Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem

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ABSTRACT: Monitoring essential marine biodiversity variables is an effective means for assessing impacts of climate change and human-related stressors such as pollution, overfishing and habitat destruction. Yet little is known about the natural variability of biodiversity in pelagic upwelling marine ecosystems, which are often subject to substantial interannual and decadal variability of ocean climate conditions. Using data from a pelagic midwater trawl survey, we quantified diversity indices of epipelagic forage species collected over 26 yr (1990 to 2015) to determine the natural variability and environmental determinants of biodiversity within the California Current upwelling ecosystem. Biodiversity time series indicate there are 2 alternate forage species assemblages that relate to differences in cool/strong and warm/weak upwelling years that vary in 3 to 5 yr cycles. Cooler years are associated with increased biodiversity of juvenile groundfish, whereas warm years coincide with increased biodiversity of coastal and mesopelagic fishes and species originating from southern and subtropical waters. During 2015, a year of anomalous warm surface ocean conditions, we observed unprecedented high levels of biodiversity and attribute it to high abundance of juvenile groundfish combined with an unusually high transport of subtropical and offshore species into neritic waters. Using a combination of remote sensing and *in situ* hydrographic data, we compare 2015 to previous anomalous ocean climate conditions and discuss how biodiversity of forage species may impact trophodynamics of upwelling ecosystems and predator–prey interactions. Attributing changes in marine biodiversity to productivity cycles and anomalous climate events, and detecting long-term biodiversity trends, provides a critical index toward understanding climate forcing on upwelling ecosystems.

KEY WORDS: Coastal pelagic species · Evenness · Forage fish · Groundfish · Marine Biodiversity Observation Network · Marine sanctuary · Monitoring · Remote forcing · Richness · Fisheries

INTRODUCTION

Marine biodiversity is threatened by climate change and increasing human-related stressors, such as pollution, overfishing and habitat destruction (Halpern et al. 2008, Tittensor et al. 2010, Beaugrand et al. 2013). The assessment of marine biodiversity is difficult because sampling methodology often varies depending on oceanographic research programs, and it is logistically difficult and expensive to maintain long-term data sets (Edwards et al. 2010, McClatchie et al. 2014, Koslow & Couture 2015).

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Furthermore, determining what aspects of biodiversity to measure and consistently monitor within and among marine ecosystems remains a challenge that often requires research involving existing long-term databases, which are rare for these ecosystems. To overcome these challenges, a recent effort was made to prioritize rules for establishing a coordinated Marine Biodiversity Observation Network (MBON) framework globally (Duffy et al. 2013, Muller-Karger et al. 2014). Developing an MBON is envisioned to quantify baseline biodiversity patterns, facilitate the identification of threats to biodiversity and provide early warning to potential perturbations from climate change and human stressors (Palumbi et al. 2009, Fautin et al. 2010). Underpinning the MBON effort is that we develop an understanding of the natural variability of biodiversity, especially for ecologically and commercially important species. Therefore, in this study, we quantify biodiversity time series (i.e. richness, diversity and evenness) for an assemblage of epipelagic micronekton (surface-oriented free-swimming organisms that are <20 cm in length, including krill and young-of-the-year [YOY] fishes) in the California Current and separate diversity metrics for juvenile groundfish and other forage species (e.g. coastal pelagic species, mesopelagic fishes and squid).

Little is known about the natural variability of biodiversity of forage species in Eastern Boundary Upwelling Ecosystems (EBUEs; Fréon et al. 2009), which are among the most productive marine habitats in the world. The 4 largest EBUEs, of which the California Current is one, account for nearly a fifth of the world's fish catch despite occupying less than 1% of the total ocean area (Fréon et al. 2009). These ecosystems are subject to substantial interannual (e.g. El Niño−Southern Oscillation [ENSO]) and decadal variability of ocean climate conditions (e.g. Pacific Decadal Oscillation [PDO]; Mantua et al. 1997, Checkley & Barth 2009). Pelagic upwelling ecosystems are in constant flux, and species assemblages and distributions often change dramatically due to the interactive effects of shifting water masses, population production patterns and life histories (Chavez et al. 2003, Hooff & Peterson 2006, Checkley & Barth 2009, Hazen et al. 2013), thus creating a myriad of challenges for assessing baselines and quantifying the natural variability in pulses of biodiversity. This challenge is especially acute in the face of global climate change that is predicted to impact these ecosystems (Rykaczewski et al. 2014, Bakun et al. 2015). Further, fisheries exploitation may impact community-level changes of marine fish

populations and influence our assessment of natural and anthropogenic drivers of marine biodiversity variability (Levin et al. 2006, Frank et al. 2016). Attributing changes in marine biodiversity to bottom-up productivity, ecosystem structure and anomalous events and detecting long-term trends are paramount to portend the future impacts of climate change.

The waters off central California comprise a productive upwelling ecosystem that supports a diverse community of marine fish, invertebrates, seabirds and mammals (Ainley & Hyrenbach 2010, Santora et al. 2012, Ralston et al. 2015) and is tightly coupled to seasonal and interannual variability of upwelling on fine spatial scales as well as variability in large-scale ocean transport at broader spatial scales (Checkley & Barth 2009). The interaction between northwest winds and coastal geomorphology influence upwelling and nutrients that stimulate the development of a rich pelagic food web involving the production of phytoplankton, zooplankton and midwater forage and predatory fish (Checkley & Barth 2009). Based on an extended survey time series, there appear to be 2 general communities in the epipelagic micronekton (forage) assemblages off central California in the late spring and early summer, largely in response to differences in warm/cool and strong/weak upwelling years (Bograd et al. 2009, Ralston et al. 2015, Sakuma et al. 2016). Strong upwelling and/or high transport of cool subarctic water is associated with enhanced production of krill, pelagic juvenile (YOY) rockfish *Sebastes* spp., market squid *Doryteuthis opalescens* and other YOY groundfish (e.g. Pacific hake *Merluccius productus* and sanddabs *Citharhichthys* spp.), whereas weak upwelling years usually coincide with increased localized abundance (or distributional shifts) of northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax* and various mesopelagic fishes (Ralston et al. 2015, Sakuma et al. 2016). Pelagic juvenile rockfish, the early life history stage of a diverse species group that is a major linchpin of the food web, display abundance cycles that relate to high transport of nutrient-rich subarctic waters and retentive patterns (Ralston & Stewart 2013, Ralston et al. 2013). Moreover, during El Niño and anomalous warm ocean events (such as the unusually low productivity conditions of 2005 and 2006; Peterson et al. 2006), the cool water community of groundfish, squid and krill is typically found at considerably lower abundance levels, and oceanic species such as the ribbonfish king-of-the-salmon *Trachipterus altivelis* and subtropical species, such as pelagic red crabs *Pleuroncodes planipes* and California lizardfish *Syn-*

odus lucioceps, are more likely to be transported into the region (Leising et al. 2015, Sakuma et al. 2016). Although these species collectively represent some of the most important forage taxa available to higher trophic level predators (piscivorous fishes, marine mammals and seabirds; Ainley & Hyrenbach 2010, Kaplan et al. 2013, Brodeur et al. 2014, Szoboszlai et al. 2015), it is unknown how variability in the diversity of this assemblage might be used to index variability in ecosystem processes and productivity resulting from anomalous ocean climate events or other impacts.

Here, we use data collected consistently over a 26 yr period by an oceanographic midwater trawl survey with the objective of establishing a record of the natural variability of biodiversity of epipelagic micronekton in the California Current, with particular attention on juvenile groundfish and other components of the forage assemblage. Specifically, we assess the degree to which our biodiversity time series reflect anomalous ocean climate events and whether there are ecologically relevant cycles and/or trends. Our overarching hypothesis is that increased biodiversity of juvenile rockfish and groundfish species will reflect production cycles during cool/strong upwelling years, whereas increased biodiversity of other forage species (e.g. northern anchovy and mesopelagic fishes) will reflect warm/weak upwelling years and influx of species from oceanic and subtropical waters. To explore potential oceanographic drivers of biodiversity, we integrate data derived from satellite observations on sea surface temperature (SST), climate indices (e.g. PDO) and oceanographic survey data. Due to the recent unprecedented climate variability experienced in the North Pacific (Bond et al. 2015, Leising et al. 2015, DiLorenzo & Mantua 2016), this long-term study highlights and compares how biodiversity changed during 2015 relative to past El Niño events. Furthermore, we discuss the contribution of epipelagic forage species diversity time series in EBUEs to better understand essential biodiversity variables integrated for the global MBON effort.

MATERIALS AND METHODS

Study area

The greater Gulf of the Farallones and Monterey Bay region (hereafter GoF/MB) extends from Point Reyes (38.5° N) to Point Sur (36° N) (Fig. 1). This region has an extensive continental shelf, particularly in the Gulf of the Farallones, and contains numerous shallow water topographies (e.g. Cordell Bank) and submarine canyon systems (e.g. Pioneer and Monterey canyons) that support a diverse food web. Located within the GoF/MB are the Farallon Islands, which contain important seabird and pinniped breeding colonies (Ainley & Boekelheide 1990) that rely on a diverse forage assemblage to raise offspring; the broader region is also a hotspot for highly migratory high trophic level predators (Block et al. 2011). Most of these predators rely extensively on coastal pelagic species (e.g. northern anchovy,
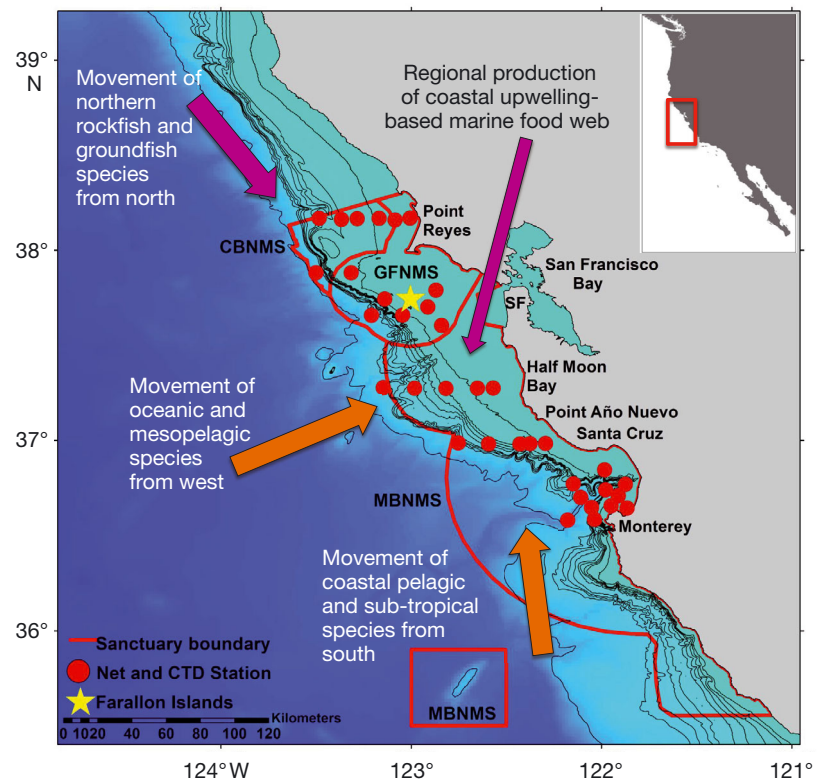

Fig. 1. Study area off central California illustrating the location of the Rockfish Recruitment and Ecosystem Assessment Survey net haul and CTD sampling stations within national marine sanctuaries. Arrows indicate generalized directional shifts of epipelagic species into the study region, representing northern, western and southern movement patterns. CBNMS: Cordell Bank National Marine Sanctuary; GFNMS: Greater Farallones National Marine Sanctuary; MBNMS: Monterey Bay National Marine Sanctuary; SF: San Francisco

Pacific sardine and market squid), krill and juvenile groundfish (particularly rockfish) and other epi-pelagic micronekton (e.g. pelagic squid and meso-pelagic fishes) as forage (Sydeman et al. 2001, Weise & Harvey 2008, Thayer et al. 2014, Glaser et al. 2015, Fleming et al. 2016), as illustrated by the high rankings of these groups in a meta-analysis of forage needs throughout the California Current eco-system (CCE) (Ainley et al. 2015, Szoboszlai et al. 2015). In addition, there are 3 national marine sanc-tuaries located in the GoF/MB: Cordell Bank, Gulf of the Farallones and Monterey Bay (Fig. 1). Under-standing the variability of biodiversity in the GoF/MB is a priority for the sanctuaries to monitor the condition of the ecosystem.

