

Phytoplankton Community Response to Changing Environmental Conditions Across Two
Central California Sites

A Senior Project

presented to

the Faculty of the Biology and Physics Departments
California Polytechnic State University – San Luis Obispo

In Partial Fulfillment

of the Requirements for the Degree
Bachelor of Science in Marine Sciences

By

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June 2021

Approval Page

Title: Phytoplankton Community Response to Changing Environmental Conditions Across Two Central California Sites

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Date Submitted: 6/11/2021

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Abstract

Understanding the role that changing environmental conditions play in altering phytoplankton abundance and community composition, and in turn ecosystem structure and function, will be increasingly important for the sustainable use and management of ocean resources in a changing climate. Characterizing change in nearshore ecosystems requires long-term studies with a broad spatial extent, with most studies sacrificing spatial extent for temporal duration. However, phytoplankton and ecosystem response can vary substantially over small spatial scales due to local oceanographic forcing and anthropogenic influence, making the application of long-term data from one site to another in the same geographic vicinity potentially challenging. In this study, we compare weekly phytoplankton abundance and community composition samples between two sites on the Central California Coast. One site, located in the San Luis Obispo (SLO) Bay upwelling shadow, is a long-term harmful algal blooms (HABs) sampling site with more than a decade of data with well characterized seasonal and interannual variability. The other site (~35 km away) is located at the mouth of Morro Bay, a seasonally low-inflow estuary with multiple aquaculture farms and long-term data from higher trophic levels, where samples were collected at high tide to capture incoming oceanic waters. Comparison of nearly a year of data shows significant correlations in abundance and temperature between sites, highlighting similarities in regional-scale oceanographic processes. Phytoplankton community response, and in particular the relative proportion of diatoms and dinoflagellates, was significantly correlated to temperature at both sites with higher temperatures associated with dinoflagellate-dominated communities and lower temperatures with diatom-dominated communities. Moreover, during large bloom events, while phytoplankton abundance differed by up to an order of magnitude between sites, likely stemming from local-scale processes, the

composition reached high levels of similarity. The relationships established here suggest that long-term phytoplankton data from the Cal Poly Pier could potentially be linked with long-term high trophic-level datasets collected in Morro Bay, although a full annual cycle with interannual realizations would provide more certainty on the relationships established.

1 Introduction

Phytoplankton form the base of the marine food web and their community structure influences coastal primary productivity, nutrient cycling, and carbon sequestration (Reynolds 2006). Phytoplankton community composition is known to change in response to variations in ocean conditions. In eastern boundary current upwelling systems, composition follows variations in nutrient availability and water column stability driven by alongshore equatorward upwelling winds (Kudela et al. 2015). In the California Current System (CCS), maximum upwelling favorable winds occur during the spring months, followed by a relaxation period in the late summer and early fall (Walter et al. 2018a). Coastal phytoplankton abundance and composition along the California Current fluctuate with these seasonal changes, allowing for trends in higher taxonomic levels to remain fairly consistent over long timescales (Taylor et al. 2015).

Interannual variability in phytoplankton composition has been linked to climate oscillations like the Pacific Decadal Oscillation (PDO), which transition between positive and negative phases that contribute to anomalously warm or cold-water temperatures (Du et al. 2015). In addition to the broader changes observed at longer time scales, finer-scale taxonomic variability and patterns of succession are observed at shorter time scales and are driven by physical changes, competition for resources, and variations in grazing (Reynolds C.S. 1989, Sommer U. 1989, Sterner R.W.

1989). These changes are often captured by the weekly sampling conducted at multiple monitoring sites along the coast and may lead to temporary deviations from the broader community trends.

Diatoms and dinoflagellates are two of the dominant phytoplankton taxa present in the CCS. Diatoms are commonly associated with cold, nutrient-rich water during periods of strong upwelling, while dinoflagellates are prevalent in warmer, more stratified water during periods of weaker upwelling (Kudela et al 2015, Barth et al 2020). Because of these differences, the ratio of dinoflagellates to diatoms has been used to link phytoplankton community dominance to changes in oceanographic conditions (McQuatters-Gollop et al. 2007, Wasmund et al. 2017, Spilling et al. 2018, Barth et al. 2020). Community dominance also has implications for food web efficiency, as diatoms represent a readily available and nutritious food source for zooplankton, while dinoflagellate mixotrophy and toxicity can complicate their reliability as food (Aberle et al. 2007). For this reason, dinoflagellates are more closely associated with harmful algal bloom (HAB) events, during which favorable conditions allow for the rapid proliferation of species that potentially produce toxins and can lead to the formation of hypoxic zones during their decomposition by heterotrophic bacteria.

