Acidifying Oceans and the Benthos:
Structural Changes in the Macroinvertebrate Community across Time

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ABSTRACT

Ocean acidification poses a serious threat to the marine biota as increasing oceanic uptake of atmospheric CO_2 alters ocean carbonate chemistry. Of particular concern is the impact that decreased carbonate saturation is having on calcareous species. Although controlled studies have elucidated the specific impacts of low pH on individual species, in-situ investigations at the ecosystem level are not as widely performed. In this study, I analyzed benthic macroinvertebrate abundance data for 166 sites along the continental shelf in the Southern California Bight over a twenty-year period. Using depth as a proxy for carbonate saturation state, I looked at taxa changes over time within four depth ranges using multivariate and univariate measures of community structure. Shannon-Weiner biodiversity indices fluctuated or slightly increased over time but did not show a net decrease in any strata. Depth fidelity of molluscs also did not show a significant migration trend. Non-metric multidimensional analysis shows a separation between the species assemblages in the first three surveys and those from the two latest, in all but the shallowest strata. These results indicate that change in taxonomic composition is a more sensitive metric for detecting disturbance in an ecological community than biodiversity or depth fidelity.

KEYWORDS

benthic macroinvertebrates, carbonate chemistry, calcification, CO_2, species composition, biodiversity, depth fidelity, non-metric multidimensional scaling.

INTRODUCTION

As the world's largest carbon sink, oceans play an important role in regulating levels of atmospheric CO_2. It is estimated oceans have absorbed ~48% of total fossil fuel and cement production-related emissions since pre-industrial times (Sabine et al. 2004). Although this absorption has greatly mitigated the pace of anthropogenic climate change, it is rapidly altering the ocean's chemistry. Models now estimate the average pH of the ocean's surface to be 0.1 unit lower than pre-industrial times (Orr et al. 2005), representing a 30% increase in $[H^+]$. This pH change is coupled to a series of reactions that shift the ratio of dissolved inorganic carbon (DIC) species away from carbonate (Figure 1), critical to shell-building and other calcification processes found in molluscs, some echinoderms, and scleractinian corals (Fabry 1990, Orr et al. 2005, Ries et al. 2009). Thus, ocean acidification will have serious implications for the health and functioning of calcareous organisms and consequently to the greater marine biota.
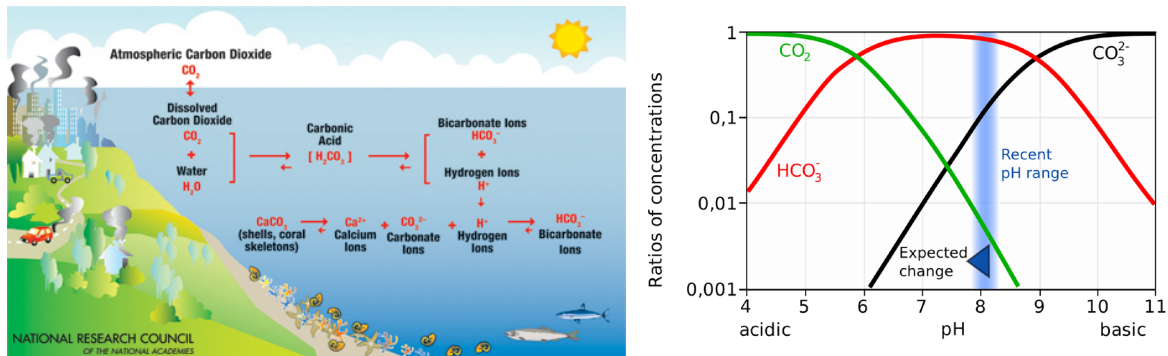

Figure 1. (Left) The series of reactions following uptake of atmospheric CO₂. (NRC [National Research Council] et al. 2010). (Right) Speciation of DIC at various pH levels. (Karbonatsystem_Meerwasser_de.svg 2010)

The impacts of shifting ocean chemistry on the fitness of any particular species will vary along with its physiology. Successful mineralization of shells and skeletons in calcareous organisms relies on the high saturation state of $CaCO_3$ ($\Omega \gg 1$); in undersaturated waters ($\Omega < 1$) shell dissolution has been observed in pteropods (Figure 2), coralline algae, conches and corals (Orr et al. 2005, Iglesias-Rodriguez et al. 2008, Ries et al. 2009). Proper shell formation is critical because calcification processes can have a high metabolic cost; shell deposition for oyster larvae in the first 48 hours after fertilization can consume 90% of their body weight (Waldbusser et al. 2013). Although these findings point to a decrease in calcareous mass, some

species demonstrate growth (Iglesias-Rodriguez et al. 2008), indicating variability in the response of marine calcifiers.

Among non-carbonate related effects of low pH, sperm motility and fertilization success are significantly reduced in the sea urchin *Heliocidaris erythrogramma* (Havenhand et al. 2008), as are the larval production and development of two oyster species (Parker et al. 2009, Barton et al. 2012). Exposure to acidic waters resulted in fewer and smaller D-veligers of the Sydney rock oyster *Saccostrea glomerata* (Parker et al. 2009). Sea stars, a keystone species, eat less and grow more slowly as juveniles when subjected to slightly elevated CO_2 levels (Appelhans et al. 2014). Because many metabolic functions operate within a narrow pH range, it is hypothesized that there will be some energetic cost to maintaining internal pH in increasingly acidic waters (NRC [National Research Council] et al. 2010).
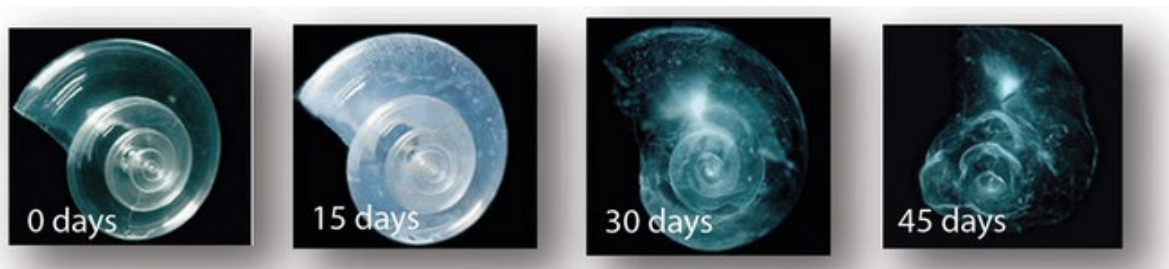

Figure 2. Time sequence dissolution of pteropod shells in decreasing CaCO3 saturation states. **(Orr et al. 2005)**

When considering the variability in individual species response and climatic and biotic variables such as temperature, upwelling, ENSO events, predation and competition, understanding impacts of ocean acidification at the ecosystem level becomes more complex. Clues in the earth's geological past support the hypothesis that marine calcifiers will decline in a high CO_2 world. Mass extinction of 35% - 50% of benthic foraminiferal species reportedly occurred during the Paleocene-Eocene Thermal Maximum (PETM), a period of rapid increase in atmospheric CO_2 and subsequent ocean acidification that occurred ~55 million years ago (Gibbs et al. 2006). The K/T extinction event from 65 million years ago also coincided with high extinction rates of calcifying organisms, although it is uncertain to what extent changes to oceanic pH were involved (NRC [National Research Council] et al. 2010). By incorporating eight years of recent coastal pH measurements from the Pacific Northwest into Markov models, significant community restructuring was found to correlate with declining pH, with non-

calcareous species more successfully displacing calcareous ones (Wootton et al. 2008). Predictions made by these models are supported by observations made of multi-species assemblages exposed to varying pH treatments. After 30 days of controlled exposure, standardized intertidal community units in low pH conditions reported lower diversity than those under ambient conditions, as well as a structural shift from calcareous to non-calcareous species (Christen et al. 2013). In benthic communities along volcanic vents near Ischia, Italy, where similar variations in pH (8.2 to 7.4) occur naturally, the relative abundance and health of calcareous organisms declined significantly with pH, while non-calcareous algal cover increased and primary production of seagrass improved (Hall-Spencer et al. 2008). Taxonomic evenness, biodiversity, and biomass were all reduced in the lowest pH zone (Kroeker et al. 2011). However, there remains a paucity of broad-scale investigations performed in-situ.

In this study I examined both temporal and spatial trends to better understand how ocean acidification may be affecting benthic macroinvertebrate communities in the Southern California Bight. The benthos contains 98% of all marine species (Widdicombe and Spicer 2008) and are valuable indicators of environmental stressors due to their limited roaming ability and wide diversity of physical and physiological attributes. Using depth as a proxy for carbonate saturation state, I examined shifts in taxonomic structure over a twenty-year period within an OA-sensitive depth range. I hypothesized that (1) biodiversity will show a decline over time, (2) peak abundance of molluscs will migrate towards shallower waters, and (3) that benthic macroinvertebrate assemblages will shift away from shelled species and towards non-calcifying organisms.