Ecosystem assessment survey

The National Marine Fisheries Service has con-ducted a midwater trawl survey of the epipelagic micronekton assemblage (Rockfish Recruitment and Ecosystem Assessment Survey [RREAS]) during late spring (typically May to mid-June) in central California waters each year since 1983 and throughout a broader expanse of California Current waters since 2004 (Ralston et al. 2015, Sakuma et al. 2016). Trawls are conducted at night at fixed stations (Fig. 1) using a modified Cobb midwater trawl with a 9.5 mm cod-end liner, typically with a headrope depth of 30 m (exceptions are made in shallower waters where 30 m tows are infeasible; see Sakuma et al. 2016 for additional survey details). Typically, 15 min tows were made at each station, although shorter-duration tows (e.g. 5 min) were made in areas with dense gelatinous zoo-plankton aggregations to avoid net damage, with data extrapolated to the standard 15 min tow dura-tion using a calibrated correction factor (less than 5% of total tows). Relative species abundance is measured as catch-per-unit-effort (CPUE). At each trawl station, a CTD cast was made using a SeaBird Electronics SeaCAT 19plus to a depth of 500 m or to 10 m from the bottom in shallower waters. Addi-tional CTD casts were done during the daytime at fixed stations bounding the nighttime trawl stations (Fig. 1); the survey also collected seabird and mar-ine mammal observational data during daylight hours and fisheries acoustics data continuously while underway. Previous studies of micronekton assemblages and oceanographic conditions from this survey highlight important subdivisions among shelf, oceanic and Monterey Bay sampling areas

(Santora et al. 2012, 2014), and these station group-ings are applied in this study.

Species selection

The RREAS was initially developed to estimate the abundance of YOY (pelagic juvenile) rockfish and other YOY groundfish during their post-larval but pre-settlement life history stage (approximately 100 to 150 d of age; Ralston et al. 2013). The survey meth-ods are also consistent with those developed in the 1960s and 1970s to assess the abundance of coastal pelagic species such as northern anchovy, Pacific sar-dine and other smaller forage fish (Mais 1974). The fine mesh on the cod-end liner also leads to high retention of other late larval/early juvenile stage fishes as well as adult stages of krill (*Euphausia* spp.), pelagic shrimps (e.g. Sergestidae and Pasiphaeidae) and gelatinous zooplankton (e.g. Scyphozoa and Tunicata). However, the smaller size of the net (rela-tive to other surveys that use surface trawls for salmon or larger coastal pelagic species) and slower towing speed (~2 knots versus ~3.5 knots for many surface trawl surveys) means that many larger and faster nekton (e.g. mackerel and saury) are able to avoid the gear, and many highly surface-oriented for-age species (e.g. salmonids and atherinopsids) are poorly sampled. Although no sampling gear is effec-tive at sampling the entire suite of organisms in any given habitat, this trawl gear is effective at catching a representative sample of the epipelagic micro-nekton. For example, species representing 12 of the 20 most frequently occurring taxa in higher trophic level predator studies are well sampled (occur in 10% or more of trawls) in this survey, including 8 of the top 10 (Ainley et al. 2015, Szoboszlai et al. 2015).

Although the survey has encountered a wide range of species throughout its duration, it was necessary to constrain the species included in this analysis for rea-sons of both consistency and common sense. For con-sistency, it was necessary to include species or taxa that were consistently enumerated to a standard taxonomic level throughout the entire time series (Table S1 in the Supplement at www.int-res.com/articles/suppl/m580p205_supp.pdf). This included 53 species of YOY groundfish (30 rockfish, 23 other groundfish), 45 species of fish (generally coastal and mesopelagic species), 4 taxa groups of cephalopods and 9 species of crustaceans. The survey did not identify krill to species level until 2002, so their taxo-nomic resolution is simply Euphausiacea. Similarly, while the market squid *Doryteuthis opalescens* has

been identified to species since 1990, all other decapods are treated as other squid, and octopods other than the blob octopus (Alloposidae) are grouped as Octopoda, which each represent multiple species or families (e.g. Gonatidae and Octopodidae). Similar to krill, data exist at a higher taxonomic resolution, but only since the mid-2000s; see Sakuma et al. 2016 for frequency of occurrence by species. Moreover, large adult stages of nekton and/or benthically oriented species, such as adult rockfish *Sebastes* spp., spiny dogfish sharks *Squalis suckleyi* or adult English sole *Parophrys vetulus*, were excluded from the analysis, as they represent species that are outside of the size range and habitats that are the focus of this analysis and are also not considered to be sampled representatively by the survey gear. By contrast, YOY and adult life history stages of coastal pelagic species (e.g. northern anchovy or Pacific sardine) were pooled into a single group for purposes of assessing diversity at the species level, as both life history stages occupy the same habitat and are preyed on by a similar assemblage of predators. Finally, despite their considerable relative abundance in survey catches (Sakuma et al. 2016) and importance with respect to ecosystem function and productivity, gelatinous zooplankton (e.g. Scyphozoa and Tunicata) were not reliably enumerated throughout the duration of the survey time series and are consequently not included in diversity metrics.

Diversity metrics and analyses

Biodiversity calculations were derived using the R Vegan package (Oksanen et al. 2013, R Core Team 2015). We quantified the following diversity indices: species richness, Shannon-Weaver diversity and Pielou's evenness (Oksanen et al. 2013). Richness provides an index of the number of species caught per trawl, diversity is a measure of the relative rarity (low) or commonness (high) of species per trawl (information including number and standardized abundance of species), and evenness is an assessment of whether abundance is equally distributed (e.g. value of 1) among species in the system. As described in 'Materials and methods: Species selection', we calculated diversity indices for (1) the entire assemblage (all catch; 111 taxa), (2) YOY groundfish (53 taxa) and (3) other forage species (primarily coastal pelagic species, mesopelagics and cephalopods; 49 taxa). Table S1 in the Supplement reports the common names, species names and frequency of occurrence (as a percentage of the number of hauls

and of years) for all species included in the analysis. Diversity indices were calculated for each individual trawl, and we aggregated all trawls per year and spatially by subregion and the entire study area (all) to calculate time series of mean diversity to describe interannual and regional variability. For diagnostics, we compared the relationships between diversity and evenness using linear regression and calculated species accumulation curves and confidence intervals to assess species richness relative to sampling effects per group (Ugland et al. 2003). Spatial climatologies of diversity indices were calculated by determining the long-term spatial mean per station over 1990 to 2015 and mapped to assess regional variability. We used ANOVA to examine regional differences in diversity indices. Furthermore, we predict that diversity time series of YOY groundfish are linearly related to their abundance, due to their synchronous production of different species during cooler productive years (Ralston et al. 2015), and are spatially consistent within the study area (Santora et al. 2014). On the other hand, during warmer and weaker upwelling years, we predict that diversity of the other forage species group within shelf habitat is nonlinearly related to their overall abundance, with higher diversity occurring at moderate levels of abundance during anomalous warm years. The mechanism behind this prediction is attributed to warm water species, which are generally lower in abundance compared to locally produced juvenile groundfish and euphausiids, becoming impinged onto the shelf during weaker anomalous warm years (Lenarz et al. 1995, Chavez et al. 2003, Santora et al. 2014, Leising et al. 2015). Due to known periodic variability of rockfish and groundfish productions and shifts in oceanic species distribution patterns, diversity time series likely reflect a combination of ocean climate anomalous events, productivity cycles and trends attributed to long-term change in large-scale transport and regional upwelling conditions (Ralston et al. 2013, 2015). Therefore, we inspected each biodiversity time series for trends with regression analyses and periodicity using autocorrelation tests with up to 12 yr lags.

Ocean climate conditions and biodiversity anomalies

We compared biodiversity variables to sea temperature variables derived from remotely sensed SST (monthly means of daily optimally interpolated advanced very high resolution radiometer SST; Rey-

nolds et al. 2007) and with the PDO to provide context on ocean climate state and to better understand cycles of biodiversity variability. Previous research revealed the importance of winter to spring ocean conditions on the variability and occurrence of species assemblages during RREAS surveys (Schroeder et al. 2009, 2014, Ralston et al. 2013, Santora et al. 2014); therefore, remotely sensed SST and the PDO were integrated over January to June for comparison with biodiversity variables. For remotely sensed SST, values were integrated within a box extending from Point Conception to Point Arena, from 34° to 40° N and from 126.7° to 120.7° W offshore. The SST box size was chosen to assess the relative importance of warm waters offshore that may influence species distribution shifts into coastal waters. SST and PDO were detrended to avoid spurious relationships and are compared to biodiversity variables using Pearson correlations to assess the relative importance of regional temperature patterns and basin-scale ocean climate conditions on biodiversity patterns. To provide greater context on the influence of ocean climate conditions on biodiversity, we compare and contrast 3 extreme climate episodes: the 1997 El Niño, the 1999 La Niña and the 2015 warm blob. The ocean climate conditions during 1997 and 1999 represent extreme warm and cool years, while 2015 was unprecedented and impacted multiple aspects of the marine food web of the North Pacific (Bond et al. 2015, Leising et al. 2015, Cavole et al. 2016, DiLorenzo & Mantua 2016). We calculated anomalies for satellite remotely sensed SST for the California Current and CTD cross-sections of temperature vertical structure to examine ocean conditions during May coinciding with biodiversity spatial anomalies during these years.

