

# Indicators of pelagic forage community shifts in the California Current Large Marine Ecosystem, 1998–2016

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## ABSTRACT

Forage fishes are ecologically and economically important in marine ecosystems worldwide and thus are a focal topic for ecosystem-based fisheries management. In the California Current Large Marine Ecosystem (CCLME), the community dynamics of forage populations have been studied at regional spatial scales, but not across regions. To evaluate indicators of the forage community at the ecosystem-wide scale, we examine temporal variability of forage assemblages in Northern (Oregon/Washington), Central (California; Point Reyes to Monterey Bay) and Southern (southern California) regions of the CCLME from 1998 through 2016 which include years with unprecedented climate variability. Forage communities fluctuated greatly between years within each region owing to regionally low abundances of common taxa in at least some years (e.g., rockfishes *Sebastes* spp. in each region). Comparison of species assemblages among regions indicate that that temporal shifts in assemblage structure were largely synchronous throughout the CCLME. However, dynamics of most individual taxa were out of phase between regions, indicating that different taxa drove the variability in each region. Within regions, taxa with similar adult ecological niches tended to co-vary, suggesting synchronous responses to environmental forcing. Major changes in forage assemblage structure are descriptively linked to large oceanographic perturbations such as the transition from El Niño to La Niña conditions in 1998, anomalous upwelling in 2005, and the onset of a large marine heatwave in fall-winter 2013–2014. Changes in forage assemblage structure are reflected in prey switching in the diet of California sea lions, *Zalophus californianus*, in the Southern region. The

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multivariate forage indices that we develop can serve as effective indicators of regional forage community composition shifts in the CCLME and provide managers with context on spatio-temporal changes in the structure of forage fish communities important to top predators in this system.

## 1. Introduction

Ecosystem-based approaches to research and management of marine resources and services have long recognized the critical role of pelagic species at intermediate trophic levels (e.g., May et al., 1979; Ecosystem Principles Advisory Panel, 1999). These taxa are often referred to as “forage,” which we define as *pelagic, schooling, nektonic stages of invertebrate or fish species that are consumed by other fishes, seabirds, or marine mammals*. Forage taxa have considerable influence on marine ecosystem structure and function, owing to their abundance and biomass, their sensitivity to environmental variability, their role in trophic energy transfer, and their importance as targets of fisheries (Cury et al., 2000; Smith et al., 2011; Rice and Duplisea, 2014). This broad influence speaks to the importance of developing holistic indicators of forage communities for inclusion in decision-making frameworks (Rice and Duplisea, 2014), such as Integrated Ecosystem Assessments (e.g., Levin et al., 2009; Harvey et al., 2017).

The diverse forage base of the California Current Large Marine Ecosystem (CCLME) forms the primary link between upwelling-driven primary productivity and a wide diversity of predators at upper trophic levels (Ruzicka et al., 2012; Kaplan et al., 2013; Szoboszlai et al., 2015; Koehn et al., 2016). Key forage species in this ecosystem include Pacific sardine (sardine) *Sardinops sagax*, market squid *Doryteuthis opalescens*, northern anchovy (anchovy) *Engraulis mordax* and Pacific herring *Clupea pallasii*, and some of these species also support valuable fisheries (PFMC, 2016a). For example, market squid has been the most valuable fishery off California in recent years (e.g., 37,100 metric tons (MT) worth \$39.2M USD was harvested off California in 2016) (CDFW, 2017). The forage community also includes pelagic early life stages of commercially important salmon *Oncorhynchus* spp. and groundfishes, including flatfishes, Pacific hake *Merluccius productus*, and many species of rockfishes *Sebastes* spp. Still other abundant forage species experience relatively little or no fishing pressure, including smelt (Osmeridae), silversides (Atherinopsidae), and mesopelagic taxa such as lanternfish (Myctophidae). More complete lists of CCLME forage species are in Szoboszlai et al. (2015) and Brodeur et al. (2014). Although euphausiids (krill) meet our definition of forage and are fed upon by a wide range of predators, this group is not evaluated here, as they were not adequately sampled in all regions of our study. The Pacific Fishery Management Council (PFMC), which makes many marine fishery regulatory decisions for species that reside between 3 and 200 nautical miles off the west coast of the United States [the Exclusive Economic Zone (EEZ)], recently implemented a precautionary prohibition on the development of new fisheries for many of these previously untargeted forage species (PFMC, 2016a,b; US Federal Register, 50 CFR § 660 2016).

Forage species in the CCLME support a diverse array of predators with a wide range of feeding strategies and foraging areas. The pelagic predator community includes numerous upper trophic level fishes (e.g., sharks; albacore *Thunnus alalunga*), marine mammals (e.g., California sea lion *Zalophus californianus* (sea lion), harbor seal *Phoca vitulina*) and seabirds (e.g., common murre *Uria aalge*; sooty shearwater *Ardenna grisea*) (Szoboszlai et al., 2015). Suites of predators feed in different parts of the water column and at different distances from shore. Some predators, particularly pinnipeds and resident breeding seabirds, are central-place foragers for much of the year, while others are more broadly distributed. Some are generalists, while others at times appear more specialized (e.g., brown pelican *Pelecanus occidentalis* depend largely on sardine and anchovy; Szoboszlai et al., 2015). Thus, changes in forage assemblages likely have variable effects on feeding conditions

across the span of predatory guilds.

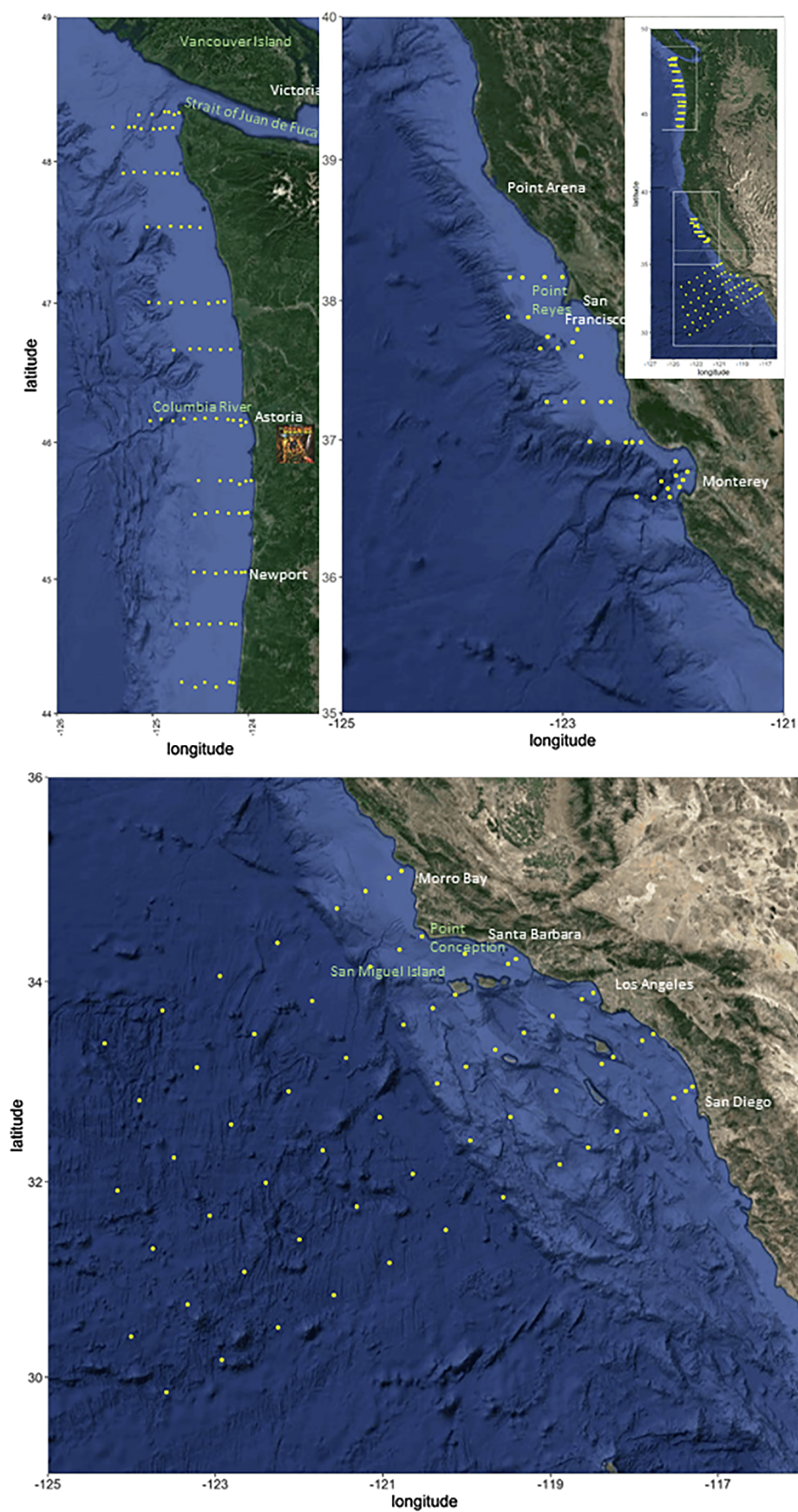
Despite the clear importance of forage species to ecosystem dynamics and fisheries in the CCLME, coast-wide indicators of forage community dynamics are lacking. Instead, forage assemblages have been delimited on regional scales (Fissel et al., 2011; Ralston et al., 2015; Thompson et al., 2017; Barcelo et al., 2018; Friedman et al., 2018), resulting in regional differences and inconsistent reporting of forage community indicators to management bodies such as the PFMC (Harvey et al., 2017). In more recent years, annual coast-wide hydro-acoustic surveys designed to target schools of sardine and other coastal pelagic species (Zwolinski et al., 2012), as well as coast-wide midwater trawl surveys to sample young of the year (YOY) groundfish and other forage species (Sakuma et al., 2016; Friedman et al., 2018) have been conducted; however, both of these time series are still rather short (< 10 years). A set of regional indicators derived with consistent statistical methods is needed to integrate existing long-term regional monitoring and to strengthen understanding of forage variability and underlying environmental and ecological drivers; through these indicators, the research community can provide improved, quantitative science support to natural resource managers on status and trends of system productivity, food availability to predators and protected species, and meaningful cross-regional comparisons (Harvey et al., 2017).