METHODS

Study system

To determine how ocean acidification is affecting marine benthic communities, I focused on macroinvertebrate populations inhabiting depths of 100 meters to 200 meters along the continental shelf and slope in the Southern California Bight (SCB) (Figure 3). The waters contained within the bend in the southern California coastline are bound to the north by Point

Conception (34° N) near Santa Barbara, to the south by Cabo Colnett (31° N) in Baja California, Mexico, and to the west by the Santa Rosa-Cortes Ridge (120° W).
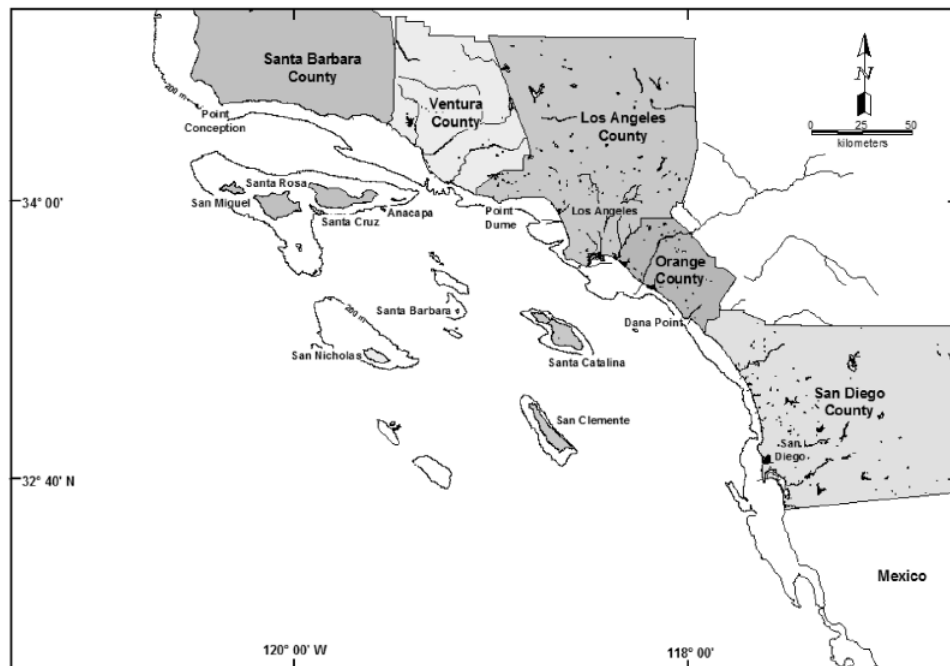

Figure 3. Southern California Bight. **(Bergen et al. 1998)**

The bight experiences weak seasonal upwelling during the spring and early summer months (Jackson 1986). Normal ocean circulation along the coastline is dominated by the California Undercurrent and Southern California Counter-current which carries warm, equatorial water that is low in oxygen and high in salinity (Browne 1994). These currents flow northwest before joining the California Current at Point Conception, which carries cold sub-Arctic water that is highly oxygenated and low in salinity southward along the Santa Rosa-Cortes Ridge. This counter-clockwise flow circumvents the study area.

Data source

Following an initial pilot survey in 1994, the Southern California Bight Regional Monitoring Program has conducted regional surveys of the soft-sediment benthic ecosystem every five years from 1998 - 2013 (Southern California Bight 2013 Regional Marine Monitoring

Survey Contaminant Impact Assessment Committee 2013). I obtained datasets from the Southern California Coastal Water Research Project (SCCWRP, D. Gillett, pers. comm).

For each survey-year, the program sampled 300-400 locations. Stations were selected using a random tessellation stratified design across 10-13 geographic zones of interest (e.g., estuaries, ports, shallow continental shelf, continental slope) to minimize clustering of sample points. At each station, samples were collected for macrobenthos, sediment chemistry, and sediment composition. At a subset of stations, sediment toxicity was measured. Latitude, longitude, and depth was recorded for each of the 1,842 stations across the sample (Table 1).

Sediment samples were collected from July to September using a 0.1 m^2 Van-Veen grab. Macrobenthic fauna were sieved on a 1-mm screen, relaxed with $NaSO_4$ and fixed with a 20% formalin solution (Southern California Bight 2013 Regional Marine Monitoring Survey Benthic Committee 2013). All infauna were sorted, identified, and enumerated following standard QA/QC protocols (Southern California Bight 2013 Regional Marine Monitoring Survey Benthic Committee 2013). All taxa were identified to the lowest possible taxonomic level, typically species, following Southern California Association of Marine Taxonomists (SCAMIT) protocols (Southern California Association of Marine Invertebrate Taxonomists n.d.) 76.8% of individuals in the final dataset were identified to the species level.

Table 1. Number of sampled stations by survey-year followed by number of reference stations selected for study.

Year		1994	1998	2003	2008	2013	Total
All sampled		251	415	397	383	396	**1842**
Reference		49	23	38	24	32	**166**
DS1	100-125m	16	13	13	2	3	47
DS2	126-150m	9	3	10	9	8	39
DS3	151-175m	11	3	5	5	12	36
DS4	176-200m	13	4	10	8	9	44

Data preparation

I limited the analysis to stations between 100 meters and 200 meters in depth to avoid effects of urban and freshwater runoff on pH near the coast and because these depths are where the most rapid pH changes are expected to occur (Caldeira and Wickett 2003). I also excluded stations designated as "Channel Islands" because this zone is an eco-tone that is subject to atypical fluctuations between cold and warm currents (Jackson 1986). To avoid effects from sediment toxicity, I excluded sites with metal and organic pollutant levels in exceedance of published Effects Range Median values (Long et al. 1995). No sediment chemistry measurements from 1994 were provided, so all sites from this year were included. After filtering for depth, location, and sediment chemistry, the total sample size was 166 stations (Table 1, second row). Station measurements were subset by year and into four depth strata at 25-meter intervals, hereafter termed DS1, DS2, DS3, and DS4 (Table 1).

Statistical Analysis

Biodiversity & species richness

To calculate taxa richness, or the number of unique taxa found at each station, I followed the protocol provided in the 2013 Macrobenthic Sample Analysis Laboratory Manual (Southern California Bight 2013 Regional Marine Monitoring Survey Benthic Committee 2013). I counted all unique taxa identified to the species level, but for taxa identified to a higher taxonomic level (e.g., genus) I counted as unique if it could be determined as distinct from any other recorded taxa at the same station. For example, individuals identified as "Onuphidae sp." would not advance the species count for that station if other individuals in the Onuphidae family were identified to the genus or species level. Then I calculated Shannon-Weiner diversity indices using natural log for each of the 166 reference stations. To determine the change in Shannon-Weiner diversity and taxa richness at various depths over time, I generated a linear regression model for each 25-meter stratum and tracked median and maximum scores in those strata over time. This and all subsequent analyses were completed in R (R Development Core Team 2017), using the package Vegan (Oksanen et al. 2017) in RStudio (RStudio Team 2016).

Depth fidelity of molluscs

I categorized species abundance measurements of molluscs and generated linear regression models for each depth strata to determine trends in raw abundance over time. Additionally, I calculated median and maximum mollusc abundance for each depth strata at eacg survey-year and generated line graphs to view fluctuations over time.

Species assemblage

I generated ordination plots using non-metric multidimensional scaling for each depth strata to explore if species assemblages changed from one survey-year to another and to determine the environmental factors correlated most strongly with the ordination.

First I generated matrices for each depth strata that included species assemblage data for each station sampled between 1994 and 2013. Then I ran the metaMDS function in k=2 dimensions and recorded stress values if convergent solutions were found. If no convergent solutions were found on the first attempt, the number of runs were increased until a successful solution was reached. I used the envfit function with the species assemblage data to identify which species were correlated most strongly with the ordination axes and spatial arrangement of the sites.

To explore the influence of environmental factors, I generated an environmental factor table for each depth strata that included depth, latitude, and percent fines for each station. I used the envfit function to determine if any variables were correlated with the ordination derived from the species assemblages. I generated ordination plots for each of the four depth strata with axes for species and environmental factors with $\alpha <= 0.05$.

