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Planktonic Diatom Species Succession in San Francisco Bay (September 2015 - December 2017)

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CHANGE THE WORLD FROM HERE

This Biology Honors Thesis

by

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TABLE OF CONTENTS

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ABSTRACT

Since Hutchinson first described the "Paradox of the Plankton" in 1961, research has been done to determine how and why the coexistence of so many different species of phytoplankton is possible. A critical part of this question is species succession, or how the assemblage of phytoplankton in a region changes over time. This study examines the succession of planktonic diatoms in San Francisco Bay, CA (USA) from September 2015 through December 2017 using phytoplankton samples and environmental data. Periodic sampling was conducted at a site in the Golden Gate Strait and taxa were identified using light microscopy and scanning electron microscopy. Relative abundance, relative biovolume, and diversity measures were calculated for each sample date. Over the course of the study, 46 unique taxa were identified, some of which persisted over time while others were seen on only one occasion. A seasonal pattern in species richness was observed, in which high species richness was consistently seen in fall and winter and low species richness was seen in spring and summer. Seasonal clusters were also seen when a non-metric multidimensional scaling (NMDS) ordination was used to visualize community similarity. Fall and spring sampling dates formed the most distinct clusters, indicating that communities during these seasons are consistently similar to one another. Diatom assemblages differed greatly between drought and non-drought periods, suggesting that certain environmental conditions (e.g., salinity) play a large role in species succession in San Francisco Bay. Further studies could examine additional environmental variables (e.g., nutrients, water column mixing, solar radiation) to determine their role in shaping phytoplankton communities.

INTRODUCTION

The vast diversity of phytoplankton species has been of interest to researchers globally for over a century; in particular many have wondered how such a large number of species can coexist in seemingly unstructured habitats (Angara et al. 2013; Nassar et al. 2015; Watanabe et al. 2017). Originally described by Hutchinson in 1961, the so-called "Paradox of the Plankton", or the ability of varied species to coexist despite the principle of competitive exclusion, has drawn attention to the cycles of phytoplankton occurrence in different parts of the world (Hutchinson 1961). This phenomenon has been examined in different marine systems across the world, with the intent to correlate phytoplankton diversity with physical and chemical factors (e.g., Cloern 1996; Gilbert et al. 2014).

A key part of understanding the diversity and coexistence of plankton species is the idea of succession. In these dynamic communities, the number of taxa present and the relative abundance of those taxa can vary greatly at different times of year (Cloern & Dufford 2005; Karentz & Smayda 1998). Several long-term studies (Cloern et al. 1985; Karentz & McIntire 1977; Karentz & Smayda 1998) have examined the temporal dynamics of phytoplankton occurrence and described both seasonal and yearly patterns in succession. Strong seasonal patterns are commonly seen in coastal areas and estuaries, but these patterns differ between sites (Cloern et al. 1985; Cloern 1996; Watanabe et al. 2017). These seasonal patterns are often characterized by "bloom" events at certain times of the year, in which a particular species rapidly

accumulates in biomass and dominates the phytoplankton community. Spring blooms have been documented in the Wadden Sea (southeastern region of the North Sea) (Cadée & Hegeman 1979), Columbia River (Washington, USA) (Small & Frey 1984), Bristol Channel (UK) (Joint & Pomroy 1981), and South San Francisco Bay (California, USA) (Cloern et al. 1985), while winter blooms have been seen in the Peel-Harvey Estuary (Western Australia) (McComb et al. 1981) and Narragansettt Bay (during the 1960s; Rhode Island, USA) (Karentz & Smayda 1998). In addition to yearly patterns, some studies have found longer term patterns, such as the five-year plankton cycles observed in Narragansett Bay between 1959 and 1974 (Karentz & Smayda 1998). Even well-established yearly cycles are subject to change in years of extreme hydrographic events like drought and flood, which were seen in 1977 and 1982, respectively, in San Francisco Bay (Cloern et al. 1985).

Correlating species succession and bloom events to physical and environmental factors has been a focus of study for many researchers (Cloern 1996; Cloern 1999; Cloern & Dufford 2005; Gilbert et al. 2014). In his early research, Smayda (1980) distinguished between allogenic factors (e.g., temperature, salinity, turbulence) and autogenic factors (e.g., nutrients, water quality, cell life cycle) affecting phytoplankton communities. He concluded that variation in the community of phytoplankton in a specific area could largely be due to allogenic factors, or changes in the physical environment, and that these changes may in turn affect autogenic pathways (Smayda 1980).

In San Francisco Bay, previous studies extending across the North and South Bay have shown that the primary factor limiting phytoplankton growth is light (Cloern 1999; Cloern & Dufford 2005). Irradiance in San Francisco Bay follows a seasonal cycle, but additional factors, such as the amount of sediment suspended in the water column, affect how deep light travels into the water (Cloern 1996; Cloern 1999). The importance of light in phytoplankton growth in San Francisco Bay was highlighted in a long-term study which found a strong correlation (r^2= 0.86) between mean water column irradiance and phytoplankton specific growth rate (Cloern et al. 1985). A later study of the bloom dynamics of San Francisco Bay established that, since nutrient levels are usually non-limiting, blooms primarily occur when light limitation is decreased by physical processes like stratification and the settling of sediment (Cloern & Dufford 2005).

Other physical factors that potentially affect phytoplankton growth or species composition include temperature, salinity, turbidity, and morphology of the estuary. A study of both North San Francisco Bay and South San Francisco Bay showed that, although certain species are found only in specific salinity or temperature ranges, the community as a whole is largely resilient to these changes (Cloern & Dufford 2005). Water circulation and mixing do appear to affect community composition in San Francisco Bay (Cloern et al. 1985). In estuarine systems, a dominant factor affecting species composition and distribution is the varying amount of freshwater discharged from rivers (Karentz & McIntire 1977; Cloern et al. 1985; Cloern 1996). In the case of South San Francisco Bay, river discharge is directly linked to phytoplankton biomass because increased river discharge creates greater stratification of the water column, which can be a factor in plankton blooms (Cloern et al. 1985). Phytoplankton communities in estuaries are also impacted by tidal patterns, the morphology of the estuary itself, turbulent mixing of fresh and salt water, and human-introduced species and chemicals (Cloern 1996; Kimmerer 2004).

San Francisco Bay has been characterized as a high-nutrient estuary (Cloern 1996; Cloern 2018; Dugdale et al. 2012; Gilbert et al. 2014; Kimmerer 2004). It is often referred to as a “shallow

coastal ecosystem" (SCE), which is defined by shallow depth, turbulent mixing, high levels of suspended particulate matter, and nutrient-rich conditions (Cloern 1996). Dissolved inorganic nitrogen (DIN), silicon (Si), and phosphorous (P) are usually present above the necessary levels for phytoplankton growth in both North and South San Francisco Bay (Cloern 1982; Cloern & Dufford 2005). In a study from 1992 to 2001, samples taken in a transect from North to South San Francisco Bay showed possible nitrogen (N) limitation on phytoplankton growth only 4% of the time (Cloern & Dufford 2005). Possible Si limitation was seen in only 1% of the samples, and P limitation was never observed. The study confirmed that light is the most important limiting factor, as light was observed as a growth-limiting factor in 74% of samples. It is also hypothesized that this nutrient-rich environment may cause larger diatom taxa to dominate the plankton community (Cloern & Dufford 2005). These nutrients have many sources, including river discharge and local inputs from the urban environment (Kimmerer 2004). N and P come from agricultural drainage and sewage, but may also be brought to the Bay through seasonal upwelling in the ocean. This high concentration of nutrients may sometimes also have adverse effects on phytoplankton productivity (Dugdale et al. 2012; Gilbert et al. 2014). Increased ammonium (NH_4) concentrations in the Bay, caused by wastewater treatment plant discharge, appear to have caused decreased phytoplankton productivity in recent years (Dugdale et al. 2012; Gilbert et al. 2014). Since NH_4 inhibits the uptake of nitrate (NO_3) by phytoplankton, the high levels of NH_4 in the Bay appear to be limiting the access of phytoplankton to NO_3 and therefore preventing phytoplankton blooms from occurring (Dugdale et al. 2012).

Phytoplankton biomass in San Francisco Bay is also negatively impacted by grazing of larger organisms (Cloern 1982; Cloern et al. 1985). A study in South San Francisco Bay found that zooplankton grazing reduced net phytoplankton growth in deeper waters but had little impact on populations in the shoals (Cloern 1982). The predominant zooplankton taxa at this time were from the copepod genus *Acartia* (Cloern 1982). In addition to zooplankton, benthic organisms like bivalves also graze on phytoplankton and can shape phytoplankton communities (Lucas et al. 2016). In South San Francisco Bay, bivalves have been shown to play a larger role in phytoplankton biomass reduction than zooplankton (Cloern 1982). Benthic grazing may also explain differences in phytoplankton species composition between North and South San Francisco Bay, where the populations of bivalves differ greatly (Cloern 1982). It has also been hypothesized that the influx of river water in the spring causes greater water column stratification in the Bay, and that the lack of benthic grazers may initiate phytoplankton blooms (Cloern 1982; Cloern et al. 1985; Kimmerer 2004).

The variety of factors potentially affecting phytoplankton species succession makes estuaries particularly interesting regions of study. San Francisco Bay is a well-studied estuary composed of four bays (South Bay, Central Bay, San Pablo Bay, and Suisun Bay) and fed by the Sacramento and San Joaquin Rivers (Kimmerer 2004) (Figure 1). It is an example of an estuary formed from a drowned river valley and subsequently altered by movements in the San Andreas and Hayward Faults. These tectonic movements have ultimately constructed a valley with four major basins, which are divided by deep, steeply-cut straits like the one under the Golden Gate Bridge (Kimmerer 2004). The geology and topography of the Bay have been further altered by human activity, both past and present. The marshes at the mouth of the San Joaquin and Sacramento Rivers were diked and dredged to create farmland after the Gold Rush, some of which exist today as islands and some of which have turned into tidal lakes (Kimmerer 2004). Some of the deeper channels have been straightened, and many are continuously dredged and deepened to create shipping routes.

Figure 1. The San Francisco Bay Estuary located in northern California (USA) (Trump 2004).