Here, we analyze forage data from three long-term, independent surveys from the northern, central and southern regions of United States waters of the CCLME (Fig. 1, Table 1). To demonstrate how prey dynamics can influence an upper trophic level species, we then compare prey data to long-term diet data for the abundant and relatively well-studied sea lions (e.g., Laake et al., 2018). Our overarching goal is to provide a unifying methodology for summarizing forage community indicators as measured by these disparate surveys. Our related objectives are to determine: (1) the degree to which forage assemblages vary within each region; (2) if there is evidence of broad-scale synchrony in forage assemblage shifts; and (3) if shifts within forage community indicators are reflected in sea lion diets. Notably, although sampling methods are consistent for the duration of the study within regions, collection methods differ greatly among regions as does the sampled life history stages. Therefore, tests of system-wide synchrony are conservative because large changes between regions would have to be evident regardless of sampling methods. Our hope is that these analyses will yield suitable indicators of forage dynamics that can help ecosystem-based management in the CCLME and inform analytical approaches in other systems that are trying to derive integrated, ecosystem-wide, management-relevant indicators from disparate survey methods.

## 2. Data & methods

### 2.1. Field sampling

We analyze data from National Oceanic and Atmospheric Administration (NOAA) surveys that off the coasts of Washington and Oregon (“Northern”), central California (“Central”) and southern California (“Southern”) over 19 years, from 1998 through 2016 (Fig. 1). In the North, we use data collected by the Northwest Fisheries Science Center’s (NWFSC) annual pelagic survey that targets juvenile salmon but quantifies all captured fishes and squids. This survey has been conducted in late June since 1998. Sampling occurs along 11 east–west transect lines off Washington and Oregon (Fig. 1), ranging from the northern tip of Washington (48.23°N) to Newport, Oregon (44.67°N). Trawls are conducted at 6–8 stations on each transect from the



**Fig. 1.** Locations of sample sites (yellow circles), cities (white font), and geographic features (green font). White boxes within the smaller, large-scale map delineate the boundaries of the larger, fine-scale maps.

**Table 1**  
Taxa analyzed in this study. Region depicts the location where each taxa was sampled. Under the Life Stage Sampled column, A = adult, L = larval, P = paralarval, and YOY = young of year. Notes explain which species were summed when taxa were grouped to a higher taxonomic level than species.

Region	Family	Common name	Scientific name	Life Stage Sampled	Adult Habitat	Note
North	Salmonidae	Coho salmon	<i>Oncorhynchus kisutch</i>	yearling	pelagic	This complex likely contains different species to some degree in each region associate with bottom when spawning
	Salmonidae	Chum salmon	<i>Oncorhynchus keta</i>	juvenile	pelagic	
	Salmonidae	Sockeye salmon	<i>Oncorhynchus nerka</i>	yearling	pelagic	
	Salmonidae	Chinook salmon	<i>Oncorhynchus tshawytscha</i>	yearling, subyearling	pelagic	
	Scorpaenidae	Rockfishes	<i>Sebastes</i> spp.	YOY	benthic	
	Anoplopomatidae	Sablefish	<i>Anoplopoma fimbria</i>	pelagic juvenile	benthic	only identified to family includes mainly <i>Bathylagus pacificu</i> , <i>Bathylagoides wesethi</i> , and <i>Lipolagus ochotensis</i>
	Loliginidae	Market squid	<i>Doryteuthis opalescens</i>	YOY, A	pelagic	
	Clupeidae	Pacific sardine	<i>Sardinops sagax</i>	A	pelagic	
	Engraulidae	Northern anchovy	<i>Engraulis mordax</i>	A	pelagic	
	Osmeridae	Herring		YOY, A	mesopelagic	
Central	Bathylagidae	Deep sea smelt				only identified to family Suite of lanternfishes excluding California headlingfish and blue lanternfish
	Bathylagidae	California smoothtongue	<i>Leuroglossus stilbius</i>	YOY, A	mesopelagic	
	Osmeridae	Smelt		A	pelagic	
	Myctophidae	Lanternfishes		YOY, A	mesopelagic	
	Myctophidae	California headlightfish	<i>Diaphus theta</i>	YOY, A	mesopelagic	
	Myctophidae	Blue lanternfish	<i>Tartarobea crenularis</i>	YOY, A	mesopelagic	This complex likely contains different species to some degree in each region <i>Citharichthys sordidus</i> and <i>C. stigmaeus</i> Mostly of <i>Glyptocephalus zachirus</i> , <i>Isopsetta isolepis</i> , <i>Lyopsetta exilis</i> , <i>Microstomus pacificus</i> , <i>Parophrys vetulus</i> , <i>Pleuronichthys coenosis</i> , <i>Pl. decurrens</i> , <i>Pl. ritteri</i> , and <i>Pl. verticalis</i>
	Merlucciidae	Pacific hake	<i>Merluccius productus</i>	YOY	epibenthic	
	Scorpaenidae	Rockfishes	<i>Sebastes</i> spp.	YOY	benthic	
	Paralichthyidae	sanddabs	<i>Citharichthys</i> spp.	YOY	benthic	
	Pleuronectidae	righteye flounders		YOY	benthic	
South	Lolliginidae	Market squid	<i>Doryteuthis opalescens</i>	YOY, A	benthic when spawning, otherwise pelagic	includes Bathylagidae ( <i>Bathylagoides wesethi</i> ); Gonostomatidae ( <i>Cyclothone signata</i> , <i>Diplophos proximus</i> ); Phosichthyidae ( <i>Vinciguerra lucetia</i> , <i>V. poweriae</i> ); Chauliodontidae ( <i>Chauliodus macouart</i> ); Myctophidae ( <i>Diogenichthys atlanticus</i> , <i>Nannobranchium ritteri</i> , <i>Protomyctophum crockeri</i> , <i>Symbolophorus californiensis</i> , <i>Trphoturus mexicanus</i> )
	Clupeidae	Pacific sardine	<i>Sardinops sagax</i>	L	pelagic	
	Engraulidae	Northern anchovy	<i>Engraulis mordax</i>	L	pelagic	
	Bathylagidae	California smoothtongue	<i>Leuroglossus stilbius</i>	L	mesopelagic	
	Bathylagidae	eared blacksmelt	<i>Lipolagus ochotensis</i>	L	mesopelagic	
	Myctophidae	Northern lampfish	<i>Stenobrachius leucopsarus</i>	L	mesopelagic	This complex likely contains different species to some degree in each region Mostly white croaker ( <i>Genyonemus lineatus</i> ) with few queenfish ( <i>Scirphus politus</i> ) and white seabass ( <i>Atractoscion nobilis</i> ) Mostly <i>Citharichthys sordidus</i> and <i>C. stigmaeus</i> ; <i>C. xanthostigma</i> presence is possible but rare
	Bathylagidae, Gonostomatidae, Phosichthyidae, Chauliodontidae, and Myctophidae	southern mesopelagics		L	mesopelagic	
	Merlucciidae	Pacific hake	<i>Merluccius productus</i>	L	epibenthic	
	Scorpaenidae	Rockfishes	<i>Sebastes</i> spp.	L	benthic	
	Carangidae	Jack mackerel	<i>Trachurus symmetricus</i>	L	pelagic	
	Sciaenidae	Croakers		L		associate with bottom when spawning
	Scombridae	Pacific mackerel sanddabs	<i>Scomber japonicus</i>	L	pelagic	
	Paralichthyidae		<i>Citharichthys</i> spp.	L	benthic	
	Pleuronectidae	Slender sole	<i>Lyopsetta exilis</i>	L	benthic	
	Pleuronectidae	English sole	<i>Parophrys vetulus</i>	L	benthic	
	Loliginidae	Market squid	<i>Doryteuthis opalescens</i>	P	pelagic	



shallowest bottom depth possible ( $\sim 30$  m) out to  $\sim 50$  km from shore, often extending beyond the continental shelf (Brodeur et al., 2005). Sampling is conducted in the upper 20 m of the water column using a 108-m pelagic rope trawl fitted with a 336-m<sup>2</sup> mouth opening (Northeastern Trawl Systems Inc., Bainbridge Island, Washington) with variable mesh sizes (162.6 cm at mouth to 8.9 cm at cod end). To retain catches of small nekton, a 6.1-m long, 8-mm mesh knotless liner is sewn into the cod end. The rope trawl is towed for 30 min at a speed over ground of approximately 6 km h<sup>-1</sup> during daylight hours (between morning civil twilight and end of evening civil twilight). Because the survey is only conducted during the day, we exclude taxa that are known to undergo diel vertical migration (notably sardine and anchovy) and thus may not be effectively sampled near the surface during the day (Krutzikowsky and Emmett, 2005). Ultimately, we evaluate the dynamics of young salmonids, pelagic juvenile sablefish *Anoplopoma fimbria*, YOY rockfish, and market squid (Table 1; see Section 2.3 for definition of life history stages), as these species undergo little or no diel vertical migrate during their early life history stages (Sakuma et al., 1999; Zeidberg and Hamner, 2002).

