 19.4 | 7.3 | 7.4 | 3.1 |
| | Spring | SNI | 1350 | 19.9 | 9.1 | 8.3 | 4.6 |
| | | SCI, SNI | 2800 | 19.6 | 8.3 | 7.8 | 3.9 |
| | | SCI | 1400 | 21.8 | 5.3 | 8.9 | 3.0 |
| | Summer | SNI | 1500 | 22.2 | 6.2 | 9.3 | 2.8 |
| | | SCI, SNI | 2900 | 22.0 | 5.8 | 9.1 | 2.9 |
| | | SCI | 1250 | 21.2 | 6.3 | 8.4 | 2.7 |
| | Autumn | SNI | 1350 | 18.3 | 5.0 | 6.6 | 2.2 |
| | | SCI, SNI | 2600 | 19.7 | 5.8 | 7.5 | 2.6 |
| | | SCI | 5450 | 20.3 | 7.3 | 7.8 | 3.3 |
| | All | SNI | 5500 | 19.4 | 6.9 | 7.6 | 3.5 |
| SCI, SNI | | 10950 | 19.8 | 7.1 | 7.7 | 3.4 | |

Table 4. Summary statistics for the Morisita index of similarity derived from comparing %SSFO of prey taxa found in seasonal CSL fecal samples. Samples were categorized into the following groups for comparison: within island = San Nicolas Island (SNI) collection Sites 1 and 2 during 1991–2015; between Island = (1) Santa Barbara (SBI), San Clemente (SCI), and SNI during 1981–2015, and (2) SBI, SCI, and SNI during summer 1981–1996; and males vs. females at SNI = male and female collection Sites 1 and 2

| Comparison | Location | Years | Sub-sample comparison | n | Min | Max | Median | Mean | SD |
|-------------------|---|---|--------------------------|-----|-------|-------|--------|-------|-------|
| Within Island | SNI | 1991–2015 | Winter | 23 | 0.758 | 0.990 | 0.917 | 0.922 | 0.049 |
| | | | Spring | 23 | 0.709 | 0.990 | 0.879 | 0.887 | 0.076 |
| | | | Summer | 21 | 0.656 | 0.983 | 0.919 | 0.864 | 0.109 |
| | | | Autumn | 23 | 0.769 | 0.997 | 0.937 | 0.915 | 0.072 |
| | | | All seasons | 90 | 0.656 | 0.997 | 0.919 | 0.898 | 0.081 |
| Between Island | SNI, SCI | 1981–2015 | Winter | 30 | 0.517 | 0.988 | 0.827 | 0.789 | 0.142 |
| | | | Spring | 32 | 0.332 | 0.953 | 0.720 | 0.691 | 0.171 |
| | | | Summer | 31 | 0.552 | 0.987 | 0.844 | 0.837 | 0.114 |
| | | | Autumn | 28 | 0.522 | 0.995 | 0.854 | 0.826 | 0.128 |
| | | | All seasons | 121 | 0.332 | 0.995 | 0.814 | 0.784 | 0.151 |
| | SCI, SBI SNI, SBI SNI, SCI All islands | 1981–1996 | Summer | 15 | 0.352 | 0.922 | 0.778 | 0.733 | 0.173 |
| | | | | 15 | 0.318 | 0.943 | 0.814 | 0.707 | 0.217 |
| | | | | 14 | 0.574 | 0.986 | 0.810 | 0.816 | 0.113 |
| | | | | 44 | 0.318 | 0.986 | 0.800 | 0.751 | 0.176 |
| | | | | 44 | 0.318 | 0.986 | 0.800 | 0.751 | 0.176 |
| Males vs. Females | SNI | 1991, 1993, 1995, 1996, 1997, 1999 & 2003 | Males vs. Site 1 females | 7 | 0.574 | 0.955 | 0.833 | 0.826 | 0.121 |
| | | | Males vs. Site 2 females | 6 | 0.466 | 0.905 | 0.798 | 0.763 | 0.159 |
| | | | All sites | 7 | 0.548 | 0.934 | 0.839 | 0.812 | 0.128 |

and 6% of production, respectively), and SNI and SMI are the largest (each producing ~45%, Lowry et al. 2017a,b). In general, diet differences between islands were more substantial than between sites within the same island, suggesting access to common prey within the southern CCE may vary across the

region. Satellite-tagged CSLs from SNI and SMI indicated that some foraged in similar areas and some did not (Melin et al. 2008, McHuron et al. 2016).