RESULTS

Baseline biodiversity patterns: events, cycles and trends

Time series of biodiversity indices for all taxa, YOY groundfish and other forage species revealed several ecologically relevant aspects of the pelagic upwelling ecosystem that relate to productivity and distribution patterns (Fig. 2a–d). In general, these results indicate that species richness covaries strongly among regions for all 3 taxonomic groupings, diversity covaries more strongly for YOY groundfish than for forage or all species, and evenness has the least amount of coherence among the regions (Fig. 2a–i). Overall, diversity is positively related to evenness, but there are distinct differences between YOY groundfish and forage species regarding the scaling of diversity and evenness (Fig. 3a). The species accumulation curve increased asymptotically, indicating that nearly all species per group may be frequently observed with only a relatively small fraction of the total hauls (e.g. <500; Fig. 3b). Moreover, the diversity of YOY groundfish is highly correlated with their abundance, while the diversity (and richness; not shown) of the forage species group within shelf habitat is non-linearly related to their abundance (Figs. 2 & 3c,d).

Above all, the time series highlight that biodiversity conditions in 2015 were extremely anomalous, and record high levels were observed for the 26 yr study period. Although diversity and species richness of all taxonomic groupings displayed record highs during 2015, evenness was not as anomalous but rather was similar to that of 1998, a strong El Niño year associated with unusually low abundance and productivity of many marine species (Fig. 2a–d). Additional results on the impact of anomalous ocean conditions during 2015 on biodiversity patterns relative to regional scale temperature anomalies and comparison to previous ENSO events are presented below in the section 'Impact of anomalous ocean climate conditions'.

Despite the high levels of biodiversity in 2015, there is a significant decline in evenness (r^2 = 0.26, r = −0.51, p < 0.007) and diversity (r^2 = 0.18, r = −0.43, p < 0.02) of the entire assemblage within the Monterey Bay region (Fig. 2b,c and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m580p205_supp.pdf). However, no trends were detected in either the YOY groundfish or the forage species group, again indicating that much of this signal may be due to the relatively high abundance of krill during 2008 to 2014. Diversity indices for the YOY groundfish group displayed marked periodicity. For example, autocorrelation tests revealed that YOY diversity in Monterey Bay and oceanic regions (Fig. 2g) displayed significant (p < 0.05) positive autocorrelation at 1 yr lag and negative autocorrelation at 3 to 5 yr lags. Similarly, YOY evenness in shelf and in oceanic regions also displayed significant positive autocorrelation at 1 yr lag and negative autocorrelation at 3 to 5 yr lags, thereby indicating potential productivity and recruitment cycles of the YOY assemblage (Fig. 2e–h). Time series of forage species richness in Monterey Bay displayed significant autocorrelation at 4 to 5 yr lags, while forage richness on the shelf displayed autocorrelation at 1 yr lag. No other time series displayed significant autocorrelation.
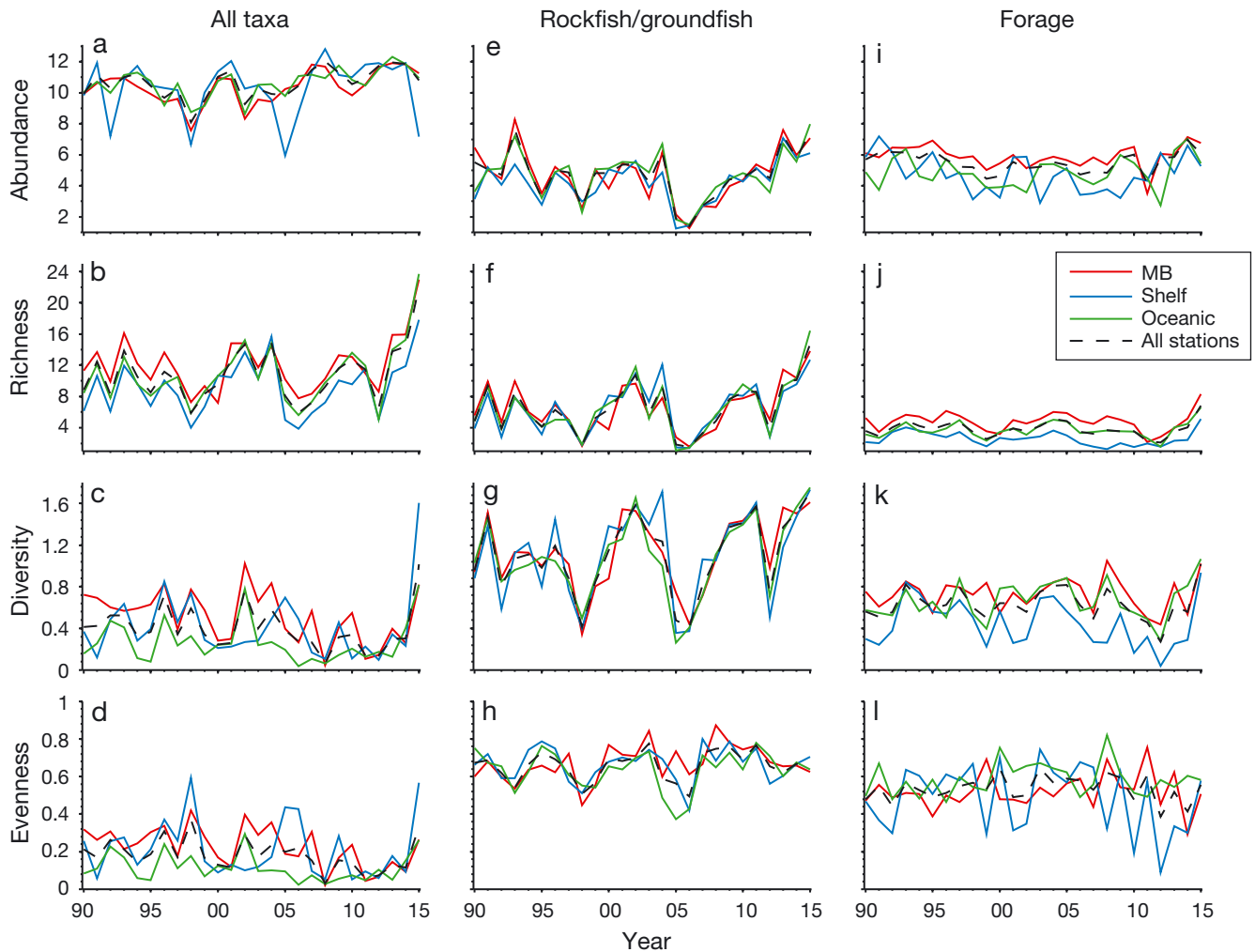
Fig. 2. Time series of total abundance (ln CPUE + 1), species richness, Shannon-Weaver diversity and Pielou's evenness for (a–d) all taxa, (e–h) young-of-the-year rockfish/groundfish and (i–l) forage species. Regional indices include the entire region (all stations), shelf, oceanic and Monterey Bay (MB)

Regional differences

Spatial average maps (e.g. climatologies for 1990 to 2015) resolved the general spatial structure of biodiversity variables, indicating regional differences and inshore–offshore gradients (Fig. 4 and Fig. S2 in the Supplement). The diversity of total taxa is greater in Monterey Bay compared to oceanic waters (p = 0.002) but not different from the shelf (p < 0.39). Evenness of total catch is significantly lower in Monterey Bay compared to the shelf (p = 0.009) and oceanic waters (p = 0.002). Species richness of total taxa is significantly higher in Monterey Bay compared to the shelf (p = 0.02) and not different compared to oceanic waters (p = 0.59). There are no significant regional differences in biodiversity indices for YOY groundfish (Fig. 4 and Fig. S2 in the Supple-

ment). Forage species diversity is significantly higher in Monterey Bay and oceanic waters in comparison with diversity on the shelf (p < 0.0001 and p = 0.002, respectively). Forage species evenness is significantly higher on the shelf compared to oceanic waters (p < 0.01) but not different from Monterey Bay (p < 0.71). Forage species richness is significantly higher in Monterey Bay compared to shelf (p < 0.001) and oceanic (p < 0.001) waters; richness in oceanic waters is higher than in shelf regions (p < 0.001).

Impact of anomalous ocean climate conditions

The richness of the forage species assemblage off central California is positively correlated (r = 0.71, p < 0.01) with SST conditions in the CCE, with highest
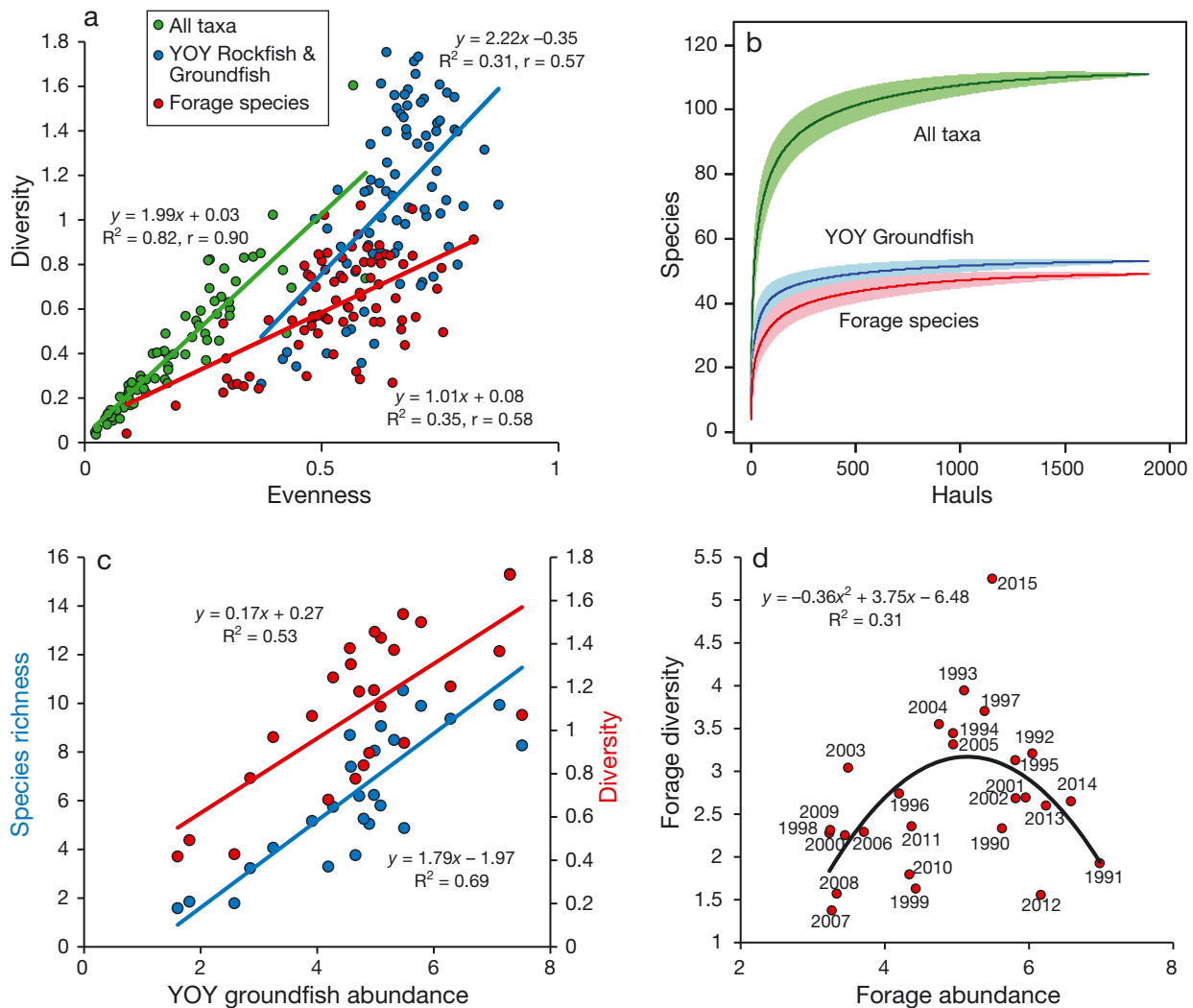
Fig. 3. (a) Relationships between annual mean species diversity and evenness per group; (b) species accumulation curves (shaded area is confidence limits) per group relative to number of net hauls; (c) relationships between species richness, diversity and total abundance (ln + 1) of rockfish and groundfish; (d) relationship between forage diversity and abundance (ln + 1) on the shelf. YOY: young of the year