RESULTS

Biodiversity & species richness

Changes in biodiversity

Shannon-Weiner diversity scores for samples obtained in DS1 and DS2 show a statistically significant increase over time, with p = 0.004 and p = 0.028 respectively (Figure 4). In DS1, the coefficient of regression is 0.034 and R^2 = 0.17. In DS2, coefficient = 0.027 and R^2 = 0.12. Linear regression models for DS3 and DS4 did not produce statistically significant results.
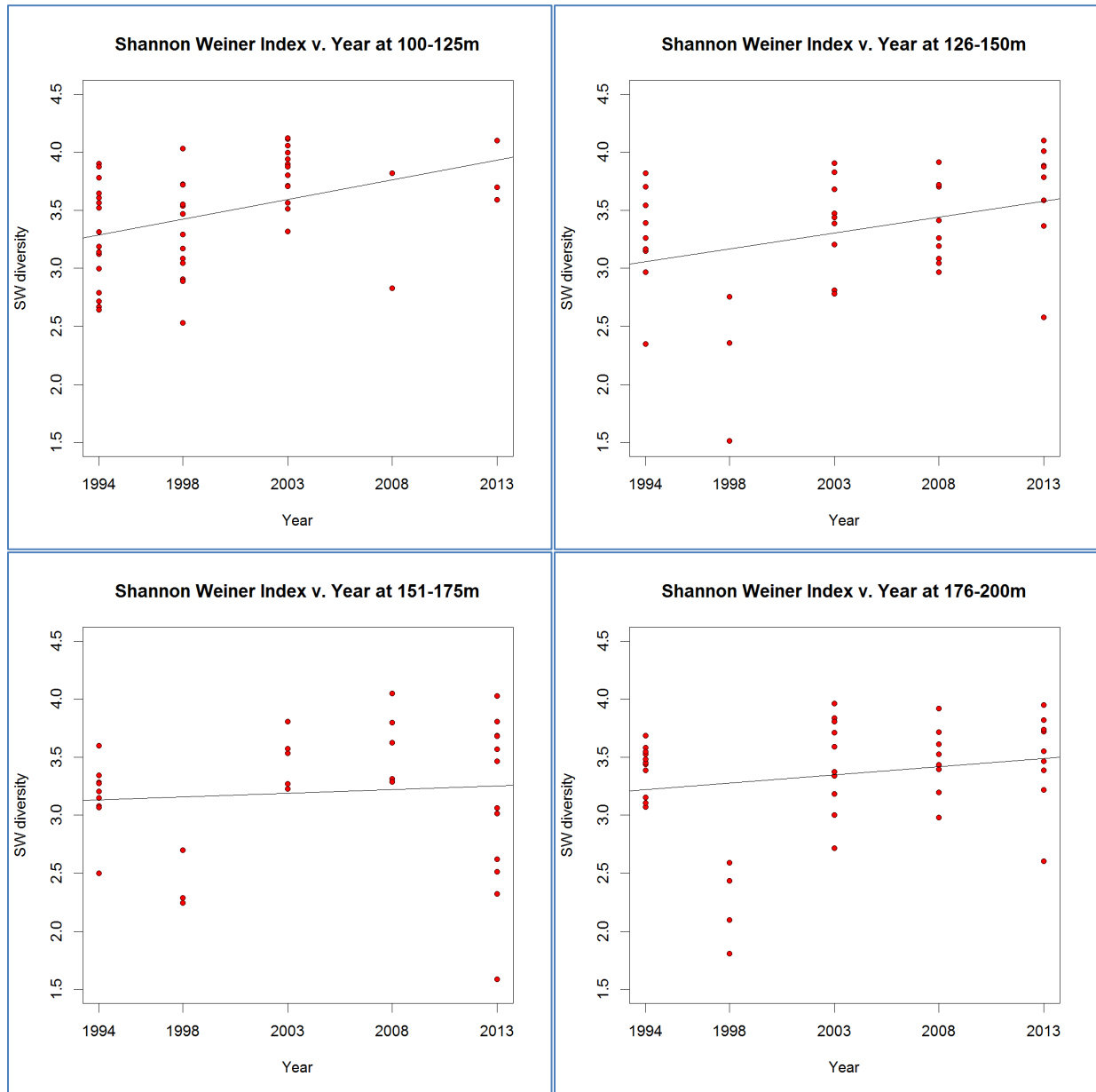

Figure 4. Shannon-Weiner diversity plotted over time. Each plot highlights changes in one depth range. (Upper right) 100-125 meters (coefficient= 0.034, p = 0.004, R^2 = 0.17). (Upper left) 126-150 meters (coefficient = 0.27, p = 0.03, R^2 = 0.12). (Bottom right) 151-175 meters (coefficient = 0.006, p = 0.59, R^2 = 0.009). (Bottom left) 176-200 meters (coefficient = 0.014, p = 0.16, R^2 = 0.05).

Median biodiversity scores for each depth range remain between 3.2 and 3.9 through all survey-years, with the exception of three strata below 125 meters in 1998; those median scores fall between 2.2 and 2.4 (Figure 5, left). Maximum biodiversity scores for each depth category range between 3.6 and 4.2 through all survey-years, with the exception of the same three strata in 1998; those fall between 2.6 and 2.75 (Figure 5, right).
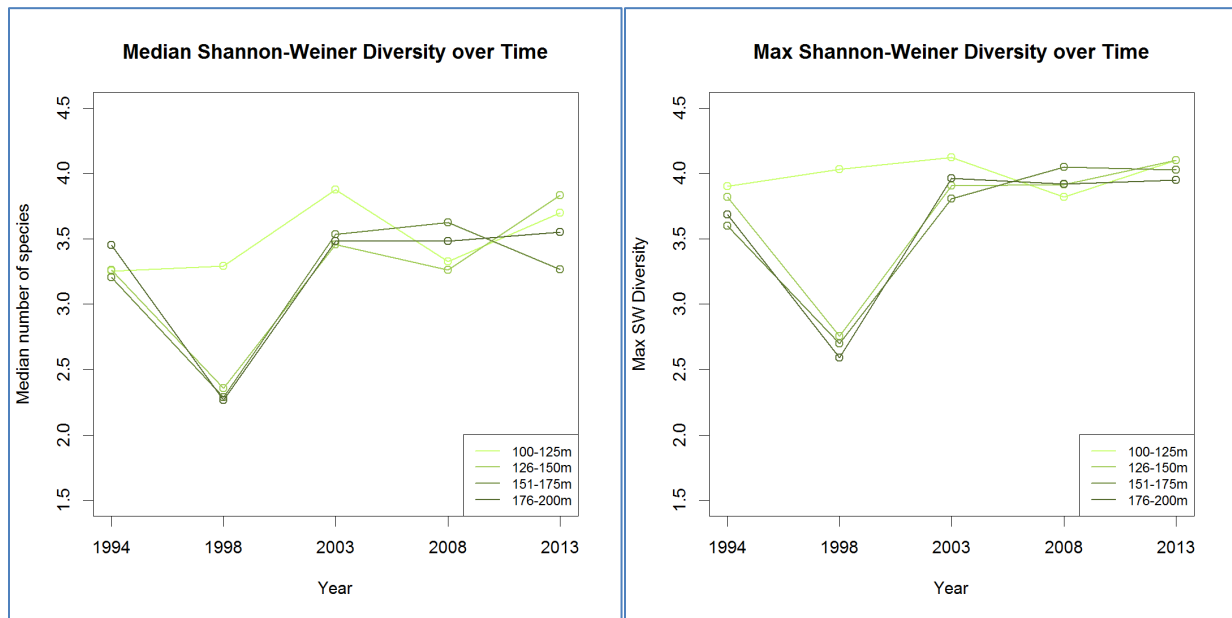
Figure 5. (Left) Median Shannon-Weiner scores over time. Each line represents a 25m-depth range (Right) Maximum Shannon-Weiner scores over time. The lowest median and maximum scores occur in 1998 in depth ranges below 125m.

