Changes in the macrobenthic infaunal community of the Southern California continental margin over five decades in relation to oceanographic factors

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Abstract

Climate change has altered the physiochemical conditions of the coastal ocean, but effects on infaunal communities have not been well-assessed. Here we used multivariate ordination to examine temporal patterns in benthic community composition from four southern California continental shelf monitoring programs that range in duration from 30 to 50 years. Temporal changes were compared to variations in temperature, oxygen and acidification using single-taxon random forest models. Species richness increased over time, coupled with a decline in overall abundance. Continental shelf macrobenthic communities from the 2010s were comprised of a broader array of feeding guilds and life history strategies than in the 1970s. Changing water temperature was associated with northward shifts in geographic distribution and increases in species abundance, while acidification was associated with southward shifts and declines in abundance of other species. Acidification was also associated with changes in depth distribution of benthic fauna, with shelled molluscs declining in abundance at depths most associated with increasing exposure to acidification. This broad-scale community-level analysis establishes causal hypotheses that set the stage for more targeted studies investigating shifts in abundance or distribution for taxa that appear to be responding to climate change-related disturbances.

Keywords

Ocean Acidification, ENSO, PDO, Range Shifts, Continental Shelf, Continental Slope

1. INTRODUCTION

Climate change has led to marked effects on the coastal ocean, with increasing water temperature (Thomson & Krassovski 2010, Sutton & Bowen 2019, Johnson & Lyman 2020, Muff et al. 2022) and enhanced intensity of El Niño and Pacific Decadal Oscillation events (Wang et al. 2017, Freund et al. 2019, Cai et al. 2021). This has led to altered circulation patterns (Thomson & Krassovski 2010, Bograd et al. 2019) and shoaling of deep basin low dissolved oxygen and low pH waters (Bograd et al. 2008, Gilly et al. 2013). The carbonate chemistry of coastal waters has been further altered by acidification of surface waters due to increases in atmospheric CO_2 (Doney et al. 2009, Hauri et al. 2013, Feely et al. 2016).

Changes in oceanographic conditions and water quality/water chemistry have been linked to changes among planktonic, pelagic, and intertidal communities (Poloczanska et al. 2016, Stiasny et al. 2016, Algueró-Muñiz et al. 2017, Lemasson et al. 2017, Espinel-Velasco et al. 2018, Leis 2018, Wang et al. 2018, Barclay et al. 2019, Pinsky et al. 2020). These changes have led to the alterations to food webs and to reduced fisheries productivity (Harley et al. 2006, Stiasny et al. 2016, Jin et al. 2020, Wilson et al. 2020). Climate-related changes in ocean waters have also been linked to the habitat compression or geographic shifts of epibenthic organisms (Sato et al. 2017).

However, the links between climate change or ocean acidification and infaunal benthic communities are less well understood. Warming waters may increase the ranges of tropical and sub-tropical fauna, while squeezing out colder water taxa (Wesławski et al. 2011, Pinsky et al. 2013, Hiddink et al. 2015, McClatchie et al. 2016, Goransson 2017). However, the microenvironments infauna create in their sediment burrows and the naturally reduced conditions of anerobic sediments may serve to de-couple infaunal adults from water column dynamics and insulate them from short-term water temperature shifts (Furukawa et al. 2001, Widdicombe & Spicer 2008, Silburn et al. 2017, Michaud et al. 2021). In contrast, there are clear effects of ocean acidification on the larvae of many benthic species, with decreases in aragonite saturation levels being particularly harmful to mollusc and echinoderm larvae (Waldbusser et al. 2015, Espinel-Velasco et al. 2018, Bednaršek et al. 2021). Furthermore there is growing evidence that overlying water with elevated temperatures and lower pH can negatively impact the functioning and productivity of adult and juvenile infauna established in the sediments – especially filter feeders (Green et al. 2009, Nixon et al. 2009, Widdicombe et al. 2009, Clements & Hunt 2017, Vlaminck et al. 2023).

Macrobenthic infauna are an ideal lens through which to view the influence of climate change on the resident biota of a location. Most species are relatively sessile and many live for multiple years, so patterns in abundance, biomass, and composition are an integrator of local environmental conditions (Gray & Elliott 2009). Furthermore, most marine benthic communities have relatively high taxonomic diversity, with a single sample containing dozens of species across multiple phyla (Ellingsen 2002, Villnäs & Norkko 2011, Gillett et al. 2021). This species diversity increases the likelihood of capturing differential responses to differing types of stress and therefore the ability to characterize stressor-specific assemblage responses (Lenihan et al. 2003, Thrush et al. 2008, Rodil et al. 2013).

The coastal ocean of the Southern California Bight provides a unique setting to track temporal changes in biotic and abiotic conditions in the benthos. It is an ecologically and oceanographically complex region situated in a biogeographic transition zone, with colder water Oregonian fauna north of Point Conception, CA and warmer water Californian fauna to the south, which leads to high biodiversity of benthic and pelagic fauna (e.g., Wares et al. 2001, Briggs & Bowen 2013, Claisse et al. 2018) (https://scb.marinebon.org/).

At broad scales, the region is oceanographically influenced at shallower depths by the cold-water California Current flowing to the south mixing with the warm-water Davidson Countercurrent flowing to the north (Bray et al. 1999), as well as seasonal upwelling of nutrient-rich water (Chhak & Di Lorenzo 2007). At depths below 300 to 400 m, the region is influenced by the northward flowing California Bottom Current, which transports relatively warmer, low oxygen Pacific Equatorial subsurface water along the continental slope (e.g., Thomson & Krassovski 2010). The relative interplay of the bottom and surface water masses is influenced by El Niño / Southern Oscillation cycling from year-to-year, with La Niña events bringing greater amounts of subsurface water to the surface along the coastal zone and El Niño events having the opposite effect (e.g., Bograd et al. 2019).

The bottom topography of the continental slope and shelf, as well as the presence of the Channel Islands, create eddies in the northern most parts of the Southern California Bight (Oey 1996, Harms & Winant 1998, Kessouri et al. 2022). These meso-scale features contribute to the oceanographic heterogeneity of the region. There are distinct north – to – south gradients in water temperature of the shallow mixed layer that become more muted with increasing depth (Gelpi & Norris 2008). Similarly, northern waters of the region are exposed to acidic conditions more frequently and at shallower depths than the southern portions of the region (McLaughlin et al. 2018).

The Southern California Bight is also a region experiencing oceanographic change, with documented temporal alterations in oxygen (Booth et al. 2014) and acidification (McLaughlin et al 2018) dynamics. Coincidentally, the Southern California Bight is home to four well-curated benthic invertebrate monitoring programs that span 30-50 years (City of Los Angeles Environmental Monitoring Division 2019, City of San Diego Ocean Monitoring Program 2020, Los Angeles County Sanitation Districts 2020, Orange County Sanitation District 2021). Here we used these four data sets to determine if there have been changes in the infaunal benthic community and to characterize the nature of those changes in the Southern California Bight. We also investigated relationships between changes in community composition and changes in oceanographic patterns and water characteristics like the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), dissolved oxygen, water temperature, and proxy-based estimates of ocean acidification.

2. METHODS

2.1 Benthic Data

Infaunal abundance and taxonomic data, as well as sediment grain size were obtained from the annual and semi-annual benthic monitoring programs of (northernmost to southernmost) the City of Los Angeles Environmental Monitoring Division (CLAEMD), the Los Angeles County Sanitation District (LACSD), the Orange County Sanitation District (OCSan) and the City of San Diego Ocean Monitoring Program (CSD). (Figure 1, Supplement 1 – Table S1). From these four programs, minimally disturbed sites used as reference condition benchmarks within these programs were selected at three different depths: mid-continental shelf (~60m), outer continental shelf (98-156m), and upper continental slope (~300m). Note that only the LACSD and OCSan locations had sites located at the continental slope depths. Summer (July – September) data were used for analysis.

The majority of the samples were collected with a $0.1m^2$ modified Van Veen grab. Samples from the Los Angeles County Sanitation Districts collected before 1980 (i.e., eight sampling events) were collected as four replicate $0.04m^2$ Shipek grabs. Given the smaller sample area of these older samples, benthic data from the first three replicate samples were summed together to approximate the samples collected with the Van Veen grab post-1980 – an approach developed by the Los Angeles County Sanitation Districts (S. Walther, pers. comm.).

Sediment from the grabs was sieved on a 1-mm screen, with the retained material fixed in buffered formalin before transfer to ethanol for preservation. All fauna were enumerated and identified to lowest possible taxonomic level, typically species. The names of all fauna from the different years were harmonized and updated to meet Southern California Association of Marine Invertebrate Taxonomists (SCAMIT) edition 12 (The Southern California Association of Marine Invertebrate Taxonomists 2018) conventions, with ambiguous taxa aggregated to higher taxonomic levels on a sample-wise basis to help ensure comparability of fauna across the temporal span of the dataset.

Sediment grain size data were available from LACSD, CLAEMD, and CSD data sets. Grain size composition by dry weight were measured as % sand (Phi -0.5 – 4.0), % silt (Phi 4.5 – 8.0), and % clay (Phi >8.5). The % sand was measured as material retained on a series of nested sieves between 2-mm and 63-µm. Percentages of silt and clay were measured by the pipette method (e.g., Plumb 1981) prior to 1990 and via a laser sediment analyzer thereafter (e.g., Beuselinck et al. 1998). Grain size data from CSD were only reported as % sand and % mud, where % mud is the sum of silts and clays.

2.2. Oceanographic Data

Patterns in ENSO and PDO were characterized using the National Oceanographic and Atmospheric Administration National Centers for Environmental Information (NOAA NCEI) SOI and PDO indices (Mantua & Hare 2002). Data were obtained from 1/1/1970 – 5/1/2020 from https://www.cpc.ncep.noaa.gov/data/indices/soi (SOI) and https://www.ncdc.noaa.gov/teleconnections/pdo/ (PDO). Monthly values for each index were averaged into quarterly seasonal values.

Sea surface and bottom water temperatures, dissolved oxygen, and salinity were obtained from the California Oceanic Fisheries Investigations (CalCOFI) hydrographic bottle dataset (https://calcofi.org/ccdata.html), which were collected quarterly using either Niskin/Wally bottles deployed on a vertical wire until 1993 or by a CTD+ bottle rosette frame after 1993. Detailed methods for collection and quality control are available at https://calcofi.org/about-calcofi/methods.html. Hydrographic data were matched to benthic sampling locations by first determining the closest CalCOFI monitoring station to each benthic station with the most available data (Figure 1). Horizontal proximity to the benthic stations was determined by calculating the geodesic distance between bottle sampling station and benthic fauna station using latitude and longitude via the distGeo function in the geosphere package (v1.5-10 [Hijmans 2019]) in R (v3.6.1). CalCOFI stations were between 16.1 (LACSD Upper-Slope) and 24.6 km (OCSan Mid-Shelf) away from their respective benthic data stations, distances that – while not directly overlying each other – represented the most reasonable approximations of the ocean water masses the benthic sites were exposed to (e.g., Dong et al. 2009, Watson et al. 2011, Bograd et al. 2015, Kekuewa et al. 2022). Data from all bottles within +/- 20m of the benthic station depth were selected and averaged to represent the bottom values for that benthic station. The temperature from the 25m bottle was used as the surface water temperature.

Ocean acidification metrics were estimated from CalCOFI temperature, salinity, and oxygen data using the proxy approach developed by Juranek et al. (2009) and Alin et al. (2012), which have been previously applied to CalCOFI time-series data in Alin et al. (2012) and McClatchie et al. (2016). Multiple linear regression equations were developed using the nortest (Gross & Ligges 2015) and robust (Wang et al. 2022) packages within R to estimate pH on the total scale (pH_T), pCO_2, aragonite saturation state (Ω_{arag}), and calcite saturation state (Ω_{calc}) from proxy temperature, salinity, and oxygen data using a calibration dataset consisting of inorganic carbon, oxygen, and CTD observations collected on NOAA West Coast Ocean Acidification (WCOA) cruises from 2007 to 2016 (Feely & Sabine 2013, Feely et al. 2015a,b, 2016, Alin et al. 2017). Models were tuned to 25–300 m depth, with separate empirical relationships for the northern (34°N–33.2°N) and southern (33.2°N–32.5°N) portions of the region. Final equations were selected on the basis of having the lowest root mean squared errors (RMSE) and highest adjusted R^2 values for the estimated parameters in the calibration data set (Supplement 1 – Table S2).