In the Central region, midwater trawls by the Southwest Fisheries Science Center are used to obtain biological samples (Table 1). This survey has been conducted since 1983 and has included nearly all of California waters south of Cape Mendocino since 2004, and most of Oregon and Washington waters since 2011. Here, we focus on 1998–2016 to overlap with surveys in the Northern region analyze night samples from fixed stations just south of Monterey Bay (approximately 36.5°N) to just north of Pt. Reyes (38.25°N; Fig. 1) from late spring of each year. At each station a modified Cobb midwater trawl net is fished at 30-m headrope depth (or 10 m at stations shallower than 60 m). The net has a square opening with a height and width of 12 m, is fitted with a 26-m headrope and has a 9.5-mm mesh cod end. The net is towed at the target depth (30 m or 10 m) at a constant speed of 3.7 km h<sup>-1</sup> for 15 min. All fish and cephalopods sampled are identified to the lowest possible taxonomic level (often species, but sometimes family or genus; Table 1).

Surveys in the Southern region are carried out in spring (March and April) by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program. CalCOFI has been monitoring physical and biological components of this region regularly since 1949, and detailed methods are described by McClatchie (2014). We analyze ichthyoplankton collected with bongo nets at 66 ‘core’ stations (Fig. 1; McClatchie, 2014) between 1998 and 2016. Ichthyoplankton sampling captures a diverse suite of forage taxa because even though adults live in a variety of habitats, larvae from most species are found in the upper 200 m of the water column day and night (Moser, 1996). Bongo nets equipped with a flowmeter, 0.71-m diameter rings, and 505- $\mu$ m mesh are lowered to 210 m (or within 20 m of the bottom at shallow stations) and towed at a constant rate at a 45° angle to the surface. Contents of the starboard net are preserved at sea in 5% tris-buffered formalin. In the laboratory, ichthyoplankton and market squid are sorted and identified to the lowest possible level of taxonomic resolution (Table 1). Most individuals are identified to species, but those that are difficult to discern based on morphology are identified to genus or family. Specifically, most rockfish larvae are morphologically indistinguishable and are categorized as *Sebastes* spp. In addition, croakers (mostly white croaker *Genyonemus linneatus*, but also a limited number of queenfish *Seriophilus politus* and white seabass *Atractoscion nobilis*) are identified as Sciaenidae.

## 2.2. Sea lion prey sampling

Forage taxa are identified in scats from adult female sea lion rookeries at San Miguel Island, California, and the frequency of the occurrence (expressed as % FO) of each prey taxa is calculated to examine the summer diet of nursing females in relation to the Central and Southern regional forage indices. These two regions represent the

foraging area of nursing adult females from San Miguel Island to Monterey Bay, CA (Melin and DeLong, 2000; Melin et al., 2008). Between 30 and 133 scat samples were collected each year between May and September. Scat samples are processed according to Orr et al. (2003); recovered fish bones, fish otoliths, and cephalopod beaks are identified, and frequency of occurrence is calculated following Melin et al. (2012). We restrict the forage index comparison to seven taxa identified as primary sea lion prey: sardine, anchovy, Pacific mackerel *Scomber japonicus*, jack mackerel *Trachurus symmetricus*, rockfishes, Pacific hake and market squid (Melin et al., 2012). Frequency of occurrence is commonly used as an index of diet for sea lions (Lowry et al., 1990; Lowry, 1991; Weise and Harvey, 2008; Melin et al., 2012) due to biases associated with extrapolating from scat contents to biomass or percent mass of prey consumed by pinnipeds (Laake et al., 2002; Joy and Tollit, 2006).

## 2.3. Data preparation

We express forage values as the number of individuals per km<sup>3</sup> of water sampled in the Northern region and as relative catch rate (by trawl) in the Central region. In the Southern region, we follow standard CalCOFI methodology to express abundances in a cylinder of water with a 10-m<sup>2</sup> cross-sectional area and a depth of 200 m (Kramer et al., 1972). Raw CalCOFI larval abundances are divided by the proportion of the sample that is sorted (samples with very high zooplankton volumes are partially sorted) and multiplied by a standard haul factor that accounts for tow depth and volume sampled. We then calculate annual means of  $\ln(x + 1)$  for each taxon in each region using the delta-mean method, which is a technique for estimating means from zero-inflated data (Pennington, 1996).

We use explicit definitions for various fish stages. In the Northern region, we analyze data from young salmonids that we classify as ‘juvenile’, ‘yearling’, and ‘subyearling’. The juvenile stage includes fishes that are just arriving in the ocean through those that have spent a year or more in the ocean but are not yet mature enough to return to freshwater to spawn in that year. ‘Yearlings’ are fish that spend a full year in freshwater (i.e., spawned in the fall, emerged in the winter, spent spring/summer/fall/winter in freshwater, migrated to sea in the spring) prior to entering the ocean; hence, some juveniles could be yearlings. Subyearlings do not spend a full year in freshwater as they emerge in winter and migrate to sea in summer. Subyearlings enter the ocean later in the year than yearlings and are younger than yearlings. Chinook salmon *Oncorhynchus tshawytscha* are the only species that are commonly found in the subyearling stage. Sablefish inhabit surface waters prior to moving to deeper water at ages 2+, and are commonly collected as pelagic juveniles in the North. YOY rockfishes are frequently caught in both the Northern and Central surveys. YOY rockfishes are typically between 50 and 150 days old and live in a pelagic environment prior to settling to the benthos where most species reside as adults. Similarly, hake, sanddabs, and righteye flounders are captured during the YOY stage as these species either move to deeper water or associate with the benthos as adults. In the Central region, anchovy and sardine are caught in both YOY and adult stages. YOY anchovy and sardine are typically between 40 and 60 mm TL while adults are > 90 mm (70–90 mm individuals are rarely captured). We do not differentiate life stages of species in the families Bathylagidae or Myctophidae in the Central region (Table 1). Fishes and market squid in the South are taken as larvae or paralarvae, respectively.

All taxa that we analyze in the Northern region (Table 1) are directly consumed as forage by a broad range of higher trophic level predators. In the Central region, most individuals are also young of the year (YOY); however, adult anchovy, smelt and sardine are also prevalent in some years (Table 1). In the southern (CalCOFI survey) data, larvae are subject to substantial predation within the macrozooplankton community (McGowan and Miller, 1980), but are generally not consumed by the same suite of predators that forage on larger

and more mobile juvenile and adult life history stages (Szoboszlai et al., 2015). Larval abundance, however, reflects the abundance of mature, spawning populations (Hsieh et al., 2005), and is treated as such in this analysis. In the case of rockfishes, most CalCOFI larvae are species that are relatively small as adults (e.g., shortbelly rockfish, *Sebastes jordani*; Thompson et al. (2016)) and are directly consumed by upper trophic level species.

Preliminary correlation results indicated that abundances of some forage species closely track one another through time. In cases where these taxa are functionally similar (Szoboszlai et al., 2015), taxa are grouped to streamline results. Rockfishes are combined as *Sebastes* spp., and sanddabs as *Citharichthys* spp. in all regions. In the Central region lanternfishes, with the exception of California headlightfish *Diaphus theta* and blue lanternfish *Tarletonbeania crenularis*, are combined as Myctophidae; deep sea smelt, with the exception of California smoothtongue *Leuroglossus stilbius*, as Bathylagidae; and right-eyed flounders as Pleuronectidae. In the Southern region, bristlemouths (Gonostomatidae), lightfishes (mostly Panama lightfish *Vinciguerria luccetta*), viperfish (Chauliodontidae) and lanternfishes (Myctophidae) with biogeographic centers of distribution that are south relative to southern California (Hsieh et al., 2005) are grouped as “southern mesopelagics,” and croakers as Sciaenidae. We exclude taxa that are found in < 5% of samples from each region and ultimately analyze the dynamics of 8–15 taxon categories per region (Table 1).