Humans have also altered the ecology of the region by introducing invasive species and changing the chemical composition of the water (Kimmerer 2004). Some of the most notable introduced species are the bivalves *Corbicula fluminea* and *Potamocorbula amurensis* (Alpine & Cloern 1992; Kimmerer 2004; Peterson & Vayssieres 2010). In certain areas, particularly in the northern reaches of San Francisco Bay, *Potamocorbula amurensis* has been linked to reductions in phytoplankton biomass (Alpine & Cloern 1992; Cloern 1996; Peterson & Vayssieres 2010). The zooplankton community composition and biomass have also been altered greatly by introduced zooplankton species, many of which originated in East Asia, but it is less clear what effect these new species have had on phytoplankton (Kimmerer 2004). In addition to foreign species, pollutant chemicals are also found in the Bay. About 40% of the area of California is drained by the San Joaquin and Sacramento River systems, which carry chemical runoff, particularly ammonium, and sediments into the Bay (Kimmerer 2004). Studies have shown that the freshwater flow carrying these contaminants has not only been affected by dams and dikes but is highly variable both seasonally and interannually and may be changing in response to climate change (Kimmerer 2004). For these reasons, the US Geological Survey has used the Bay for several decades as a study area for the synergistic effects of human usage and climate change on a complex estuarine system.

A number of US Geologic Survey projects have examined the bloom dynamics and temporal dynamics of phytoplankton in the San Francisco Bay Area (Cloern et al. 1985; Cloern 1996; Cloern & Dufford 2005; Cloern 2018), and these studies have contributed to our understanding of phytoplankton species succession and estuary dynamics. The sample sites used in these studies, however, have been limited to the interior of the Bay, along a transect from South Bay through Suisun Bay. The study described in this paper examines the phytoplankton community at a geologically and hydrographically unique location near the Golden Gate Strait (Figure 2). This study aims to contribute to what is known about planktonic diatom species succession by

analyzing taxonomic and hydrographic data collected from a unique sampling location over a two-and-a-half-year period that included both drought and non-drought years.

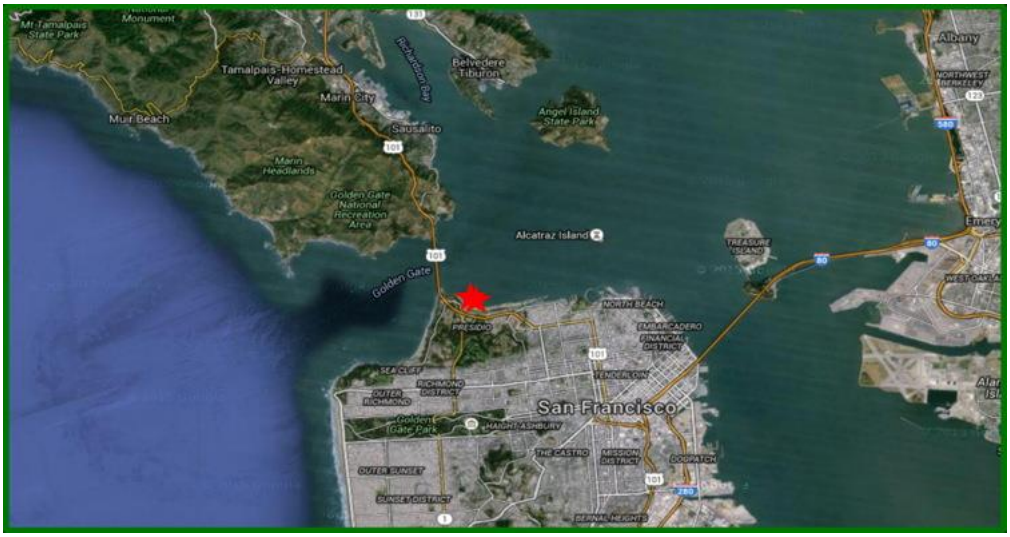

Figure 2. The sampling locations: Torpedo Wharf, Fort Point and Gulf of the Farallones Visitor Center (NOAA), San Francisco, CA USA (Google Maps 2017).

METHODS

Location of Sample Sites

The Golden Gate Strait connects the Pacific Ocean and San Francisco Bay Estuary and is 115 m at its deepest point (Dartnell et al. 2006). The sampling sites were located along the shallow edge on the south side of the Strait (Figure 2). Sampling was conducted from two closely located docks in San Francisco, CA (USA). Samples from 10 Sept 2015 – 22 Sept 2016 were collected at Torpedo Wharf (37.809049º N, 122.470288º W) and samples from 11 Oct 2016 – 5 Dec 2017 were collected at the Gulf of the Farallones Visitor Center (NOAA) dock (37.806394º N, 122.466083º W). Tides in San Francisco Bay are mixed semidiurnal and have a median daily tidal range of 1.8 m (Kimmerer 2004, NOAA 2018). Sampling occurred across different tidal heights.

Sampling Protocol

Phytoplankton samples were collected from the dock using a phytoplankton net with 64 µm mesh. The net was deployed to the middle of the water column and held while water passed through. When the current was not strong enough to flow through the net, the net was either walked along the dock or dragged up and down in a “yo-yo” method (Table 1).

Table 1. Sampling dates showing number of diatom taxa observed, location sampled (Torpedo Wharf (TW) or Gulf of the Farallones Visitor Center (GFVC), and method for using the plankton net (current-deployed = C, yo-yo method = Y, and walking with the net = W).

Date	Location	Method
10 Sep 2015	TW	C
24 Sep 2015	TW	C
8 Oct 2015	TW	Y
21 Oct 2015	TW	C
5 Nov 2015	TW	Y
26 Nov 2015	TW	C
19 Jan 2016	TW	Y
11 Feb 2016	TW	C
26 Feb 2016	TW	C
9 Mar 2016	TW	Y
20 Apr 2016	TW	C
11 May 2016	TW	C
14 Sep 2016	TW	Y
11 Oct 2016	GFVC	W
22 Nov 2016	GFVC	W
31 Jan 2017	GFVC	Y
28 Feb 2017	GFVC	W
21 Mar 2017	GFVC	W
30 Mar 2017	GFVC	W
11 Apr 2017	GFVC	C
9 May 2017	GFVC	W
6 Jul 2017	GFVC	C
7 Sep 2017	GFVC	C
13 Sep 2017	GFVC	C
4 Oct 2017	GFVC	C
18 Oct 2017	GFVC	C
31 Oct 2017	GFVC	W
15 Nov 2017	GFVC	C
5 Dec 2017	GFVC	W

Hydrographic measurements including water temperature, salinity, and water clarity were taken on each sampling date. Temperature and salinity measurements were taken using a conductivity-temperature-depth (CTD) meter (Sontek CastAway®, Xylem Inc.) deployed from the dock. Water clarity was measured using a Secchi disk deployed from the dock (Preisendorfer 2003). Additional temperature and salinity measurements were obtained from the Fort Point Bodega Ocean Observing Node (BOON) operated by the University of California Davis Bodega Marine Laboratory (BOON 2018). The BOON mooring samples Bay water continuously for temperature, salinity, light transmittance in the water column and fluorescence (proxy for chlorophyll *a* concentration); these data were used for analyses. Precipitation data for San Francisco from January 2014 through February 2018 were obtained from the National Weather Service Forecast Office (NOAA) (National Weather Service 2018). Tide data from August 2015 through December 2017 were obtained from the NOAA Tides and Currents website (NOAA 2018).

Phytoplankton net samples were further concentrated in the lab by sieving through a 64 µm mesh. Concentrated samples were preserved in 50% ethanol. To obtain relative abundance counts, slides were made from the preserved samples. To ensure that slides were representative of the whole sample, the vials with sample were inverted several times to evenly resuspend all material that had settled to the bottom. Diatom cells were counted by light microscopy (LM) at 400× magnification and smaller taxa were more closely examined at 600× and 1000× magnification. Phytoplankton specimens were identified to genus or species primarily using the works of Cupp (1943) and Tomas et al. (1996). The number of cells of different taxa was determined by identifying and counting the first 500 cells seen on the slide (100-300 cells is a recommended minimum number of cells required for achieving statistical significance) (Alverson et al. 2003; McIntire & Overton 1971). Cell numbers were used to calculate the relative abundance of each taxa on each sample date.

Numerous centric diatoms that could not be identified by light microscopy were grouped together as the "Centrics" in the cell counts. Similarly, all *Thalassiosira* species were grouped together. Species difficult to identify via light microscopy were further examined using scanning electron microscopy (SEM) (Hitachi TM3030, Hitachi High-Technologies). To prepare cells for viewing under SEM, cells were acid-cleaned (Taylor et al. 2007). Cells were mounted on stubs with a black background and examined at 1000-5000× magnification.

Species biovolumes (as a proxy for biomass) were calculated using published data from a US Geologic Survey (USGS) study of phytoplankton in San Francisco Bay between 1992 and 2014 (Nejad et al. 2017). This database lists a cell volume calculation for 337 dates at 31 stations from the lower South Bay to the Delta. For our purposes, cell volumes for each species or taxonomic group (e.g., Centrics, *Thalassiosira* spp.) were estimated by averaging all of the cell volumes for that species (or group) listed in the USGS database. This mean cell volume for each species was then multiplied by the relative abundance of the species in our study to calculate the relative biovolume of each species on each sampling date. For unknowns and species not observed in the Nejad et al. study, the Hillebrand et al. (1999) method was used to calculate biovolume.

Data Analysis

Three biodiversity measures were used to analyze the species data: species richness (S), the Shannon-Wiener Index (H), and evenness (E). Species richness is calculated by counting the total number of species observed on a given date. The Shannon-Wiener Index is calculated by

$$H = -\sum[(P_i)\ln(P_i)]$$

where P_i is the total number of individuals of a given species on a certain day divided by the total number of individuals of all species counted in the sample. Evenness is calculated by

$$E = \frac{H}{\ln(S)}$$

The program R (version 3.5.0) (The R Project for Statistical Computing**,** https://www.r-project.org) was used, along with the "vegan" package for multivariate data analysis. The relationship between environmental factors and community composition was visualized using non-metric multidimensional scaling (NMDS). Permutational multivariate analysis of variance (PERMANOVA) using distance matrices was applied to quantify variation between clusters generated by NMDS.

RESULTS

Species Composition

A total of 46 taxa were identified in this study, with 6 to 24 different taxa observed on each sample date (Table 2, Figure 3). Of these taxa, 37 were identified to species, and an additional six were identified to genus. A number of centric diatoms that have the classic "round" morphology appeared on 100% of the sampling dates (Figure 4). These individuals could not be identified to species under LM and were therefore grouped together in the cell counts. Further examination under SEM indicated that this group is comprised of > 20 taxa, many of which co-occurred across sample dates. The taxa occurring in this group will be collectively referred to as "the Centrics". Another dominant taxon was *Ditylum brightwelli*, which appeared on 93% of the sampling dates. The taxa *Biddulphia mobiliensis*, *Chaetoceros decipiens, Chaetoceros curvisetus, Pseudo-nitzschia* sp., *Skeletonema costatum, Thalassiosira* spp., *Pleurosigma* sp. 1, and *Rhizosolenia setigera* also all appeared more than 50% of the time. Six taxa were seen on only one occasion. The most well-represented genera were *Chaetoceros* (8 species), *Rhizosolenia* (4 species), *Biddulphia* (3 species), and *Nitzschia* (3 species). Of the taxa observed, 41 were also seen in the USGS survey of San Francisco Bay between 1992 and 2014 (Nejad et al. 2017) (Table 2). Four species identified in this study were not previously observed in the USGS survey (*Bacillaria paradoxa, Chaetoceros tortissimus, Rhizosolenia calcar-avis,* and *Stephanopyxis turris*).