In comparison with the methods and results in Alin et al. (2012): 1) we did not standardize variables within equations by subtracting mean parameter values, 2) higher standard error (SE) values on coefficients likely reflect the very small numbers of calibration observations for this study (n = 21 and 42 samples, in the northern and southern regions, respectively), and 3) RMSE and R^2 values remain excellent, as the calibration data were tightly constrained to bottom depths of 25–300 m within northern and southern regions so that the calibration data would be most appropriate for this nearshore, benthos-focused study. It should be noted that the application of these equations to data collected prior to the calibration dataset cruises (i.e., 2007) will likely underestimate Ω and pH and overestimate pCO_2 values to some degree for the earliest parts of the time-series because we did not account for the increase in anthropogenic CO_2 content across the decades of this study (cf. Feely et al. 2016). As a consequence, the magnitude of change in ocean acidification metrics (Ω, pH, and pCO_2) across the decades are likely underestimated by our results, as similarly noted in McClatchie et al. (2016). Furthermore, there was most likely some degree of inter-relatedness between ENSO and PDO cycles with water temperature, dissolved oxygen and low pH bottom water (via upwelling) at the sampling sites. However, separating the source of changes in carbonate chemistry and temperature (atmospheric vs. upwelled) were beyond the scope of this work, which was focused on their (aggregate) effects on the fauna.

For most of the years within the 1970-2020 period of interest, water quality data were collected during four quarterly cruises per year. However, due to changes within the CalCOFI program, there were no measures of temperature, dissolved oxygen, or acidification variables for 1970, ’71, ’73, ’77-’80, and ’82-’83. For bottom dissolved oxygen, surface temperature, and bottom water temperature, summer (July – September) values (i.e., concurrent with the benthic sampling period) were selected for comparison to benthic faunal patterns. For the acidification variables, the least acidified estimates (i.e., highest pH, Ω_{arag}, and Ω_{calc}, or lowest pCO_2) across the four quarterly sampling events in a given year were selected to compare to benthic faunal patterns.

2.3. Analytical Approach

Changes in benthic faunal community composition were characterized using non-metric Multidimensional Scaling (nMDS) ordination. Bray-Curtis dissimilarity values were calculated based on presence-absence data (equivalent to Sørensen dissimilarity) through time at each sample site. Dissimilarity values were ordinated 2-d nMDS across a minimum of 250 iterations.

A 1-way Permutation Analysis of Variance (PERMANOVA) was then used to quantify the influence of time on community structure from each sampling site. PERMANOVAs were conducted (10,000 permutations) on Bray-Curtis dissimilarities as the response variable and year of collection as the predictor variable. The correlation between year of collection and the pattern in 2-d ordinations was also calculated across 1,000 permutations. All similarity calculations, ordinations, PERMANOVAs, and correlations were conducted in the vegan package (v2.6-2) (Oksanen et al 2022) in R (v3.6.1) using the metaMDS, adonis2, and envfit functions.

Taxa from each sample site were grouped in categories of shelled and non-shelled organisms. The relationships of these taxonomic groups with water quality/chemistry and oceanographic patterns at each site were quantified using random forest regression. Regression models were structured with faunal abundance as the response variable and the water quality and oceanographic variables detailed in Table 1 as the potential predictor variables across 10,000 trees per relationship. The relative influence of each predictor variable on the abundance of the taxonomic groups through time was quantified from % Mean Square Error change values for each predictor in the models. Random forests regressions were calculated using the randomForest and importance functions within the randomForest package (v4.6-16) (Liaw & Wiener 2002) in R (v3.6.1).

Changes in the presence and absence of frequently observed individual taxa throughout time were characterized using logistic regression. The presence of each taxon observed in 10 or more years at each sampling site was treated as the response variable, with year of collection as the predictor variable. An alpha value of 0.05 was used to select taxa whose presence significantly changed over the span of the sampling period. Taxa were characterized as increasers – more likely to be observed in modern samples – or decreasers – less likely to be observed in modern samples – based upon the sign of the beta term in the logistic regression equation. Polychaetes, crustaceans, echinoderms, and molluscs that were identified to the level of family or higher were omitted from consideration. The abundance of each increaser or decreaser taxon was then modeled with the suite of water quality/chemistry, sediment, and oceanographic variables detailed in Table 1 as predictor variables across 10,000 trees in a random forest regression. The relative influence of each predictor variable on the abundance of each taxon through time was quantified from % Mean Square Error change values for each predictor in the models. Random forests regressions were calculated using the randomForest and importance functions within the randomForest package (v4.6-16) (Liaw & Wiener 2002) in R (v3.6.1).

Changes in species richness and total abundance at each sample site and depth zone were both characterized using simple linear least squares regression. Species richness or total abundance were set as the response variable, with year of collection as the predictor variable. Regressions were done using the lm function in R (v3.6.1).

Geographic changes through time among frequently observed taxa were characterized using linear least squares regression. Abundance-weighted latitude for each taxon observed in 10 or more years was treated as the response variable and the year of collection was the predictor variable. Year-specific, abundance-weighted latitude for each taxon was calculated by summing across all four sampling sites the product of latitude at a sample site multiplied by relative abundance (sample abundance/total abundance) of a taxon within that year (EQ 1). An alpha value of 0.05 was used to select taxa whose location significantly changed over the span of the sampling period. Taxa were characterized as shifting northwards – taxa centered in higher latitudes in more modern samples – or shifting southwards – taxa centered in lower latitudes in more modern samples – based upon the sign of the beta term in the linear regression equation.

EQ1 - $Abundance\ Weighted\ Latitude\ (Sample\ Site\ i(CLAEMD \rightarrow CSD)$

$$\sum_{i} Latitude\ at\ Sample\ Site * \frac{Abundance\ at\ Sample\ Site}{Total\ Abundance}$$

Abundance of each northward or southward taxon was then modeled with the suite of water quality/chemistry and oceanographic variables detailed in Table 1 as predictor variables across 10,000 trees in a random forest regression. The relative influence of each predictor variable on the abundance of each taxon through time was quantified from % Mean Square Error change values for each predictor in the models. Random forests regressions were calculated using the randomForest and importance functions within the randomForest package (v4.6-16) (Liaw & Wiener 2002) in R (v3.6.1).

3. RESULTS

3.1 Patterns in Oceanographic Data

From the 1970s through the 2010s there was greater spatial variability in the selected oceanographic measures across the different depth zones and sampling sites than temporal variability at any given location. (Figure 2). Spatial patterns largely followed expectations, with the water masses being colder, saltier, denser, more acidified, less oxygenated, and with more nitrate as depth increased. The mid-shelf depth waters (~60m) were the most variable from year to year, while the slope depth waters (~300m) were the most stable. Inspection of the time-series data in Figure 2 suggests an increasing trend in temperature of mid-shelf depth waters at the northern sampling sites and in the upper-slope depth waters at the southern sampling site.

Furthermore, there is a suggestion of declining dissolved oxygen across all depths and sampling sites from the early 1980's through 2010's. The pattern amongst the modelled carbonate chemistry variables suggests a more acidified/corrosive conditions in the outer-shelf depth waters (~150m) of the northern sample sites. The carbonate chemistry variables fluctuated year-to-year from the 1970s – 2010s, but were non-corrosive at mid-shelf depths across all three sampling sites.

3.2 Patterns in Benthic Data

The nMDS plots (Figure 3) illustrate a pattern of changes in benthic community composition through time in all four sampling regions and across all depth zones. While there is year-to-year variation in ordination space, the general trend, as illustrated by the year correlation vector, is a relatively unidirectional change from the 1970s through the 2010s. The most visually distinct patterns are observable in the northernmost sample locations (LACSD and CLAEMD) (Figure 3, panels A-E). Quantitatively, both the multivariate correlation (Table 2) and the PERMANOVA (Table 3) results support the visual interpretation that the year of collection was significant ($\alpha = 0.05$) from the perspective of both the 2-D ordination (correlation) and the underlying dissimilarity relationships among samples (PERMANOVA). Analysis of these patterns using either presence/absence data, as done here, or abundance data (Supplement 2) did not change the clear pattern of community composition change through time.

The top-ten most abundant taxa for each decade within each depth zone from the LACSD and OCSan samples sites are presented in Table 4. Tracking these taxa through time presents a similar pattern to the nMDS ordinations of Figure 3, where there was a shift in community dominants across the decades. Of the 10 taxa that were community dominants at a given depth and location in the 1970s, an average of only 3.6 of these across the two programs were still dominant taxa in the 2010s. At mid-shelf depths, there was a shift from bivalves, polychaetes (cirratulids, lumbrinerids, and terebellids), and ostracods in the 1970s, giving way to ophiuroids, amphipods, and spionid polychaetes in the 1980s and 1990s. The mid-shelf communities of the 2000s and 2010s were dominated by ophiuroids and a variety of polychaetes, with no shelled molluscs among the top-ten most abundant taxa. The outer-shelf communities show a similar break between 1970s and 1980s taxa in contrast to more modern samples. The outer-shelf was a bivalve and ophiuroid dominated community before 1990 that shifted to an ophiuroid and polychaete dominated community in the 2000s and 2010s. The dominant taxa of the upper-slope from the 1970s and 1980s were relatively persistent through 2000s compared to the other depth zones. The upper-slope communities had a mix of polychaetes and amphipods consistently in the top-10 taxa through the 2000s, with a shift to different species of polychaetes and molluscs in the 2010s.

Many taxa were inconsistently observed through time, with only 8 to 25% of the taxa at a given site occurring in 10 or more years (Table 5a). It is important to note that the consistency of detection of a given taxon through time within our data set may have potentially been impaired for some taxa due to the regional standard operating practice of using only a single benthic grab to characterize benthic communities combined with high biodiversity of the region. Despite this, the logistic regressions of taxa presence vs. absence indicated that 105 taxa had an increasing probability of being observed in more modern years – increaser taxa – and 44 had a decreasing probability of being observed in more modern years – decreaser taxa (details in Supplement 3 – Table S5). These patterns can be illustrated by the ampeliscid amphipod *Ampelisca hancocki* or the travisiid polychaete *Travisia brevis* – both increasers – versus the tellinid bivalve *Macoma carlottensis* or entropneusts -both decreasers (Figure 4). Nearly all of the taxa that displayed a temporal trend had consistent increaser/decreaser patterns across all sampling locations and depth zones, with the exception of three taxa that increased in some sites and decreased in others: the bivalve *Axinopsida serricata* decreased in the mid-shelf and upper-slope of northern sites (CLAEMD and LACSD), while increasing in the outer-shelf of the southern location (CSD); the sigalionid polychaete *Sthenelanella uniformis* decreased in southern outer-shelf depths while increasing at the northern mid-shelf locations; lastly, the spionid polychaetes in the *Spiochaetopterus costarum* complex decreased in mid-shelf central locations (OCSan) but increased in outer-shelf depths.

The random forest models of the individual increaser and decreaser taxa through time indicates that there were relatively distinct influences on the two types of taxa. The most influential predictors (based upon their effect on model mean square error) of the abundance of decreaser taxa through time were associated with ocean acidification or dissolved oxygen at all three depth zones, as well as ENSO/PDO oceanographic variables for decreaser taxa from the outer-shelf and sediment composition for decreaser taxa from the upper-slope (Figure 5). Conversely, the top three most influential variables for increaser taxa were related to changes in temperature in all depth zones and ENSO/PDO in the mid and outer-shelf zones. Relatively few increaser taxa were influenced by acidification or dissolved oxygen patterns. Sediment grain size was an important predictor for approximately 20% of the taxa, most commonly among polychaetes at upper-slope depths. Supplement 3 (Tables S6 and S7) contains the detailed variable importance data for each increaser or decreaser taxon.