Changes in species richness

None of the linear regression models from any depth range reveals a statistically significant trend in species richness over time (Figure 6). Median species richness for all strata in all survey-years ranges between 47.5 and 96 species with the exception of DS2, DS3, and DS4 (20, 23, and 27.5, respectively) in 1998 (Figure 7, left). Maximum species richness in each strata ranges from 71 to 143 species in 1994 and then drops to 30-40 species in 1998 for DS2, DS3, and DS4 (Figure 7, right). For all strata, maximum richness scores reach between 87 and 129 species in 2013.
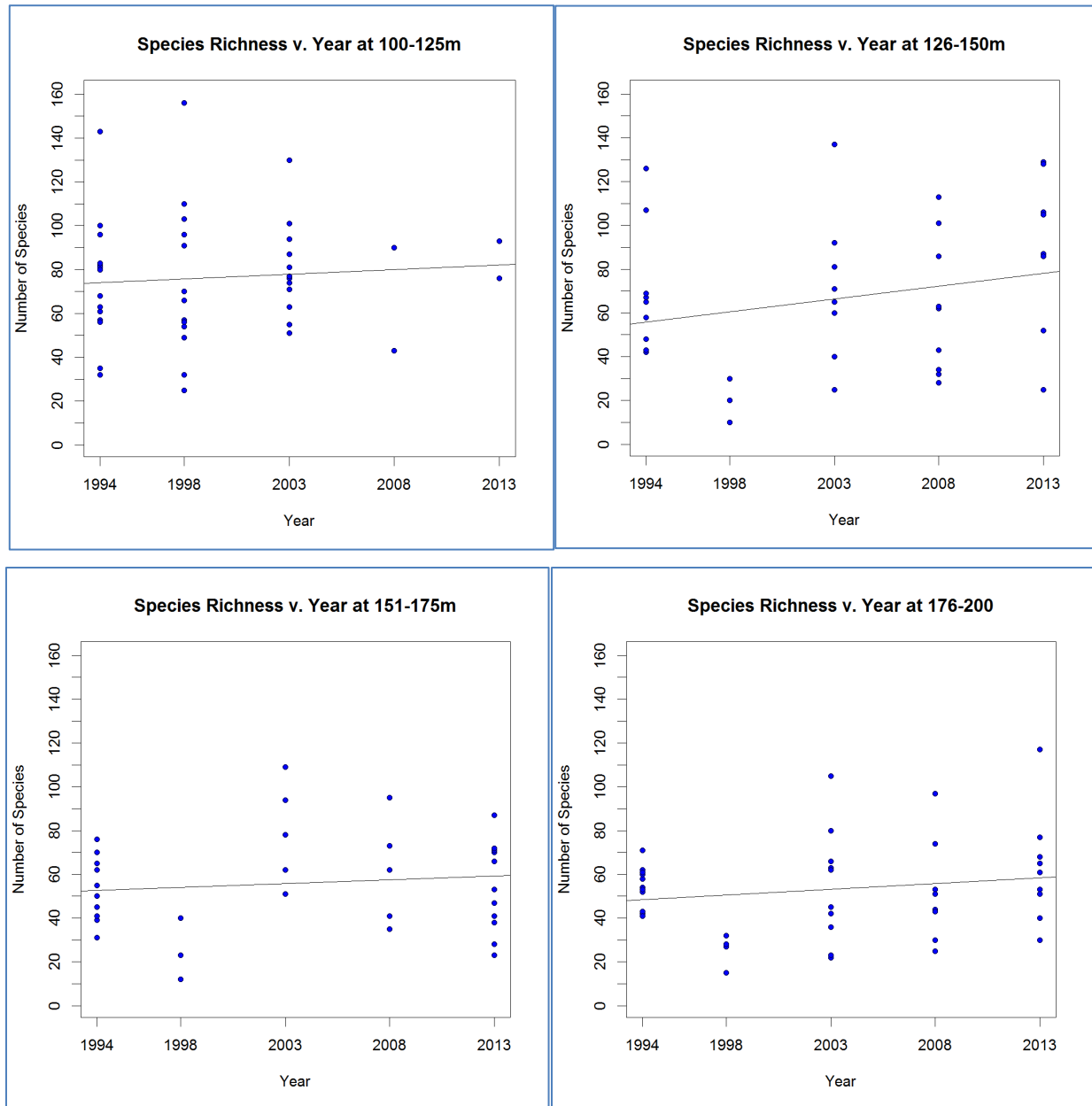
Figure 6. Species richness plotted over time. Each plot highlights changes in one depth range. (Upper right) 100-125 meters (coefficient of regression line = 0.42, p = 0.57, R^2 = 0.007). (Upper left) 126-150 meters (coefficient = 1.17, p = 0.15, R^2 = 0.006). (Bottom right) 151-175 meters (coeffficient = 0.34, p = 0.47, R^2 = 0.016). (Bottom left) 176-200 meters (coefficient = 0.52, p = 0.26, R^2 = 0.030).
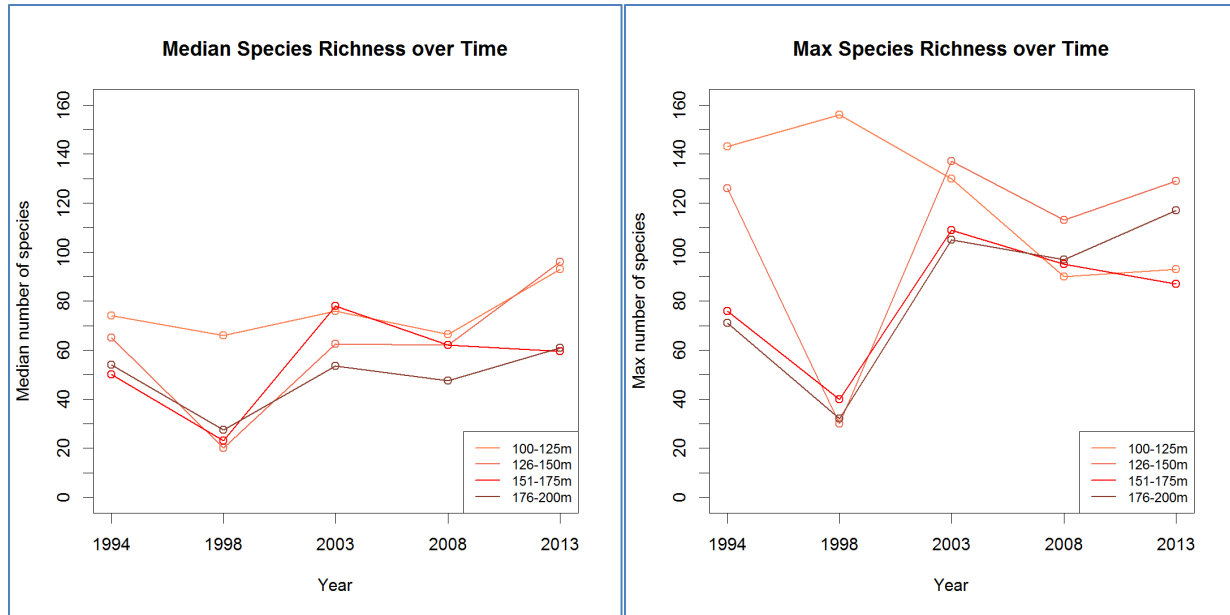
Figure 7 (Left) Median species richness over time for each depth range. (Right) Maximum species richness over time for each depth range.