correlations located adjacent to coastal upwelling waters (Fig. 5), and broadly reflects ocean climate signals associated with the PDO ($r = 0.75$, $p < 0.01$). That is, anomalous warm SST along the California coast corresponds with an increase in forage species richness, most likely due to the transport of species from oceanic waters from the west and subtropical waters from the south. Moreover, the diversity and evenness of all taxa are significantly related to SST and the PDO (Table 1), indicating that the entire species assemblage becomes less even during warm and positive PDO years. However, we found that neither SST nor the PDO correlates significantly with any diversity indices for YOY groundfish (Table 1), indicating that biodiversity of this group of locally produced species does not reflect regional SST patterns or the PDO.

Temperature anomalies during May 1997, 1999 and 2015 provide insight on how anomalous ocean climate conditions may influence diversity patterns (Fig. 6). During 1997, a strong El Niño year, positive SST anomalies extended across the entire California Current, and off central California, temperature anomalies extended deep within the water column (Fig. 6). As a result, increased anomalies of forage diversity occurred north of Monterey Bay within the region of strongest positive SST anomalies (Fig. 6a,d,g). As expected during a strong La Niña event, an opposite pattern occurred during 1999, and negative temperature and diversity anomalies occurred throughout the study area (Fig. 6b,e,h). The distributions of temperature and diversity anomalies during 2015 are in stark contrast to those in 1997 and 1999 and were
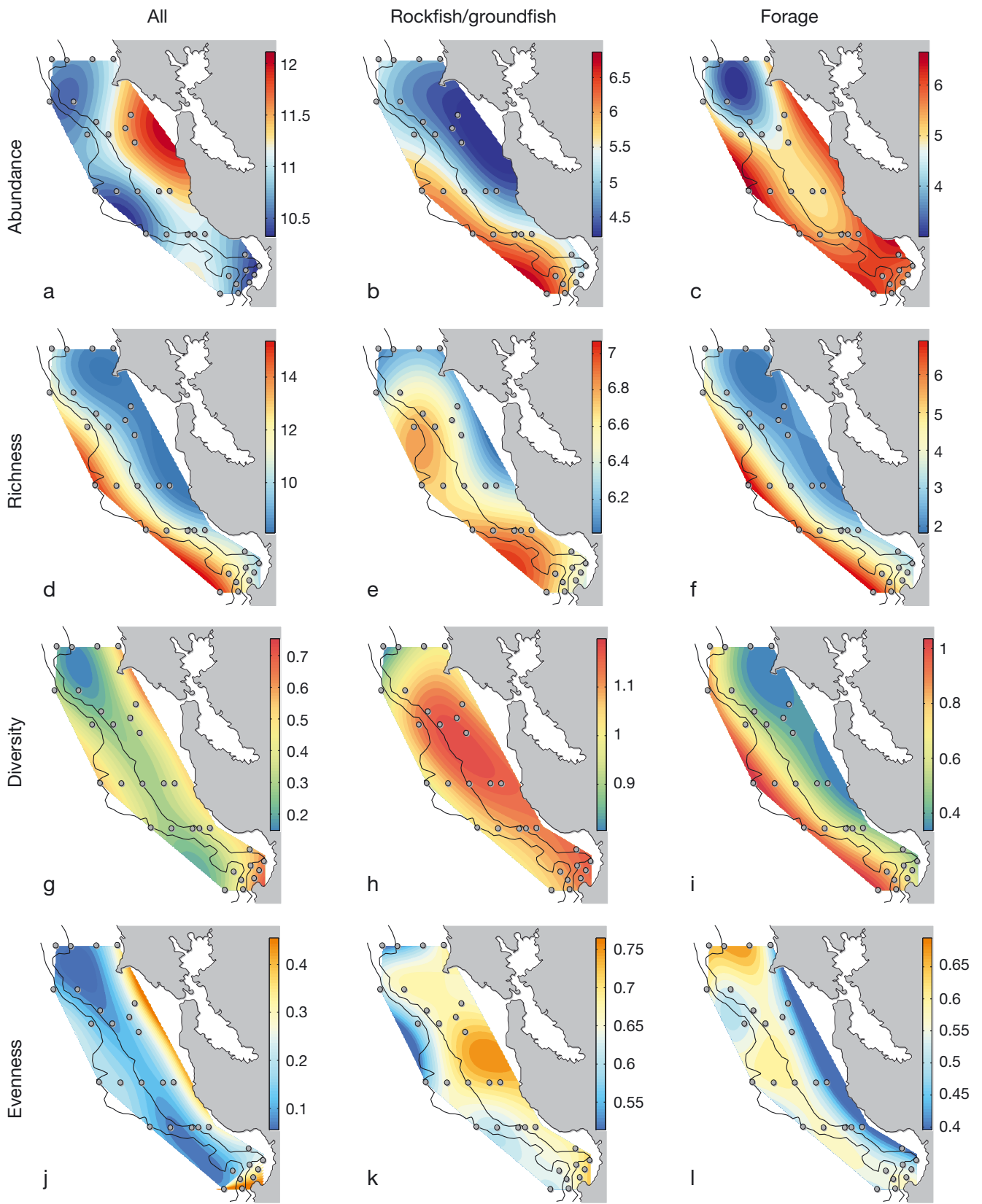
Fig. 4. Spatial climatology of (a–c) mean total abundance (ln CPUE + 1), (d–f) species richness, (g–i) Shannon-Weaver diversity and (j–l) Pielou's evenness per all taxa, young-of-the-year rockfish/groundfish and forage species. Note range of scale bar differs for each panel to highlight the different regional variability of biodiversity indices
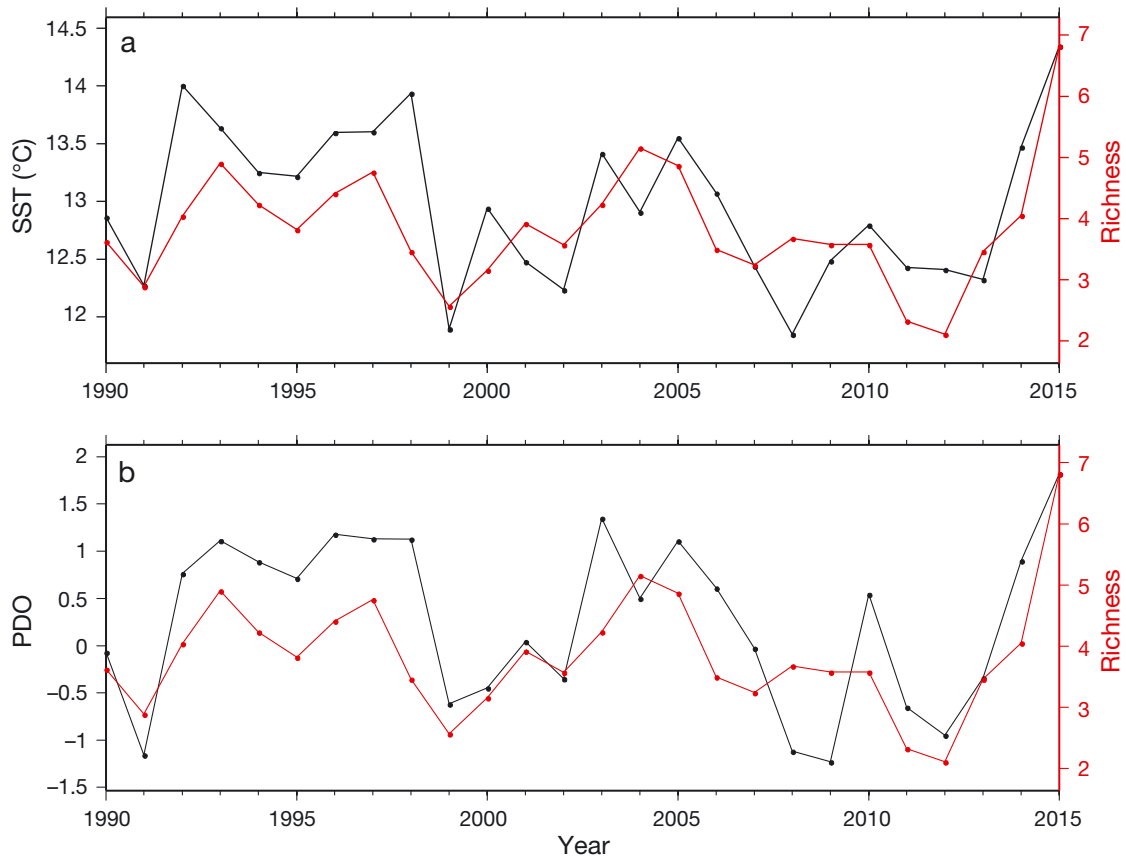
Fig. 5. Temporal coherence among time series of forage species richness, winter to spring (January to June), with (a) remotely-sensed sea surface temperature (SST) time series and (b) the Pacific Decadal Oscillation (PDO)

strongly positive throughout all regions (Fig. 6, Figs. S3–S5 in the Supplement). The effect of the warm water blob as a mixing pot for biodiversity in the North Pacific is clearly evident (Fig. 6c,f,i), and compared to May 1997 the vertical distribution of temperature anomalies are weaker and more shallow in their extent. Moreover, although cool upwelled water was not present along the coast during 1997, upwelling remained normal during 2015. Therefore, the unprecedented high diversity and richness of all taxa observed during 2015 are attributed to high pro-

duction of YOY groundfish as well as the influx of oceanic and subtropical forage species (Figs. 2 & 6 and Figs. S3–S5 in the Supplement).