Diets between male-dominated and female-dominated sites were slightly dissimilar. Sub-adult and juvenile males that comprise a small proportion

of non-pups occupying reproductive sites may have contributed fecal samples at these areas. The higher proportion of sub-adult males in Site 1 in particular may be why diet similarity was slightly higher there than the comparison at Site 2. However, adult male contribution to fecal samples within Sites 1 and 2 is likely negligible, as they spend most of their time patrolling aquatic zones within female reproductive areas for a few days between foraging trips (S. Melin pers. comm.). Nonetheless, we observed significant differences in the consumption of common and non-common prey species between sexes during the summer breeding season. During the summer breeding season, adult females at SNI consumed more energy rich prey such as anchovy and sardine than males, while males consumed more prey with lower energy content such as non-common cephalopods and non-common fishes. The intra-population variation in diet we observed in our study may help improve estimates of biomass removal by sea lions of commercially important forage species. Ignoring these differences may over- or underestimate consumption of prey species by the CSL population. Additional sampling of male- and female-dominated haulout sites across seasons would allow for even finer detections in sex-specific diets that may be useful to resource managers.

The diet data showed that CSLs shifted from an anchovy-based diet in the 1980s to a market squid-based diet in the 1990s and 2000s, with 5 other common prey taxa being heavily utilized in years when the 2 main prey diminished (Fig. 4). Generally, CSLs rely on market squid in autumn and fall when squid concentrate to spawn and consume a variety of other common prey during the other seasons. A wide array of less common cephalopod and/or fish prey collectively represented a sizeable portion of the CSL diet. CSLs fed mostly on epipelagic prey in the 1980s, and then more on epipelagic–mesopelagic prey and benthic–demersal prey in the 1990s and 2000s. There were occasional periods when benthic–demersal prey taxa were the most important prey. However, some prey, such as Pacific hake and shortbelly rockfish, inhabit epipelagic and demersal–benthic zones. Pacific hake, categorized as an epipelagic species, and shortbelly rockfish, categorized as a demersal species, inhabit the demersal zone during the day and the epipelagic zone during night (Bailey et al. 1982, Love et al. 2002). CSLs are daytime and nighttime feeders (McHuron et al. 2016), so it's not possible to determine where they foraged on these 2 taxa from the fecal sample data.

Changes in the diet were pronounced during extremely warm oceanographic conditions in 1982–

1983, 1997–1998, 2009, and 2013–2015, during which more non-common cephalopods and non-common fishes were consumed. Others have observed similar changes for the CSL population (DeLong et al. 1991, Weise & Harvey 2008, Melin et al. 2010, Robinson et al. 2018). Multiple explanations for spatial and temporal diet variability of CSL have been proposed: (1) prey movement and life history characteristics (Weise & Harvey 2008); (2) differences in energy content of prey (McClatchie et al. 2016); (3) abundance and availability of prey (Lowry et al. 1990, 1991), and (4) individual and rookery differences in foraging strategy (Melin et al. 2008, McHuron et al. 2016). The influx of sub-adult and adult males at Channel Islands' rookeries during the summer breeding season may have density dependent effects on the diet, especially during warm water events when abundance of forage is reduced. This body of evidence suggests CSLs may increasingly rely on a greater array of less common prey taxa as oceans warm.

The eastern North Pacific Ocean undergoes decadal cold and warm periods lasting 10 to 30 yr that have 3 to 7 yr El Niño Southern Oscillation (ENSO) cycles embedded within them (Fiedler 2002). These decadal periods are punctuated by regime shifts, 2 of which have been proposed to have taken place in 1988–1989 and 1998–1999 (Hare & Mantua 2000, Fiedler 2002, Jo et al. 2013). The ENSO cycle has warm (El Niño), neutral, and cold (La Niña) sequences. During past moderate and severe warm-water El Niño periods, CSLs spent more time at sea, dove deeper and longer, traveled farther from the island rookery and farther offshore (i.e. increased travel costs), and consumed fewer Pacific hake, Pacific sardine, northern anchovy, and market squid than they consumed during cold-water La Niña periods (Feldkamp et al. 1989, Heath et al. 1991, Melin et al. 2000, 2008, Weise et al. 2006, Kuhn & Costa 2014). Warm-water periods associated with or without El Niño periods also have affected CSL pup production, pup survival, pup weights, and juvenile survival (DeLong et al. 1991, 2017, Francis & Heath 1991, Melin et al. 2012, Lowry et al. 2017a). Coincidentally, the shift we found in this study from an anchovy-based diet in the 1980s to a diet dominated by market squid in the 1990s and 2000s occurred during the proposed 1988–1989 regime shift. Further analyses of this dataset could evaluate the relationship between prey variation and ENSO or other decadal effects and determine which prey taxa or combinations of them are optimal for pup production and population growth. Changes in the abundance and availability of forage species in the CCE have previously been linked to