Depth fidelity of molluscs

Linear regression models from DS1, DS2, and DS3 do not reveal a significant trend in mollusc abundance over time (Figure 8). In DS4, there is a statistically significant increase in abundance over time (p = 9.9e-6). The coefficient of regression is 1.99 and R^2 = 0.375. Median abundance values are lowest in DS2, DS3, and DS4 in 1998 (n=15, n=11, and n=7, respectively) and highest in DS2, DS3, and DS4 in 2013 (n=55, n=36, and n=52, respectively) (Figure 9). Maximum abundance values show the greatest range in 1994 (n=57 to n=390), which includes the greatest reported abundance values (n=390) in both DS1 and DS2 (Figure 9). The range of maximum abundance values are narrowest in 2013 (n=55 to n=100)
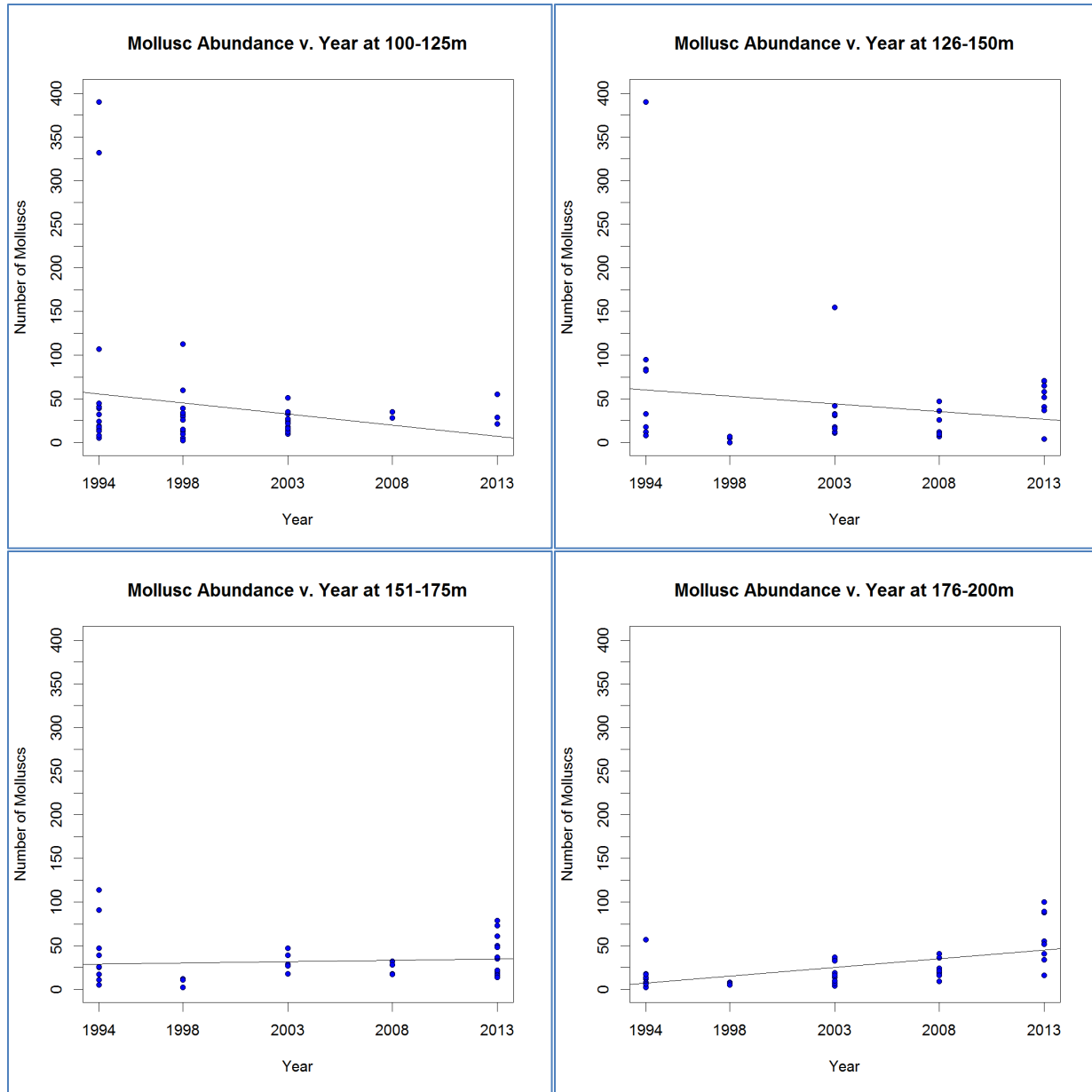
Figure 8. Mollusc abundance over time. Each plot highlights changes in one depth range. (Upper right) 100-125 meters (coefficient of regression line = -2.50, p = 0.19, R^2 = 0.04). (Upper left) 126-150 meters (coefficient = -1.75, p = 0.26, R^2 = 0.034). (Bottom right) 151-175 meters (coeffficient = 0.30, p = 0.57, R^2 = 0.009). (Bottom left) 176-200 meters (coefficient = 1.99, p = 9.9 e -6, R^2 = 0.375).
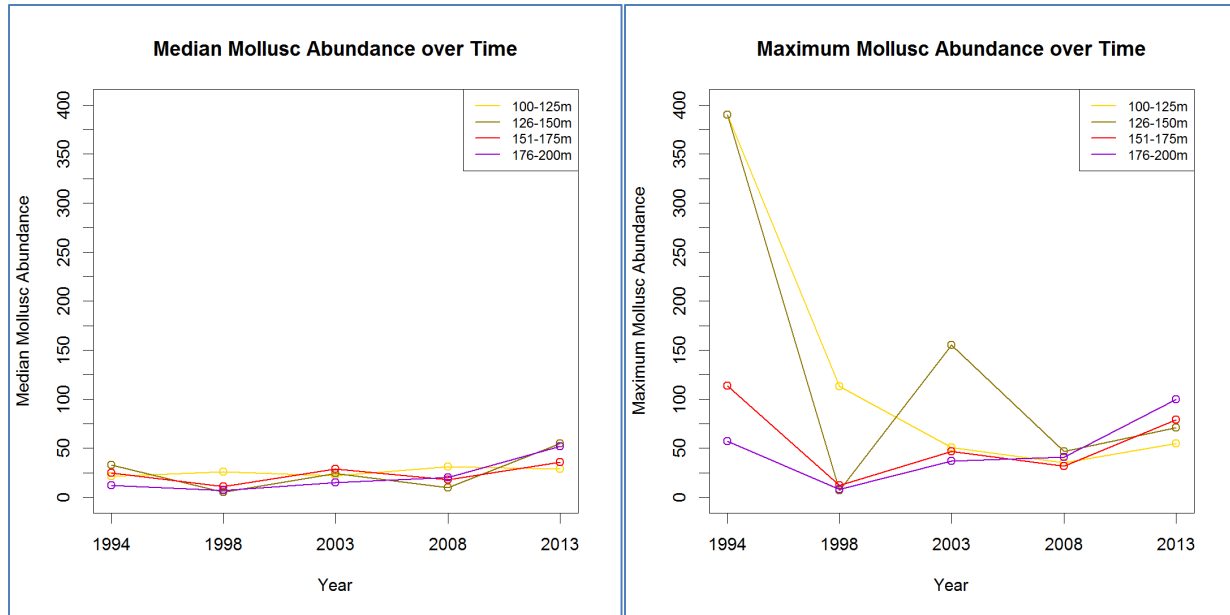
Figure 9. (Left) Median mollusc abundance over time for each depth range. (Right) Maximum mollusc abundance over time for each depth range.

Non-metric multi-dimensional spatial analysis of species assemblage

Spatial arrangement of sites based on species assemblage in DS1 (Figure 9) do not indicate any distinction between survey-years, however sites sampled in 2008 and 2013 are negatively correlated with the presence of *Brissopsis pacifica* (r=0.367, p=0.041).

In the remaining three depth strata, species assemblages in sites from 1994, 1998, and 2003 sites show a clear distinction those sampled in 2008 and 2013 (Figure 10 - Figure 12).

In DS2, sites sampled in 2008 and 2013 appear on the positive side of NMDS1 while all other sites appear on the negative side of NMDS1 (Figure 10, right). Sites in 2008 and 2013 are most negatively correlated with the presence of *Paraprionospio pinnata* (r=0.426, p=0.027) and *Pinnixa occidentalis* (r=0.382, p=0.047) and most positively correlated with the presence of *Monticellina siblina* (r=0.417, p=0.004), *Ampelisca brevisimulata* (r=0.405, p=0.046), *Aphelochaeta* sp. (r=0.492, p=0.006), *Chaetozone* sp. (r=0.397, p=0.34), *Westwoodilla tone* (r=0.433, p=0.019), *Mooreonuphis segmentispadix* (r=0.470, p=0.007), *Zygeupolia rubens* (r=0.401, p=0.032), and *Synidotea magnifica* (r=0.412, p=0.027).

In DS3, most of the sites sampled in 2008 and 2013 appear on the positive side of NMDS1 while all other sites appear on the negative side of NMDS1 (Figure 11, right). Sites in

2008 and 2013 are most negatively correlated with the presence of Maldanidae (r=0.445, p=0.021), *Monticellina* sp. (r=0.458, p=0.023), *Eranno lagunae* (r=0.458, p=0.024), and Polynoinae (r=0.449, p=0.029) and most positively correlated with the presence of *Paraprionospio alata* (r= 0.424, p=0.038), *Sternaspis affinis* (r=0.471, p=0.020), and *Polyschides quadrifissatus* (r=0.489, p=0.013).

     In DS4, sites sampled in 2008 and 2013 appear on the positive side of NMDS1 and on the negative side of NMDS2, while most other sites appear on the negative side of NMDS1 and on the positive side of NMDS2 (Figure 12, right). Sites in 2008 and 2013 are most negatively correlated with the presence of *Spiophanes kimballi* (r=0.499, p=0.004), *Paraprionospio pinnata* (r=0.502, p=0.004), and Chaetodermatidae (r=0.483, p=0.005), and most positively correlated with the presence of *Paraprionospio alata* (r=0.684, p=0.001), *Praxilella pacifica* (r=0.461, p=0.005), *Malmgreniella sanpedroensis* (r=0.491, p=0.003), *Scoletoma tetraura Cmplx*(r=0.666, p=0.001), *Pista wui* (r=0.428, p=0.013), *Compressidens stearnsii* (r=0.573 , p=0.001), and *Rhabdus rectius* (r=0.450, p=0.012).
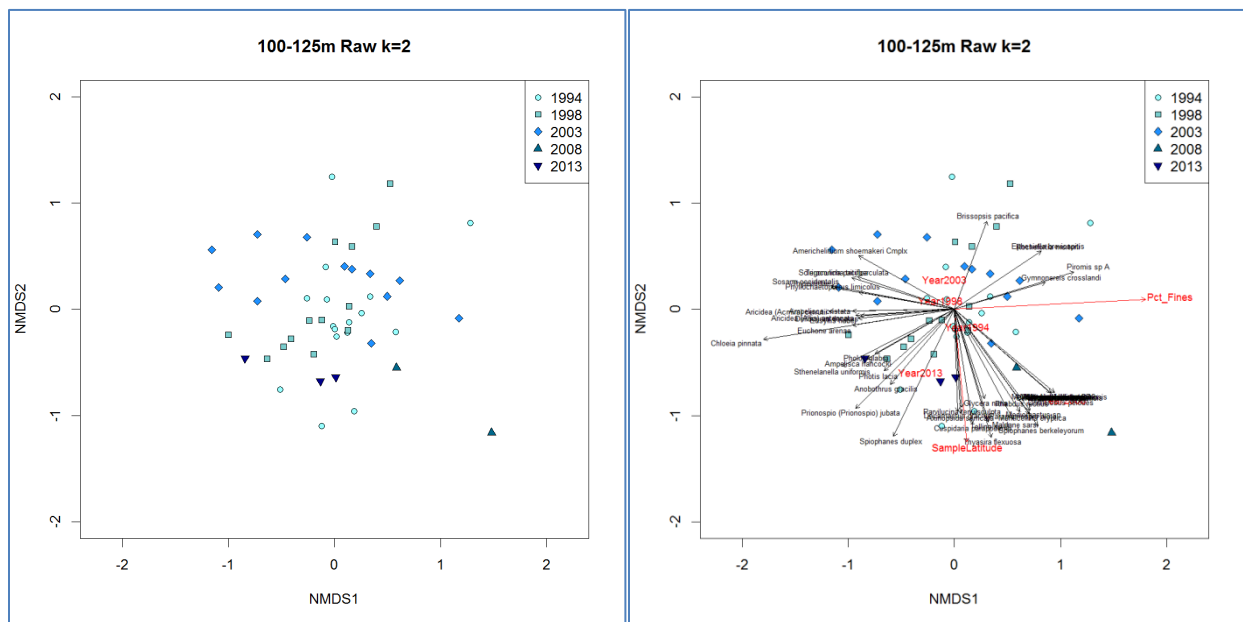