The greater number of increaser taxa versus decreaser taxa across the sampling sites was echoed in the overall trend of species richness through time. All sites had significantly ($\alpha = 0.1$) increasing taxa richness through time except mid-shelf depths at CSD and upper-slope depths at

LACSD (Figure 6). In contrast, the total abundance within a given sample significantly ($\alpha = 0.1$) declined through time in the mid-shelf depths of the CLAEMD, OCSan, and CSD sites, as well as at the outer-shelf and upper-slope depths of the LACSD site (Figure 7). Total abundance increased at the OCSan outer-shelf sites and there was no discernable trend at the other sample sites.

Eighty-six taxa shifted their geographic center of abundance northward or southward across the study region (Supplement 3 – Table S8). Most shifts occurred among mid-shelf taxa, with 37 taxa shifting northward and only 7 shifting southward (Table 5b). Conversely, the distributions of more taxa from the outer-shelf (29) and upper shelf (3) shifted southward than shifted northward (18 and 0, respectively). These patterns are illustrated in Figure 8 with the northward shifts in distribution of the spionid polychaete *Prionospio dubia* and the ampharetid polychaete *Asabellides lineata* (both mid-shelf). Conversely, southward shifts in distribution are illustrated by the spionid polychaete *Prionospio jubata*, the ampeliscid amphipod *Ampelisca pacifica*, and the thyasirid bivalve *Adontorhina cyclia* along the outer-shelf, or the scaphopod mollusc *Rhabdus rectius* on the upper-slope. The center of distribution for 51 of the 86 taxa shifted by more than 1 degree of latitude (a maximum of 1.24 degrees) north or south within our sampling area.

The random forest models of individual taxa whose distributions shifted northward or southward indicated a mix of influences on the two types of taxa (Figure 9). Of the taxa whose distribution shifted northward, temperature and acidification variables were the most influential predictors of abundance for more than 50% of the taxa on the mid-shelf and the outer-shelf, while oceanographic and dissolved oxygen predictors were less (<30%) frequently important to mid-shelf and outer-shelf taxa. Among those taxa whose distribution shifted southwards, acidification was the only clearly important predictor for outer-shelf taxa and acidification and dissolved oxygen were similarly important for mid-shelf taxa. As noted above, only 3 upper-slope taxa had significantly southward shifted distributions and only 1 taxon had a northward shifted distribution. For these taxa acidification and dissolved oxygen predictors were important for all of the northward and southward taxa, with temperature also important for 2 of the 3 southward taxa (full details in Supplement 3 – Tables S9 and S10). Note that ENSO/PDO oceanographic variables were not influential predictors for any southward shifting taxa at upper-slope depths.

A visual inspection of the relative abundance of shelled and non-shelled taxa through time showed distinct changes in the fauna through time. Figure 10 highlights the pattern in all three depth zones from the LACSD sampling sites. The upper-slope location, where there is the greatest, consistent exposure to acidified waters, and the outer-shelf location, where exposure has increased in more recent decades, showed relatively high abundance of shelled organisms in the 1970s and early 1980s. This was then followed by an initial sharp decline in the mid-1980s, short-term recovery, and a longer-term decline in the mid 1990's (Figure 10). In contrast, the abundance of non-shelled organisms showed a less distinct pattern through time, with fluctuating abundance that would be expected with most fauna. At mid shelf depths, where there is little expected exposure to corrosive waters, the relative abundance of shelled organisms declined briefly in the early 1990s, but recovered to normal levels soon after, while the abundance of non-shelled organisms was relatively consistent through time. Plots of shelled and non-shelled organisms from all depths and sites are presented in Supplement 4. The decline in shelled organisms at outer-shelf depth was not as drastic at the centrally located OCSan site, with a muted decline in the mid-1990s and recovery through the 2000s. It was not apparent at all at the southern-most, CSD sampling site.

The random forest regression models of total shelled fauna abundance indicated in the northern and centrally located mid-shelf stations (CLAEMD, LACSD, and OCSan) that acidification predictors were most frequently selected as influential variables. Temperature and oceanographic variables were most influential at the southern mid-shelf station. At outer-shelf depths, acidification variables were never identified as influential predictors of shelled fauna abundance, whereas DO, temperature and oceanographic variables were. In the upper-slope locations, acidification variables were most frequently identified as influential predictors, though DO, temperature, and oceanographic variables were all selected once too. Of the individual shelled taxa that could be classified as increaser or decreaser taxa, the likelihood of observing 8 taxa decreased through time and 13 increased (Supplement 3 – Table S5) across all three depth zones. Of the individual shelled taxa that could be classified as northward or southward shifting taxa, the distribution of 4 shifted northwards and 8 shifted southwards (Supplement 3 – Table S8).

4. DISCUSSION

This study presents empirical evidence for ongoing temporal changes in the composition of the macrobenthic communities of the coastal ocean of Southern California. The changes appear to be gradual and relatively unidirectional at a decadal scale, with oscillation of community dominants and secondary taxa from year-to-year at all of the sampling locations and depth zones. Beyond demonstrating the change, we were able to characterize the nature of the change. Some taxa became more frequently observed in modern samples than in the past, while others commonly observed in the past were rarely observed in modern times. Similarly, there were detectable shifts in the geographic distribution of a number of taxa, shifting either northward or southward across the breadth of the Southern California Bight. Most significantly, we were able to provide insight into the relative influence of changing ocean conditions on these appearances, disappearances, or geographic shifts. The bulk of the decreasing taxa were driven by changes in carbonate chemistry and dissolved oxygen regimes of their habitats, while the increasing taxa were more frequently linked to changes in water temperature and ENSO/PDO cycles.

Our findings for benthic fauna are similar to that of Hale et al. (2018) on the Atlantic Coast of the US. When considering the autecology and natural history of the taxa across the decades, there were shifts away from a bivalve (thyasirids, lucinids, tellinids) and polychaete (spionids and cirratulids) dominated community towards a community dominated by amphiurid ophiuroids, amphipods, and a more functionally diverse array of polychaetes. These data indicate that the communities of the continental shelf and slope of the Southern California Bight are, within recent record, comprised of a majority of deposit and interface feeding taxa, which makes sense given the depth of the water and separation from the photic zone. However, the shifts from a community dominated by lucinid bivalves (i.e., *Axinopsida serricata* and *Parvilucina tenuisculpta*) and deposit/interface-feeding polychaetes to one with an array of additional feeding modes from predatory polychaetes (e.g., *Lumbrineris* spp., *Scoletoma tetraura*) and crustaceans (e.g., *Metaphoxus frequens*, *Rhepoxynius* spp.) to true filter feeders (e.g.. *Phoronis* sp.) represents a broadening of the realized ecological niche space in the habitat. The broadening of niche space occupied by the fauna, may in part account for the increasing species richness combined with declining total abundance observed across the decades in the dataset (Cardinale et al. 2009, Niklaus et al. 2017).

We would suggest that the scope of the temporal community composition changes we observed was ecologically relevant. To give that change context, the difference in composition between samples from the 1970s and the 2010s was equivalent to differences in composition between a reference condition site and one disturbed by anthropogenic activities. As an illustration, the Bray-Curtis dissimilarity of presence/absence data between the 1974 and 2018 sample from the LACSD mid-shelf site was 0.75. The same dissimilarity measure between a mid-shelf reference condition site and a disturbed site from a 2018 Southern California Bight regional survey – using a similar type of grab, as well as the same sieve size and taxonomic standard – was 0.73 (Gillett et al. 2022). The nature of the changes was different – one is a shift from an older community to a more modern community, the other a shift from an intact modern assemblage to a pollution tolerant assemblage – but both pairs represent an approximately 75% difference in sample composition.

There are likely multiple mechanisms for the change in community composition and increase in species richness observed over the decades. All of the sample sites were selected to minimize influence of local human disturbance (i.e., wastewater outfalls, dredging, trawling). However, the dominance of the lucinid bivalves and deposit feeders in older samples (i.e., typical indicators of organic matter enrichment) versus a broader array of feeding types in newer samples could be reflective of regional recovery from anthropogenic pollution in the earlier part of the 20th century (Leonard-Pingel et al. 2019, Los Angeles County Sanitation Districts 2020, Orange County Sanitation District 2021). This recovery could partially explain the species richness and abundance patterns that were observed (e.g., Diaz et al. 2008). However, the degree of disturbance observed at the sampling sites across the length of the dataset was relatively minimal, with nearly all of the samples within a reference or low disturbance category (following Smith et al. 2001, Gillett et al. 2022) (Figure 11).

An alternative, non-environmental explanation one could posit for both the increased species richness and the differences in taxa observed across time might be changes in the science of taxonomy (Isaac et al. 2004, Agapow & Sluys 2005, Morrison et al. 2009). Taxonomy changes as new species are erected from within old polyphyletic “species”, local taxonomic precision changes, or the names change due to refined precedence of descriptions. This can be of particular concern with data records as long as those used in this study, during which the taxonomist personnel in each of the monitoring program has changed numerous times. However, that does not appear to be a major contributing factor to the patterns observed in the present study. The nature and magnitude of community change we observed was similar across four independent programs whose taxonomists did not change at the same times. Furthermore, the declines in abundance that were observed concurrently with the increases in species richness are unlikely to occur if species names were just being split or refined from family to species. In fact, the relative taxonomic stability across our data sets is a tribute to the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT, www.scamit.org) who work diligently to ensure consistency in nomenclature over time and who assisted in assembling these data sets prior to analysis to limit any taxonomic confounding.

Beyond any changes in regional pollution levels or shifts in taxonomic nomenclature, our analyses indicate that temperature and carbonate chemistry appear to have been important factors affecting the benthic composition over time. Temperature was an important predictor for taxa whose geographic distribution shifted, as well as those that increased in frequency of occurrence in the more modern samples. We would suggest that a combination of range expansions within the study area and from outside of the region to inside of it created the increase in overall species richness observed within the dataset. This would follow patterns observed in benthic communities along the Atlantic coast of US (Hale et al. 2017) and the Kattegat (Goransson 2017), as well pelagic communities in the Atlantic and the Pacific (e.g., ter Hofstede et al. 2010, McClatchie et al. 2016). Of the taxa whose range did shift, temperature was more frequently important for those moving northwards than southwards (predominantly crustaceans, as well as spionid and maldanid polychaetes), which follows with the encroachment of warmer waters into the northern parts of the Southern California Bight (e.g., Fumo et al. 2020) (Figure 2). The scale of range shifts for benthic species has been documented up to 70km per decade (Birchenough et al. 2015). These rates are in line with observations of the taxa in the present study, where more than two-thirds of the taxa that had northward or southward shifts in their distribution changed by 1-1.2 degrees latitude (approximately 111 – 133km) across the five decades of our study.

There is less evidence in the literature for geographic shifts in benthic infauna related to changes in carbonate chemistry, though the patterns from our study suggest that carbonate chemistry and dissolved oxygen can shape the distribution of benthic taxa as strongly as the more well documented changes related to water temperature noted above. Sato et al (2017) demonstrated habitat compression for motile benthic epifauna on the continental shelf of the Southern California Bight as a product of changes in carbonate chemistry and dissolved oxygen. The gradient in exposure to low pH waters across relatively short spatial scales in the region (Hauri et al. 2013, McLaughlin et al. 2018, Kessouri et al. 2022) may contribute to the range shifts we observed. Conversely, the influence of carbonate chemistry on changes in community composition related to local extirpations and appearances we observed in the macrobenthos has been predicted or observed in other systems (e.g., Kroeker et al. 2011, Busch et al. 2013, Nagelkerken & Connell 2022). A large number of the decreaser taxa influenced by carbonate chemistry were bivalve and gastropod molluscs, which makes sense given their calcium carbonate shells (Green et al. 2009, Clements & Hunt 2017). In contrast, the increaser taxa influenced by carbonate chemistry were mostly spionid or cirratulid polychaetes and crustaceans, most of which were also deposit/interface feeders and could be filling the niche and physical space vacated by the disappearing bivalves and gastropods.