Hsieh et al. (2005) found that abundances of fishes with similar adult habitats tend to track one another through time. Adult habitat affinity, therefore, could serve as an indicator of taxa dynamics, and we assign to each taxon a classification of adult habitat similar to Hsieh et al. (2005). Taxa are considered epibenthic if they associate with the benthos during a majority of their adult lives. Pelagic taxa, by contrast, spend their entire adult lives in the open ocean. Mesopelagic taxa reside (at least during the day; many vertically migrate to the surface at night) in waters between approximately 200–1000 m.

#### 2.4. Regional forage assemblage dynamics

Our first objective is to pinpoint when changes occurred in forage assemblages within each region and which taxa drive these changes. To determine when changes in assemblage structure took place, we run chronological cluster analyses based on Bray-Curtis dissimilarity matrices calculated from  $\ln(x + 1)$ -transformed annual delta mean abundances of each taxon (Grimm, 1987). Delta means are better suited than simple averages for computing means from zero-inflated data (Grimm, 1987). Chronological clustering identifies which years have similar assemblages with the constraint that years are sequential. The relatively short duration of sampling precludes the use of statistics such as broken stick (Bennett, 1996; Morse et al., 2017) or multivariate regression trees (De'ath, 2002; Perretti et al., 2017) to delineate significant assemblage changes. Thus, we qualitatively identify years where deep transitions are found in the chronological clusters. To help visualize patterns of taxa dynamics, we couple the chronological dendrograms with heat maps showing taxa Z-scores of abundance in each year. Taxa on the heat maps are grouped by hierarchical clustering based on Bray-Curtis dissimilarity matrices of calculated means; this approach also helps identify which taxa are correlated through time. To assist with biological interpretation of these results, we qualitatively note if taxa that tracked one another through time have similar adult habitat affinities. In addition, we create non-metric multidimensional scaling (NMDS) plots to evaluate which years have similar forage assemblages independent of sequential time. Finally, we create bar plots that quantified mean abundances of each taxon in each year for the three regions.

#### 2.5. Cross-regional synchrony of forage dynamics

Our second objective is to determine whether forage assemblages change at similar times among regions. If assemblages fluctuate in

synchrony across regions, then we would expect years that differ in one region to also differ in another region (e.g., if assemblage structure differs greatly between 1998 and 1999 in the North, it should also differ greatly between these years in the Central region). To determine if there is significant correlation among the dissimilarity matrices (derived for objective 1) between each pair of regions, we use Mantel tests (Legendre and Legendre, 1998). Significance of the Mantel  $r$  statistics are assessed using 10,000 bootstrap resamples.

Next, we evaluate synchronicity of individual taxa across regions by calculating significance of Pearson correlations ( $p$ -value < 0.005 following sequential Bonferroni correction for multiple testing) between pairs of regions for taxa that are found in multiple regions (e.g., sanddab abundance in the Central vs. Southern regions paired by year). Recognizing that different surveys targeted different life history stages, we limit taxa-specific inter-region comparisons to five taxa that are consistently abundant in at least two regions: paralarval/juvenile/adult market squid, larval/adult anchovy, larval/adult Pacific sardine, and larval/ pelagic YOY stages of rockfishes and sanddabs.

#### 2.6. Sea lion diet as a forage indicator

Our final objective is to evaluate as a case study whether forage dynamics correspond to variability in diets of sea lions at San Miguel Island (Fig. 1). We first characterize changes in adult female sea lion diet, expressed as % FO by forage taxa in scat samples, using the same analyses described above for prey: chronological clustering, heat map, and NMDS. We then evaluate whether changes in abundance of the seven focal forage taxa in the Central and Southern regions correlate with the frequency with which those taxa occur in the sea lion diet using Redundancy Analysis (RDA; Borcard et al., 2011). Forage data from both regions are used because female sea lions from San Miguel Island forage in both regions during periods of gestation and nursing (Section 2.2; Melin and DeLong, 2000). To discern which forage taxa best predicts sea lion diet, we perform both forward and backward stepwise selection based on AIC values derived from RDA sum of squares. Because stepwise selection in RDA models can be sensitive to the order in which independent variables are entered into the model (Oksanen, 2007), we also manually explore several models containing various forage taxa based on initial stepwise results. We ultimately present the most plausible RDA model based on the minimization of AIC scores.

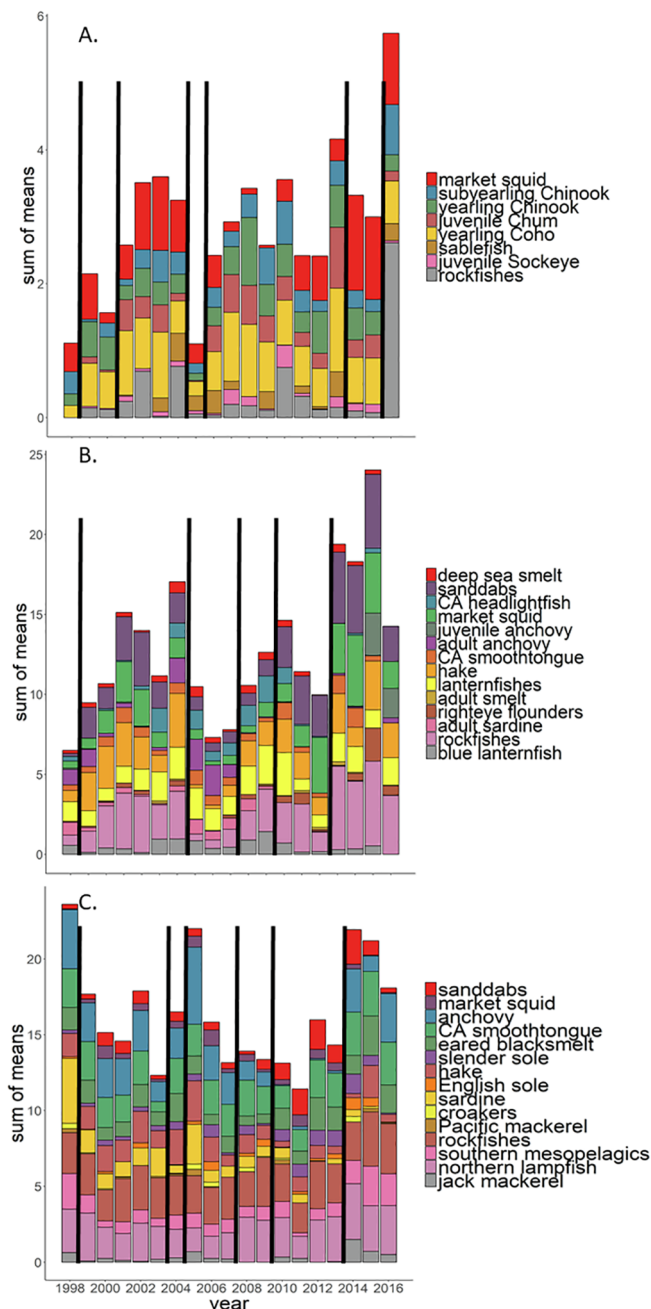
#### 2.7. R packages

We use R version 3.4.3 (R Core Team, 2017) to perform all analyses and generate plots. RDA and NMDS analyses are done using the package ‘vegan’ (Oksanen et al., 2017). Chronological clusters are created with the package ‘rioja’ (Juggins, 2015) while the heat maps and species cluster dendrograms are made with the packages ‘gplots’ (Warnes et al., 2016), ‘cluster’ (Maechler et al., 2017) and ‘dendextend’ (Galili, 2015). The NMDS, RDA, and chronological cluster dendrograms are created with ‘ggplot2’ (Wickham, 2009) and the maps with ‘ggplot2’ and ‘ggmap’ (Kahle and Wickham, 2013).

### 3. Results

#### 3.1. Forage assemblage dynamics

In all 3 regions of the CCLME forage taxa abundances were highly dynamic between 1998 and 2016 (Fig. 2), and there was a strong tendency for taxa with similar adult habitats to shift concurrently. The deepest transition in the Northern region's chronological cluster tree occurred after 1998, 2000, 2004, 2005, 2013 and 2015; examination of the heat map, NMDS plot, hierarchical clustering dendrograms, and bar graphs of mean abundances (Table 1; Figs. 2 and 3) show that juvenile sockeye salmon *Oncorhynchus nerka*, yearling Chinook salmon *O.*



**Fig. 2.** Summed mean abundances of taxa from the A) Northern, B) Central, and C), Southern regions. Black lines depict years when strong changes in assemblage structure were detected with chronological clustering analyses. Note that units are different for each region.