Networks of sampling sites have been established to monitor phytoplankton communities in order to detect HAB events and build datasets characterizing trends at the base of the food web. Sampling at discrete locations provides a snapshot of the phytoplankton composition, but the patterns within one location may be not generalizable to the surrounding areas. Geographically adjacent systems may experience localized blooms stemming from site-specific local oceanographic variability that differentially favor particular taxa. Moreover, having reliable characterizations of phytoplankton community structure is valuable for various industries

including aquaculture. Previous aquaculture studies describe the importance of phytoplankton concentrations in maintaining growth rates of shellfish and the deleterious effects of HAB events that can trigger closures due to the buildup of toxins in bivalve tissues (Kirby-Smith & Barber 1974, Mizuta & Wikfors 2020). Thus, understanding the role that local oceanographic variability plays in structuring phytoplankton community composition in geographically similar sites subject to the same regional upwelling forcing is particularly important for the development of predictive relationships that can be used to estimate compositions at sites that do not have a long-term phytoplankton monitoring program.

This study compares the phytoplankton composition between two sites (~ 35 km apart) located in the Central California region: San Luis Obispo Bay (SLO Bay) and Morro Bay. SLO Bay is a small coastal embayment and is home to a long-term harmful algal bloom sampling site, with approximately weekly phytoplankton measurements going back to 2008. Morro Bay is a seasonally low-inflow estuary with significant tidal influence and is home to long-term datasets of higher trophic level organisms (e.g., invertebrates) as well as multiple aquaculture facilities. In order to make comparisons between these sites, phytoplankton communities were characterized from weekly samples collected from both sites starting in September 2020. Multiple parameters were investigated between the sites to quantify similarity in composition, abundance, and response to changing conditions. This study also investigates whether the ratio of dinoflagellates to diatoms developed in SLO Bay is applicable to Morro Bay, and how community dominance could be predicted using other measured parameters. Exploring these relationships is not only beneficial for making inferences in the phytoplankton community structure at local sites lacking consistent monitoring, but can also serve as a step towards making connections between long-term plankton datasets and higher trophic-level datasets that are spatially separated.

2 Methods

2.1 Site Considerations

Phytoplankton sampling was conducted at the Cal Poly Pier in San Luis Obispo Bay (35.170°N, 120.741°W) and at the end of the Coast Guard T-pier near the mouth of Morro Bay (35.370°N, 120.858°W). SLO Bay is a small (length and width scales < 20 km, cf. Largier 2020), semi-enclosed upwelling embayment that is partially sheltered from the prevailing northwesterly upwelling winds by coastal peaks and hence is termed an “upwelling shadow” system (Walter et al. 2017, Walter et al. 2018a). This system is prone to enhanced retention of warm waters and increased stratification, often leading to harmful algal blooms and hypoxic events (Walter et al. 2018a; Barth et al. 2020; Valera et al. 2020). Morro Bay is a tidally-forced seasonal low-inflow estuary (LIE), where freshwater input is negligible during the extended dry season (~April to October) and intermittent during the winter wet season (~November to March) (Walter et al. 2018b, Walter et al. 2020). In this system, the tides and tidal currents are in near quadrature such that during the rising tide, oceanic waters are transported into the estuary (Walter et al. 2018b).

Weekly samples were collected from the Cal Poly Pier since August 2008 as part of the Southern California Coastal Ocean Observing System (SCCOOS) HABs monitoring program, while weekly sampling in Morro Bay began in September 2020. Starting in September 2020, samples from the two sites were collected on the same day whenever possible. In Morro Bay, samples were collected within an hour of a high tide to ensure oceanic source water. Due to this constraint, Morro Bay sampling times ranged from 4:30am to 7:30pm, while the Cal Poly Pier sampling times ranged from 7:30am to 3pm. Sampling plans were generated in advance using

tidal height predictions from the NOAA Port San Luis station (<https://tidesandcurrents.noaa.gov/noaatidepredictions.html?id=9412110>).