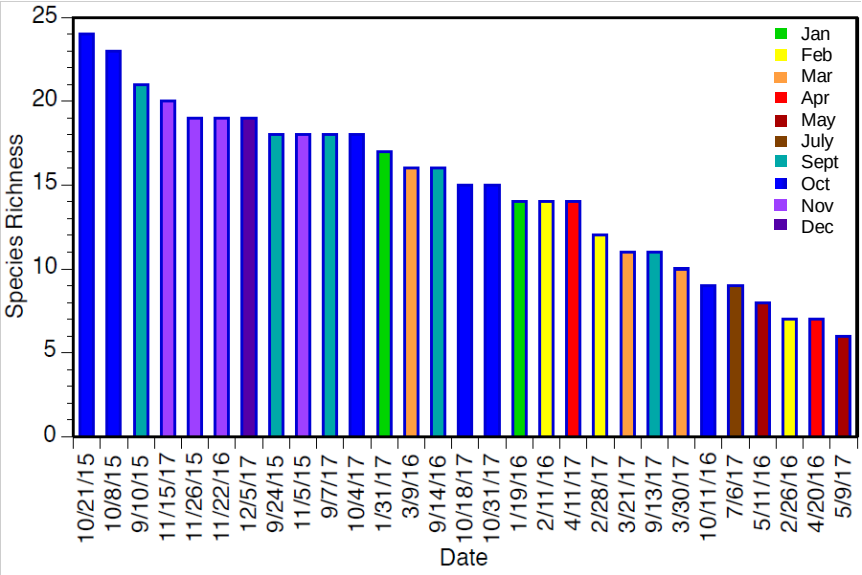

Figure 3. The species richness of each diatom assemblage sampled in San Francisco Bay, ordered from highest to lowest and color coded by month (purple/blue colors code for fall months, yellow/red/orange colors code for winter/spring months).

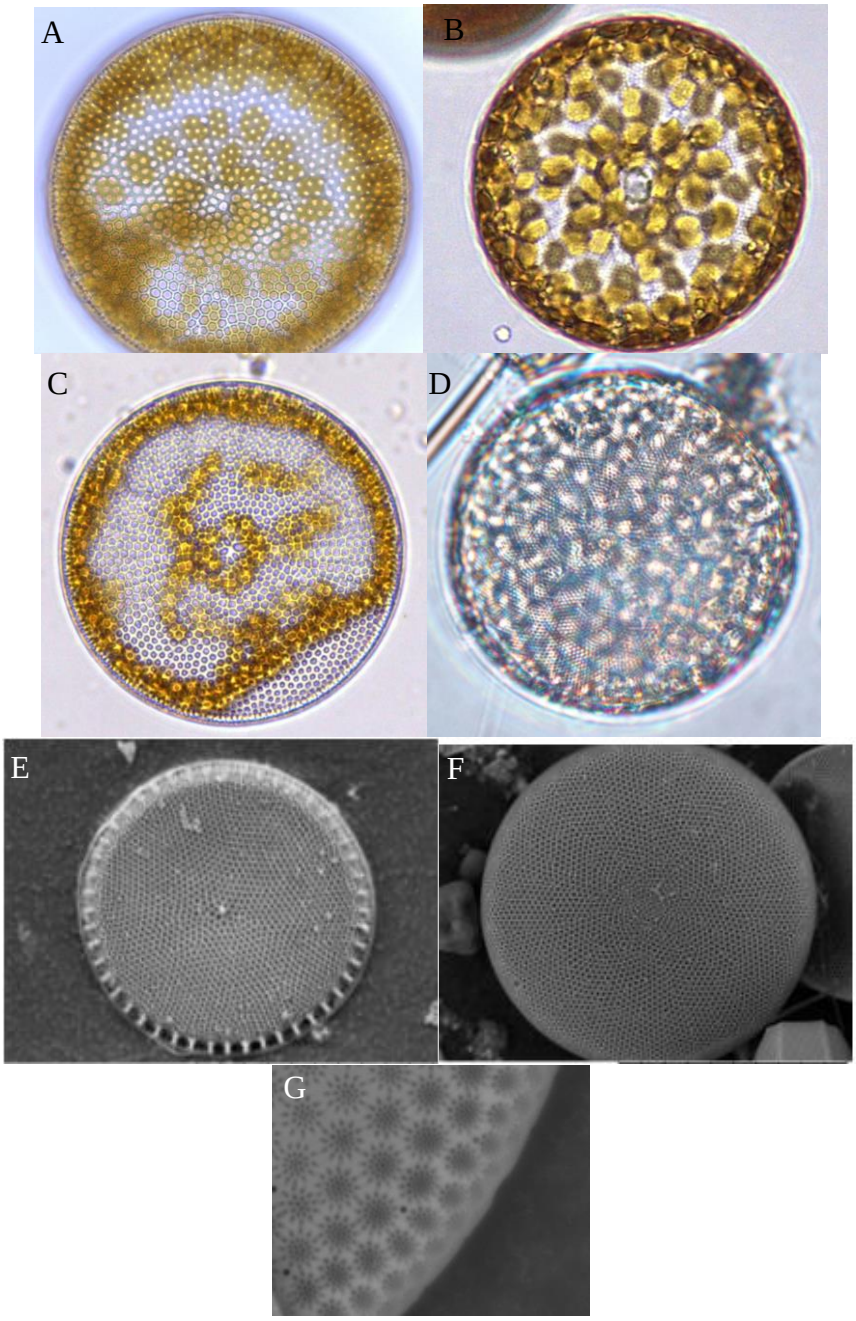

Figure 4. LM and SEM images of representative cells in the group "Centrics". (A) LM image of live cell taken at 400× from the 8 Oct 2015 sample, (B) LM image of live cell taken at 100× from the 21 Oct 2015 sample, (C) LM image of live cells taken at 400× from the 30 Mar 2016 sample, (D) LM image of preserved cell taken at 400× from the 21 Oct 2015 sample, (E) SEM image of acid-washed cell taken at 3000× from the 10 Sept 2015 sample, photo by Dr. Deneb Karentz, (F) SEM image of acid-washed cell taken at 1800× from the 10 Sept 2015 sample, photo by Dr. Deneb Karentz, (G) SEM image of the pattern on an acid-washed cell taken at 4800× from the 21 Oct 2015 sample.

Table 2. List of diatom species observed in this study (Sept 2015-Dec 2017), percentage of samples (%) each taxon was observed in for this study, years in which taxa were observed during a 22-year US Geologic Survey (USGS) investigation of phytoplankton in San Francisco Bay (Nejad et al. 2017), and taxonomic synonyms. Years with an * indicate that the diatom was not identified to species in our study but members of that genus were observed in the USGS investigation.

species observed	% this study	USGS (1992- 2014)	Synonym
Asterionella formosa Hassall	7	1993, 1994, 1996-2000, 2002, 2004, 2010, 2011, 2014	
Asterionella japonica Cleve	45	1992-1996, 1998-2014	*Asterionellopsis glacialis*
Bacillaria paradoxa Gmelin	7		
Biddulphia alternans (Bailey) Van Heurck	17	1994, 2001, 2003, 2004	*Trigonium alternans*
Biddulphia aurita (Lyngbye) Brébisson	17	1993, 1995, 1999-2004, 2006-2009, 2011-2014	*Odontella aurita*
Biddulphia longicruris (Greville) Hoban	38	1992, 2002, 2004, 2005, 2008, 2009	*Odontella longicruris*
Biddulphia mobiliensis (Bailey) Grunow	59	1992, 1993, 1996, 1998, 2001, 2002, 2005-2007, 2009-2014	*Trieres mobiliensis*
Centrics	100	1992-2014*	
Chaetoceros affinis Lauder	10	2006, 2008, 2010-2013	
Chaetoceros constrictus Gran	3	2008	
Chaetoceros curvisetus Cleve	55	2008	
Chaetoceros debilis Cleve	34	1992-1994, 1998, 1999, 2003-2006, 2008, 2011, 2012	
Chaetoceros decipiens Cleve	86	1994, 1998, 1999, 2003, 2005, 2008-2011	
Chaetoceros didymus Ehrenberg	48	1992, 1993, 1995, 2003, 2010-2014	
Chaetoceros socialis Lauder	3	1992-1996, 1999, 2001-2003, 2006, 2008, 2011, 2013	
Chaetoceros tortissimus Gran	3		
Corethron hystrix Hensen	17	2002, 2003, 2005, 2008, 2010	
Detonoula confervacea (Cleve) Gran	14	2010	
Ditylum brightwellii (West) Grunow	93	1992-2014	
Eucampia zodiacus Ehrenberg	34	1992-1994, 1996, 1999, 2002, 2004, 2005, 2009, 2011, 2013	
Grammatophora marina (Lyngbye) Kützing	7	1994, 1995, 2005, 2013	
Gyrosigma balticum (Ehrenberg) Rabenhorst	10	1992, 1994, 1995, 2008, 2011	
Isthmia nervosa Kützing	10	1994	
Lauderia sp.	34	1998, 1999*	
Leptocylindrus danicus Cleve	38	1992, 1993, 1999, 2004-2006, 2009, 2010, 2012, 2013	
Lithodesmium undulatum Ehrenberg	41	1992, 1993, 1996, 2001, 2002, 2011-2014	
Melosira moniliformis (Müller) Agardh	31	1992, 1995, 1996, 2003, 2004, 2006, 2010-2013	
Melosira sulcata (Ehrenberg) Kützing	10	1992-2014	
Navicula sp. Bory de Saint-Vincent	3	1992-2014*	
Nitzschia longissima (Brébisson) Ralfs	17	1992-2001, 2003, 2008-2012	
Nitzschia sigma (Kützing) W. Smith	38	2003, 2008-2014	
Nitzschia sp. Hassall	10	1992-2014*	
pennate sp.	3		