*tsawytscha*, yearling coho salmon *O. kisutch*, and juvenile chum salmon *O. keta* tended to flux congruently as all load negatively on NMDS1 and cluster together on the dendrogram. In 1998, these taxa were all relatively low but increased in 1999–2000. The transition after 2000 reflected an increase in market squid, yearling coho, and juvenile sockeye but a decrease in yearling Chinook. In 2005, all of the sampled taxa decreased but most rebounded in 2006. The assemblage was relatively stable from 2006 to 2013, but all salmon, rockfishes, and sablefish decreased, while market squid increased, from 2013 to 2014. The transition from 2015 to 2016 was mainly caused by a large increase in rockfishes. The two taxa in the North with epibenthic adult habitats (rockfishes and sablefish) tended to fluctuate congruently as did four of five salmon groups.

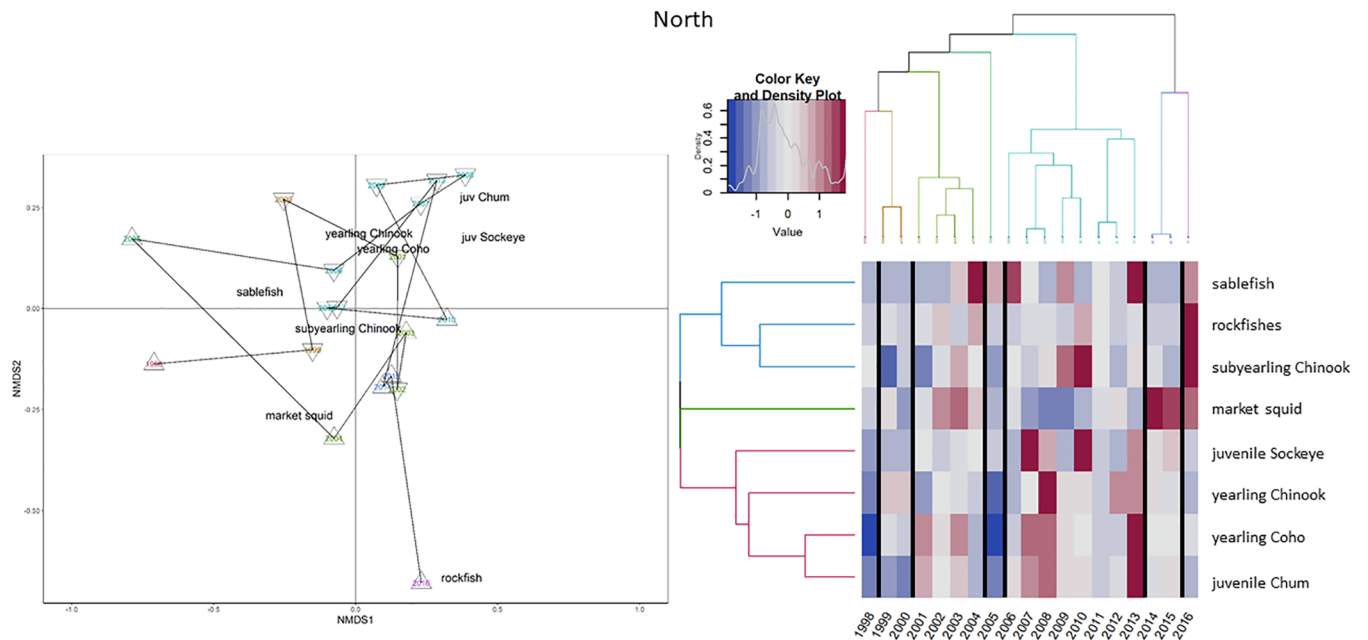
In the Central region, the abundances of several taxa that live in pelagic habitats (adult sardine and adult anchovy; Table 1) and mesopelagic habitats (deep sea smelt and lanternfishes; Table 1) tended to temporally cluster together relative to those that are associated with epibenthic adult habitats (hake, righteye flounders, rockfishes and sanddabs) (Table 1, Fig. 4). YOY anchovy and market squid, however, did not follow this pattern as they also cluster with taxa with epibenthic adult habitats. Chronological clustering defines major assemblage transitions after 1998, 2004, 2007, 2009, and 2012 (Fig. 4). The 1998–1999 transition was characterized by decreases in many of the pelagic/mesopelagic taxa such as sardine and lanternfishes but increases in most of the epibenthic taxa (Figs. 2 and 4). During the 2004–2005 transition most of the pelagic taxa increased while many of the epibenthic taxa decreased (Figs. 2 and 4). The 2007–2008 transition saw an increase in most mesopelagic taxa, and a marked decline for adult anchovy. The 2009–2010 transition was then driven by an increase in most epibenthic taxa as well as mesopelagic California smoothtongue. The transition after 2012 was driven by deepsea smelt, lanternfish and California smoothtongue (mesopelagic), and hake, rockfishes, and sanddabs (epibenthic) increases.

In the Southern region taxa with mostly pelagic (Table 1) adult habitats clustered together (jack mackerel, croakers, Pacific mackerel, sardine and anchovy; hake were the exception) as did several taxa that associate with epibenthic adult habitats (market squid, English sole *Paraphrys vetulus*, slender sole *Lyopsetta exilis*, and sanddabs) (Fig. 5). The third cluster contained taxa with mesopelagic adult habitats (eared blacksmelt *Lipolagus ochotensis*, northern lampfish, southern mesopelagics and California smoothtongue) as well as rockfishes (Table 1, Fig. 5). Chronological clustering in the Southern region defines assemblage transitions after 1998, 2002, 2003, 2007, 2009, and 2013 (Figs. 2 and 5). The 1998–1999 transition was characterized by decreases of most taxa in the mesopelagic and pelagic clusters. The 2002–2003 transition saw decreases in most taxa in the epibenthic and mesopelagic groups. California smoothtongue, in particular, fell to very low levels in 2003. After 2003, most taxa increased with the exception of sardine. The main driver of the 2007–2008 transition was a marked increase in northern lampfish (Figs. 2 and 5). The 2009–2010 transition was the deepest in the Southern region time series and marked decreases of anchovy to almost non-detectable levels as well as a decrease in hake to the lowest level in the time-series. The final deep transition (2013–2014) was mainly characterized by increases in three of four epibenthic taxa (English sole, slender sole and sanddabs; market squid declined), three of four mesopelagics (only eared blacksmelt declined) and all pelagics except Pacific mackerel (anchovy and jack mackerel had the largest increases).

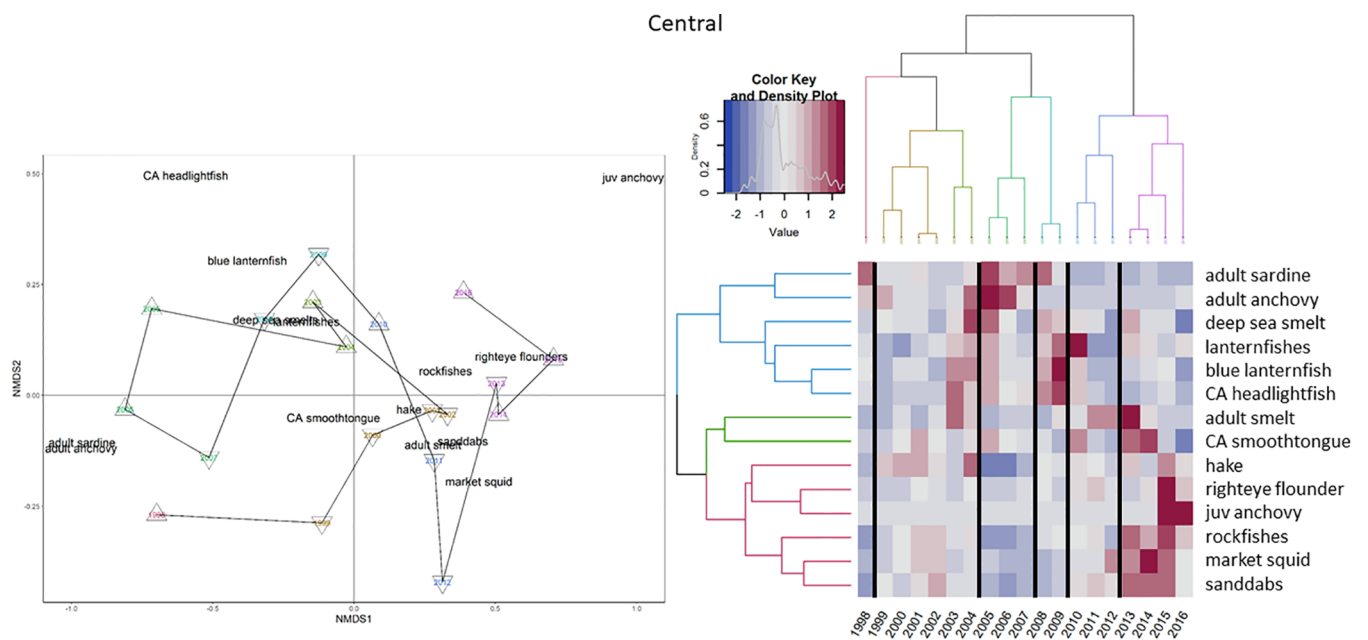
### 3.2. Synchrony of forage dynamics

Changes in forage assemblage structure were largely concordant among regions as dissimilarity matrices correlated significantly among adjacent regions (Northern versus Central: Mantel  $r = 0.25$ ,  $p = 0.02$ ; Central vs. Southern Mantel  $r = 0.27$ ,  $p = 0.007$ ), although the correlation between the Northern and Southern regions was not quite significant (Mantel  $r = 0.18$ ,  $p = 0.11$ ). While assemblage composition changed in synchrony between adjacent regions, there is little evidence that individual taxa fluctuated synchronously among regions (Table 2). Of the five taxa sampled in at least two locations and 9 correlation analyses, only larval/juvenile sanddabs in the Central and Southern regions were significantly correlated following Bonferroni correction for multiple testing.