The specific impacts of the observed changes in macrobenthic community composition on the functioning of the soft-sediment continental shelf and slope ecosystem are hard to quantify within the scope of the present study. However, experiments exposing different types of infauna to altered temperature and pH conditions have demonstrated changes in behavior and allocation of energetic resources within individual fauna (Wood et al. 2008, Widdicombe et al. 2009, Christensen et al. 2017). When these climate change- and ocean acidification-driven impacts are extrapolated to the whole of the benthic ecosystem (e.g., Busch et al. 2013, Morley et al. 2022, Weinert et al. 2022), decreases in rates of secondary production, nutrient cycling, and carbon sequestration are predicted. Our data indicate that the macrobenthic community of the Southern California continental margin has changed compositionally and that total abundance has declined. When viewed through the lens of the aforementioned studies, the patterns we observed could be suggestive of the potential for a reduction in ecosystem functioning (e.g., bioturbation/nutrient cycling and secondary productivity). However, the accompanying increase in taxonomic and feeding guild diversity suggests that there may have been some degree of community compensation against the influence of climate change and acidification (e.g., Hendriks et al. 2010, Lavergne et al. 2010, Kroeker et al. 2011).

One of the more striking examples of community change we observed was the decline of shelled organisms over time in the northern portions of the region (see also Tomašových & Kidwell 2017, Leonard-Pingel et al. 2019). The northern parts of our sample area have greater exposure to acidic waters (Hauri et al. 2013, McLaughlin et al. 2018) due to the oceanographic currents of the region (Harms & Winant 1998, Bray et al. 1999). However, the abundance patterns of shelled fauna, especially in the 1970s and early 1980s, at the northern sample sites did not perfectly track the patterns in Ω_{arag}. This is, in part, due to the unfortunate lack of consistent data at our water quality/chemistry sites during the early years of the benthic monitoring data record that prevents us from drawing quantitative conclusions. McClatchie et al. (2010) highlight the 1970s and 1980s as a period of increased oxygen concentrations in the Southern California Bight as a whole, from which one could infer generally lower pCO_2 and less acidic conditions. The four data points prior to 1984 where we estimate low Ω_{arag} values may represent local anomalies or influence of legacy organic matter pollution in the continental shelf of the region.

An additional level of complexity to consider when interpreting these patterns is that water column acidification most likely affects the veliger larvae and freshly settled infaunal molluscs more acutely than the adults buried deeper in the sediment (Green et al. 2009, Widdicombe et al. 2009, Waldbusser et al. 2015). This differential impact would create a lag where the adults – which are detected in the benthic monitoring data – persist through acidified conditions but are not being replaced at the population level by juveniles and larvae – which are not detected in the benthic monitoring data. Illustrating this potential lag in population-level response, the abundance of a many of the molluscs classified as decreasers in our data set (e.g., *Acila castrensis*, *Chaetoderma* sp, *M. carlottensis, P. tenuisculpta*) were influenced in our random forest analyses by ocean acidification variables from one and three years prior to their collection rather than measurements from the same year of their collection (Supplement 3 – Table S7).

There has been increasing recognition among managers of the need to monitor and track both the exposure to and potential effects of climate change and acidification in coastal waters (Boehm et al 2015, Cross et al. 2019, Tilbrook et al 2019). The present study could represent the first steps towards developing specific benthic indicators of dissolved oxygen, temperature, or acidification. We have identified a number of species that appear to be either sensitive to or indicative of exposure to these different water chemistry/quality stressors. These species could be used as the subjects of focused exposure or physiological studies to support the statistical relationships we observed in this retrospective study, much as Bednarsek et al. (2017) suggested pteropods as sentinels for midwater taxa. Alternatively, the patterns in abundance of the benthic species could be combined into multi-species metrics or used to create a stressor-specific assemblage models in a benthic index of acidification exposure. These types of experiments and assessment tools would combine nicely with existing chemical and biological monitoring efforts in the water column to create a holistic perspective on the exposure and effects of climate change on the coastal ocean.

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Figures

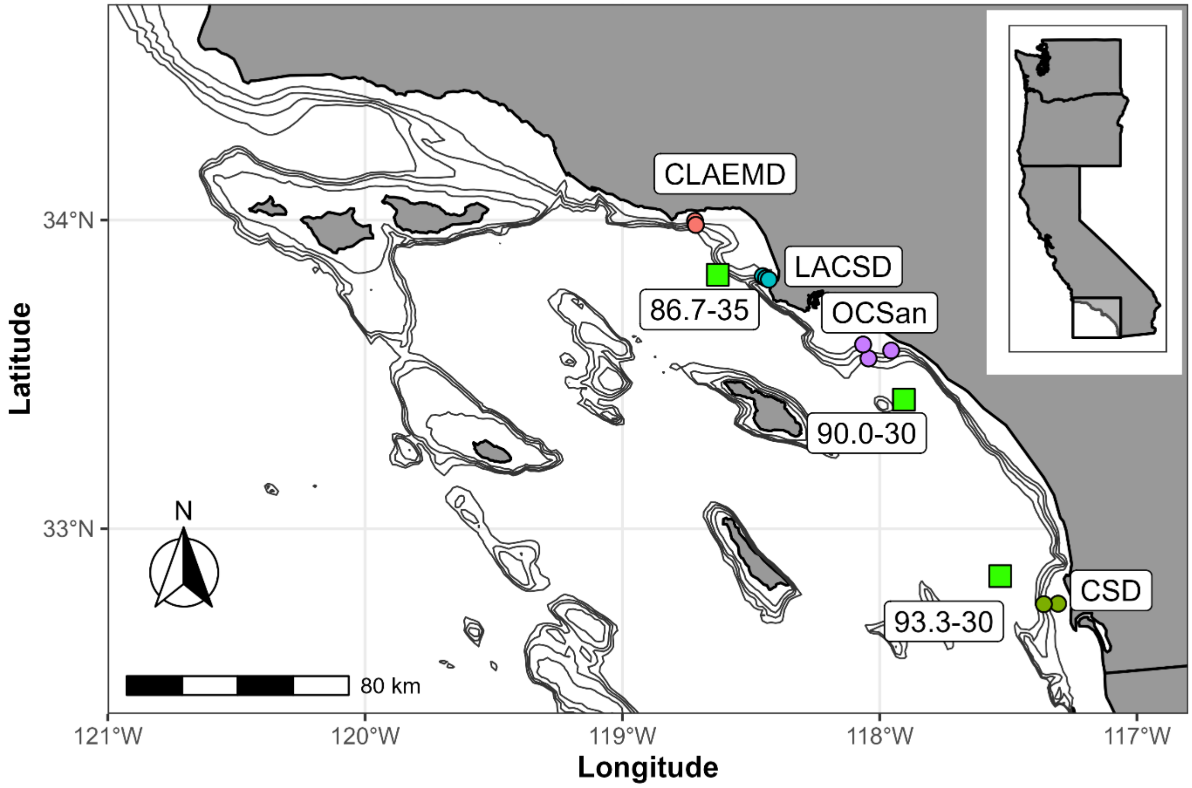


Figure 1 A map of the Southern California Bight illustrating the locations of the ten benthic sampling sites, color-coded by their sampling locations/data sources. The green squares represent the location of the CalCOFI water quality monitoring stations labelled with their transect number-station ID. The black lines represent the 100-m isobaths between 100 and 400 m deep. The inset shows the position of the Southern California Bight relative to the California and eastern Pacific coasts.

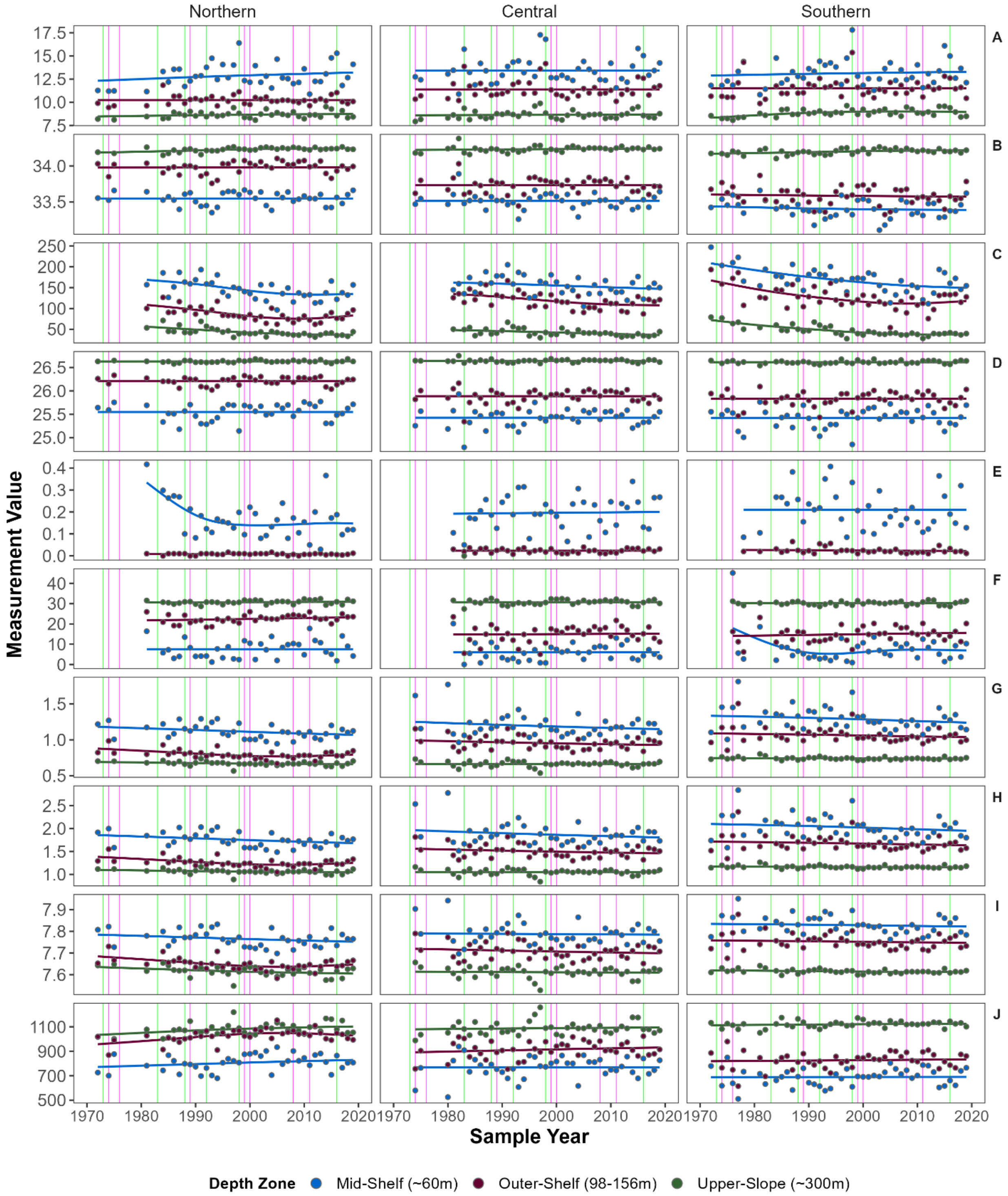


Figure 2 Water quality and water chemistry (summarized from quarterly bottle samples) at each of the three CalCOFI water monitoring stations (see Figure 1) used in subsequent analyses of benthic fauna. A trend line (general additive model for smoothing) for each set of data is

presented only to help the reader follow the patterns amongst the individual points. Bottles were selected within 20m of the depth of the associated benthic sample locations. A = maximum bottom water temperature (C), B= median salinity (PSU), C= minimum dissolved oxygen (µmol kg^{-1}), D=median water density (σ_T), E=median chlorophyll a (µg L^{-1}), F= median nitrate (µg L^{-1}), G=minimum estimated aragonite saturation State, H=minimum estimated calcite saturation State, I=minimum estimated pH, and J=maximum estimated pCO_2. The green vertical lines indicate years with strong to very strong El Niño events. The magenta lines indicate years with strong La Niña events. ENSO designations based upon NOAA Oceanic Niño Index (https://psl.noaa.gov/data/correlation/oni.data).