Table 2. (continued)

species observed	% this study	USGS (1992- 2014)	Synonym
Pleurosgima sp. 1 W. Smith	66	1992-2014 *	
Pleurosgima sp. 2 W. Smith	7	1992-2014 *	
Pseudo-nitzschia sp. Peragallo	52	1992- 2014*	
Rhizosolenia calcar-avis Schultze	7		
Rhizosolenia setigera Brightwell	55	1992-1997, 1999-2003, 2005-2014	
Rhizosolenia stolterfothii Peragallo	24	1992-1194, 1998, 2002, 2004, 2005, 2007, 2009-2012, 2014	*Guinardia striata*
Rhizosolenia styliformis Brightwell	17	1992, 1994, 1997, 1999, 2002	
Skeletonema costatum (Greville) Cleve	76	1992-2014	
Stephanopyxis turris (Greville) Ralfs	3		
Streptotheca tamensis Shrubsole	45	1992-1994, 2011, 2013	
Thalassionema nitzschioides (Grunow) Mereschkowsky	14	1992-1995, 1997-2014	
Thalassiosira spp. Cleve	52	1992-2014*	
Tropidoneis antarctica (Grunow) Cleve	28	1996, 2011	*Membraneis challengeri*

Relative Abundance

The diatom assemblages in San Francisco Bay were repeatedly dominated by several groups (Figure 5). The Centrics accounted for more than 50% of the cells counted on seven dates (19 Jan 2016, 11 Feb 2016, 14 Sept 2016, 11 Oct 2016, 22 Nov 2016, 18 Oct 2017, and 31 Oct 2017) and more than 25% of the cells counted on an additional six dates (10 Sept 2015, 5 Nov 2015, 26 Nov 2015, 26 Feb 2016, 15 Nov 2017, and 5 Dec 2017). In samples that the Centrics did not dominate, the species *Chaetoceros didymus*, *Skeletonema costatum*, and *Leptocylindrus danicus* made up high percentages of the cells observed. *C. didymus* rose to over 50% of cells counted on two dates (24 Sept 2015 and 21 Oct 2015), *L. danicus* on one date (28 Feb 2017), and *S. costatum* on four dates (9 March 2016, 20 Apr 2016, 11 May 2016, and 9 May 2017). *S. costatum* was the only species to make up more than 90% of a sample on a given day. This occurred both on 20 Apr 2016 (91.91%) and 9 May 2017 (93.08%). Of the 46 taxa, ten had a relative abundance of greater than 25% on at least one sampling date and 21 had a relative abundance of greater than 5% on at least one sampling date.

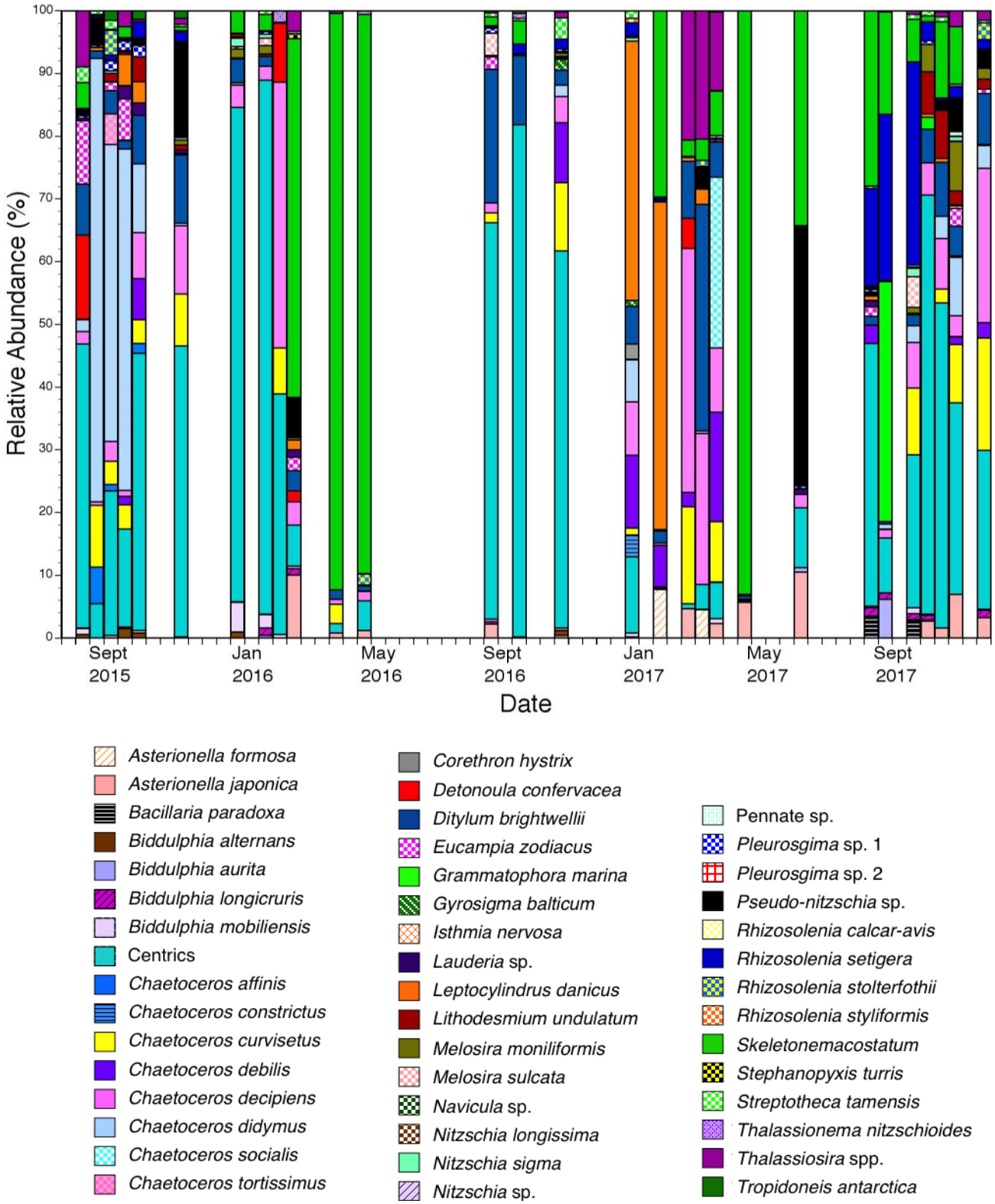

Figure 5. The relative abundance of diatom taxa in San Francisco Bay from September 2015 to December 2017.

Biovolume (proxy for biomass)

On every sampling date, either the Centrics or *Ditylum brightwellii* contributed more than 25% of the biovolume (Figure 6). Both groups contributed more than 25% of the biovolume on seven of the sample dates. Additionally, either the Centrics or *Ditylum brightwellii* contributed over 50% of the biovolume of the sample on 12 of 29 sampling dates (Centrics on seven dates, *Ditylum brightwellii* on five dates). The only other taxa to contribute more than 25% of the biovolume on a given day were *Corethron hystrix* (31 Jan 2017 and 28 Feb 2017), *Pleurosigma* sp. 1 (21 Oct 2015 and 9 May 2017), *Thalassiosira* spp. (21 March 2017), *Pseudo-nitzschia* sp. (6 July 2017), and *Tropidoneis antarctica* (8 Oct 2015).

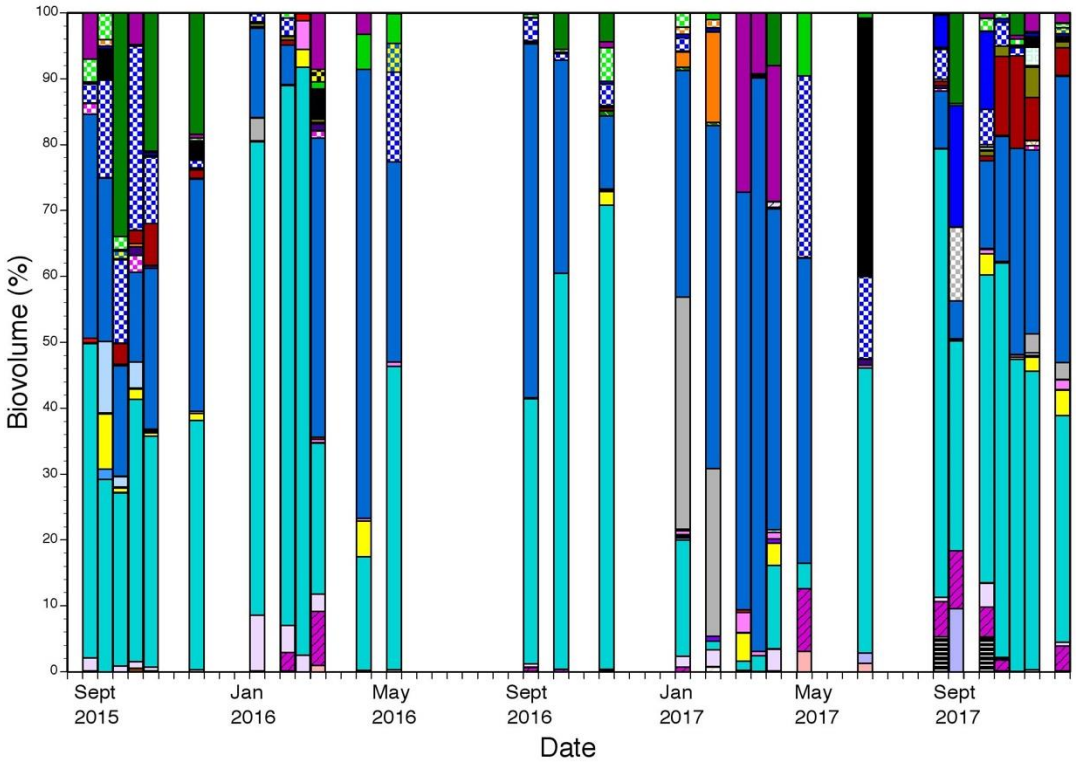

Figure 6. The relative biovolume of diatom taxa in San Francisco Bay from September 2015 to December 2017. Refer to legend of Figure 5.

Centrics

The Centrics were the only taxa to appear in every sample (Figure 5). Although they were treated as a single unit for relative abundance counts because of their similar appearance under the light microscope, analysis using SEM revealed that this group is likely made up of more than 20 species. These species include representatives primarily from the genera *Coscinodiscus* and *Thalassiosira* (Figure 4). This group persisted throughout the different seasons in which we sampled and never disappeared entirely, even while other species underwent blooms. For example, on 9 May 2017 when *Skeletonema costatum* made up 93.08% of the cells counted, the Centrics persisted at a low frequency (0.2%).

This group is notable because it frequently dominated the relative abundance counts, making up 60-85% on different days (Figure 7). Although high throughout much of the year, relative abundance of this group was low between the months of March and June in both 2016 and 2017. There was also a

dramatic but short-lived decline in relative abundance during September and October of these years (Figure 7).

Since many of the cells in this group are large (60 to over 100µm in diameter) they also dominated the biomass on many occasions, contributing over 25% on 21 sampling dates (Figure 6). In one instance, the group rose to over 70% of the biomass for three consecutive sampling dates: 19 Jan 2016 (71.87%), 11 Feb 2016 (81.97%), and 26 Feb 2016 (89.27%) (Figure 7).