DISCUSSION

Biodiversity has been hypothesized to fundamentally enhance ecosystem resilience to climate change and human disturbance in both terrestrial and marine systems (Fischer et al. 2006, Palumbi et al. 2009,

Table 1. Pearson correlations between biodiversity variables and detrended remotely sensed sea surface temperature (SST) and the Pacific Decadal Oscillation (PDO). Values in **bold** are significant (p < 0.05). YOY: young-of-the-year

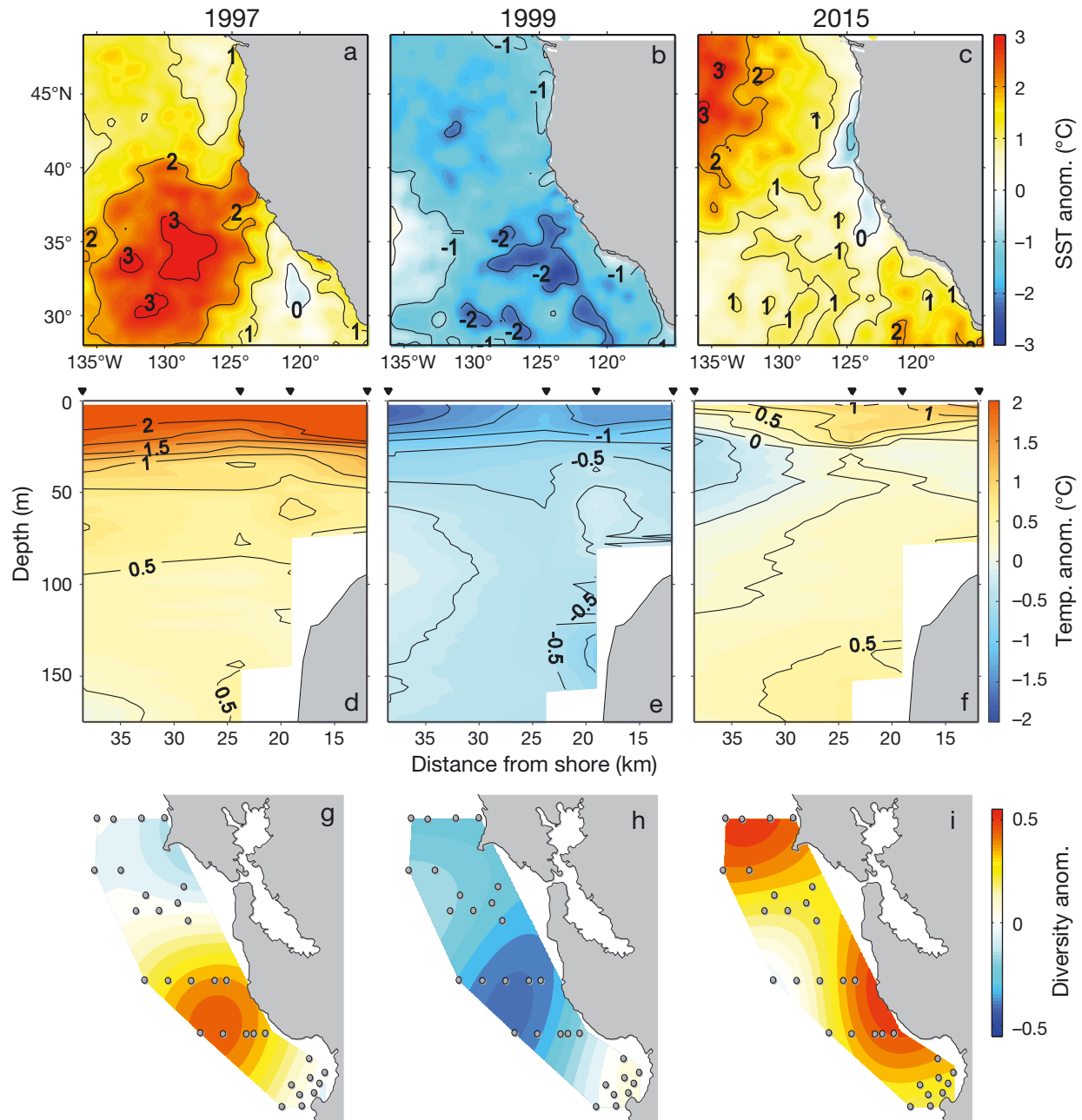| | SST | | | | | | PDO | | | | | |
| | All taxa | | YOY groundfish | | Forage | | All taxa | | YOY groundfish | | Forage | |
Variable	r	p	r	p	r	p	r	p	r	p	r	p
Abundance	−0.3	0.13	0.07	0.72	0.4	0.05	−0.37	0.06	0.05	0.79	0.31	0.12
Richness	0.23	0.26	−0.02	0.93	0.71	**<0.01**	0.26	0.2	−0.02	0.92	0.75	**<0.01**
Diversity	0.56	**<0.01**	−0.14	0.49	0.51	**<0.01**	0.55	**<0.01**	−0.13	0.52	0.56	**<0.001**
Evenness	0.62	**<0.01**	−0.33	0.1	0.03	0.9	0.59	**<0.01**	−0.35	0.08	−0.02	0.93

Fig. 6. Comparison of North Pacific (a–c) sea surface temperature (SST) anomalies (from satellite) and (d–f) vertical temperature anomalies (derived from survey CTD stations; black triangles indicate sampling points) during the 1997 El Niño, 1999 La Niña and 2015 warm water blob. (g–i) Impact of these anomalous conditions on forage species diversity anomalies off California

Beaugrand et al. 2013, Duffy et al. 2013). Determining the connection between the production and distribution of marine populations to assess how and when thresholds in biodiversity are reached is critical for predicting future consequences of biodiversity loss and gains in marine ecosystems (Palumbi et al. 2009, Fautin et al. 2010) and the establishment of monitoring networks (Duffy et al. 2013, Muller-

Karger et al. 2014). Due to their importance in global marine food webs, biodiversity time series of forage fish will fill key information gaps in global maps of biodiversity and in assessing declines that may impact fishery resources (Cury et al. 2000, Hiddink & Hofstedeter 2008, Bakun et al. 2015). However, to use biodiversity as an indicator for future changes in pelagic systems requires long-term studies to under-

stand past natural variability and how it relates to ocean climate conditions (Jetz et al. 2012) as well as fishery exploitation patterns that may impact biodiversity (Levin et al. 2006, Lindegren et al. 2013, Frank et al. 2016). There are few long-term data sets on juvenile fish biodiversity, despite their high importance both in food webs and as drivers of fisheries productivity; so, understanding the influence of ocean climate conditions on this critical life history stage is important for predicting future changes to marine ecosystem functioning and resilience (Worm et al. 2006, Pikitch et al. 2014, Asch 2015).

The baseline variability of biodiversity quantified here yielded several insights on the trends and cycles that relate to the productivity of the epipelagic forage community in the California Current and the impact of anomalous climate events on biodiversity. Strikingly, the biodiversity indices observed during 2015 reached unprecedented levels in the 26 yr time series and appear to be the result of an ocean climate event in the North Pacific that resulted in a convergence of northern, southern and oceanic species assemblages (Leising et al. 2015, Sakuma et al. 2016). Our study confirms that epipelagic biodiversity of micronekton off central California is driven by ocean climate conditions that favor successful recruitment and production of YOY groundfish at regional scales, while increased biodiversity during warmer periods reflects anomalous transport patterns of oceanic and subtropical species into coastal habitats. This alternating pattern reflects the pulse of biodiversity of epipelagic fish guilds and has consequences for trophodynamics in this ecosystem. During cooler periods, the high biodiversity of YOY groundfish is related to their combined high abundance and reflects a typical upwelling food web in the CCE, where these species represent key conduits of energy transfer to upper-level predators (Santora et al. 2014, Wells et al. 2017). The increased diversity of coastal mesopelagic forage species into the ecosystem during warm years results in overall higher biodiversity anomalies but is not strictly correlated with abundance — high diversity is generally observed during warmer, lower productivity years, such as El Niño years. Furthermore, we found that forage species diversity, and not YOY groundfish diversity, is positively related to remotely sensed SST and the PDO, indicating that large-scale ocean basin conditions are the predominant drivers of biodiversity patterns off central California. Regarding biodiversity as an index to monitor healthy or resilient marine ecosystems, anomalously high biodiversity of micronekton

species within the CCE upwelling ecosystem often indicates that ecological conditions are poor, and higher trophic level predators may have difficulties (e.g. failed breeding by seabirds; Ainley & Boekelheide 1990), although even this generality may not have held during the unusual conditions of 2015.

Trophic considerations of epipelagic fish biodiversity

The biodiversity patterns quantified here are also reflected in the long-term food habit studies of higher trophic level predators in this ecosystem. For example, breeding seabirds such as common murres *Uria aalge* on Southeast Farallon Island (Fig. 1) feed primarily on YOY rockfish when they are abundant and switch to target northern anchovy when YOY rockfish are unavailable (Ainley & Boekelheide 1990, Sydeman et al. 2001). When YOY rockfish are less available, breeding success tends to be lower, although the most severe declines occur during periods of unusual environmental conditions (such as El Niño events) that correspond with both very low YOY rockfish abundance and low productivity throughout the ecosystem more generally (Field et al. 2010, Wells et al. 2017). Similarly, humpback whales *Megaptera novaeangliae* may alter their foraging behavior between krill and northern anchovy as a function of climate-driven ocean conditions that determine which prey type is abundant, such that krill are preyed on more frequently in cool, high upwelling years and northern anchovy in years of lower productivity and warmer SST (Fleming et al. 2016). Finally, Thayer et al. (2014) showed that diets of adult Chinook salmon *Oncorhynchus tshawytscha* correspond to the forage assemblage quantified from the RREAS and that diet diversity had declined over time and was somewhat correlated with productivity. However, the declines were largely driven by low rockfish abundance in the mid-2000s, and the study did not include data past 2007, when YOY rockfish and other forage abundance returned to high levels. Regardless, the results of the diversity analysis here, combined with the observations from those predator studies, suggest that the 2 broadly defined assemblages may represent functional complementarity in the mid trophic level of the pelagic ecosystem. In the southern CCE, Lindegren et al. (2016) examined divergent responses to opposing environmental drivers by functionally similar species and found they can provide stability and resilience to dependent predators by helping to maintain functioning at a commu-

nity level. The role of functional complementarity in promoting community stability and resilience merits additional attention in pelagic marine ecosystems, and the biodiversity metrics presented here may serve as key indicators of ecosystem health (Palumbi et al. 2009, Duffy et al. 2013). Thus, future analyses should explore the relationship between diversity at the mid trophic level forage assemblage and the productivity of higher trophic level predators that rely on that assemblage (Pavoine & Bonsall 2011, Kaplan et al. 2013).

Insights from epipelagic fish biodiversity

We derived several diversity indices to quantify the variability of epipelagic forage species biodiversity to provide insight on their dynamics in an upwelling-dominated marine ecosystem. Time series of biodiversity indices provide support for the alternating dominance of YOY groundfish and forage species during cool and warm periods (Ralston et al. 2015, Sakuma et al. 2016). The abundance of YOY groundfish is positively linearly related to diversity, while forage species abundance is non-linearly related to forage diversity. These contrasting abundance and diversity relationships possibly indicate there are different physical and biological drivers acting on these species groups. Many species of juvenile rockfish seem to exhibit synchronized abundance fluctuations, so it is not surprising that their diversity is higher during cool and more productive upwelling years (Ralston et al. 2013). However, our indicators suggest the fluctuation of forage species diversity is dependent on their origin and transport from warmer offshore or southern waters, and although peak diversity occurs during strong El Niño and warm water events, these years coincide with overall less abundance of epipelagic species.