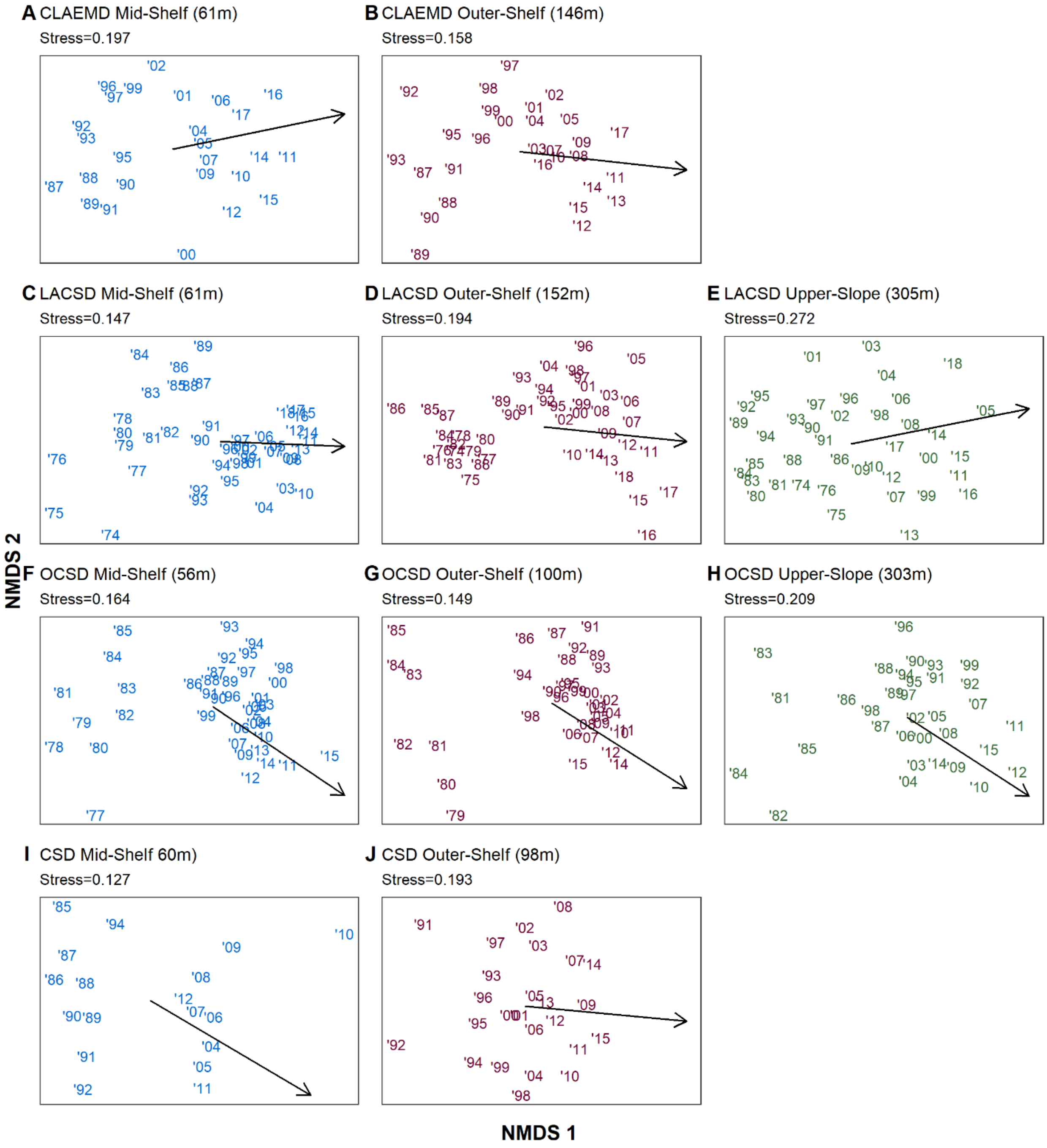


Figure 3 A series of 2-D nMDS ordination plots of Bray-Curtis dissimilarity values of benthic infauna communities at each of the sampling sites from each year across the breadth of the data set. The two-digit number represents the year of collection (i.e., 1998=98, 2001=01). The black

arrows indicate the trend of time across the different ordinations based upon multivariate correlations (Table 2). Ordinations based upon dissimilarities of presence-absence transformed community data with a minimum of 250 iterations.

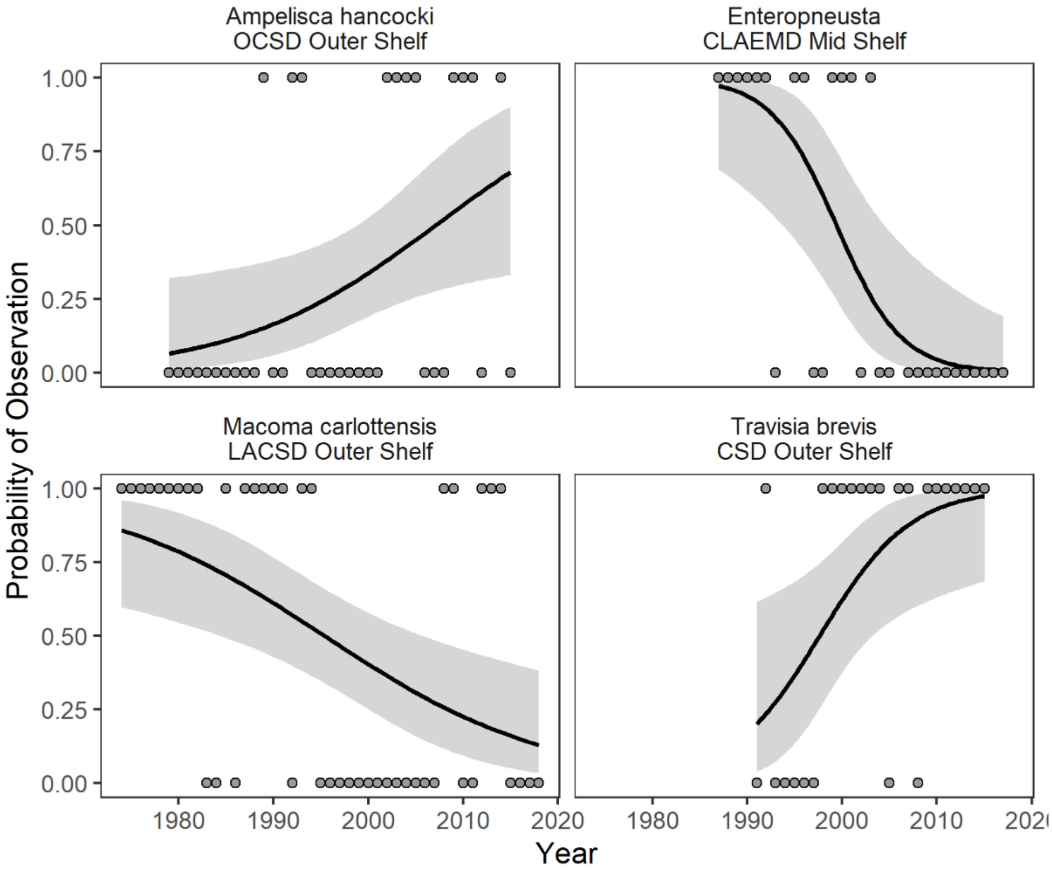


Figure 4 Logistic regression curves of four example taxa illustrating patterns of increasing probability of observation through time (*Ampelisca hancocki* and *Travisia brevis*) and decreasing probability of observation through time (Enteropeneusta and *Macoma carlottensis*). Each of these taxa, as well as all taxa identified in Supplement 3 – Table S5, had a regression with a beta term significantly different than 0 (α=0.05). The grey ribbon represents the standard error of the probability estimate. The grey dots in the rug represent the presence (1) or absence (0) of that taxon in a given year at the site.

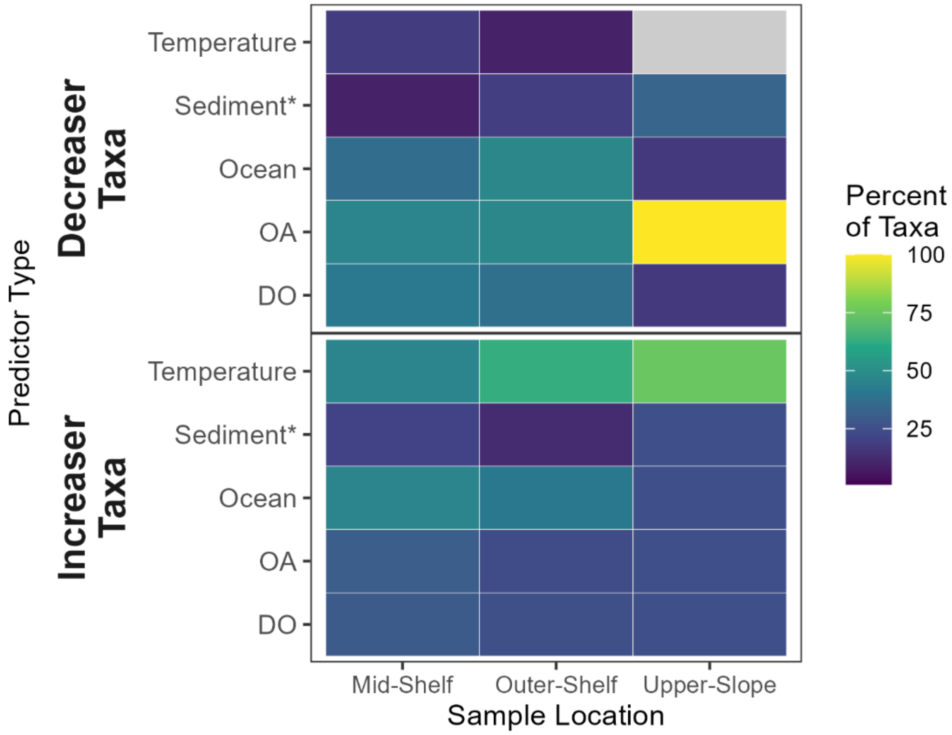


Figure 5 A heat map summarizing the most important variables in predicting the abundance patterns of benthic infauna classified as decreasing or increasing in abundance through time (see Supplement 3 – Tables S6 and S7) across all four sample locations and divided by depth zone. Predictors included measures of temperature (surface water temperature, bottom water temperature), oceanographic patterns (ENSO, PDO), bottom water ocean acidification (aragonite saturation, calcite saturation, pH, pCO_2), bottom water dissolved oxygen, or sediment grain size (%Sand, %Silt, %Clay). Their predictive importance was derived from random forest regression variable importance outputs. Warmer colors indicate a predictor that was important for more taxa within a given depth zone. Cooler colors indicate a predictor that was important for fewer taxa. No temperature variables were important predictors for decreaser taxa from the upper-slope. See Table 1 for a full list of all potential predictor variables. Note that sediment* grain size data were only available for the CLAEMD, LACSD, and CSD sample sites.