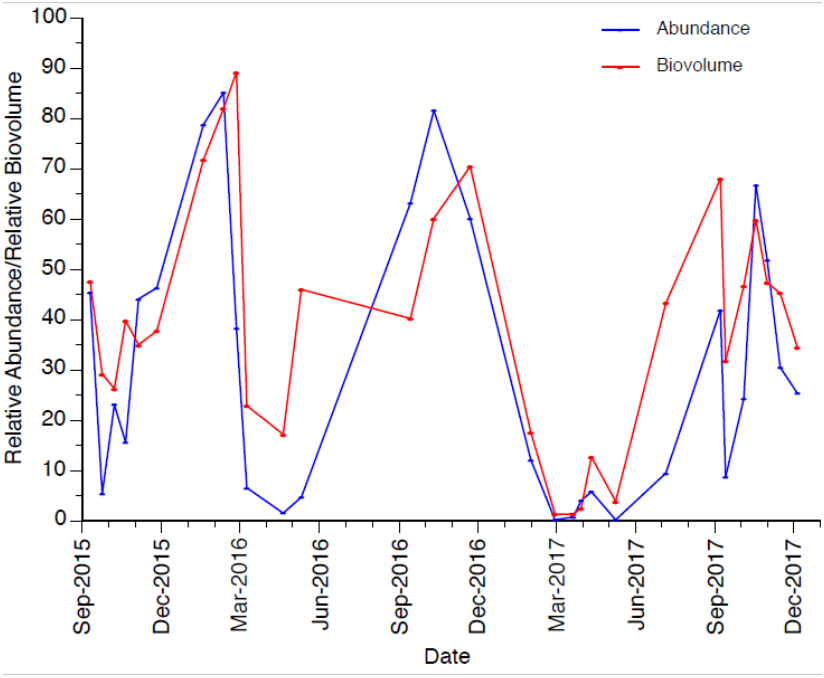

Figure 7. Relative abundance and relative biovolume of the Centrics in San Francisco Bay from September 2015 to December 2016.

Ditylum brightwellii

Behind the Centrics, *Ditylum brightwellii* was the species that appeared most frequently in our samples, occurring on 27 of 29 sampling dates (Figures 5 and 8). Although it appeared almost constantly, *D. brightwellii* almost always occurred in small numbers, making up less than 10% of the plankton assemblages based on cell counts on 23 occasions. *D. brightwellii* made up more than 25% of the sample on only one occasion (30 March 2017, 36.17%) (Figure 9). Despite its low relative abundance, *D. brightwellii* was important to the overall biomass of the phytoplankton (Figure 6). This species accounted for more than 25% of total biomass in 11 samples and more than 50% of total biomass in an additional five samples. On 30 March 2017, *D. brightwellii* represented 86.96% of the total biomass of the sample despite reaching only 36.17% relative abundance on that day. The two greatest contributions of *Ditylum* to biomass occurred in April of 2016 and March of 2017 (Figure 9). In samples where this species was not observed, the Centrics and *Pseudo-nitzschia* sp. made up a large portion of the total biomass.

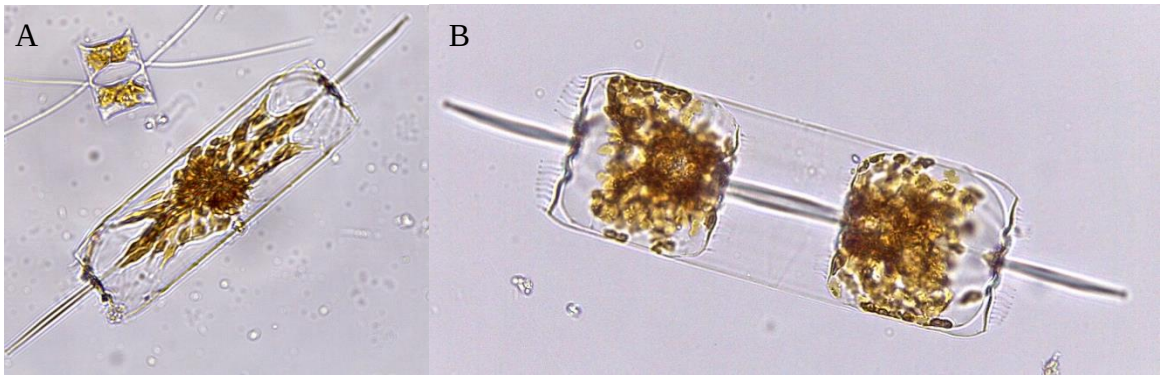

Figure 8. (A) LM image of *Ditylum brightwellii* taken at 100× from the 14 Sept 2016 sample, (B) image of dividing *Ditylum brightwellii* taken at 100× from the 8 Oct 2015 sample.

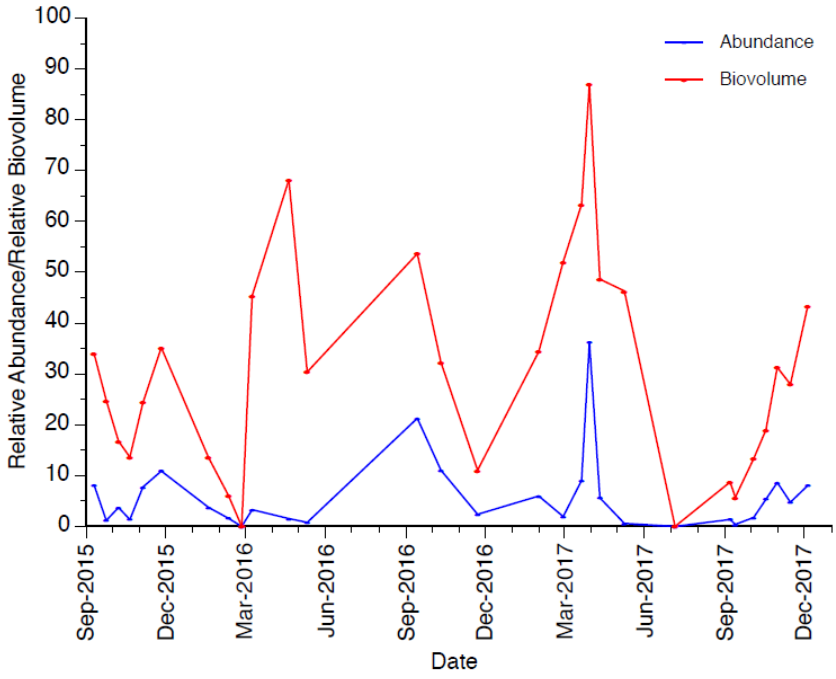

Figure 9. Relative abundance and relative biovolume of *Ditylum brightwellii* in San Francisco Bay from September 2015 to December 2017.

Chaetoceros Species

Eight species in the genus *Chaetoceros* were observed throughout the course of the study: *Chaetoceros affinis*, *Chaetoceros constrictus*, *Chaetoceros curvisetus*, *Chaetoceros debilis*, *Chaetoceros decipiens*, *Chaetoceros didymus*, *Chaetoceros socialis*, and *Chaetoceros tortissimus* (Figures 5 and 10). This genus was represented in 93.1% of the samples and was absent in only two samples (9 May 2017 and 11 Oct 2016) (Figure 11). Species of this genus often co-occurred, and up to five species were found together in a sample (8 Oct 2015, 5 Nov 2015, and 31 Jan 2017) (Figure 12).

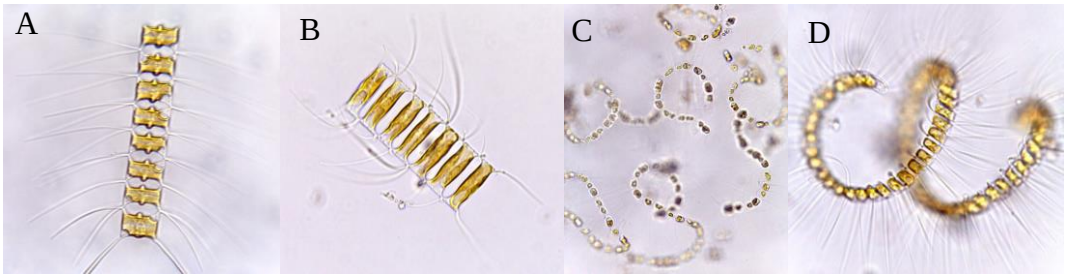

Figure 10. LM images of various species in the genus *Chaetoceros*. (A) *C. didymus* taken at 400× from 8 Oct 2015 sample, (B) *C. decipiens* taken at 400× from 31 Jan 2017 sample, (C) *C. socialis* taken at 400× from 10 Sept 2015 sample, (D) *C. debilis* taken at 400× from 26 Feb 2016 sample.

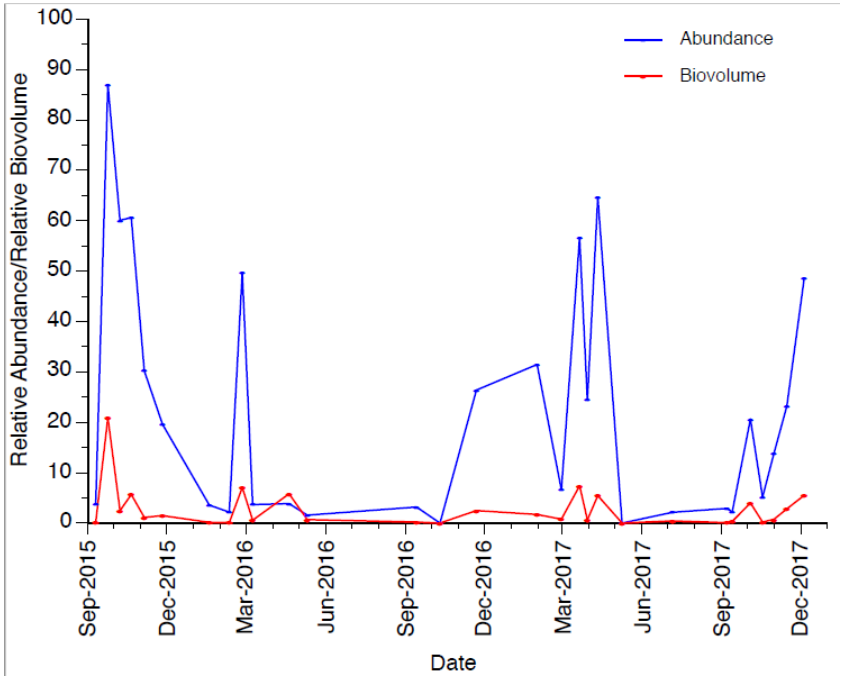

Figure 11. Relative abundance and relative biovolume of cells in the genus *Chaetoceros* in San Francisco Bay from September 2015 to December 2017. Data shown include cell counts for *C. affinis, C. constrictus, C. curvisetus, Chaetoceros debilis, C. decipiens, C. didymus, C. socialis,* and *C. tortissimus.*