The springtime upwelling season in the CCE is a critical period for ecosystem functioning and biodiversity of the pelagic fish assemblage and clearly reflects periodic and annual variability of ocean climate conditions. In the California Current, both meta-analyses and model results have projected changes in upwelling dynamics (Sydeman et al. 2014, Rykaczewski et al. 2015). For instance, increased spatial and temporal variance of key biological components (e.g. krill, rockfish and seabirds) may be an indicator of climate change (Sydeman et al. 2013). In closed systems, an increase in variance has been an important indicator of impending regime shifts and ecosystem reorganization (Car-penter & Brock 2006). A combined effect of increased variance and changes in biodiversity may provide more insight into whether upwelling ecosystems are facing impending reorganization. However, continued monitoring of key forage species needs to separate the signal of climate variability from long-term change. The recent warm water anomaly and El Niño event may provide a window into future conditions, such that we can examine the extreme events to better understand how changes in both trend and variability in bottom-up dynamics will translate to ecosystem response. Some of the longest time series for pelagic ecosystems (e.g. California Cooperative Oceanic Fisheries Investigations ichthyoplankton survey) have shown that unfished species have discernible trends in population abundance over the past 50 yr (McClatchie et al. 2014, Asch 2015). With continued monitoring, the biodiversity indices described here may be well suited to monitor changes in resilience in the CCE in the face of increased variability and secular trends.

Ocean climate-driven variability of biodiversity

Ocean temperature patterns and the PDO appear to be key drivers of patterns of biodiversity of forage species but not of YOY groundfish in the California Current. This is consistent with the observation that SSTs tend to be the most reliable predictors of diversity across marine taxa (Tittensor et al. 2010). Range limits are often set by thermal tolerance, with the diversity of oceanic taxa typically peaking at latitudes between 20° and 40°. Warming temperatures are likely to introduce more subtropical species than they exclude cooler water species in this ecosystem, providing some context for why temperature correlates so well with diversity over time in this particular ecosystem. Determining the natural variability of pelagic fish biodiversity is necessary for understanding the impact of global climate change. Although there is significant periodicity of YOY groundfish biodiversity, which reflects production patterns for this assemblage (Lenarz et al. 1995, Ralston et al. 2013, Santora et al. 2014), biodiversity of YOY groundfish did not appear to be clearly related to SST or the PDO. In part, this is due to the complicated life history of long-lived groundfish species, for which the best indicators of recruitment tend to be anomalous transport patterns, although such patterns do not explain a tremendous fraction of the variability in observed recruitment (Ralston et al. 2013, Stachura et al. 2014).

During ENSO events, we found that diversity levels of either species group generally displayed opposing anomalies because cool ocean conditions favored the production of groundfish and warm conditions favored the transport and occurrence of subtropical species (Lenarz et al. 1995, Chavez et al. 2003). Stronger north-to-south transport (e.g. La Niña years) would predict lower forage diversity, while local warming events (e.g. via onshore transport from the subtropical gyre) lead to lower YOY groundfish diversity (Ralston et al. 2013, Sakuma et al. 2016). However, we found that biodiversity reached unprecedented levels during 2015, which was an unusual year, as it had a high diversity of YOY groundfish and forage species and was largely driven by localized upwelling in coastal waters and regional warming attributed to the warm water blob. This resulted in record high diversity of YOY groundfish and forage species given the mixing of cool and warm waters. These anomalous ocean warming events have increased globally in recent years (Chust et al. 2014, Hobday et al. 2016, Scannell et al. 2016), and in the California Current anomalous climate and ocean events have been predicted to occur more frequently (DiLorenzo & Mantua 2016). With shifting species distributions, including the overlap of warm and cold water species shown here, there is the possibility that ecological relationships (predator–prey dynamics and competition) may change as well (Urban et al. 2012). Specifically, as new species overlap or prey shift quicker than predators, there are likely to be ecosystem consequences to shifting species distributions. Indices of biodiversity may be important both to index changing ocean conditions and to understand patterns in species distributions that may result in changes to the ecosystem.

Monitoring marine biodiversity

Developing a global MBON will benefit from the integration of many biodiversity studies, across all trophic and functional levels of marine ecosystems, to highlight and organize essential biodiversity variables in a meaningful framework (Sala & Knowlton 2006, Stachowicz et al. 2007, Pereira et al. 2013). Our study establishes a long-term perspective for monitoring changes in biodiversity of an epipelagic forage assemblage in a highly productive upwelling ecosystem that is likely to be experiencing increased variance of biophysical conditions associated with global climate change (Sydeman et al. 2013). Maintaining marine biodiversity has been defined as a pri-

ority for sustaining ecosystem health and resilience, especially as anthropogenic climate change continues to impact these ecosystems (Palumbi et al. 2009, Duffy et al. 2013). Biodiversity provides a portfolio effect to monitoring marine ecosystems, offering a suite of trophic pathways that maximize resiliency and reduce extinction probability (Schindler et al. 2010, Lindegren et al. 2016). Most studies of biodiversity have focused on terrestrial or benthic communities (e.g. tropical forests and coral reefs), yet biodiversity may play a similar role in pelagic systems as well (Fisher et al. 2008, ter Hofstede et al. 2010). Our biodiversity indices of epipelagic fish and their context for understanding marine food web dynamics should be included in the global MBON framework of essential biodiversity variables, which would benefit the monitoring of community composition and ecosystem structure and function (Pereira et al. 2013). Thus, monitoring biodiversity indices of key forage communities, as well as species composition changes, may provide important insight into the severity of ecosystem responses to climate fluctuations and benefit the coordination of global MBONs (Scholes et al. 2008, Duffy et al. 2013).

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Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem

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Table S1: Taxa, group classification list and their frequency of occurrence (positive trawls) utilized in the calculation of biodiversity indices.

Group	Scientific name	Common name	Frequency Occurrence
YOY.rockfish	*Sebastes auriculatus*	Brown rockfish	13.1%
YOY.rockfish	*Sebastes aurora*	Aurora rockfish	0.1%
YOY.rockfish	*Sebastes babcocki*	Redbanded rockfish	0.1%
YOY.rockfish	*Sebastes crameri*	Darkblotched rockfish	2.5%
YOY.rockfish	*Sebastes dallii*	Calico rockfish	0.1%
YOY.rockfish	*Sebastes diploproa*	Splitnose rockfish	64.1%
YOY.rockfish	*Sebastes elongatus*	Greenstriped rockfish	0.4%
YOY.rockfish	*Sebastes entomelas*	Widow rockfish	23.3%
YOY.rockfish	*Sebastes flavidus*	Yellowtail rockfish	14.7%
YOY.rockfish	*Sebastes goodei*	Chilipepper	30.2%
YOY.rockfish	*Sebastes hopkinsi*	Squarespot rockfish	7.9%
YOY.rockfish	*Sebastes jordani*	Shortbelly rockfish	57.2%
YOY.rockfish	*Sebastes levis*	Cowcod	3.8%
YOY.rockfish	*Sebastes melanops*	Black rockfish	5.2%
YOY.rockfish	*Sebastes melanostomus*	Blackgill rockfish	0.2%
YOY.rockfish	*Sebastes miniatus*	Vermillion rockfish	0.2%
YOY.rockfish	*Sebastes mystinus*	Blue rockfish	16.7%
YOY.rockfish	*Sebastes paucispinis*	Bocaccio	11.1%
YOY.rockfish	*Sebastes pinniger*	Canary rockfish	16.4%
YOY.rockfish	*Sebastes rastrelliger*	Grass rockfish	0.7%
YOY.rockfish	*Sebastes ruberrimus*	Yelloweye rockfish	0.4%
YOY.rockfish	*Sebastes rufus*	Bank rockfish	1.3%
YOY.rockfish	*Sebastes saxicola*	Stripetail rockfish	24.0%
YOY.rockfish	*Sebastes semicinctus*	Halfbanded rockfish	9.0%
YOY.rockfish	*Sebastes serranoides*	Olive rockfish	1.8%
YOY.rockfish	*Sebastes wilsoni*	Pygmy rockfish	8.3%
YOY.rockfish	*Sebastes zacentrus*	Sharpchin rockfish	1.2%
YOY.rockfish	*Sebastomus spp*	Rosefish group	3.1%
YOY.rockfish	*Sebastes caurinus complex*	Copper rockfish complex	11.6%
YOY.rockfish	*Sebastes emphaeus*	Puget sound rockfish	0.5%
YOY.groundfish	*Liparididae*	Snailfish	2.0%
YOY.groundfish	*Lycodapus mandibularis*	Pallid eelpout	3.4%
YOY.groundfish	*Anarrhichthys ocellatus*	Wolf eel	1.8%
YOY.groundfish	*Anoplopoma fimbria*	Sablefish	0.8%
YOY.groundfish	*Atheresthes stomias*	Arrowtooth flounder	0.4%
YOY.groundfish	*Citharichthys sordidus*	Pacific sanddab	63.3%
YOY.groundfish	*Citharichthys stigmaeus*	Seckled sanddab	4.8%
YOY.groundfish	*Cottidae*	Sculpin	4.8%