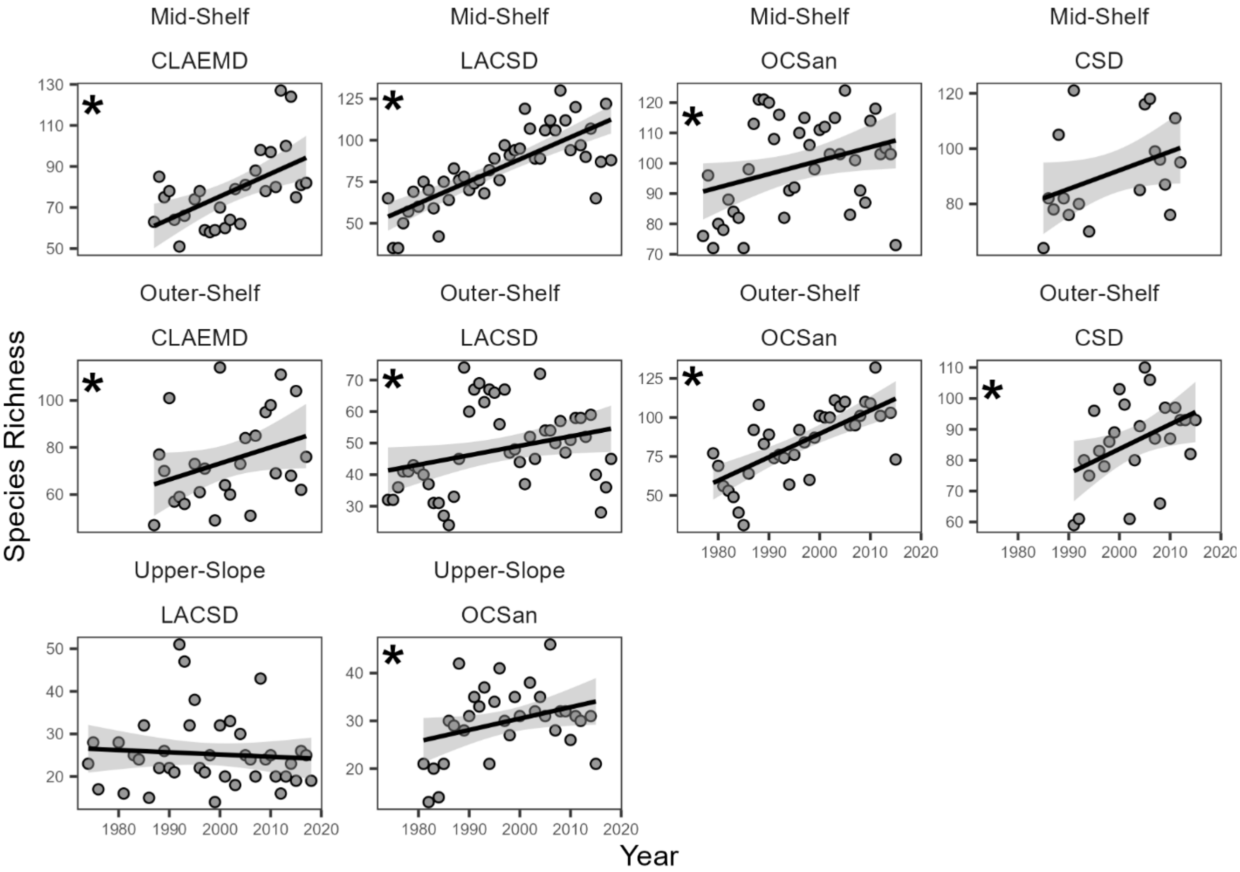


Figure 6 Least squares linear regression plots of taxa richness through time at each of the sampling sites at the three depth zones. An asterisk indicates a slope significantly (α = 0.1) different than zero. The grey ribbon indicates the standard error of the predicted values.

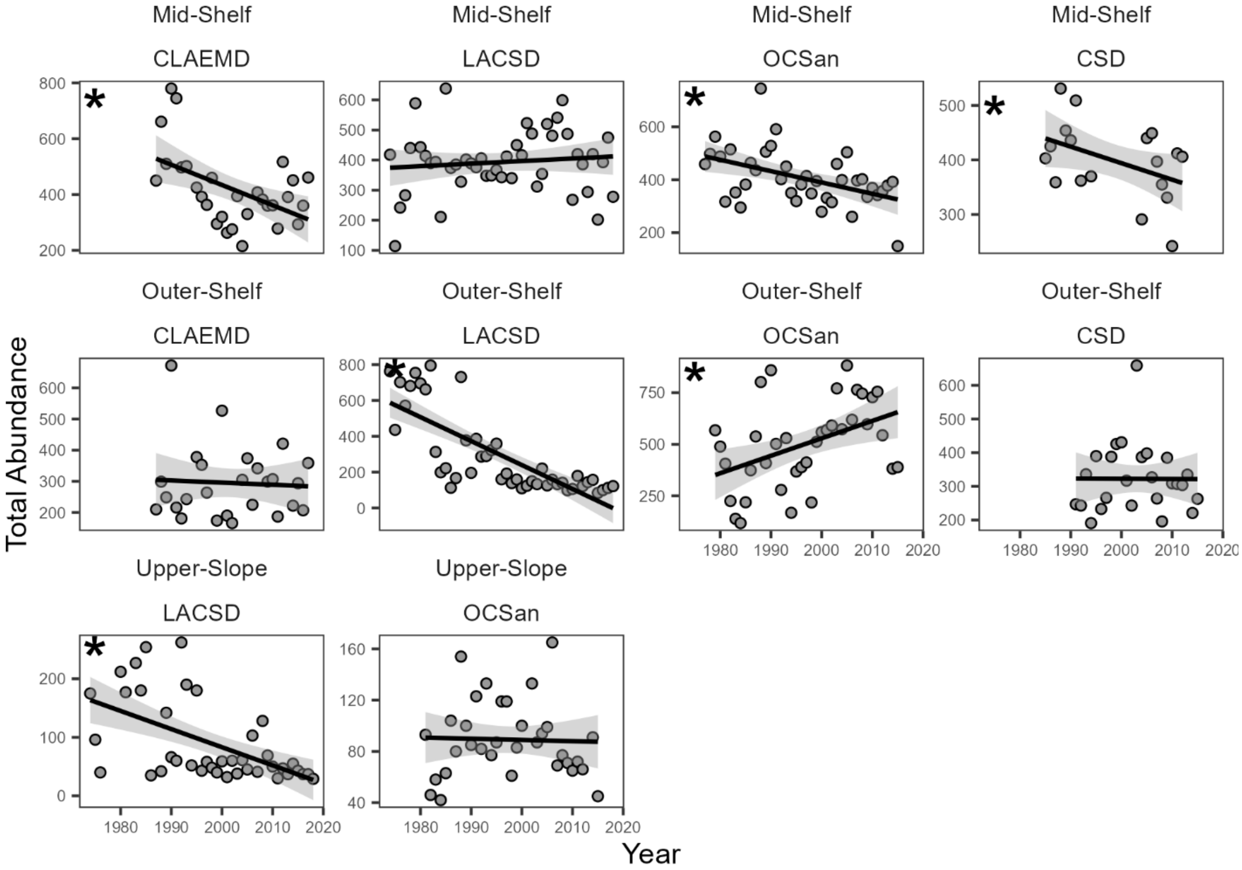


Figure 7 Least squares linear regression plots of sample abundance through time at each of the sampling sites at the three depth zones. An asterisk indicates a slope significantly (α = 0.1) different than zero. The grey ribbon indicates the standard error of the predicted values.

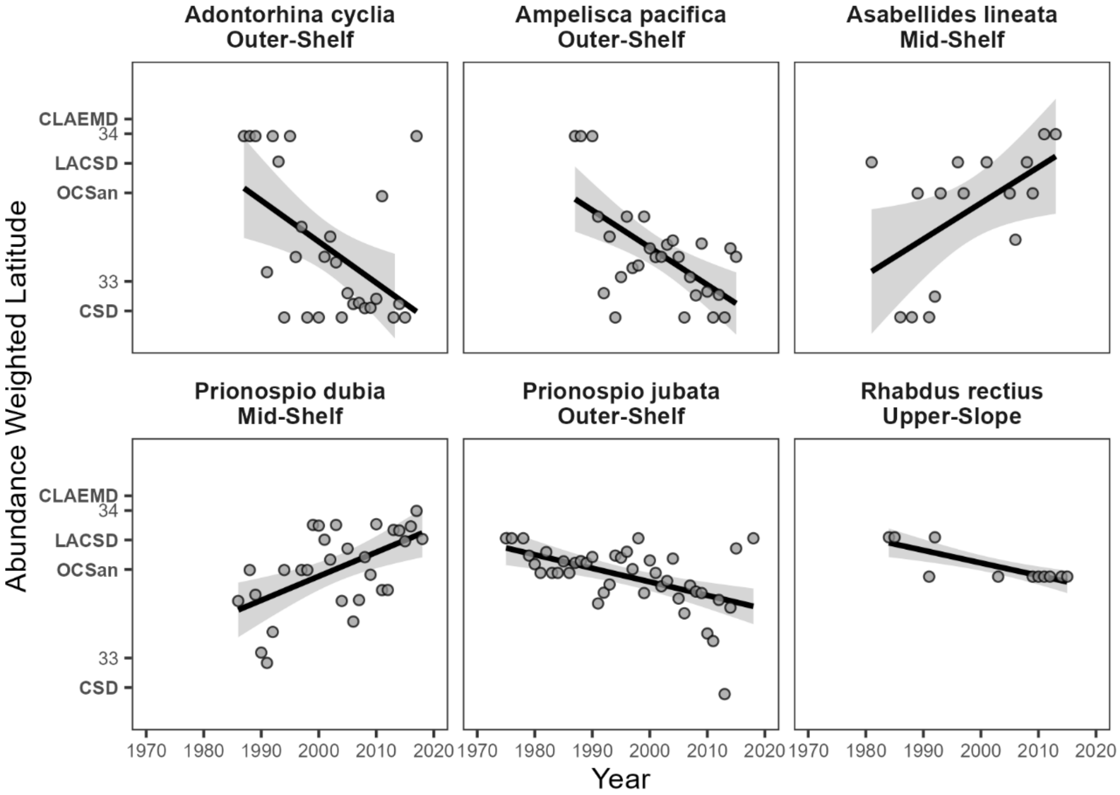


Figure 8 Least squares linear regression of abundance weighted latitude through time for six taxa illustrating a trend of a taxon whose distribution has shifted northwards (*Asabellides lineata* and *Prionospio dubia*) or a taxon whose distribution has shifted southwards through time (*Prionospio jubata*, *Adontorhina cyclia*, *Ampelisca pacifica*, and *Rhabdus rectius*). Each of these taxa, as well as all taxa identified in Supplement 3 – Table S8, had a regression with a slope significantly different than 0 (α=0.05). The grey ribbon indicates the standard error of the predicted values. The average latitudinal position of the four sampling sites is indicated on the y-axis for reference.