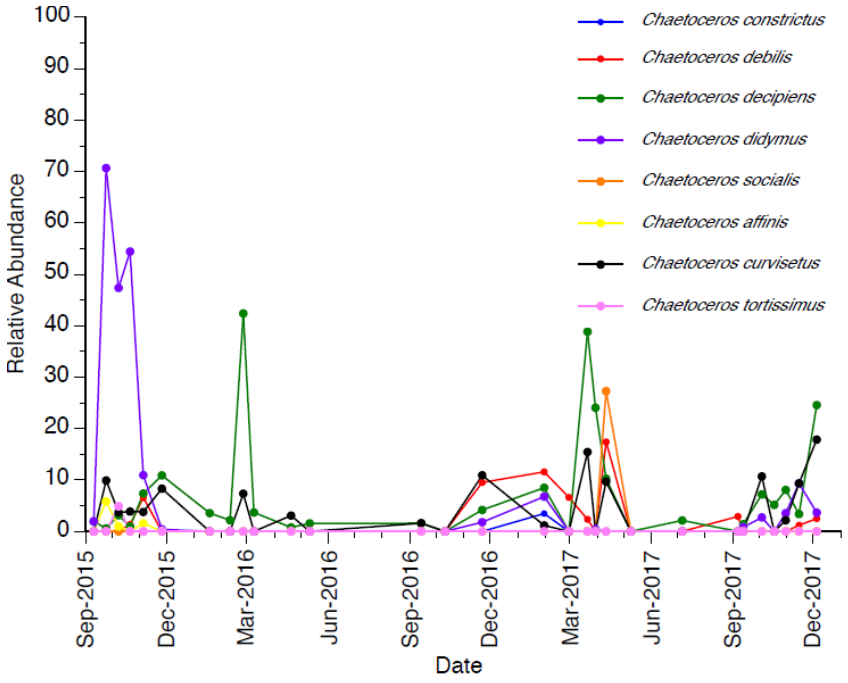

Figure 12. Relative abundance and relative biovolume of eight *Chaetoceros* species in San Francisco Bay from September 2015 to December 2017.

The most common *Chaetoceros* species was *C. decipiens*, which occurred 86.21% of the time (Figure 13). Despite its common occurrence, this species had a relative abundance of greater than 25% on only two occasions. On the other hand, the species *C. didymus* occurred in only 48.28% of the samples, but had very high relative abundances (70.68%, 47.36%, 54.44%) on three consecutive sample dates (24 Sept 2015, 8 Oct 2015, and 21 Oct 2015). *C. debilis* and *C. curvisetus* also appeared regularly (34.48% of the time and 55.17% of the time, respectively). Of the other species, *C. affinis* appeared only three times, and *C. constrictus, C. socialis,* and *C. tortissimus* appeared only once.

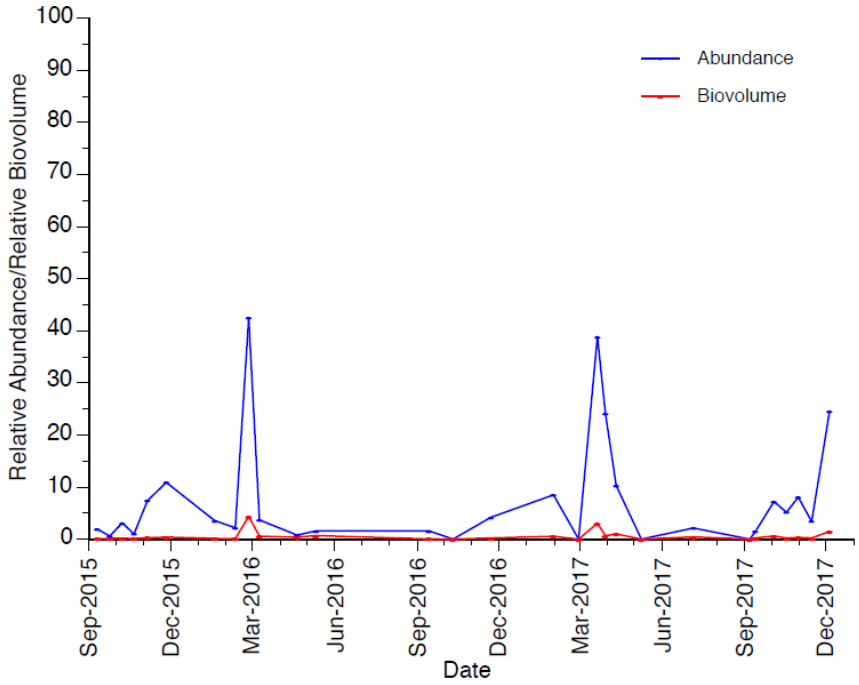

Figure 13. Relative abundance and relative biovolume of *Chaetoceros decipiens* in San Francisco Bay from September 2015 to December 2017.

Individually, the *Chaetoceros* species are relatively small cells and contributed little to total biovolume on any of the sample dates (Figure 6). Even the most abundant *Chaetoceros* species never contributed greater than 10% of the biovolume of a given sample. When all *Chaetoceros* species are grouped together, they accounted for greater than 10% of the biovolume of a sample only once (24 Sept 2015, 20.88%) (Figure 11).

Skeletonema costatum

Skeletonema costatum was a unique species because of large changes in its relative abundance throughout the sampling period (Figures 5 and 14). The species was observed in 75.86% of the samples but fluctuated between 0% and 93.08% relative abundance (Figure 15). High relative abundance was observed between March and September of 2016 and 2017, with blooms observed in April of 2016 and May of 2017. During these seasonal highs, relative abundance exceeded 50% on four dates and exceeded 85% on three dates. Much lower relative abundances were seen between October and February of these years, with relative abundance exceeding 15% on only one occasion (28 Feb 2017).

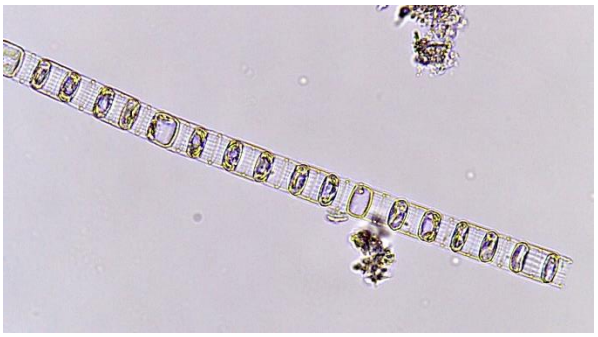

Figure 14. LM image of *Skeletonema costatum* taken at 400× from the 21 Oct 2015 sample.

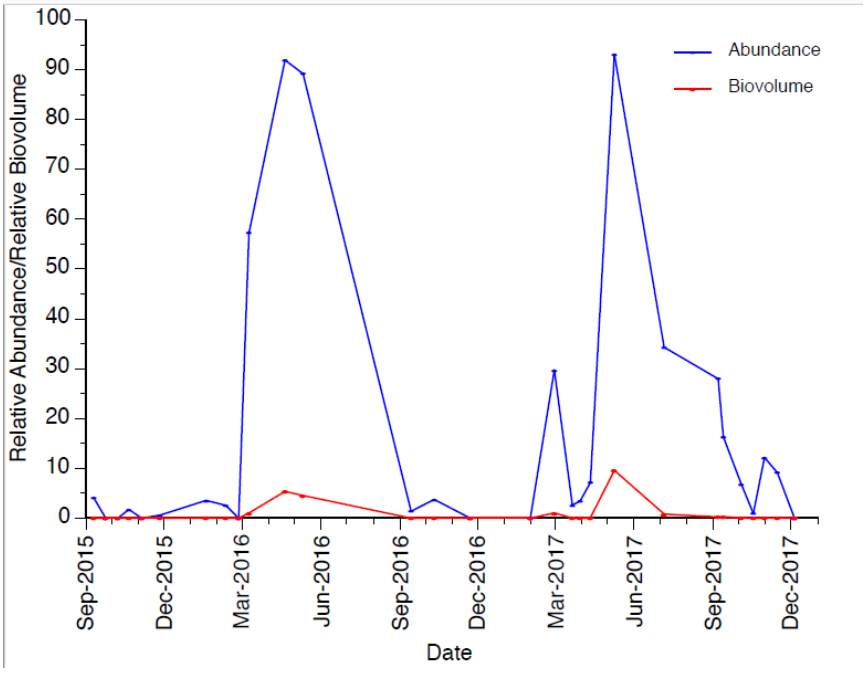

Figure 15. Relative abundance and relative biovolume of *Skeletonema costatum* in San Francisco Bay from September 2015 to December 2017.

Despite seasonal increases in the relative abundance of *Skeletonema costatum*, it never exceeded 10% of the biovolume of a sample (Figures 6 and 15). Even when this species made up 93.08% of the cells seen on 9 May 2017, it only accounted for 9.59% of the biomass of the diatoms due to its small size.

Pseudo-nitzschia sp.

The *Pseudo-nitzschia* sp. seen in this study occurred in 51.72% of the samples, but on most of these occasions only a few cells were observed (Figures 5 and 16). There was one notable exception in which this species made up 41.47% of the cells observed and 39.17% of the biovolume (6 July 2017) (Figure 17). Throughout most of the year both the relative abundance and biovolume of this taxon were quite low when it was observed. *Pseudo-nitzschia* sp. was seen, although at varying abundances, every September and March during the sample period.