The overall lack of correlation between individual taxa indicates that although the timing of shifts in forage community composition was approximately the same among regions, these changes were driven by different taxa among regions. For example, there was a strong change between 2004 and 2005 in both the Northern and Central regions, but in the Northern region it was highly driven by decreases in most salmon



**Fig. 3.** Multivariate analyses of forage dynamics in the Northern Region. The plot on the left depicts NMS2 results where years are color coded to correspond with the horizontal chronological clustering branches on the top right. Upward and downward triangles depict years when the Pacific Decadal Oscillation (PDO) index was high and low, respectively. The vertical dendrogram in the middle characterizes taxa that tended to exhibit similar dynamics. The heatmap is colored based on the Z-score for each taxon. Dark vertical bars on the heatmap demarked deep breaks in assemblage structure between years. NMS2 stress = 0.14.



**Fig. 4.** Multivariate analyses of forage dynamics in the Central Region. Plot components are the same as Fig. 3. NMS2 stress = 0.08.

as well as market squid and rockfish (Figs. 2 and 3) whereas in the Central region the major change was an increase in sardines and anchovies (Figs. 2 and 4).

### 3.3. Sea lion diet

As with forage community dynamics, sea lion diet varied dramatically from 1998 to 2016. Diet composition differed among four periods with transitions after 1998, 2001 and 2007 (Fig. 6). In 1998, diet was largely comprised of sardine and rockfishes. In 2000 and 2001, hake and market squid dominated sea lion diet. Between 2002 and 2007 diet was mainly comprised of sardine and anchovy. From 2009 onward,

market squid, hake and rockfishes were common in diet samples, although the prevalence of anchovy increased in 2016 (Fig. 6).

Sea lion diet correlated significantly with forage assemblage dynamics in the Central and Southern regions. The most parsimonious RDA model included anchovy and sardine in the South and market squid from the Central region (Fig. 7; RDA  $F = 3.81$ ,  $p = 0.002$ , adj.  $R^2 = 0.35$ ). The RDA result indicates that sea lions consumed large amounts of anchovy, sardine and market squid when these species were abundant in the environment.



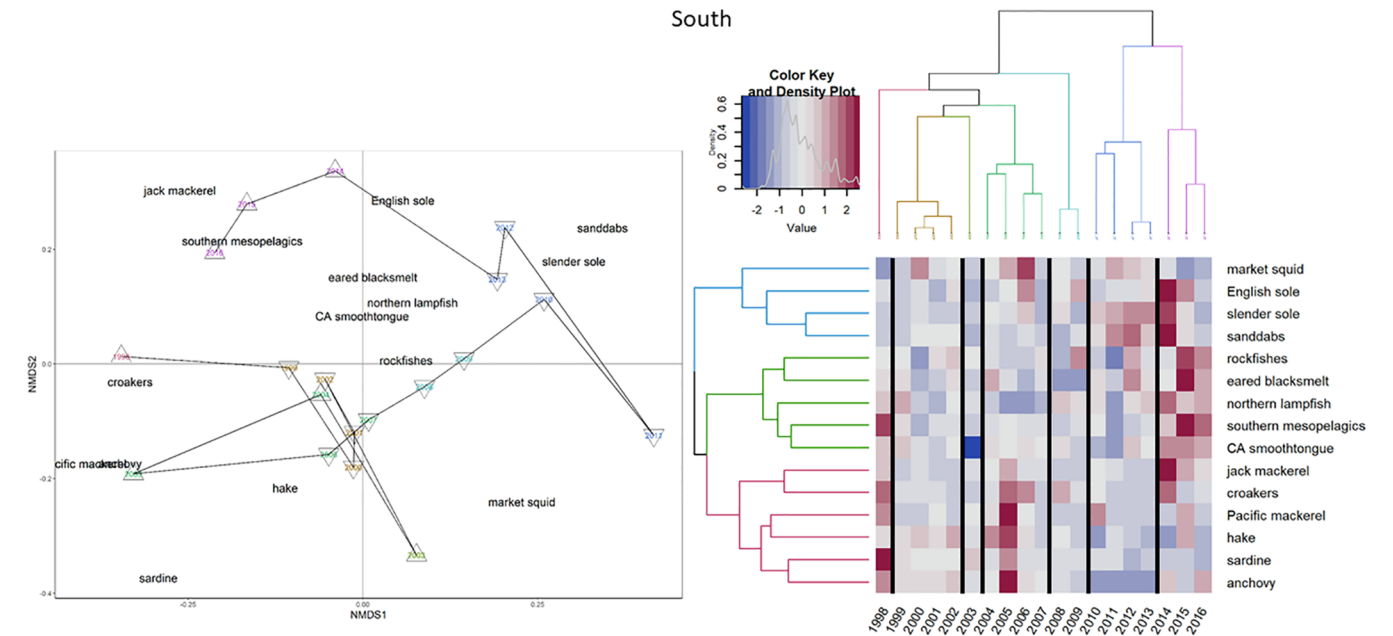


Fig. 5. Multivariate analyses of forage dynamics in the Southern Region. Plot components are the same as Fig. 3. NMDS stress = 0.13.

**Table 2**  
Pearson correlation coefficients and p-values for taxa found in at least two regions. The threshold for significance following Bonferroni correction is  $p < 0.005$ .

Taxa	Region 1	Region 2	r	p
Sanddabs	Central	South	0.66	0.0022
Market squid	North	Central	0.59	0.0074
	North	South	-0.35	> 0.05
	Central	South	-0.15	> 0.05
Anchovy	Central	South	0.01	> 0.05
Sardine	Central	South	0.6	0.0062
Rockfish	North	Central	0.26	> 0.05
	North	South	0.29	> 0.05
	Central	South	0.28	> 0.05

4. Discussion

Our results indicate that forage communities are highly dynamic throughout the CCLME, but that there is concordance in inter-regional community shifts. Despite major differences in sampling methodologies across the three regions, we gain valuable insight about forage dynamics in different regions through the statistical integration of multiple monitoring programs. The indices we derive, therefore, should be useful to management efforts that must account for changes in lower trophic level productivity that supports target and protected species.

4.1. Forage assemblages

We detect significant correspondence in changes to the overall

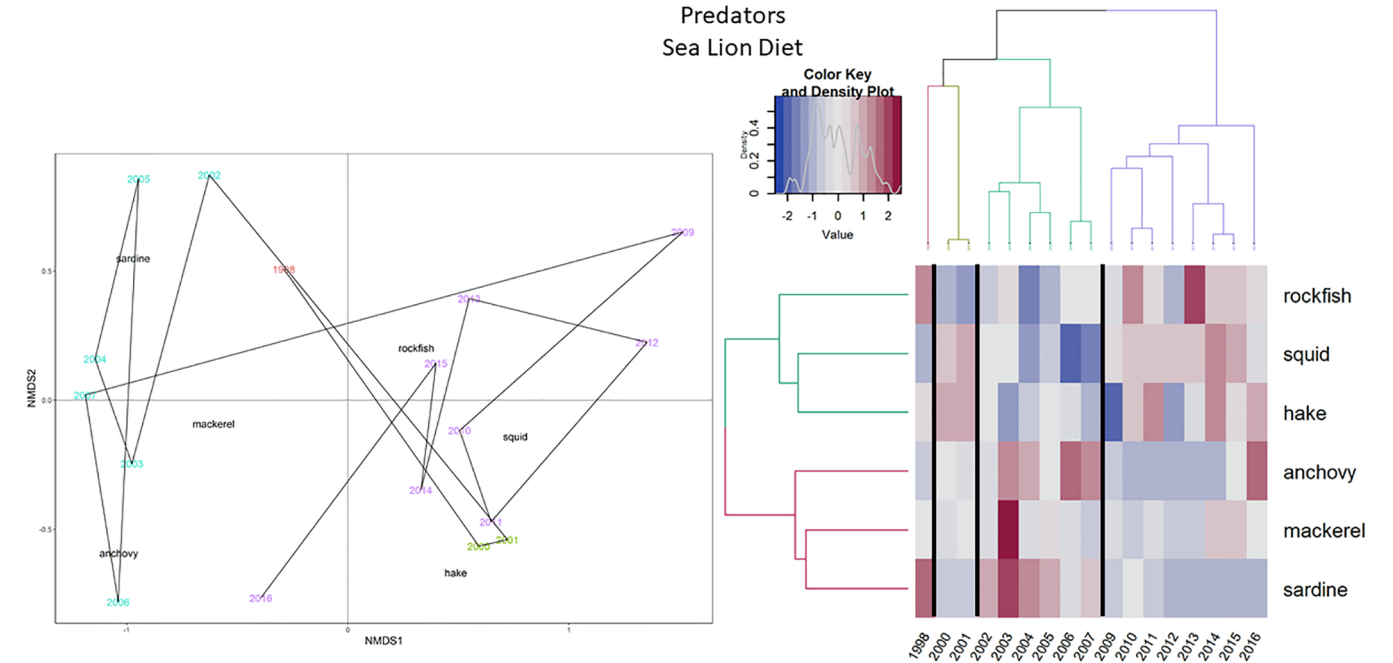


Fig. 6. Multivariate analyses of sea lion diet on San Miguel Island, California. Plot components are the same as Fig. 3. NMDS stress = 0.03.