2.2 Field Sampling

Surface water samples at both sites were collected using a plastic bucket, from which temperature measurements were taken immediately using a Traceable Digital Thermometer (CAT# 4344). After recording the temperature, 1 L Nalgene bottles were used to collect subsamples from the bucket. For the fixed phytoplankton sample, 90 ml was measured into a glass beaker, which was then transferred to a French square bottle containing 10ml 37% formaldehyde (stabilized with 10-15% methanol). Two 100ml subsamples were then collected from the bucket in replicate for chlorophyll filtration. For chlorophyll, samples from the Cal Poly Pier were filtered on site and samples from Morro Bay were filtered in the lab after transporting them in dark amber bottles. Chlorophyll samples were filtered onto 25 mm GF/F Whatman filters (CAT# 1825-025) and stored in cryovials (CAT# 1050025) at -20 °C until further analysis.

2.3 Laboratory Analysis

Formalin-fixed surface samples (25 ml) were settled for 24 hours onto microscope slides using Utermöhl chambers (Edler & Malter, 2010). The samples were enumerated using an Olympus IX70-S8F2 microscope. Ten fields of view were observed at 100X total magnification (10X eyepiece and 10X optical). Phytoplankton were counted and recorded to the genus level and occasionally the species level if distinguishing features were evident. Phytoplankton concentrations (cells/L) were calculated from the raw totals following Edler & Malter (2010).

Chlorophyll samples were extracted in 7 ml of 90% acetone and analyzed using a Turner 10-AU fluorometer. Chlorophyll-a concentrations were derived from fluorescence using the acidification method (Strickland and Parsons, 1972).

2.4 Statistics and Data Analysis

All taxa were grouped into two categories, by genus and by broader taxonomic category (diatom vs dinoflagellate). The dinoflagellate to diatom ratio was also calculated by dividing total dinoflagellate concentration by total diatom concentration.

All data management, figure generation, and statistical analyses were conducted using R version 4.0.3. In order to compare compositions of each sample between sites, percentage similarity values were calculated using the ‘vegan’ package with square root transformed genus-level phytoplankton data. Percentage similarity was chosen as the appropriate ecological resemblance metric due to its quantitative and asymmetrical characteristics (Legendre & Legendre, 2012). Over 70 genera were compared to obtain the percent similarity values, although not all genera were observed over the course of the study and were therefore excluded from the asymmetrical analysis. Linear regression models were used to obtain statistical significance for several different environmental and compositional correlations.

3 Results

3.1 Phytoplankton Abundance and Environmental Patterns

SLO Bay and Morro Bay displayed consistent temporal patterns in phytoplankton abundance, chlorophyll-a concentration, and temperature (Figure 1). While the magnitude of