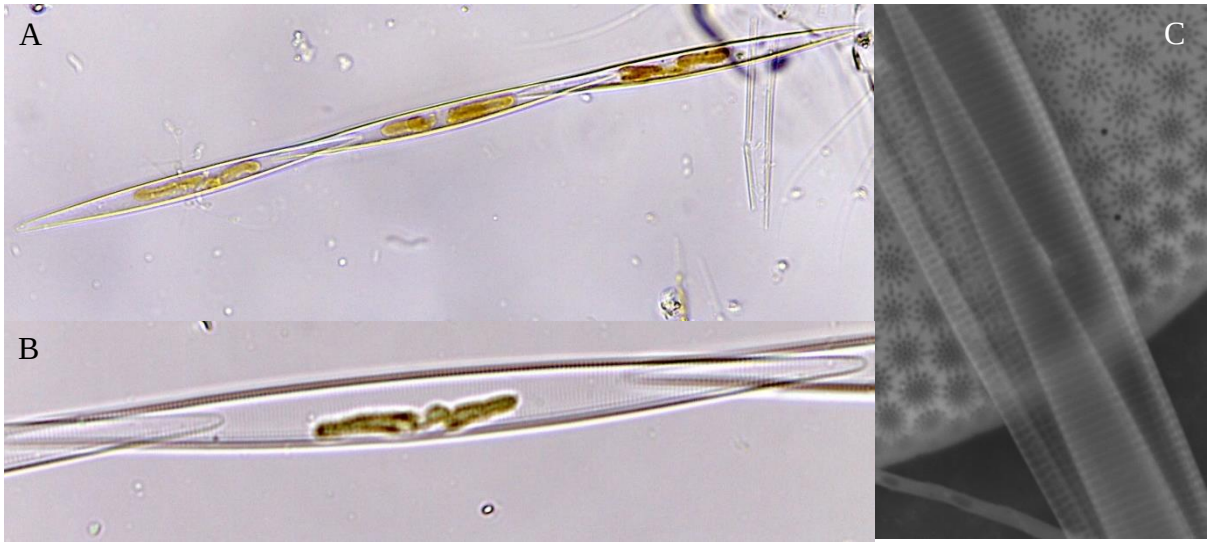

Figure 16. (A) LM image of *Pseudo-nitzschia* sp. taken at 100× on 10 Sept 2015, (B) LM image of *Pseudo-nitzschia* sp. taken at 400× from the 10 Sept 2015 sample, (C) SEM image of *Pseudo-nitzschia* sp. taken at 4000× from the 21 Oct 2015 sample.

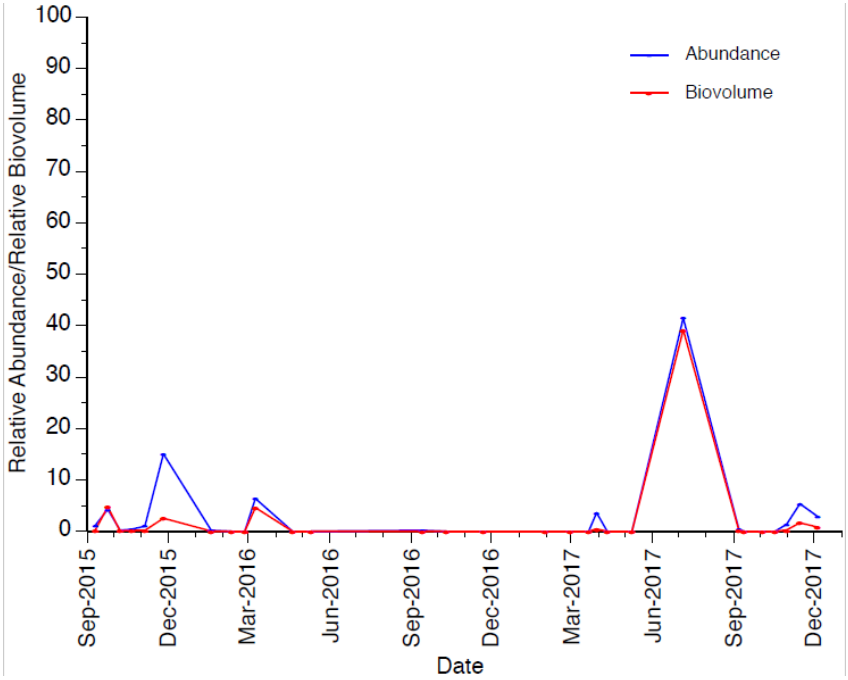

Figure 17. Relative abundance and relative biovolume of *Pseudo-nitzschia* sp. in San Francisco Bay from September 2015 to December 2017.

Species Diversity and Evenness

Several measures of diversity were calculated for each sample. Species richness varied substantially, from a high of 24 (21 Oct 2015) to a low of 6 (9 May 2017) (Figure 3). The majority of the samples

(65.52%) had a species richness between 10 and 19, with a smaller number of dates below 9 (20.69%) and above 20 (13.79%). Species richness appeared to vary seasonally, generally reaching higher values in the fall and lower values in the spring and summer (Figure 3). Of the 16 samples with species richness greater than 15, 14 were from the months of September through December. Conversely, 11 of the 13 samples with a species richness of 14 or lower were collected between January and July.

Diversity, measured by the Shannon-Wiener Index, also varied greatly throughout the year from a high of 2.37 (15 Nov 2017) to a low of 0.30 (9 May 2017) (Figure 18). A majority (62.1%) of the samples showed a diversity between 1 and 2. Only 17.24% of the samples showed diversity above 2, and 20.69% showed diversity below 1. Seasonal patterns in diversity were less defined than in species richness, although it is important to note that the two highest diversity values were calculated in samples from November and December and the three lowest diversity values were calculated in samples from April and May (Figure 18). The evenness of the samples varied throughout the year, from a high of 0.79 (15 Nov 2017) to a low of 0.17 (9 May 2017) (Figure 18). Most of the samples (72.41%) had an evenness of above 0.50. Of the samples with an evenness of less than 0.50, half of them were very low, less than 0.30.

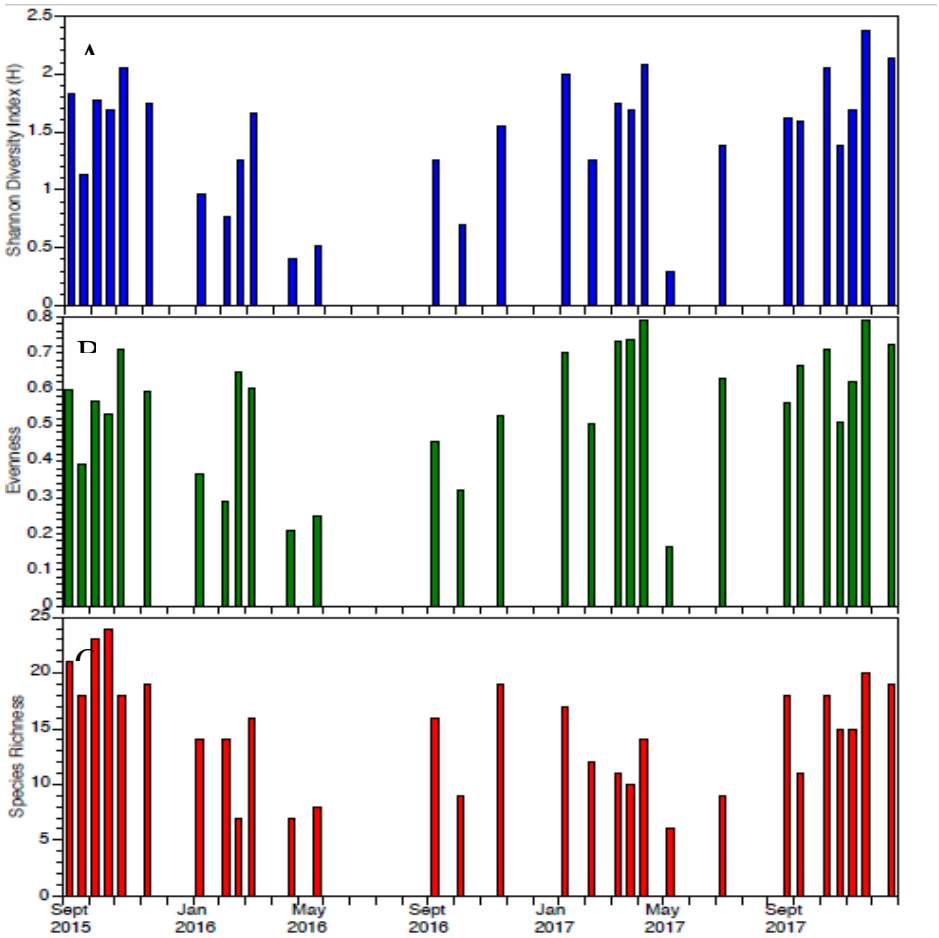

Figure 18. Diversity measures of diatom assemblages in San Francisco Bay from September 2015 through 2017. (A) The Shannon-Weiner Index of diversity, (B) evenness, (C) species richness.

Environmental Data

Temperature, salinity, and rainfall data from before, during, and after the sampling period demonstrated consistent seasonal yearly trends within San Francisco Bay and showed the effect of the recent drought on these trends (Figure 19). There were four yearly cycles in both salinity and temperature. Each year, temperature climbed consistently through the spring and summer and peaked in August or September. Temperature peaks during this time period were 18.96 C (26 Sept 2014), 18.73 C (31 Aug 2015), 16.97 C (1 Sept 2016), and 17.87 C (18 Sept 2017). Water temperature cooled more rapidly during the winter, reaching its lowest point in January or February. The lowest temperature recorded each winter was 10.68 C (1 Jan 2014), 12.46 C (6 Jan 2015), 11.06 C (31 Jan 2016), and 9.63 C (28 Feb 2017). Sampling for this study occurred across a wide range of temperatures (Figure 19). The highest temperature on a sample date was 17.71 C (13 Sept 2017) and the lowest was 9.63 (28 Feb 2017).