Figure 10. Ordination plots for all sites sampled in the 100 – 125 meter depth range between 1994 and 2013. Stress value = 0.226. Right plot shows all environmental factor and species correlations with p < 0.05.
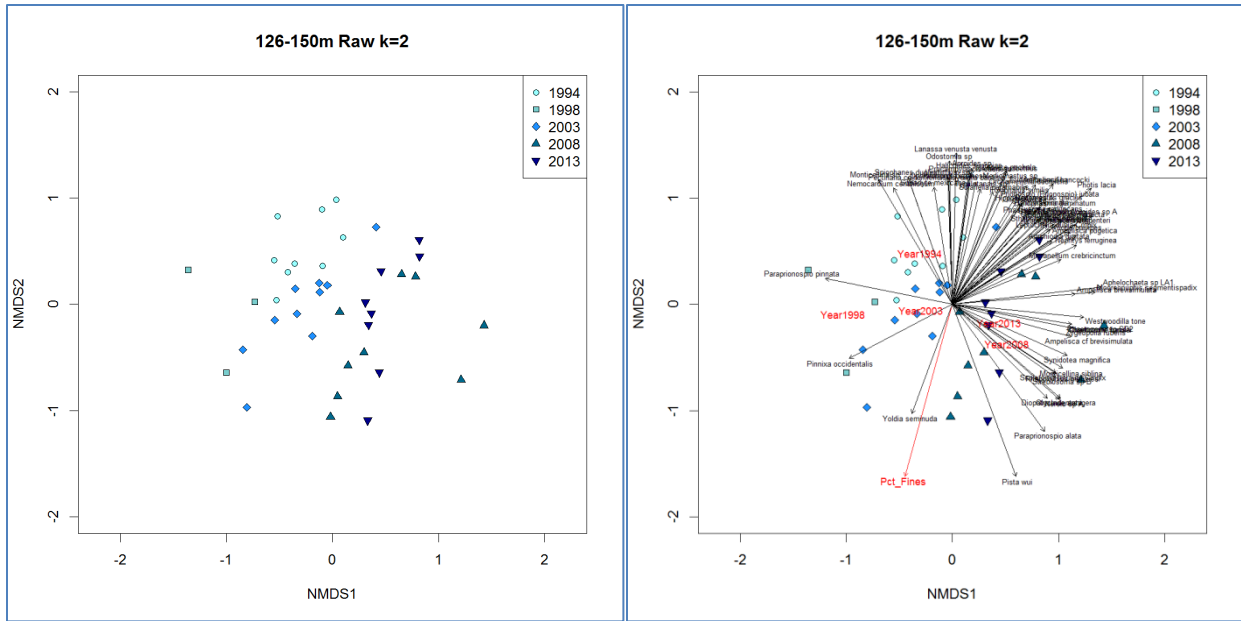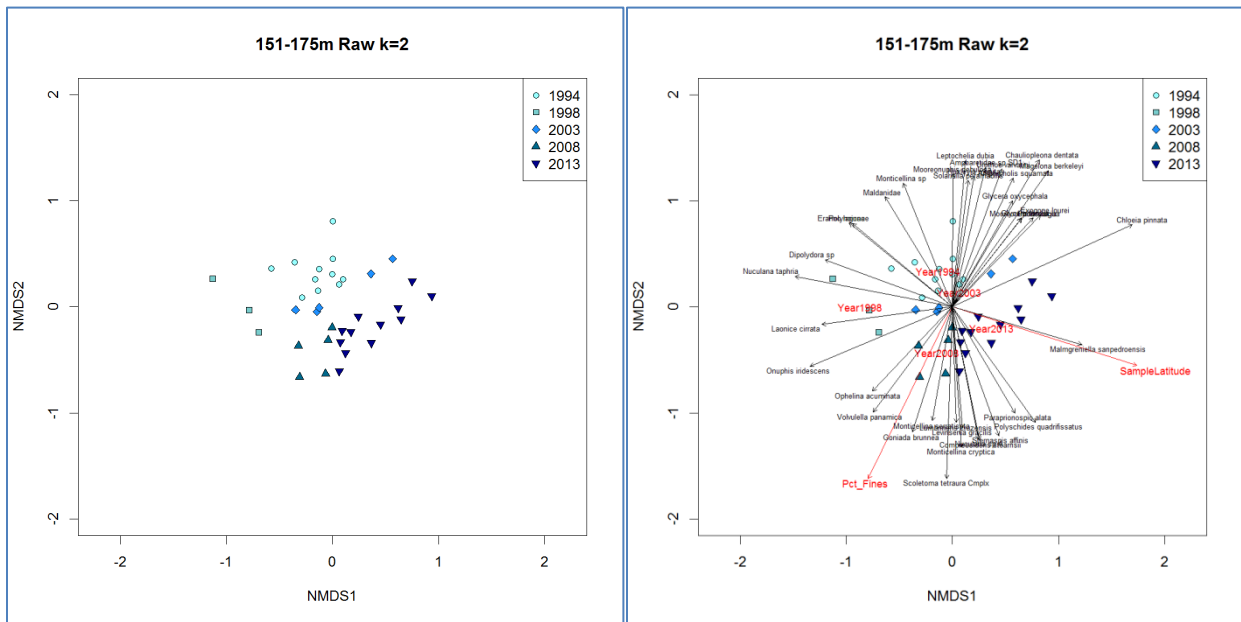
Figure 11. Ordination plots for all sites sampled in the 126-150 meter depth range between 1994 and 2013. Stress value = 0.221. Right plot shows all environmental factor and species correlations with $p < 0.05$.
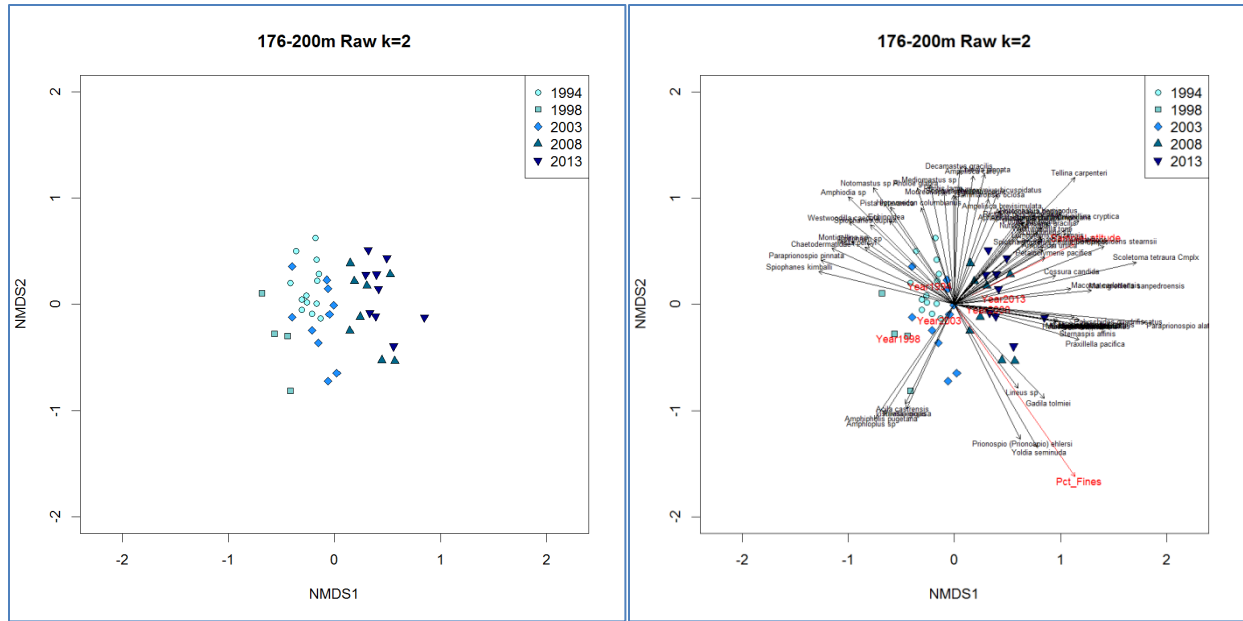

Figure 12. Ordination plots for all sites sampled in the 151-175 meter depth range between 1994 and 2013. Stress value = 0.229. Right plot shows all environmental factor and species correlations with $p < 0.05$.