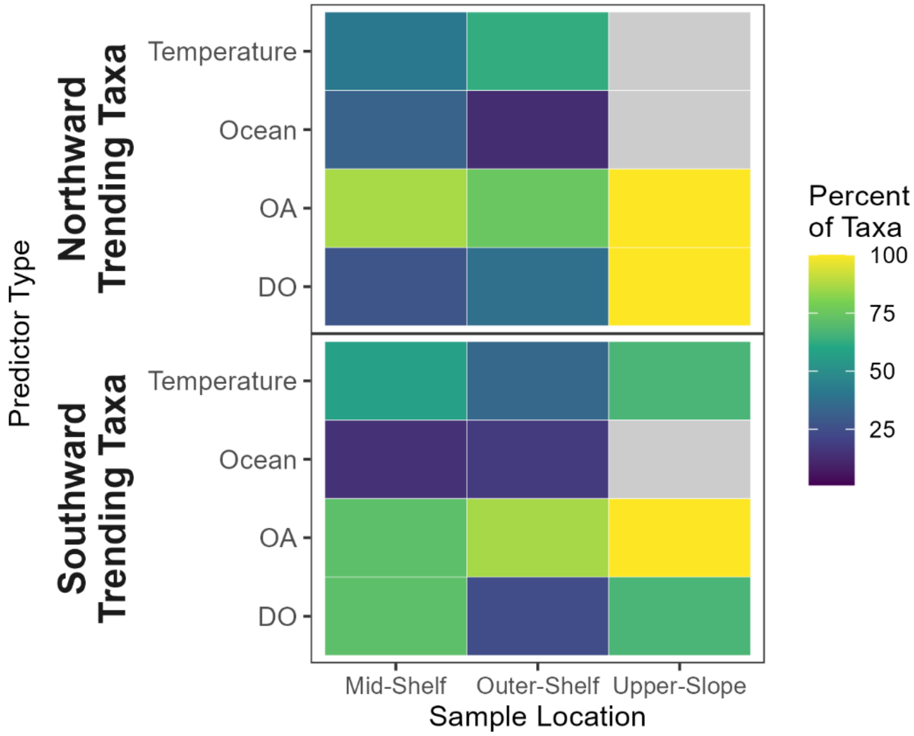
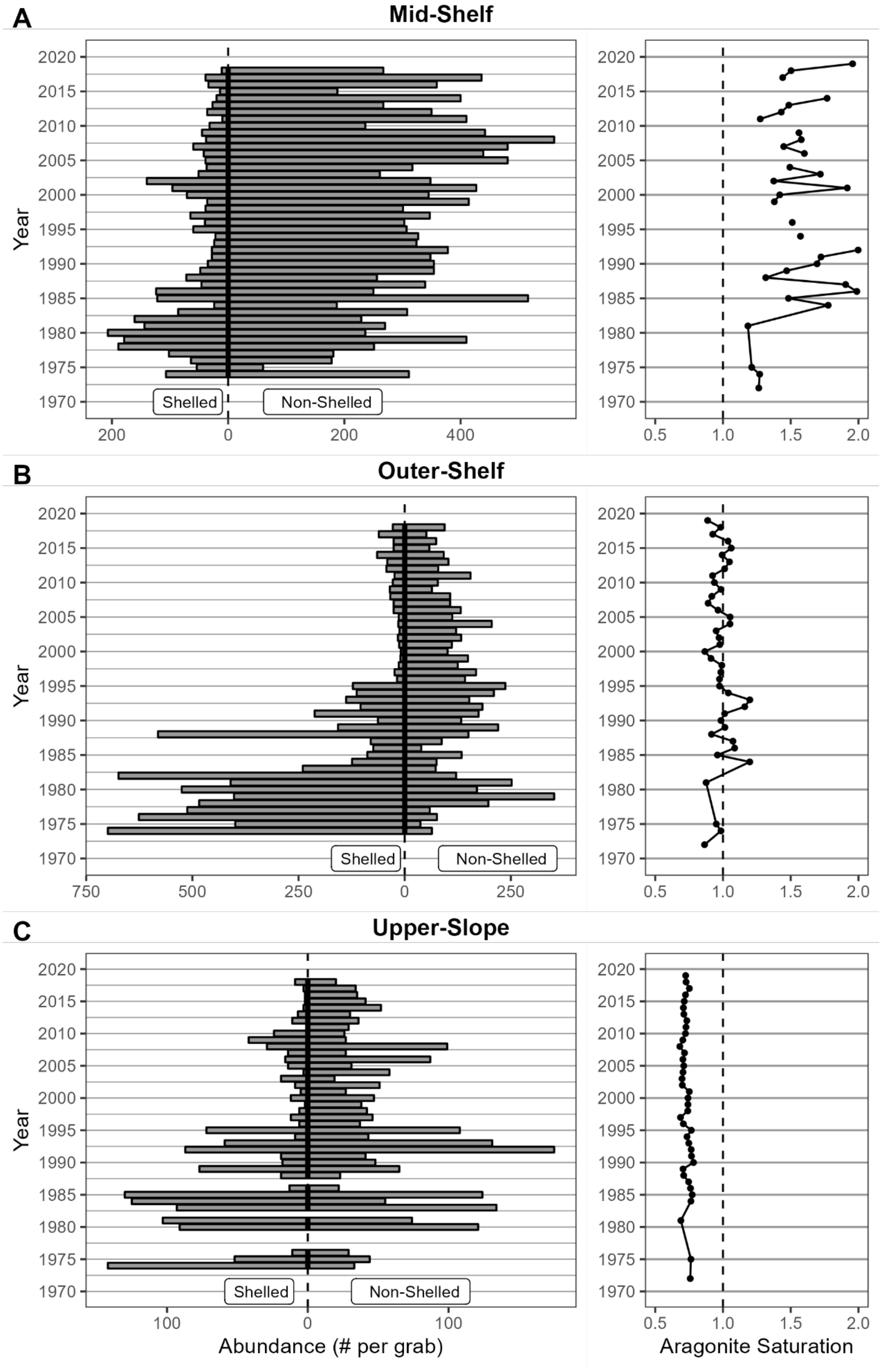


Figure 9 A heat map summarizing the most important variables in predicting the abundance patterns of benthic infauna classified as northward or southward shifting taxa through time (see Supplement 3 – Tables S9 and S10) within each of the three depth zones. Predictors included measures of temperature (surface water temperature, bottom water temperature), oceanographic patterns (ENSO, PDO), bottom water ocean acidification (aragonite saturation, calcite saturation, pH, pCO_2), or bottom water dissolved oxygen. Their predictive importance was derived from random forest regression variable importance outputs. Warmer colors indicate a predictor that was important for more taxa within a given depth zone. Cooler colors indicate a predictor that was important for fewer taxa. Only one northward trending taxon was observed from the upper-slope and oceanographic variables were not important predictors for southward shifting taxa from the upper-slope. See Table 1 for a full list of all potential predictor variables.


A
Mid-Shelf
B
Outer-Shelf
C
Upper-Slope
Year
2020
2015
2010
2005
2000
1995
1990
1985
1980
1975
1970
Shelled
Non-Shelled
200
0
200
400
750
500
250
0
250
100
0
100
0.5
1.0
1.5
2.0
Abundance (# per grab)
Aragonite Saturation

974

Figure 10 An illustration of the change in abundance of shelled and non-shelled organisms at Mid-Shelf (A), Outer-Shelf (B), and Upper-Slope (C) sample sites relative to modeled aragonite saturation values at the LACSD location through time. The dashed vertical line on the aragonite saturation plots highlight a value of 1.0, below which aragonite will dissolve into seawater from a solid form.

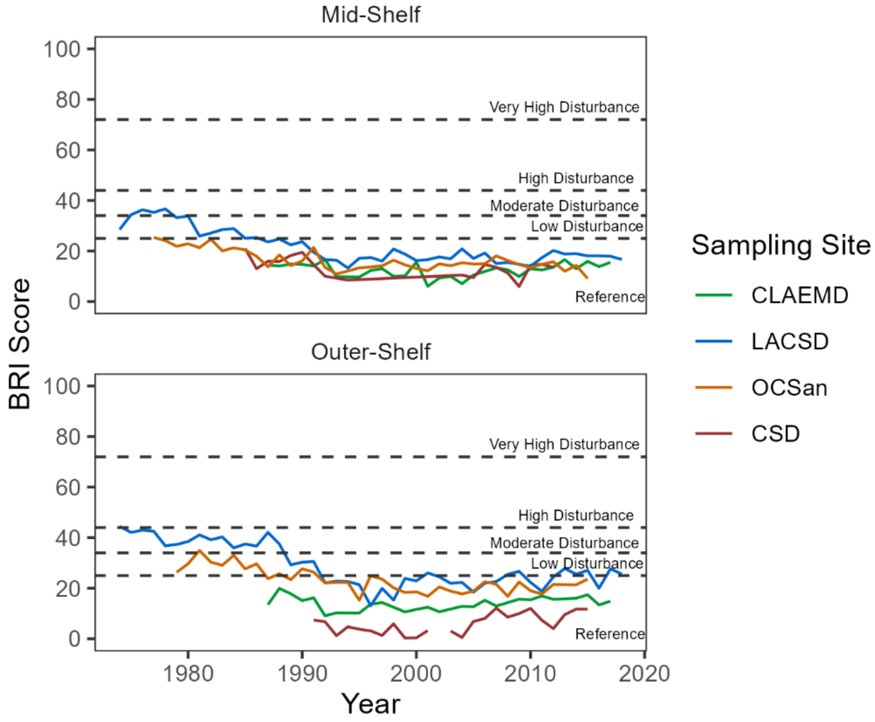


Figure 11 Benthic condition scores through time at each of the sampling sites in the mid-shelf and outer-shelf depth zones using the Benthic Response Index (BRI) of Smith et al. (2000). A higher score indicates a more disturbed sample. The dashed lines indicate the different thresholds of community impact that were linked to compositional changes in addition to loss of taxonomic and functional diversity with high levels of disturbance. The BRI is not calibrated to Upper-Slope habitats.

Tables

Table 1. Environmental variables used as potential predictors of change in macrobenthic community composition through time, the sources of those data, and the coverage of those variables at each of the four sampling locations. PDO - Pacific Decadal Oscillation index value. SOI - Southern Oscillation Index value. *CSD sediment data were reported in % sand and % mud, where % mud = % silt +% clay. 1- and 3-year time lags were selected for consideration, as most of the benthic infauna are thought to live from 1 to 3 years at a maximum, though some of larger bivalves may persist longer.

Data Type	**Potential Predictor Variables**	**Data Source**	**CLAEMD**	**LACSD**	**OCSan**	**CSD**
Local Sediment	% Sand	Discharger	X	X		X
	% Silt	Discharger	X	X		X*
	% Clay	Discharger	X	X		X*
Regional Oceanography	Mean Springtime PDO	NOAA	X	X	X	X
	Mean Spring PDO One Year Prior	NOAA	X	X	X	X
	Mean Spring PDO Three Years Prior	NOAA	X	X	X	X
	Mean Springtime SOI	NOAA	X	X	X	X
	Mean Springtime SOI One Year Prior	NOAA	X	X	X	X
	Mean Springtime SOI Three Years Prior	NOAA	X	X	X	X
Local Temperature	Mean Summer Surface Water Temperature	CalCOFI	X	X	X	X
	Mean Summer Surface Water Temperature One Year Prior	CalCOFI	X	X	X	X
	Mean Summer Surface Water Temperature Three Years Prior	CalCOFI	X	X	X	X
	Mean Summer Bottom Water Temperature	CalCOFI	X	X	X	X
	Mean Summer Bottom Water Temperature One Year Prior	CalCOFI	X	X	X	X
	Mean Summer Bottom Water Temperature Three Years Prior	CalCOFI	X	X	X	X

Local Dissolved Oxygen	Mean Summer Bottom Water Dissolved Oxygen	CalCOFI	X	X	X	X
	Mean Summer Bottom Water Dissolved Oxygen One Year Prior	CalCOFI	X	X	X	X
	Mean Summer Bottom Water Dissolved Oxygen Three Years Prior	CalCOFI	X	X	X	X
Local Acidification	pCO2	Modelled	X	X	X	X
	pCO2 One Year Prior	Modelled	X	X	X	X
	pCO2 Three Years Prior	Modelled	X	X	X	X
	pH	Modelled	X	X	X	X
	pH One Year Prior	Modelled	X	X	X	X
	pH Three Years Prior	Modelled	X	X	X	X
	Aragonite Saturation	Modelled	X	X	X	X
	Aragonite Saturation One Year Prior	Modelled	X	X	X	X
	Aragonite Saturation Three Years Prior	Modelled	X	X	X	X
	Calcite Saturation	Modelled	X	X	X	X
	Calcite Saturation One Year Prior	Modelled	X	X	X	X
	Calcite Saturation Three Years Prior	Modelled	X	X	X	X

Table 2 Multivariate correlation of year of sampling with the nMDS ordinations presented in Figure 3. Correlations were calculated across 1,000 permutations.

Depth Zone	Sample Location	r	p-value
Mid-Shelf	CLAEMD	0.93	0.002
	LACSD	0.96	0.002
	OCSan	0.92	0.002
	CSD	0.91	0.002
Outer-Shelf	CLAEMD	0.95	0.002
	LACSD	0.91	0.002
	OCSan	0.84	0.002
	CSD	0.88	0.002
Upper-Slope	LACSD	0.80	0.002
	OCSan	0.86	0.002

Table 3. Outputs of 1-way PermANOVAs testing the differences in macrobenthic community structure through time at the different depth zones of each of the four sampling locations based upon Bray-Curtis dissimilarities of taxon presence-absence over 10,000 permutations.

Depth Zone	Sample Location	Term	Df	SS	R^2	pseudo-F	p-value
Mid-Shelf	CLAEMD	Year	1	0.92	0.20	6.79	<0.0001
		Residual	27	3.64	0.80		
	LACSD	Year	1	1.99	0.23	12.87	<0.0001
		Residual	43	6.65	0.77		
	OCSan	Year	1	1.12	0.16	6.86	<0.0001
		Residual	37	6.04	0.84		
	CSD	Year	1	0.76	0.26	5.56	<0.0001
		Residual	16	2.20	0.74		
Outer-Shelf	CLAEMD	Year	1	0.84	0.17	4.97	<0.0001
		Residual	24	4.05	0.83		
	LACSD	Year	1	1.94	0.19	10.31	<0.0001
		Residual	43	8.09	0.81		
	OCSan	Year	1	0.98	0.17	6.77	<0.0001
		Residual	34	4.91	0.83		
	CSD	Year	1	0.50	0.15	3.92	<0.0001
		Residual	23	2.92	0.85		
Upper-Slope	LACSD	Year	1	0.94	0.09	3.79	<0.0001
		Residual	38	9.41	0.91		
	OCSan	Year	1	0.96	0.13	4.44	<0.0001
		Residual	31	6.72	0.87		

Table 4. Top-10 most abundant taxa in descending rank order (with ties) for each decade 1970s – 2010s at Mid-Shelf, Outer-Shelf, and Upper-Slope depth zones from the LACSD and OCSan sampling sites. Taxa are color-coded based upon the decade during which they first appeared in the top-10 of the sample site. ^ denotes taxa indicative of disturbed conditions based upon Smith et al. (2001). # denotes taxa indicative of non-disturbed conditions based upon Smith et al. (2001). (c) = crustacean, (e) = echinoderm, (h) = hemichordate, (l) = phoronid, (m) = mollusc, and (p) = polychaete. Note that that no samples were collected from the OCSan Upper-Slope site in the 1970s.