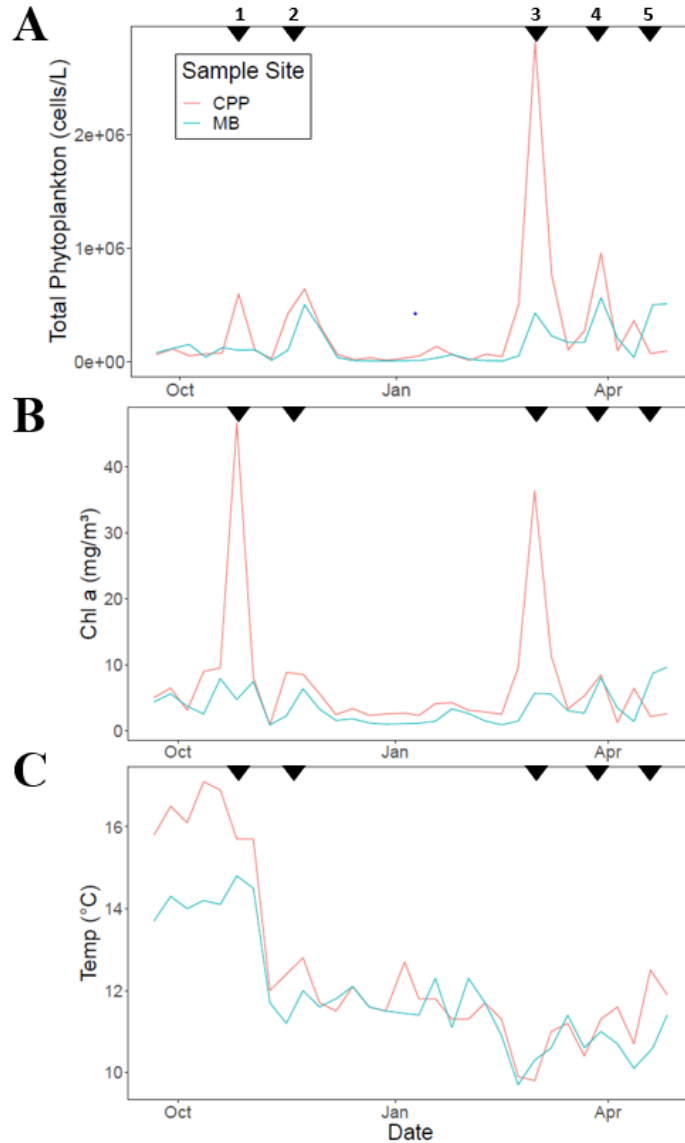


Figure 1. (A) Total phytoplankton abundance, (B) chlorophyll-a concentration, and (C) temperature in SLO Bay (red) and Morro Bay (blue). The black arrows at the top of each panel denote the five large bloom events referenced in the text.

phytoplankton blooms differed between sites (Figure 1A), phytoplankton abundances were significantly correlated ($R^2 = 0.2398$, $p = 0.005$). There were five main bloom events observed during the course of the study, three of which occurred concurrently between sites (Events 2,3,4; Figure 1A) and two that were site-specific (Cal Poly Pier for Event 1 and Morro Bay for Event 5; Figure 1A). During bloom events, SLO Bay typically had higher overall phytoplankton and

chlorophyll-a concentrations, with late April serving as an exception (Figure 1A, B). Of particular note were two peaks in chlorophyll observed in SLO Bay reaching over 30 mg/m³ that were not observed in Morro Bay (Figure 1B). Both sites exhibited similar seasonality in sea surface temperature (SST; Figure 1C). SST ranged from approximately 14-17 °C during the late fall months followed by a drop to approximately 10-12 °C during the winter and early spring months. SLO Bay SST was typically about 2 °C higher than Morro Bay during the fall months.

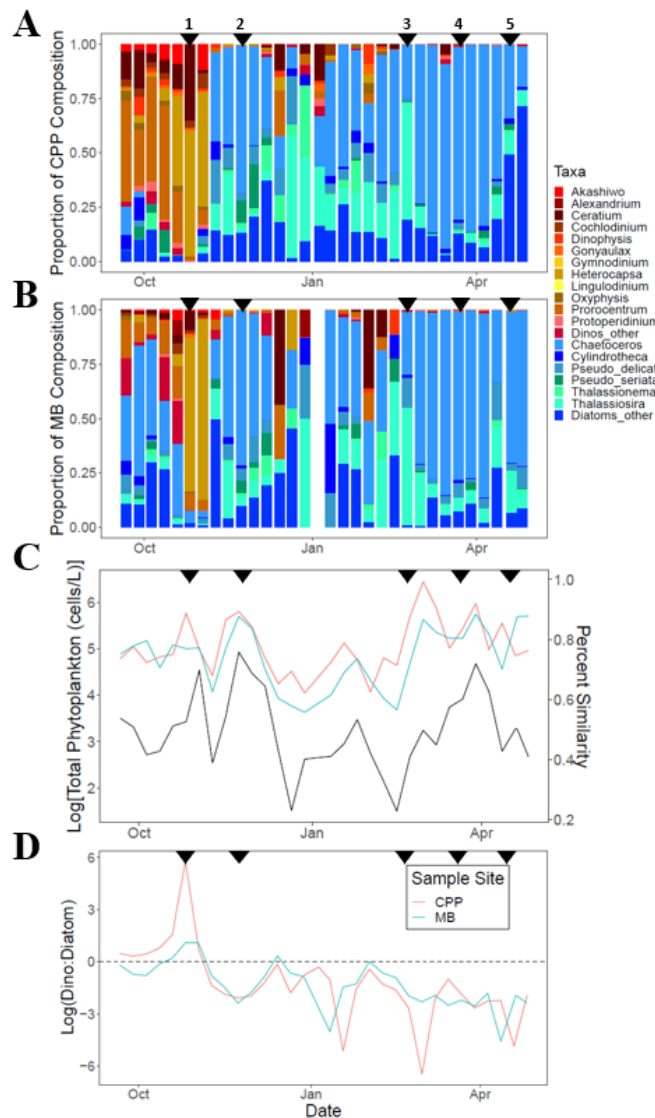


Figure 2. Relative abundance of phytoplankton grouped at the genus level by sample date for (A) SLO Bay and (B) Morro Bay. (C) Transformed total phytoplankton abundance for SLO Bay (red) and Morro Bay (blue), with percent similarity (black) on the second y-axis. (D) Log-transformed dinoflagellate to diatom ratio for SLO Bay (red) and Morro Bay (blue). The black arrows at the top of each panel denote the five large bloom events referenced in the text.