Figure 13. Ordination plots for all sites sampled in the 176-200 meter depth range between 1994 and 2013. Stress value = 0.222. Right plot shows all environmental factor and species correlations with p < 0.05.

DISCUSSION

Data did not support the hypotheses that increasing ocean acidification has negatively impacted biodiversity and taxa richness within the observed depth ranges, nor that peak mollusc abundance has migrated towards shallower waters over time. Nevertheless, results from multivariate analysis suggest a shift in species assemblage occurring at some point in time between 2003 and 2008, in three of the fourth depth strata.

The absence of a significant downward trend in biodiversity and taxa richness runs contrary to observations of multi-species assemblages exposed to increasingly acidic waters (Hall-Spencer et al. 2008, Kroeker et al. 2011, Christen et al. 2013). It is important to note, however, that the range of pH in those studies was much larger and extended much lower than the range of pH fluctuations experienced in the SCB (Hofmann et al. 2011). This indicates that biodiversity and depth fidelity are fairly crude metrics of ecological disturbance, and their use for measuring impacts of ocean acidification are more suited to greater magnitudes of pH change, although sampling artefacts should also be considered. Biodiversity, richness, and mollusc abundance values decrease sharply in DS2, DS3, and DS4 in 1998 and then rebound the following sample-year (Figures 5, 7, 9). Upon deeper inspection, the most likely cause of this

anomaly is geography: the samples with the lowest biodiversity and taxa richness were obtained in the southeastern boundary of the study area, near Cabo Colnett. In no other years were samples obtained below the California-Mexico border (Appendix A).

It is more likely that the nature of changes occurring presently is related to species turnover rather than the number of species or individuals. Despite the absence of expected trends in univariate analyses, the results of ordination show a clear delineation between the taxonomic structure of communities in 1994 through 2003 and those in 2008 through 2013, in all strata but DS1. Since carbonate saturation decreases with depth due to increasing pressure (Mucci 1983), this finding supports the idea that deeper communities, being closer to the aragonite and calcite compensation depths, will experience acidification earlier and at greater magnitudes before communities closer to the surface (Hofmann et al. 2011).

Polychaetes dominated the list of taxa which turned over between earlier and later survey-years. This is a roughly proportionate to the representation of polychaete species identified in the surveys. (Approximately 41–42% of species identified in the final taxa list were polychaetes, while 64% of "transitional" taxa were polychaetes.) The emergence of mollusc species in communities of later survey-years was unexpected, however the numbers (n=3 species with declining correlation, 1 species with increased correlation) are too low to be very meaningful.

Limitations

Although this dataset spans twenty years, the five-year interval between sampling efforts may have produced too few points to withstand the variance introduced by a single anomalous year in 1998. Having data from more survey-years, whether by more frequent sampling or with continued monitoring, would help reduce uncertainty concerning trends amidst noisy data. This is especially important given that this region is influenced by seasonal upwelling and El Nino Southern Oscillation events that contribute to greater fluctuations in pH than what is observed in the open ocean (Hofmann et al. 2011)

Compounding the issue of low temporal resolution was uneven sampling distribution and coverage across the depth spectrum from year to year. Some years there were as few as 2 stations within a critical depth range, some there were as many as 16. The geographic distribution of

stations from 1998 was notably distinct from other years (Appendix A-2); there were very few beyond 125 meters, none beyond 200 meters and almost all stations between the two depths were clustered off the coast of Mexico. In all other years, stations were distributed similarly along the continental shelf and slope from Santa Barbara to San Diego (Appendix A-1, 3-5). Inconsistent sampling may have accounted for the dramatic fluctuations in abundance counts and biodiversity metrics in 1998. A more even distribution across the depth spectrum and perhaps incorporating a higher percentage of station revisits could strengthen this dataset considerably.

Broader implications

Although this study did not reveal a signature of change in marine benthic macroinvertebrates in response to ocean acidification via sampling depth, there still exists a great need to explore community response to ocean acidification. Each ecosystem is unique with regards to the combination of species and local environmental factors which shape it. From this natural variability, we can learn about which characteristics lend resiliency to communities and apply this knowledge to protect fragile ecosystems.

However with the current trajectory of atmospheric CO_2 levels and oceanic uptake, we will soon arrive at a catastrophic tipping point for ocean chemistry with unknowable consequences. An equal or greater effort must be addressed to limiting carbon emissions and restoring equilibrium to the carbon cycle.

fellow students for much-needed moral support along the way. I wish everyone the best of luck in their science careers as we march forward.