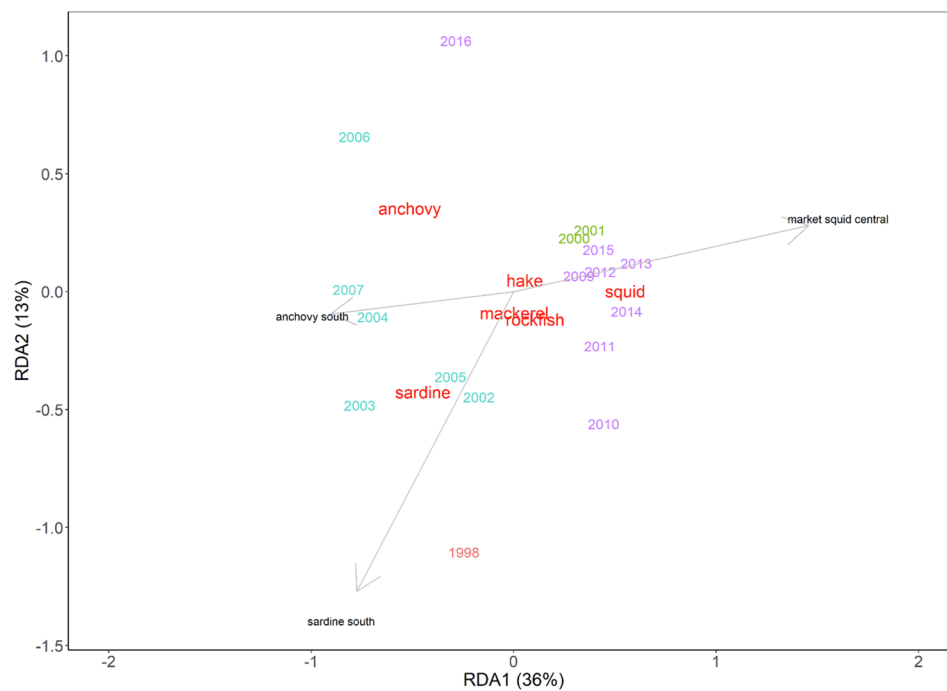


Fig. 7. Redundancy Analysis (RDA) relating forage availability (black font) with prey occurrence in sea lion fecal matter (red font).

forage fish assemblage throughout the CCLME. At the level of individual taxa that are found throughout the CCLME, however, fluctuations show little interregional similarity. This indicates that although large changes commonly occur at about the same time across the regions, the taxa that change within each region are not necessarily the same. These patterns could be explained in part by differences in sampling gear that targets different ontogenetic stages in each region (which could lead to lags in the community response for adults, relative to larval or juvenile abundance shifts), by local physical or biological processes, or by distributional shifts of taxa among these regions. In particular, forage fish assemblages changed in all regions from 1998 to 1999, when there was a transition from El Niño to La Niña conditions, and again around 2013–2014 when ocean temperatures rapidly warmed throughout the CCLME (although the prey assemblage shifted a year earlier in the Central region).

In general, when conditions are warm in the CCLME some taxa move north or shoreward relative to their typical distribution (Hsieh et al., 2009; Santora et al., 2017; Auth et al., 2018). However, because biogeographic ranges differ among taxa, the response to warming and cooling may differ among locations. For example, during the unusual ocean conditions and water temperatures subsequent to 2013 (Jacox et al., 2018) water temperature in the north increased and environmental conditions likely became suitable for market squid. In the south, however, the water was probably too warm for market squid and abundances substantially decreased. Thompson et al. (2014) also found that there was little to no correlation between dynamics of larval fishes sampled off Oregon and off southern California from 2004 to 2011. However, earlier research suggests that the CCLME can be a cohesive system, and that similar processes affect the entirety of the region. For example, Mendelssohn and Schwing (2002) demonstrated that monthly sea surface temperatures within 2° longitude-latitude boxes between 1946 and 1990 were highly correlated along the west coast of North America at all locations between 23°N (south tip of Baja California Sur, Mexico) and 47°N (northern Washington, USA). Further, Bernal and McGowan (1981) found that zooplankton biomass varied in concert throughout the entirety of the coastal ocean off California between 1949 and 1969. Given that different sampling methods are used to collect forage fish data in each region in our study, our finding of

system-wide cohesion suggests that broad climatic changes affect all life phases of forage fish in the CCLME. Our results provide further support for broad-scale biological synchrony, but they also demonstrate that the entire assemblage must be considered to illuminate how this trend is expressed by the forage community within a particular region.

Within each region taxa with similar adult habitats tend to exhibit similar dynamics, likely because taxa in similar habitats are exposed to similar ocean conditions. Previous analysis of CalCOFI larval data from 1951 to 2010 also demonstrated that taxa with similar adult habitats (oceanic, coastal-oceanic and coastal habitats) are apt to track one another through time (Hsieh et al., 2005). This coherence was well explained by environmental variability for the oceanic group (we refer to this group as mesopelagic in this study) as abundance of almost all species increased during warm periods and vice versa (Hsieh et al., 2005), but there was little evidence of linear environmental effects for the coastal-pelagic or coastal groups. Hsieh et al. (2005) suggested that a lack of simple correlation was due to more complex, nonlinear relationships between species and the environment. Further evidence for cohesion in the dynamics of population fluctuation was discovered in juvenile rockfishes (Ralston et al., 2013) as the abundances of 10 YOY rockfish taxa were almost all significantly correlated with one another between 1983 and 2010. Although interannual variability in upwelling and basin scale indices such as the Pacific Decadal Oscillation did not explain changes in YOY abundances, equatorward transport tended to be high when abundances were large (Ralston et al., 2013). These results and ours suggest that groups of taxa with similar adult habitats often fluctuate fairly coherently in the CCLME, but that the relationships to oceanographic drivers can be complex over long time periods.

Wide fluctuations are a hallmark of forage species population dynamics worldwide (Peck et al., 2014). Due to their economic and ecological importance, fluctuations of anchovy and sardine populations are particularly well documented. Both of these species ranged from being by far the most abundant forage fishes to being nearly undetectable during parts of the 20th century in northwestern, northeastern and southeastern Pacific LMEs (Schwartzlose et al., 1999). Fluctuations of similar magnitude for species such as herring *Clupea harengus* and sprat *Sprattus sprattus* were also documented over the past six decades in the North Sea LME (Akimova et al., 2016). Similarly, populations of

Japanese sardine *Sardinops melanostictus*, Japanese anchovy *Engraulis japonicus*, round herring *Etrumeus teres*, horse mackerel *Trachurus japonicus*, chub mackerel *Scomber japonicus*, and walleye pollock *Theragra chalcogramma* in the Tsushima, Kuroshio, and Oyashio current LMEs around Japan changed greatly between 1955 and 2010 (Tian et al., 2014). The volatile nature of forage populations over decadal time periods throughout the globe emphasizes the need for continuous monitoring of forage assemblages as changes in forage populations have can have far-reaching ecological and economic effects throughout ecosystems.

#### 4.2. Oceanographic drivers

Synchronous changes in assemblage structure throughout the CCLME suggest that large-scale oceanographic dynamics impacted multiple regions in a similar manner between 1998 and 2016. There were several major large-scale oceanographic transitions during this period. First, there was a transition from a major El Niño (warm conditions) to a strong La Niña (cold conditions) between 1998 and 1999, and a concurrent change in forage assemblage was observed in each region. La Niña conditions persisted through 2002, and the forage assemblage was relatively stable in each region during this time. Moderate El Niño conditions prevailed between 2003 and 2005, and the assemblage composition fluctuated in each region during this time. In addition, delayed upwelling occurred in the North and Central regions in 2005 (Schwing et al., 2005; Sydeman et al., 2006), and changes in assemblage composition were documented following 2004 in these regions. Conditions were mostly Niño-neutral in 2006 and 2007, but a strong La Niña occurred in 2008 and persisted through mid-2009. Forage assemblages in the Central and Southern regions also changed between 2007 and 2008. From mid-2009 to mid-2010 there was a strong, but short-lived El Niño (Kim et al., 2011), and the Central and Southern assemblages changed in 2010. Another strong La Niña occurred in 2012 but transitioned to more neutral conditions at the beginning of 2013. The Central but not the Northern nor Southern assemblages changed between 2012 and 2013. In late 2013 a marine heatwave (McClatchie et al., 2016b; Fiedler and Mantua 2017; Santora et al., 2017), also known as “The Blob” (Bond et al., 2015), was characterized by anomalously warm surface waters that began in the Gulf of Alaska and spread to the south by late 2014. The warm water was then influenced by an El Niño event during the winter of 2015 that persisted into 2016, and the 2014–2016 period had the warmest ocean temperatures over a 3-year period on record (Jacox et al., 2018). Forage composition changed greatly between 2013 and 2014 in the North and South and between 2012 and 2013 in the Central Region, and remained similar within each region during the prolonged warming events except in the Northern region where another shift occurred between 2015 and 2016.