reduced reproductive success and survival of young CSLs, and sometimes survival of adult CSLs (DeLong et al. 1991, Melin et al. 2008, 2010, McClatchie et al. 2016).

During 2013–2015, the CCE experienced a record-breaking marine heatwave (Bond et al. 2015, Di Lorenzo & Mantua 2016) that was followed by an extreme El Niño event (Jacox et al. 2016). Arrival of large numbers of emaciated CSL pups on the southern California mainland resulted in the declaration of an unusual mortality event by the National Oceanic and Atmospheric Administration in 2013¹. At that time, fecal sample data showed increased consumption of benthic and demersal taxa, decreased consumption of epipelagic taxa, and increased consumption of non-common cephalopods and fishes. If warm-water events intensify or become more prevalent in the future, the CSL population is predicted to experience negative growth (Laake et al. 2018) as they experience decreased pup production and increased pup and yearling mortality (DeLong et al. 2017), likely driven by dietary changes similar to those observed in 2013–2015 and to other warm-water events that took place during 1981–2012. Current forecasts indicate that the CCE will experience increased surface and near-surface temperatures, increased stratification along the west coast that may affect upwelling, cooler temperatures below 70m depth, increased numbers of extreme El Niño occurrences, and higher frequencies of central Pacific El Niño events (Aquad et al. 2006, Yeh et al. 2009, Cai et al. 2014).

Decreased abundance of high-energy forage, such as anchovy and sardine, during 2004–2014 was found to result in reduced CSL pup weights that led to pup die-offs in 2013–2014 (McClatchie et al. 2016). However, the long-term 35 yr diet data shows that market squid dominated the diet of sea lions for many years while the US CSL population increased until it peaked in 2012 (Lowry et al. 2017a, Laake et al. 2018). Though cephalopods and fish have similar percentage protein values, percentage fat value (i.e. lipid) varies by species (Sidwell 1981), which can affect their total energy content. Market squid and other cephalopods have low fat content, while anchovy and sardine have the highest fat content of forage species consumed by CSLs. In addition, seasonal variation in fat content has been found for anchovy (Garcia-Franco et al. 1999), thus it is likely that other fish and squid consumed by CSLs have temporal variations in fat con-

tent as well. Further analyses could be conducted to evaluate relationships between protein and fat content of forage (or their ratio) and CSL population growth and decline.

Seasonal differences in CSL diet are governed by prey abundance, prey distribution, prey selection, density dependent responses by CSLs, and climatic effects on oceanographic conditions. Market squid is primarily consumed by CSLs during autumn and winter when they form dense spawning aggregations and are more abundant. As their fetus develops, CSL adult females consume protein-rich market squid in autumn and winter, then increase their consumption of energy-rich northern anchovy and Pacific sardine in the spring (as market squid abundance decreases) prior to giving birth in late-May and June. Northern anchovy was consumed most often in spring when this species congregates inshore of the Southern California Bight to spawn (Demer et al. 2012). Sub-adult and adult male CSLs exhibit a density-dependent response when they arrive at the Channel Islands for the summer breeding season (increasing the number of CSLs at the Channel Islands) where they consume fewer energy-rich forage such as northern anchovy and Pacific sardine than adult females and greater amounts of energy-poor non-common fish and cephalopods. Seasonal variability is also influenced by annual differences in distribution of prey species in the CCE (Zwolinski et al. 2012, Dorval et al. 2016). Thus, CSL seasonal consumption of these species, and perhaps others may be altered.

As global oceans warm due to climate change, the distributions of many marine species, including CSL common prey taxa, are predicted to shift poleward (Cheung et al. 2009) and in some cases parts of their range would become uninhabitable (Howard et al. 2020). Poleward shifts have recently been documented for tropical species within the southern CCE during warm-water El Niño episodes (Lea & Rosenblatt 2000) and for some pelagic species (Hsieh et al. 2009). For CSLs at the Channel Islands, the northward shift in their common forage species may lead to increased consumption of non-common prey taxa, increased diet diversity, and possibly a northward shift in the CSL breeding population as individuals follow the northward shift of their forage. Recent increases in CSL pups born at Año Nuevo Island and at the Southeast Farallon Islands in central California indicate that a northward population shift is already beginning to occur (Lowry et al. 2017a, 2021).