YOY.groundfish	*Glyptocephalus zachirus*	Rex sole	21.4%
YOY.groundfish	*Hexagrammidae*	Greenling	1.4%
YOY.groundfish	*Lyopsetta exilis*	Slender sole	18.9%
YOY.groundfish	*Merluccius productus*	Pacific hake	59.6%
YOY.groundfish	*Microstomus pacificus*	Dover sole	10.0%
YOY.groundfish	*Ophiodon elongatus*	Lingcod	15.7%
YOY.groundfish	*Oxylebius pictus*	Painted greenling	3.8%
YOY.groundfish	*Platichthys stellatus*	Starry flounder	0.2%
YOY.groundfish	*Pleuronichthys spp.*	Turbot	5.5%
YOY.groundfish	*Psettichthys melanostictus*	Sand sole	9.0%
YOY.groundfish	*Rhamphocottus richardsonii*	Grunt sculpin	0.1%
YOY.groundfish	*Scorpaenichthys marmoratus*	Cabezon	3.5%
YOY.groundfish	*Microgadus proximus*	Pacific tomcod	3.4%
YOY.groundfish	*Hemilepidotus spp.*	Irish lord	1.6%
YOY.groundfish	*Stichaeidae*	Prickleback	3.1%
Forage	*Leptocephalus larva*	Eel larvae	0.4%
Forage	*Clupea pallasii*	Adult Pacific herring	1.3%
Forage	*Ammodytes hexapterus*	Pacific sandlance	1.2%
Forage	*Atherinops affinis*	Topsmelt	0.5%
Forage	*Atherinopsis californiensis*	Jacksmelt	1.0%
Forage	*Bathophilus flemingi*	Highfin dragonfish	0.9%
Forage	*Bathylagidae*	Blacksmelt	15.8%
Forage	*Bathymasteridae*	Ronquil	0.7%
Forage	*Chauliodus macouni*	Pacific viperfish	0.1%
Forage	*Cololabis saira*	Pacific saury	0.0%
Forage	*Diaphus theta*	California headlightfish	0.1%
Forage	*Gasterosteus aculeatus*	Threespine stickleback	0.1%
Forage	*Gobiidae*	Goby	16.7%
Forage	*Icichthys lockingtoni*	Medusafish	5.6%
Forage	*Icosteus aenigmaticus*	Ragfish	0.4%
Forage	*Petromyzontidae*	Lamprey	1.2%
Forage	*Leuroglossus stilbius*	California smoothtongue	0.1%
Forage	*Lyopsetta exilis*	Slender snipefish	57.2%
Forage	*Melamphaidae*	Bigscale	0.2%
Forage	*Melanostomiidae*	Dragonfish	0.1%
Forage	*Nemichthyidae*	Snipe eel	0.2%
Forage	*Paralepididae*	Barracudina	8.2%
Forage	*Peprilus simillimus*	Pacific Pampano	8.4%
Forage	*Opisthoproctidae*	Spookfish	0.2%
Forage	*Porichthys notatus*	Plainfin midshipman	15.8%
Forage	*Sygnathidae*	Pipefish	1.1%
Forage	*Synodus lucioceps*	California lizardfish	0.1%
Forage	*Tactostoma macropus*	Longfin dragonfish	4.7%
Forage	*Tarletonbeania crenularis*	Blue laternfish	18.2%
Forage	*Tetragonurus cuvieri*	Smalleye squaretail	0.1%
Forage	*Trachipterus altivelis*	King-of-the-salmon	8.3%
Forage	*Zaniolepididae*	Combfish	7.3%
Forage	*Doryteuthis opalescens*	Market squid	51.6%
Forage	*Octopoda*	Octopus	28.7%
Forage	*Argentina sialis*	Pacific argentine	11.2%
Forage	*Malacosteidae*	Loosejaw	1.7%
Forage	*Idiacanthidae*	Blackdragon	3.8%
Forage	*Eurypharyngidae*	Umbrellamouth gulper	0.1%
Forage	*Stomias atriventer*	Blackbelly dragonfish	0.1%
Forage	*Phosichthyidae*	Lightfish	0.3%
Forage	*Alloposidae*	Blob octopus	0.2%
Forage	*Oncorhynchus spp.*	Total YOY salmon	2.1%

|			
Forage	*Teuthoidea*	Other squid	43.9%
Forage	*Myctophidae*	Other myctophid	37.3%
Forage	*Sardinops sagax*	Total Pacific sardine	16.2%
Forage	*Engraulis mordax*	Total northern anchovy	31.6%
Forage	*Osmeridae*	Total smelt	2.1%
Forage	*Scomber japonicus*	Total Pacific mackerel	1.7%
Forage	*Trachurus symmetricus*	Total Jack mackerel	1.1%
Crustacean	*Mysidacea*	Mysid	0.5%
Crustacean	*Caridea*	Caridean shrimp	1.1%
Crustacean	*Pleuroncodes planipes*	Pelagic red crab	0.7%
Crustacean	*Phyllosoma*	Phyllosoma	0.5%
Crustacean	*Pandalus jordani*	Pandalid shrimp	1.7%
Crustacean	*Bentheogennema burkenroadi*	Red shrimp	0.3%
Crustacean	*Pasiphaea pacifica*	Glass shrimp	4.1%
Crustacean	*Sergestid*	Sergestid	27.6%
Crustacean	*Euphausiacea*	Total krill	90.1%
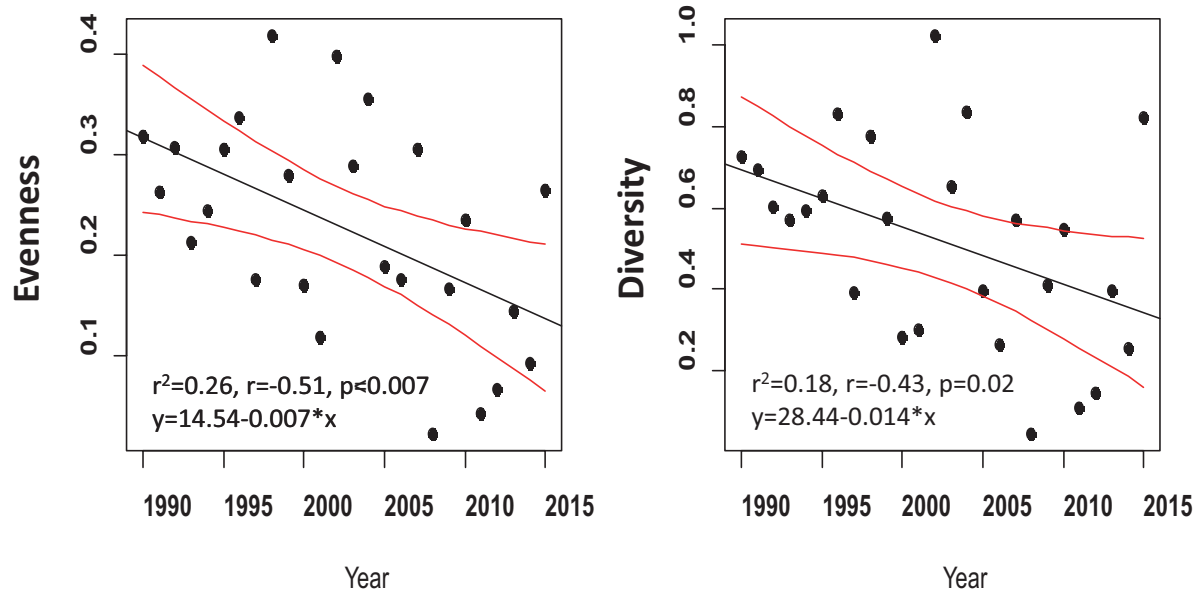
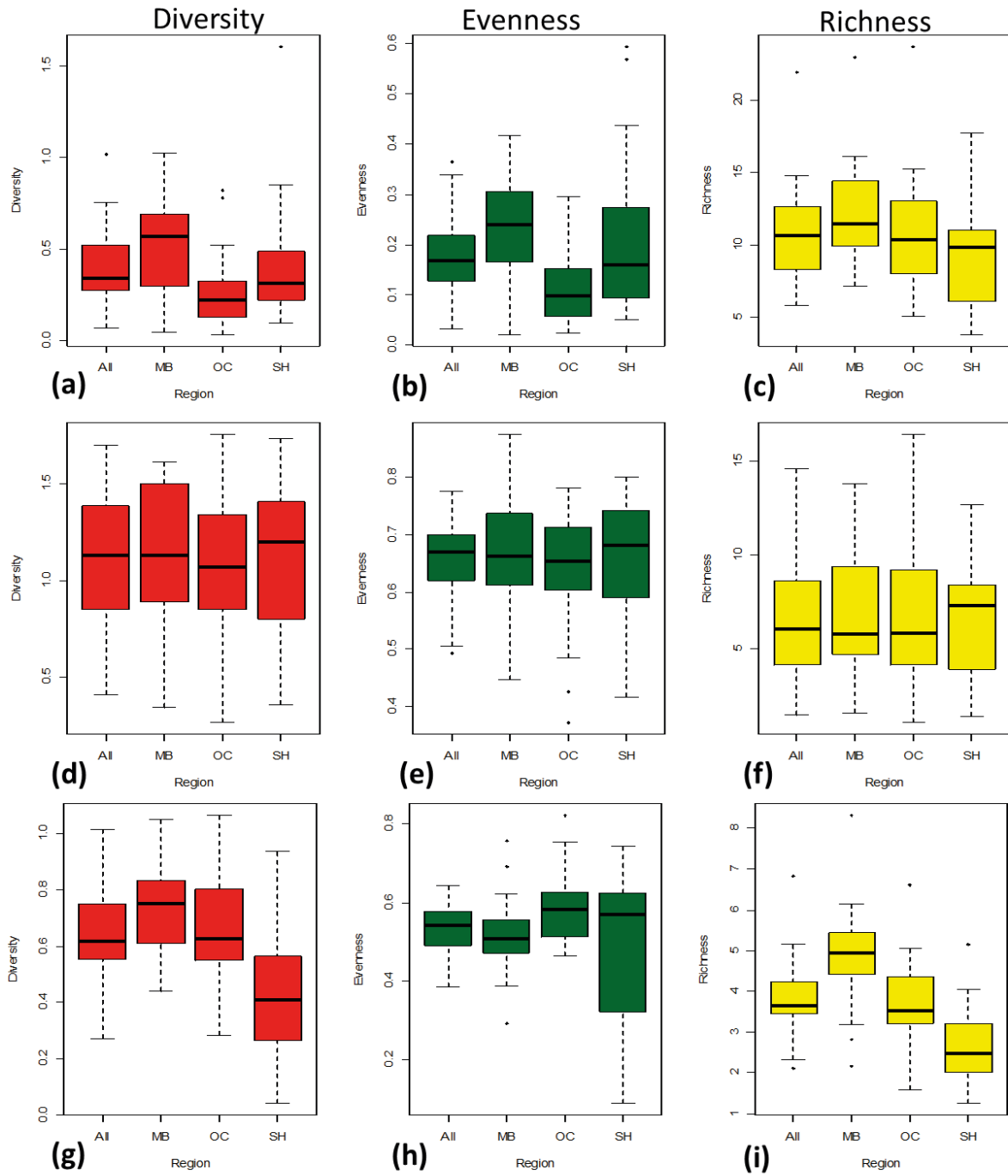Figure S1: Long-term trends of all taxa in Monterey Bay, (a) evenness and (b) diversity.