3.2 Compositional Comparisons

Seasonal patterns in phytoplankton composition were similar between sites, with a clear shift from mostly dinoflagellates to mostly diatoms in early November (Figure 2A,B).

Phytoplankton community percent similarity was significantly correlated with bloom magnitude in SLO Bay ($R^2 = 0.2056$, $p = 0.01042$) and Morro Bay ($R^2 = 0.4798$, $p < 0.0001$), with a higher percent similarity during large bloom events (Figure 2C). The mean percent similarity over the study period was 0.495 and mean values were not disproportionately higher during the warm phase (0.519) or the cool phase (0.488) of sampling. The phytoplankton community was most similar between sites (e.g., highest percent similarity values) during large *Chaetoceros* spp. blooms, with values of 0.759 on 23 November and 0.720 on 29 March (Events 2 and 4, respectively). During these blooms, both sites experienced total phytoplankton concentrations over 5×10^5 cells/L. The phytoplankton community was least similar between sites (e.g., lowest percent similarity values) when both sites had total phytoplankton concentrations under 5×10^4 cells/L (0.230 on 15 February and 0.232 on 21 December).

SLO Bay was dinoflagellate-dominated until early November and then diatom-dominated for the rest of the study period (Figure 2D). Morro Bay followed SLO Bay closely with occasional deviations on sampling dates with low phytoplankton abundance. Community dominance (i.e., the ratio of total dinoflagellates to total diatoms) was significantly correlated between sites ($R^2 = 0.374$, $p = 0.0003$).

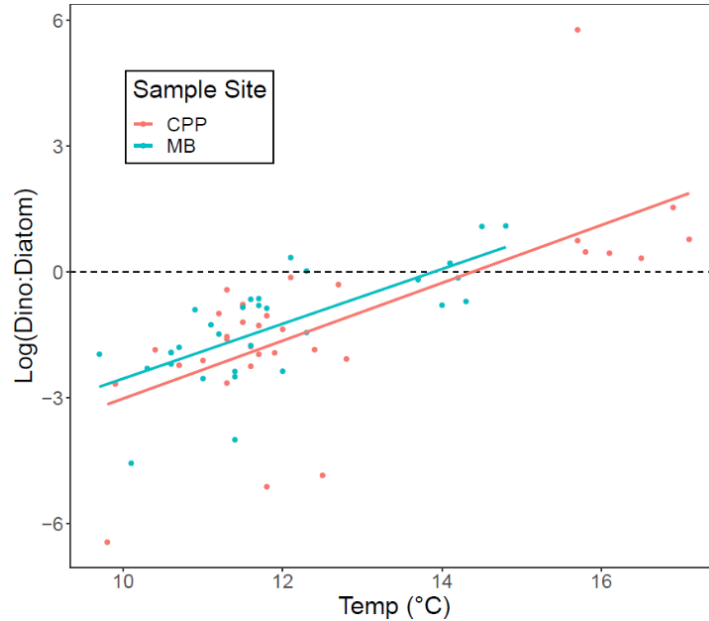


Figure 3. Log-transformed dinoflagellate to diatom ratio as a function of SST for SLO Bay (red) and Morro Bay (blue).

3.3 Linking Environmental Patterns to Compositional Data

SST was strongly correlated with the log of the diatom-dinoflagellate ratio in SLO Bay ($R^2 = 0.4677$, $p < 0.0001$) and Morro Bay ($R^2 = 0.5175$, $p < 0.0001$). SLO Bay had a larger temperature range than Morro Bay; however, they both were typically diatom dominated below 12°C and dinoflagellate dominated above 14°C .

4 Discussion

4.1 Similarities in Composition

This study compared the phytoplankton composition and abundance between a small semi-enclosed coastal embayment and a tidally-forced seasonal low inflow estuary from late fall to spring. Both sites (~35 km apart) are located in the same geographic region of the California Current System and experience the same regional upwelling forcing (e.g., Checkley and Barth,

2009; Garcia-Reyes and Largier, 2012). However, local forcing drives site-specific differences. During the fall, the SLO Bay upwelling shadow retains warmer water at the surface for long periods of time, resulting in enhanced stratification (Walter et al. 2017, Walter et al. 2018a). The mouth of Morro Bay has much shorter residence times due to strong tidal currents, which leads to strong vertical mixing (Walter et al. 2018b). In Morro Bay, sampling was performed at high tide to capture incoming oceanic waters for comparison with SLO Bay (e.g., Walter et al. 2018b).