While fecal analysis provides high taxonomic resolution of prey consumed, there is some uncertainty in the spatial and temporal resolution in prey consump-

¹<https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events>

tion that can be inferred from this method. Satellite tag and time-depth recorder data have shown that adult female CSLs from the Channel Islands spend ~1 to 5 d at sea foraging within a range of depths (~30–150 m) and foraged within 26.1 and 623.7 km of the rookery (Melin et al. 2008, Kuhn & Costa 2014, McHuron et al. 2016). Males tagged at Monterey, in central California, on average spend 0.8 to 2.4 d at sea and foraged up to 820 km from the tagging site (Weise et al. 2006). Captive feeding studies of CSLs have indicated that not all prey hard parts pass through the digestive tract, and that while most of the passage occurs within 48 h, it may take up to 120 h for prey remains to pass through the digestive tract (Orr & Harvey 2001, Sweeney & Harvey 2011). Therefore, while defecation occurs in the water, fecal samples collected on land for diet analysis represent foraging by CSLs over a 1 to 5 d period at various depths over a wide geographic area.

It is important to note that CSL diet quantified in other regions has been shown to reflect the abundance of primary prey species within those regions (as indexed by fisheries-independent trawl surveys; Robinson et al. 2018). This may be true for the southern California region as well, as one study linked CSL foraging patterns to the abundance of Pacific sardine and northern anchovy in the southern CCE (Fiechter et al. 2016). Shortbelly rockfish abundance was found to be reflected in the diet of CSLs (Field et al. 2007). It is possible that abundance estimates of other CSL common prey taxa such as market squid, Pacific hake, and Pacific mackerel, as well as non-common mesopelagic taxa, may show short-term and long-term temporal changes (Crone et al. 2009, Hill et al. 2011, Dorval et al. 2013, Koslow et al. 2013, Taylor et al. 2015, MacCall et al. 2016) that may be reflected in the diet of CSLs upon further analysis.

Several consumption indices have been used to describe the diet of pinnipeds from fecal samples. Frequency-based metrics, such as %FO and %SSFO used in this study, assume independent sampling (i.e. one sample represents one individual) and depict the proportion and percentage, respectively, of what the population consumed. Number or percentage of individual prey consumed may also be used, but this metric is biased by prey size—smaller individuals consumed in greater quantities are overestimated, while larger prey consumed in fewer quantities are underestimated. Mass of prey has also been used to describe pinniped diets (Weise & Harvey 2008) by relating otolith or cephalopod beak size to fish or cephalopod length and mass for a few species fed to

CSLs during captive feeding studies (e.g. Orr & Harvey 2001, Sweeney & Harvey 2011) and making hard part survival estimates for others. However, a re-analysis of those captive feeding data (Curtis et al. 2022) estimates fish otolith and cephalopod beak survival during the digestive process for all fish and cephalopod prey found in our study by applying otolith morphometrics and size and mass of CSL prey (Lowry et al. 2020). Biomass reconstruction of the CSL diet data presented here is now possible and can provide highly resolved inputs for food web and ecosystem models.

This 35 yr CSL foraging ecology study highlights temporal and spatial patterns of a significant marine predator in the southern CCE. Future studies should address causes of observed dietary variability and dietary impact on the US population of CSLs by integrating the oceanographic, climate, and prey abundance correlates with this time series. These data can also be used to understand the effects of climate change on apex predators, changes in abundance of forage taxa that are ecologically significant to many predators in the CCE, how diets of marine mammals affect their production and population growth, and the effects of prey consumption by predators on commercial fish abundance. While consumption estimates have been made for CSLs in central California (Weise & Harvey 2008), biomass reconstruction of this CSL diet dataset, in addition to the application of caloric energy of CSL forage species to the times series, will make it possible to generate consumption estimates for CSLs at the Channel Islands where the largest proportion of the US population resides. These future analyses will help us understand the mechanisms affecting predator foraging and population responses in dynamic upwelling environments, provide data for fish stock assessments, and ultimately contribute to multi-trophic level management of species in the CCE.

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