District	Depth Zone	1970s	1980s	1990s	2000s	2010s
LACSD	Mid-Shelf	*Parvilucina tenuisculpta*^ (m)	*Spiophanes duplex* (p)	*Amphiodia* sp (e)	*Amphiodia* sp (e)	*Amphiodia* sp (e)
		Aphelochaeta-Kirkegaardia Cmplx^ (p)	*Parvilucina tenuisculpta*^ (m)	*Spiophanes duplex* (p)	*Spiophanes duplex* (p)	*Lumbrineris cruzensis* (p)
		Axinopsida serricata (m)	*Axinopsida serricata* (m)	*Amage scutata* (p)	*Axinopsida serricata* (m)	*Spiophanes duplex* (p)
		Prionospio jubata (p)	*Amphiodia* sp (e)	*Axinopsida serricata* (m)	*Mediomastus* sp (p)	*Aphelochaeta-Kirkegaardia* Cmplx^ (p)
		Mediomastus sp (p)	*Myriochele striolata* (p)	*Phoronis* sp	*Thyasira flexuosa* (m)	*Mediomastus* sp (p)
		Euphilomedes producta (c)	*Lumbrineris sp* (p)	*Pectinaria californiensis* (p)	*Paraprionospio alata* (p)	*Cossura candida* (p)
		Lumbrineris sp (p)	*Marphysa disjuncta* (p)	*Marphysa disjuncta* (p)	*Prionospio jubata* (p)	*Prionospio dubia* (p)
		Hamatoscalpellum californicum (c)	*Prionospio jubata* (p)	*Prionospio jubata* (p)	*Phoronis* sp (l)	*Prionospio jubata* (p)
		Euphilomedes carcharodonta (c)	*Heterophoxus sp* (c)	*Paraprionospio alata* (p)	*Lumbrineris cruzensis* (p)	*Gymnonereis crosslandi* (p)
		Pectinaria californiensis (p)	*Cossura candida* (p)	*Glycera nana* (p)	*Maldane sarsi* (p)	*Eclysippe trilobata#* (p)
						Lumbrineris sp (p)
						Phoronis sp (l)
OCSan	Mid-Shelf	*Amphiodia* sp (e)	*Amphiodia* sp (e)	*Amphiodia* sp (e)	*Amphiodia* sp (e)	*Amphiodia* sp (e)
		Euphilomedes carcharodonta (c)	*Pectinaria californiensis* (p)	*Prionospio jubata* (p)	*Prionospio jubata* (p)	*Prionospio jubata* (p)
		Pectinaria californiensis (p)	*Prionospio jubata* (p)	*Chloeia pinnata* (p)	*Mediomastus* sp (p)	*Euphilomedes carcharodonta* (c)
		Kirkegaardia serratiseta^ (p)	*Spiophanes duplex* (p)	*Pectinaria californiensis* (p)	*Aricidea (Acmira) catherinae* (p)	*Lumbrineris cruzensis* (p)
		Heterophoxus oculatus (c)	*Euphilomedes carcharodonta* (c)	*Rhepoxynius bicuspidatus* (c)	*Euphilomedes carcharodonta* (c)	*Chloeia pinnata* (p)
		Chloeia pinnata (p)	*Heterophoxus oculatus* (c)	*Amphideutopus oculatus* (c)	*Leptochelia dubia* Cmplx (c)	*Scoloplos armiger* Cmplx (p)
		Lumbrineris sp (p)	*Ampelisca brevisimulata* (c)	Phoronida (l)	*Rhepoxynius bicuspidatus* (c)	*Aricidea (Acmira) catherinae* (p)
		Prionospio jubata (p)	*Tellina modesta* (m)	*Ampelisca brevisimulata* (c)	*Chloeia pinnata* (p)	*Sthenelanella uniformis* (p)
		Sabellidae (p)	*Goniada maculata* (p)	*Aricidea (Acmira) catherinae* (p)	*Lumbrineris ligulata* (p)	*Stereobalanus* sp (h)
		Axinopsida serricata (m)	*Rhepoxynius bicuspidatus* (c)	*Euclymeninae* sp A (p)	*Paraprionospio alata* (p)	*Photis californica* (c)
LACSD	Outer-Shelf	*Parvilucina tenuisculpta*^ (m)	*Parvilucina tenuisculpta*^ (m)	*Axinopsida serricata* (m)	*Paradiopatra parva* (p)	*Aphelochaeta-Kirkegaardia* Cmplx^ (p)
		Axinopsida serricata (m)	*Axinopsida serricata* (m)	*Spiophanes fimbriata* (p)	*Paraprionospio alata* (p)	*Paraprionospio alata* (p)
		Acila castrensis (m)	*Acila castrensis* (m)	*Spiophanes kimballi* (p)	*Spiophanes berkeleyorum* (p)	*Spiophanes kimballi* (p)
		Macoma carlottensis^ (m)	*Tellina* sp B (m)	*Paraprionospio alata* (p)	*Mediomastus* sp (p)	*Axinopsida serricata* (m)
		Pectinaria californiensis (p)	*Spiophanes berkeleyorum* (p)	*Aphelochaeta-Kirkegaardia* Cmplx^ (p)	*Aphelochaeta-Kirkegaardia* Cmplx^ (p)	*Nuculana* sp A (m)
		Aphelochaeta-Kirkegaardia Cmplx^ (p)	*Pectinaria californiensis* (p)	*Pectinaria californiensis* (p)	*Tellina* sp B (m)	*Tellina* sp B (m)
		Spiophanes berkeleyorum (p)	*Aphelochaeta-Kirkegaardia* Cmplx^ (p)	Lumbrineridae (p)	*Spiophanes fimbriata* (p)	*Chloeia pinnata* (p)
		Spiophanes duplex (p)	*Lumbrineris sp* (p)	*Tellina* sp B (m)	*Axinopsida serricata* (m)	*Brisaster* sp (e)
		Onuphis sp (p)	*Onuphis sp* (p)	*Heterophoxus affinis* (c)	*Spiophanes duplex* (p)	*Mediomastus* sp (p)
		Tellina sp B (m)	*Macoma carlottensis*^ (m)	*Parvilucina tenuisculpta*^ (m)	*Marphysa disjuncta* (p)	*Polyschides quadrifissatus* (m)
			Maldane sarsi (p)		*Spiophanes kimballi* (p)	

					🟧
OCSan Outer-Shelf	*Pectinaria californiensis (p)*	*Amphiodia* sp (e)	*Pectinaria californiensis* (p)	*Aphelochaeta glandaria* Cmplx^ (p)	🟧
	Amphiodia sp (e)	*Parvilucina tenuisculpta^* (m)	*Spiophanes berkeleyorum* (p)	*Axinopsida serricata* (m)	🟦
	Chloeia pinnata (p)	*Aphelochaeta glandaria* Cmplx^ (p)	Euryalida (e)	*Spiophanes berkeleyorum* (p)	🟩
	Parvilucina tenuisculpta^ (m)	*Kirkegaardia serratiseta^* (p)	*Aphelochaeta glandaria* Cmplx^ (p)		🟧
	Axinopsida serricata (m)	*Spiophanes duplex* (p)	*Spiophanes duplex* (p)	*Petaloclymene pacifica* (p)	🟦
	Lumbrineris sp (p)	*Spiophanes berkeleyorum* (p)	*Parvilucina tenuisculpta^* (m)	*Prionospio jubata* (p)	🟪
	Maldanidae (p)	Lumbrineris sp (p)	*Prionospio jubata* (p)	*Pectinaria californiensis* (p)	🟨
	Glycera nana (p)	*Prionospio jubata* (p)	*Scoletoma tetraura* Cmplx (p)	*Lumbrineris cruzensis* (p)	🟧
	Mediomastus sp (p)	*Prionospio lighti* (p)	*Glycera nana* (p)	*Rhepoxynius bicuspidatus* (c)	🟧
	Praxillella pacifica (p)				
LACSD Upper-Slope	*Parvilucina tenuisculpta^* (m)	*Lirobittium rugatum* (m)	*Lirobittium rugatum* (m)		🟩
	*Macoma carlottensis^* (m)	*Pectinaria californiensis* (p)	*Paraprionospio alata* (p)	*Cyclopecten catalinensis* (m)	🟧
					🟧
	Onuphis sp (p)	*Parvilucina tenuisculpta^* (m)	*Ampelisca unsocalae* (c)	*Yoldia seminuda* (m)	🟨
	Bipalponephtys cornuta (p)	*Axinopsida serricata* (m)	*Onuphis* sp (p)	*Onuphis* sp (p)	🟨
	Paraprionospio alata (p)	*Paraprionospio alata* (p)	*Delectopecten vancouverensis* (m)		🟩
	Harpiniopsis galera (c)	*Bipalponephtys cornuta* (p)	*Axinopsida serricata* (m)	*Mediomastus* sp (p)	🟨
	Amphipoda (c)	*Macoma carlottensis^* (m)	*Bipalponephtys cornuta* (p)		🟩
	Malmgreniella sp (p)	*Aoroides columbiae#* (c)	*Aoroides columbiae#* (c)	*Bipalponephtys cornuta* (p)	🟨
	Goniada brunnea (p)	*Aphelochaeta-Kirkegaardia* Cmplx (p)	*Myriochele gracilis* (p)	*Delectopecten vancouverensis* (m)	🟨
	Pectinaria californiensis (p)				
OCSan Upper-Slope					🟦
		Pectinaria californiensis (p)	*Aphelochaeta monilaris* (p)	*Aphelochaeta monilaris* (p)	🟨
		Paraprionospio alata (p)	*Ampelisca unsocalae* (c)	*Ampelisca unsocalae* (c)_	🟨
		Ampelisca unsocalae (c)	*Paraprionospio alata* (p)	*Myriochele gracilis* (p)	🟦
		Aphelochaeta glandaria Cmplx (p)	*Melinna heterodonta* (m)	*Paraprionospio alata* (p)	🟨
		Melinna heterodonta (m)	*Spiophanes kimballi* (p)	*Spiophanes berkeleyorum* (p)	🟪
		Kirkegaardia serratiseta (p)	*Limifossor fratula* (m)	*Spiophanes kimballi* (p)	🟨
		Prionospio ehlersi (p)	*Eudorella pacifica* (c)	*Melinna heterodonta* (m)	🟨
		Aphelochaeta monilaris (p)	*Caecognathia crenulatifrons* (c)	*Eudorella pacifica* (c)	🟦
		Lumbrineris sp (p)	*Onuphis* sp A (p)	*Caecognathia crenulatifrons* (c)	🟦
					🟨

Table 5 Inventories of the number of taxa from the data set whose likelihood of occurrence increased or decreased through time (A) or whose geographic distribution shifted northward or southward through time (B). Total Richness is the count of all distinct taxa observed at a site or depth zone. Frequent Taxa are those observed ten or more times at a site or depth zone and were considered for classification as increaser/decreaser or northward/southward.

A

Depth Zone	Sample Site	Total Richness	Frequent Taxa	Increaser	Decreaser	Other
Mid-Shelf	LACSD	547	129	51	9	69
	CLAEMD	415	73	18	4	51
	OCSan	602	135	33	13	89
	CSD	496	90	7	1	82
Outer-Shelf	LACSD	389	66	14	16	36
	CLAEMD	441	66	10	7	49
	OCSan	468	107	37	3	67
	CSD	460	115	15	9	91
Upper-Slope	LACSD	259	29	1	6	22
	OCSan	266	22	3	2	17

B

Depth Zone	Total Richness	Frequent Taxa	Northward	Southward	Neither
Mid-Shelf	861	246	37	7	202
Outer-Shelf	773	207	15	29	163
Upper-Slope	365	50	1	3	46