Phytoplankton showed signs of responding to the same oceanic conditions at both sites, with variations in magnitude likely stemming from differences in local conditions. The timing of bloom events was highly correlated between sites; however, phytoplankton concentrations were often several orders of magnitude different. This could be explained by differences in residence times, nutrient availability, and turbulence levels in the two systems. For example, longer residence times promote the retention of phytoplankton in a particular area, which may enhance the magnitude and duration of bloom events (Alpine & Cloern 1992, Ryan et al. 2008). In addition, as described in the Monod Model, nutrient limitation effects the reproductive rate of phytoplankton, which may contribute to varying abundance between sites with different nutrient availabilities (Monod 1950, Tilman et al. 1982). Turbulence changes nutrient availability through both vertical and lateral mixing, as well as providing a source of mechanical disturbance that may limit or increase phytoplankton growth, depending on the present taxa (Estrada & Berdalet 1998).

Temporal variations in the dominant phytoplankton taxa (e.g., diatoms and dinoflagellates) were also correlated between sites (Figure 2D), indicating that higher taxonomic levels are likely structured by regional-scale oceanographic processes such as wind-driven

coastal upwelling. Bloom events are often related to shifts in upwelling strength and may therefore influence sites similarly within the same region. Dominance trends have implications for inferring food availability, which is critical for aquaculture farms and fisheries since particular taxa may serve as a preferred food source for filter feeders or larval fish (Rossi et al. 2006). On the other hand, similarities between sites at the genera-level were highly dependent on bloom magnitude (Figure 2C). When phytoplankton exhibit lower concentrations, localized oceanography may be more important than strong regional forcing in structuring the community. Bloom events have a greater significance from ecological and management perspectives, as they are more closely associated with HAB events and higher trophic-level responses (Anderson 2009, Moore et al. 2019). However, it is important to note that there are limitations for detecting phytoplankton taxa with microscopy. Phytoplankton enumeration using light microscopy is likely to pick up on the primary taxa present (e.g., diatom vs. dinoflagellate) during high concentration events, while particular groups at low concentrations may be missed during counting since they are not abundant enough to show up within the limited fields of view.

4.2 Linking Patterns to Environmental Variability

It has been well-established that changes in SST are linked with variations in the dominant phytoplankton taxa (McQuatters-Gollop et al. 2007, Wasmund et al. 2017, Spilling et al. 2018, Barth et al. 2020). Both sampling sites exhibited a significant correlation between SST and phytoplankton dominance, with higher temperatures associated with dinoflagellate-dominated communities and lower temperatures with diatom-dominated communities. The transition between diatom to dinoflagellate dominance occurs around 14°C for both sites, although it is not as clearly delineated in Morro Bay. In addition, since there is only a minimal difference in percent similarity between the warm and cool phases observed during the study

(both are approximately 0.5), it may be possible to infer the main genera present in the water regardless of the temperature regime.

The relationships established here suggest that long-term phytoplankton data from the Cal Poly Pier could potentially be linked with long-term high trophic-level datasets collected in Morro Bay, although a full annual cycle with interannual repetition and further exploration of the patchiness of the blooms would provide more certainty on the relationships established (Venrick 1998, Stauffer et al. 2020). Site-specific differences in local-scale oceanography likely limit the applicability of the results presented here to other locations. However, the methodology presented could be used in other locations with long-term monitoring programs. The ability to estimate compositional data between sites in the same geographic region is critical for a range of applications including aquaculture, nearshore fisheries management, and general ecosystem function. The continuation of sampling for another year will reduce the uncertainty in the length of the dataset and further elucidate the extent to which spatial patchiness influences site-specific community composition.

Acknowledgments

We acknowledge support from the NOAA IOOS program through SCCOOS (HABs) for data collected at the Cal Poly Pier. Funding for the Morro Bay sampling was provided by Cal Poly Strategic Initiatives funding. We also acknowledge Ian Robbins and Elysa Romanini for their help in the field. I would also like to thank Dr. Pasulka and Dr. Walter for their help throughout this project, which has been the most valuable learning experience in my college career and would not have been possible without their guidance.

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