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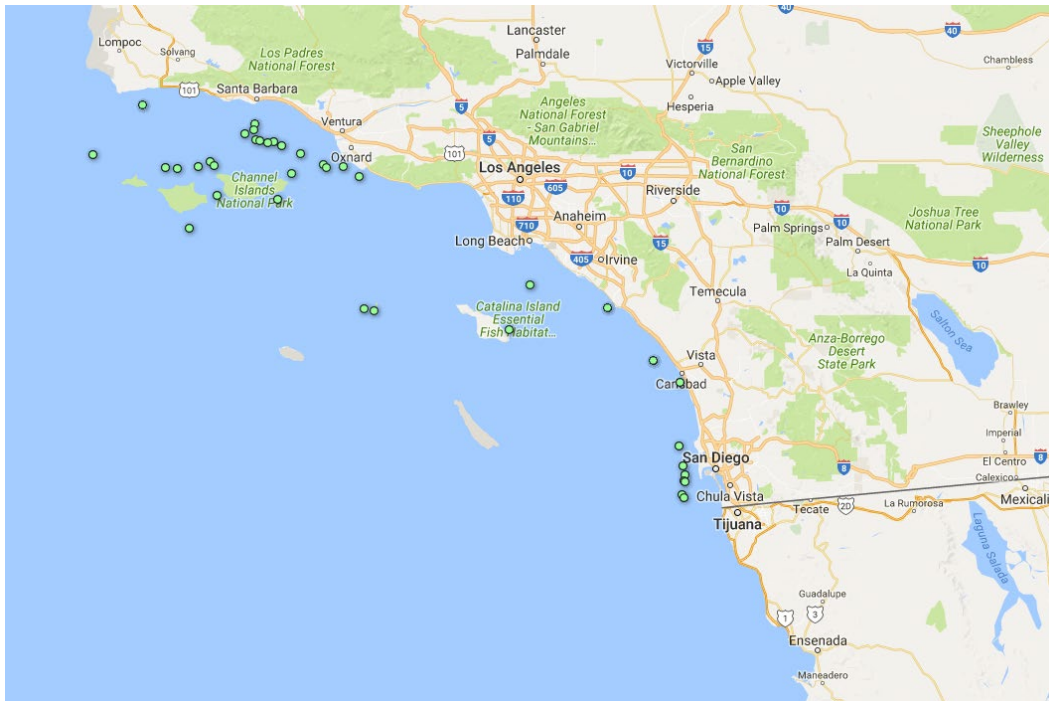
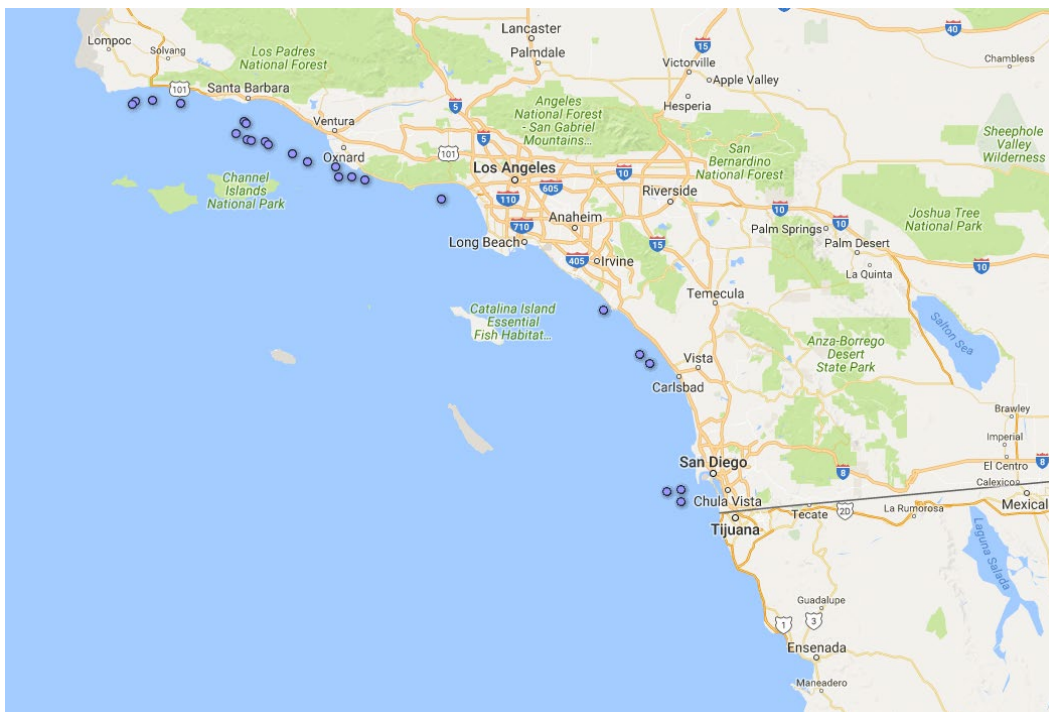**APPENDIX A: Geographical Distribution of Sampling Stations by Year**
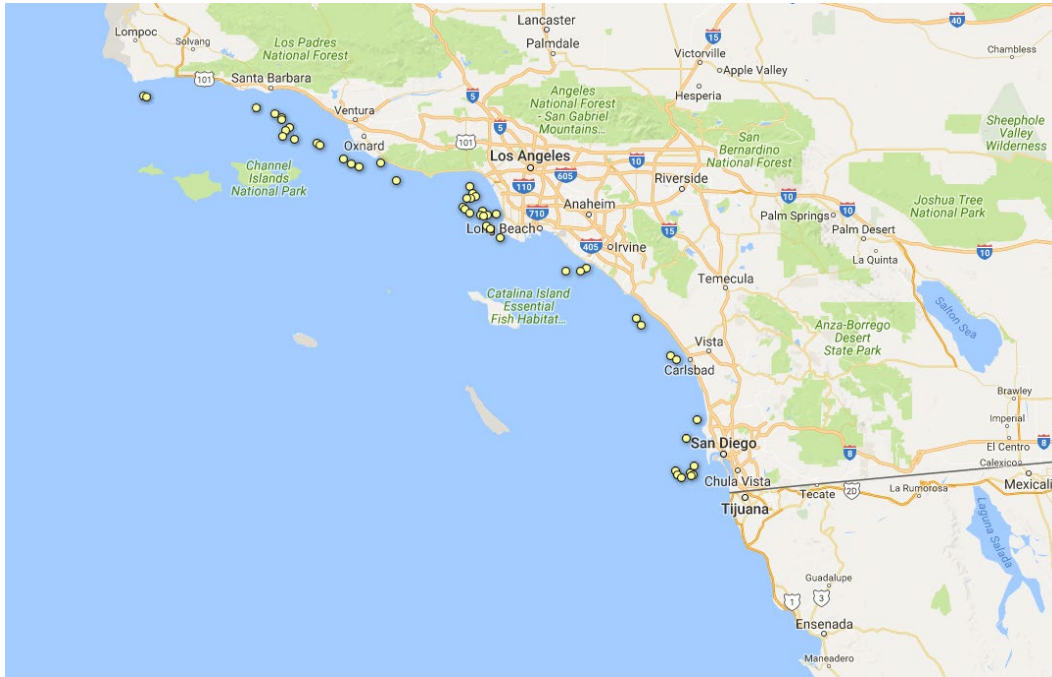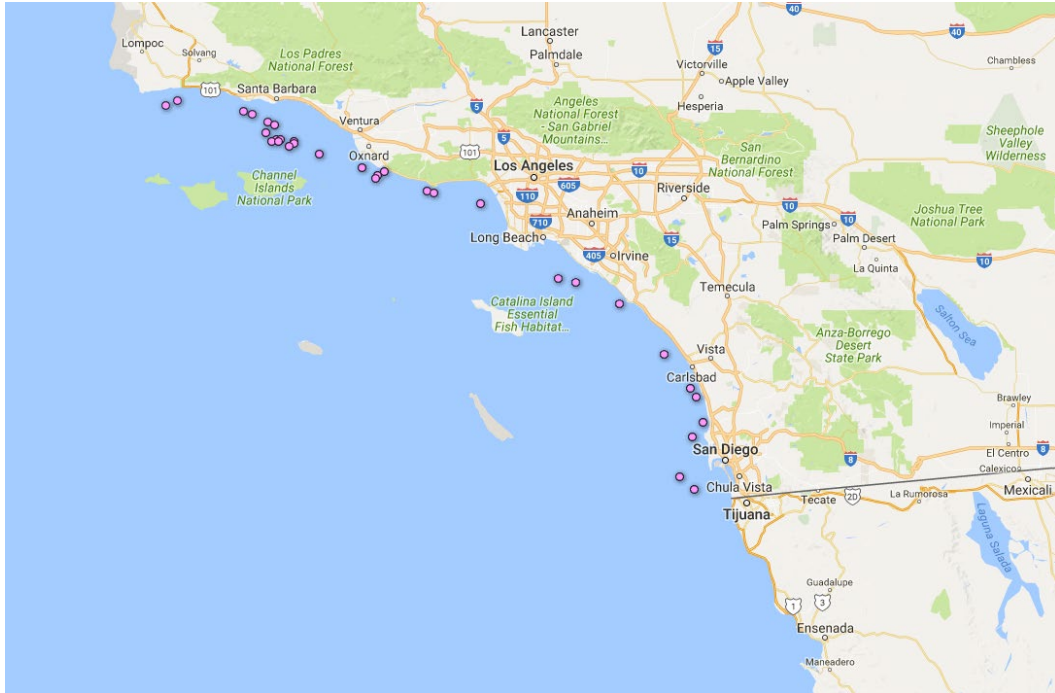

Appendix 1. 1994 Sampling Stations.
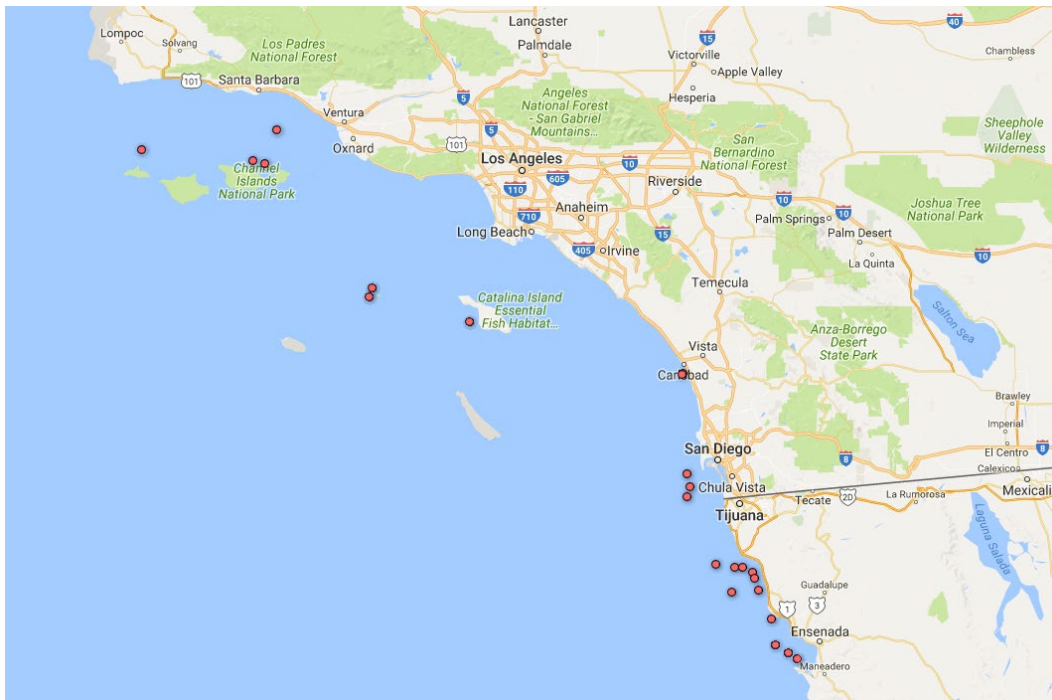
Appendix 2. 1998 Sampling Stations.

Appendix 3. 2003 Sampling Stations.

Appendix 4. 2008 Sampling Stations.

Appendix 5. 2013 Sampling Stations.