Figure S2: Regional comparison of diversity indices (box plots): (a-c) all taxa, (d-f) YOY rockfish and groundfish, and (g-i) forage species
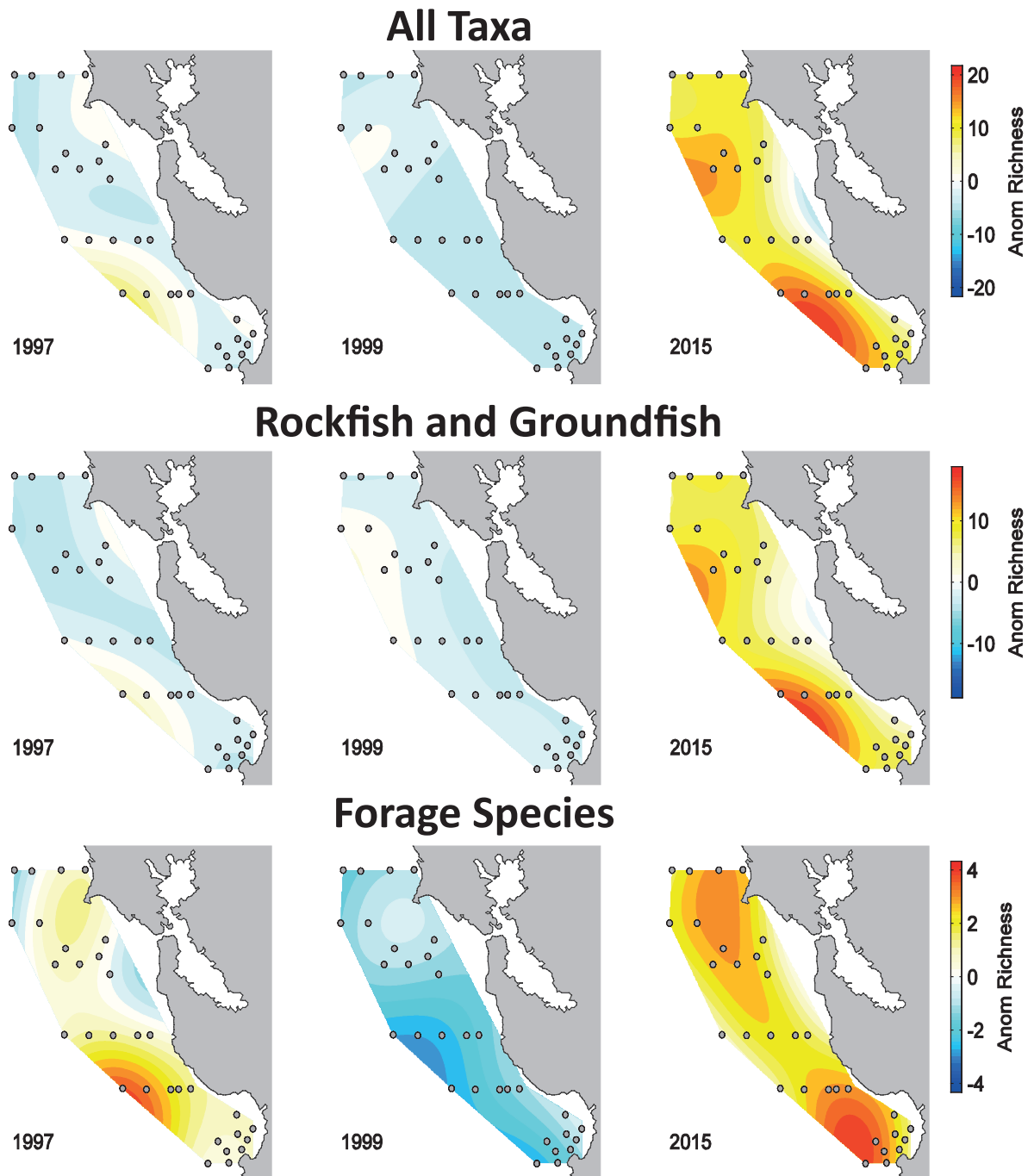
Figure S3: Spatial anomalies of species richness for (top) all taxa, (middle) YOY rockfish and groundfish and (bottom) forage species during the 1998 El Niño, 1999, La Niña and 2015 warm water blob.

All Taxa
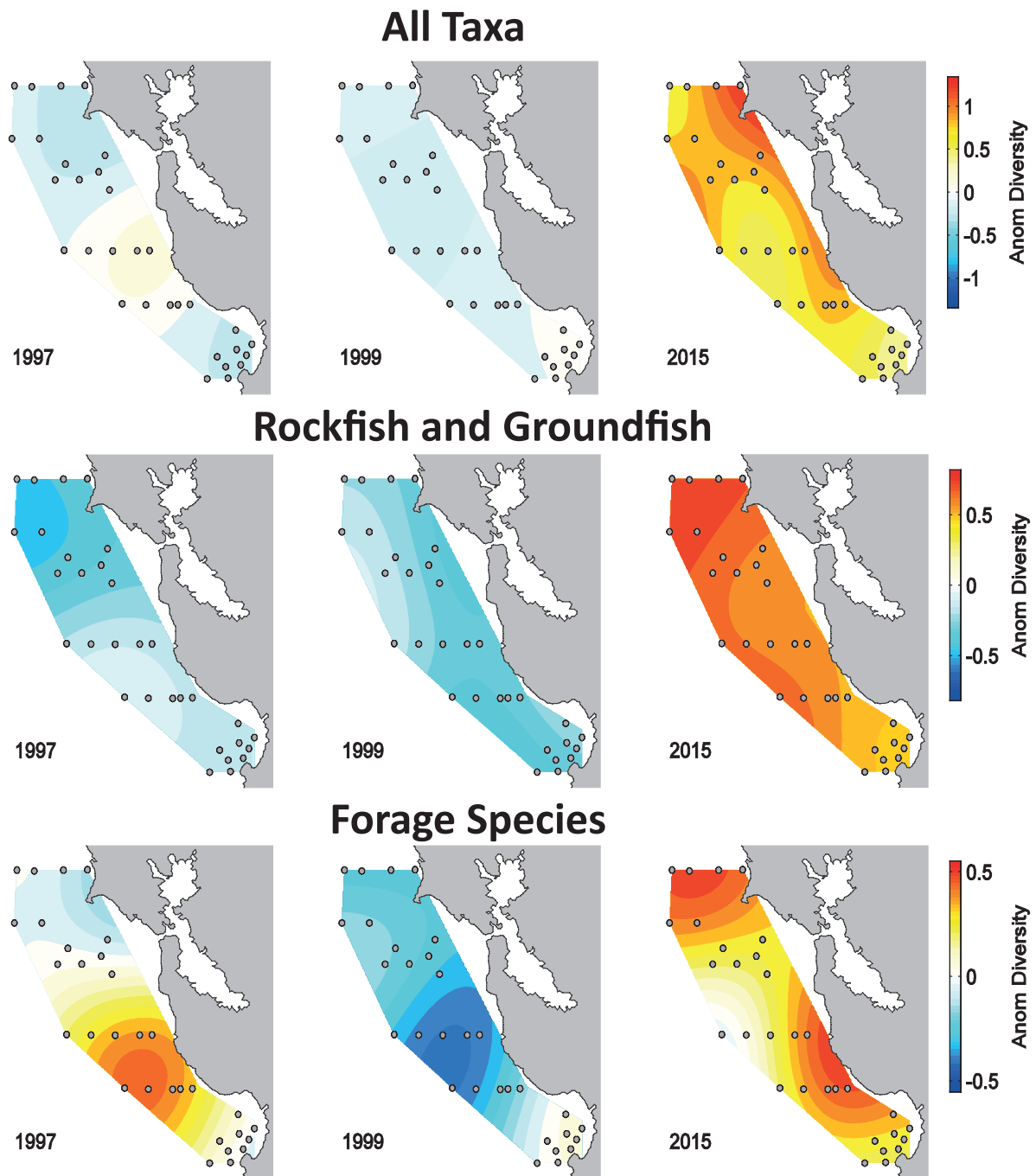

Rockfish and Groundfish

Forage Species

Figure S4: Spatial anomalies of diversity for (top) all taxa, (middle) YOY rockfish and groundfish and (bottom) forage species during the 1998 El Niño, 1999, La Niña and 2015 warm water blob.
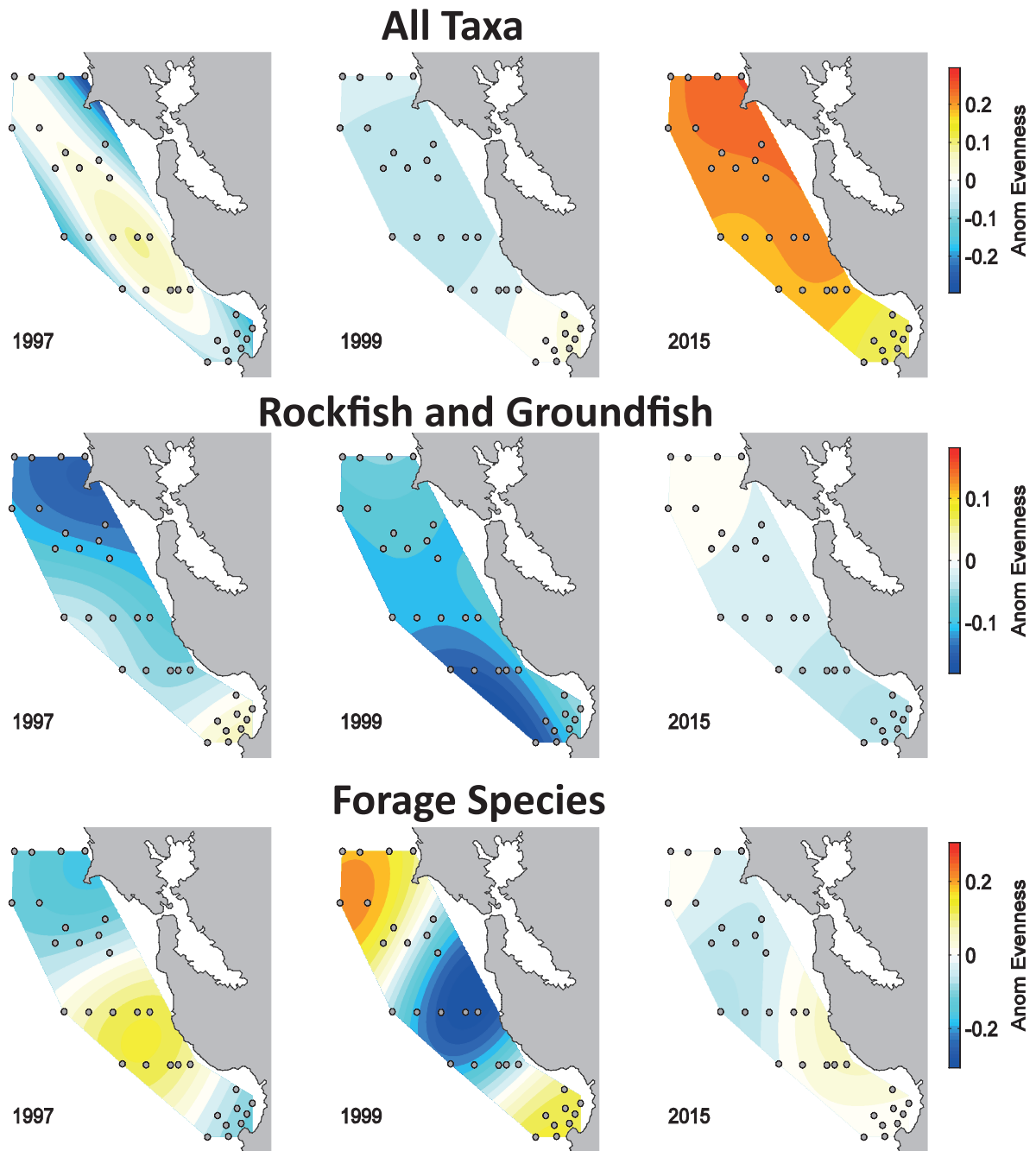
Figure S5: Spatial anomalies of evenness for (top) all taxa, (middle) YOY rockfish and groundfish and (bottom) forage species during the 1998 El Niño, 1999, La Niña and 2015 warm water blob