Previous research in the CCLME showed that the assemblage breaks identified here were concurrent with shifts for additional ecosystem components. The 1998–1999 El Niño/La Niña transition has been described as a potential regime shift in the California Current (Peterson and Schwing, 2003); thus, it was not surprising that it was the only event showing complete CCLME synchrony. This event resulted in changes from warm-water to cold-water zooplankton and an increase in abundance of a number of adult fish stocks (Peterson and Schwing, 2003). The record warm years between 2014 and 2016 (Jacox et al., 2016) also resulted in a multitude of ecosystem effects throughout the CCLME. For example, northern copepod abundances were at record low levels during this period in the North, whereas myctophids reached record high abundances in both the Central and Southern regions (Cavole et al., 2016; McCabe et al., 2016; McClatchie et al., 2016b; Peterson et al., 2017; Jacox et al., 2018).

Although large-scale forcing affected much of the CCLME during some periods, other breakpoints may have been associated with more local forcing. For example, the month-long delayed upwelling of 2005

(Schwing et al., 2006; Sydeman et al., 2006) coincided with changes in the North and Central assemblages, but not in the South as upwelling is less of a driver in the southern California ecosystem (Checkley and Barth, 2009). In addition to our work, Brodeur et al. (2006) documented anomalously high abundances in 2005 of taxa such as anchovy, jack mackerel, and Pacific mackerel in the Northern region and sardine and myctophids in the central region. Some of the other synchronous intermediate break points (e.g. 2007–2008 and 2009–2010 in the central and southern CCLME) may represent regional differences in temperature expression that in turn would be expected to lead to differential responses, both regionally and across life-history stages.

Quantitatively linking environment to assemblage changes was beyond the scope of our study, but more detailed analyses describing how changes in environmental conditions impact forage fish assemblages have been conducted within each region of the CCLME. In the Northern region, epipelagic forage fish assemblage structure was correlated with ocean temperature and salinity between 1999 and 2009 (Litz et al., 2014). Similarly, ichthyoplankton surveys off Oregon reveal that forage species such as YOY sanddabs, anchovy, and YOY rockfish correlated positively with ocean temperature (Auth, 2008; Brodeur et al., 2008; Thompson et al., 2014), and that sardine were highly abundant during the extremely warm winter of 2015 (Auth et al., 2018). In the Central region, the midwater forage assemblage structure was correlated with oceanographic conditions: higher densities of YOY rockfishes and market squid were associated with greater advection (transport) of subarctic waters in the California Current (as indicated by water properties and relative sea level anomalies) between 1990 and 2012, while sardine and/or anchovy as well as lampfish were associated with low transport (more subtropical ocean conditions) years (Ralston et al., 2015). The forage community of 2015 stood out from previous years in the Central region as it had high overall abundance and very high species diversity (Santora et al., 2017). In the Southern region, CalCOFI ichthyoplankton surveys revealed that mesopelagic taxa that primarily reside seaward of the continental shelf move shoreward and impinge on the CalCOFI sampling area during warm conditions associated with El Niños (Moser et al., 1987; Hsieh et al., 2009; Thompson et al., 2012). Overall, our work and previous analyses demonstrate that forage fish assemblages can shift dramatically in response to environmental forcing throughout the CCLME.

#### 4.3. Impact of forage fluctuation on predators

Fluctuations in forage fish assemblage structure have major implications for predator diets and population dynamics. We find that sea lion diets consist largely of sardine, anchovy and market squid when these taxa are abundant in either Central or Southern California. A very comparable result is reported by Robinson et al. (2018), who found substantial coherence between sea lion diets off of Año Nuevo Island (central California) and the abundance of various forage taxa from the central California midwater trawl survey. When anchovy, sardine and hake in sea lion diets were low, other species, such as rockfishes, myctophids, sanddabs, and slender barracudina (*Lestidiops rigens*) increased. Because these latter species are less nutritious than anchovy and sardine, females were malnourished when anchovy and sardine were scarce, and there was elevated pup mortality (Melin et al., 2010; McClatchie et al., 2016a). As such, it is now well appreciated that forage abundance and composition are important indicators of sea lion status (Melin et al., 2012). In addition to sea lions, forage availability is also linked to diet and survival of piscivorous birds such as rhinoceros auklet *Cerorhinca monocerata* (Thayer and Sydeman, 2007; Santora et al., 2014), common murre (Ainley et al., 1996; Wells et al., 2008; Wells et al., 2017) and Brandt's cormorant *Phalacrocorax penicillatus* (Elliot et al., 2016) in the CCLME. In addition, the survival of salmon transitioning from river to ocean habitat correlates with abundance (Friedman et al., 2018) and type (Daly et al., 2017) of forage species in the central and northern CCLME. These results and ours demonstrate

that changes in abundance and structure of forage assemblages can permeate through marine ecosystems and further emphasizes the need to understand forage fluctuations to elucidate predator dynamics.

#### 4.4. Management applications

The necessity of documenting forage dynamics in a palatable manner to inform Ecosystem-Based Management (EBM) is now widely appreciated around the globe (Peck et al., 2014). A major motivation for this study, therefore, is to examine how forage community indicators from different regions of the CCLME could be evaluated in a manner conducive to improving resource managers' understanding of ecosystem dynamics that support productivity of target and protected species at upper trophic levels. In the United States, fisheries management decisions within the EEZ are made by regional councils such as the PFMC, where voting members need to assimilate information on a myriad of marine regulatory issues and make informed decisions on, among many other items, EBM. As such, the PFMC relies on clear reports to quickly assimilate a large amount of information. We hope that our work will aid this process.

The PFMC largely relies on NOAA's California Current Integrated Ecosystem Assessment (CCIEA) team to provide ecological and social contexts for EBM (Harvey et al., 2017). Unfortunately, the CCIEA team has struggled to identify effective indicators of the forage community. In part, this is because the large number of forage species results in a potentially overwhelming number of abundance time series to present to managers; moreover, these time series cannot be compared directly across regions due to differences in survey methods and life history stages collected (larval vs. juvenile or adult). The analyses here integrate each region's many forage species time series into a manageable number of multivariate indices of forage community status. Thus, even in the absence of consistent coast-wide forage monitoring surveys, we now provide the PFMC with multivariate indices relating regional forage composition in a given year to community compositions in previous years or climate/oceanographic regimes, and quantitatively identify when especially strong shifts occur. Specifically, we anticipate presenting the PFMC with annual updates of the heatmaps and dendrograms shown in Figs. 3–6 to summarize forage dynamics in different parts of the CCLME, and similar figures are included in the 2018 CCIEA report (Harvey et al., 2018). The common statistical approach used across all regions should enable comparison of the timing of shifts in regional forage community composition, and thus helps connect forage community dynamics to major changes in climate or ocean conditions. As such, we believe that our results on forage indicators will augment PFMC understanding of an important component of the CCLME. Our work could also serve as a template for documenting forage dynamics in other LMEs around the world where regional monitoring efforts must be integrated to support ecosystem-scale management.

#### 5. Conclusions

Forage species are centrally important to the function of marine ecosystems, particularly in LMEs driven by strong seasonal pulses of production that can vary substantially between years (Checkley and Barth, 2009). Monitoring their status and understanding their responses to environmental variation at different spatial and temporal scales will facilitate ecosystem-based management of fisheries that target forage species and their predators, and also support conservation of top predators such as marine mammals and seabirds. Under the PFMC's Fishery Ecosystem Plan, the CCIEA team has been producing annual California Current ecosystem status reports, which include indicators of forage species (Harvey et al., 2017, 2018). The approach we offer here synthesizes information on dozens of species collected by multiple, disparate regional survey approaches into a small number of biologically meaningful multivariate indices, which should lessen the burden of interpretation on the PFMC and other management partners. This

approach should be readily transferable to LMEs around the world where forage species are monitored via piecemeal regional efforts, and where management bodies and research groups are working together to develop robust mechanistic indicators to support ecosystem-based management of fisheries and other marine resources.

#### Declaration of Competing Interest

The authors have no competing interests to declare.

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