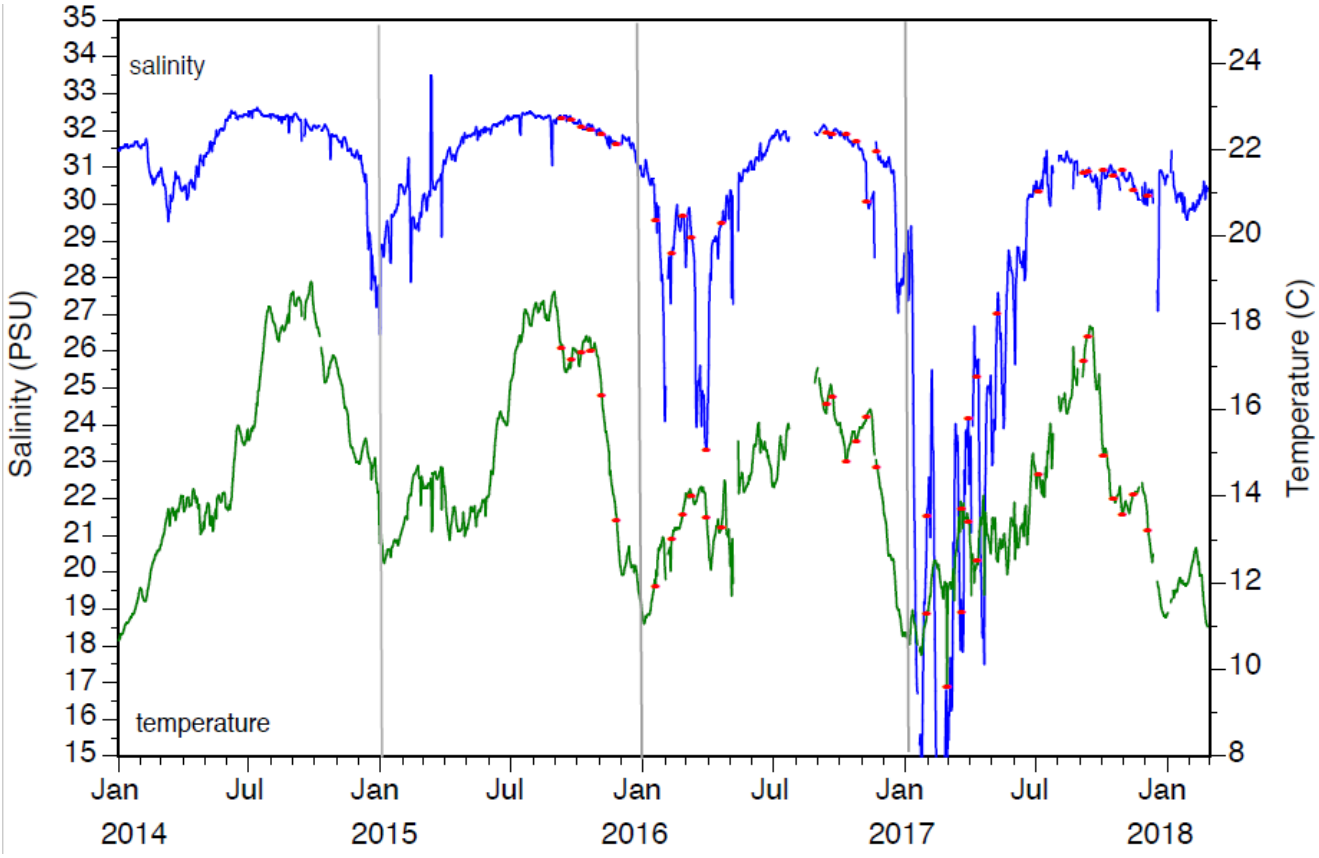

Figure 19. Salinity and temperature in San Francisco Bay from January 2014 to February 2018. Sampling dates indicated by red symbols. (Data from the Bodega Ocean Observing Node (BOON))

Salinity also followed a yearly pattern from 2014-2016. At the beginning of 2017, however, the pattern altered and there was a massive reduction in salinity for a sustained period of time. During the usual yearly cycle, seen in 2014-2016, salinity remained high from May through December, ranging between 31 and 33 PSU. In these years salinity peaked at 32.62 PSU (13 July 2014), 32.50 PSU (28 July 2015), and 32.15 PSU (9 Sept 2016). This was followed by a decline in salinity characterized by drastic and repeated reductions between December and March. From 2014-2016, salinity never fell below 23.25

PSU. Beginning in January of 2017, a different pattern is seen in which salinity drops to much lower levels and continued to show periodic downward spikes through June. During this period salinity was reduced to a low of 7.24 PSU (22 Feb 2017). This pattern corresponded to increased rainfall during this time (Figure 20).

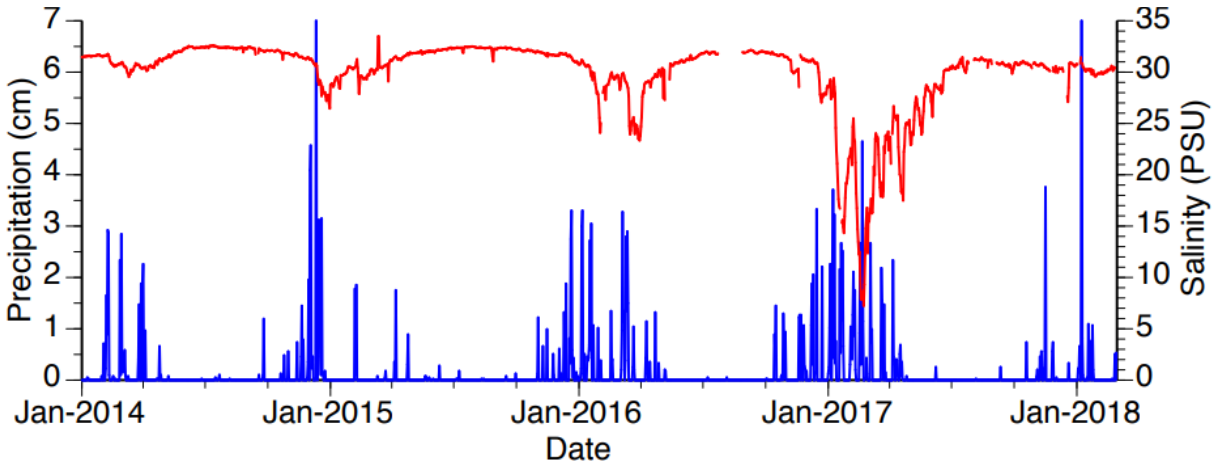

Figure 20. Precipitation and salinity in San Francisco Bay from January 2014 to February 2018. (Data from National Weather Service Forecast Office (NOAA) and the Bodega Ocean Observing Node (BOON)).

The pattern of rainfall in San Francisco Bay was inversely correlated with salinity (Figure 20). Similar seasonal rainfall patterns occurred in 2014, 2015 and 2016. During these years, rainfall was observed periodically between the months of September and March, but the low amounts represented drought conditions. Changes in salinity mirrored these rainfall patterns. At the end of 2016 and the beginning of 2017, rainfall between December and June was nearly constant, reflecting the end of the drought in this part of California. The corresponding changes in salinity were drastic and extended past the rainy season (Figure 20).

Other environmental data including light transmittance in the water column, fluorescence of chlorophyll, and tidal patterns throughout the sampling period were also examined (Figures 21, 22 and 23). Sampling occurred across a wide range of conditions and at various points across the tidal cycle. Relative light transmittance ranged from 0 (10 Oct 2014) to 3.21 (16 Oct 2015), and fluorescence values exhibited a high of 1.85 (30 Aug 2016) to non-detectable levels (12 Jan 2018). The highest tidal height during sampling was 2.16 m (13 Dec 2016) and the lowest was -0.51 m (27 May 2017).

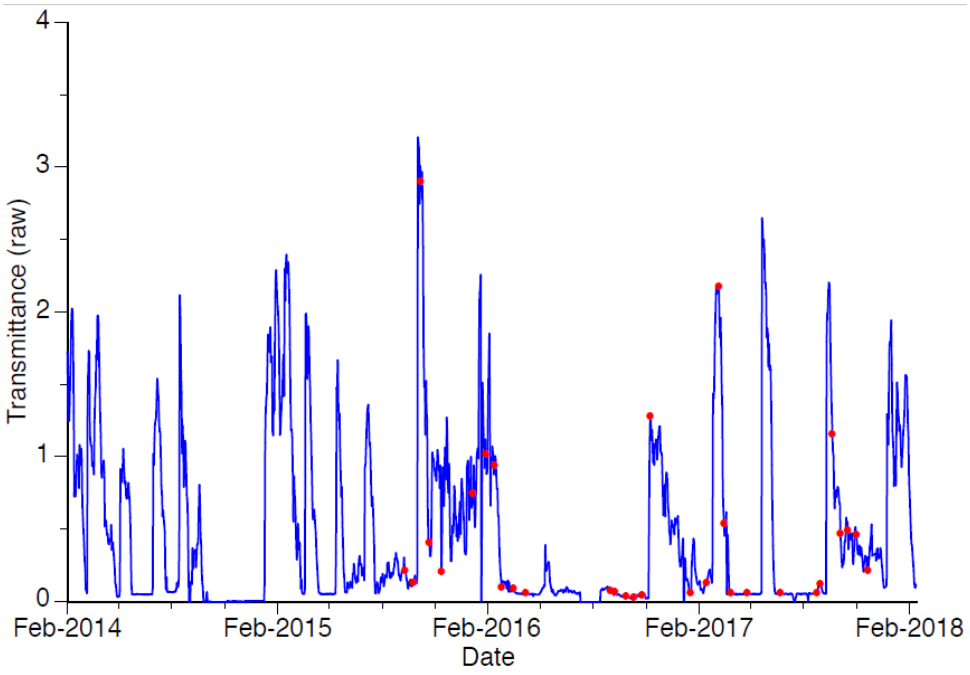

Figure 21. Raw transmittance values (relative values of water clarity) in San Francisco Bay from February 2014 to February 2018. Sample dates indicated with red symbols.

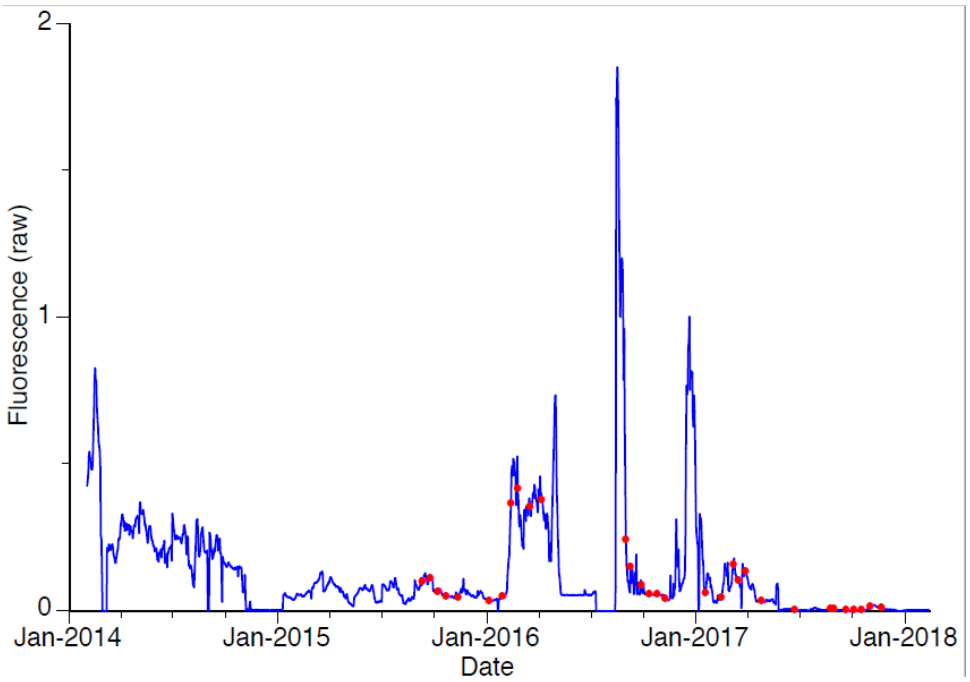

Figure 22. Raw fluorescence values (proxy for chlorophyll *a* concentrations) in San Francisco Bay from January 2014 to February 2018. Sample dates indicated with red symbols.

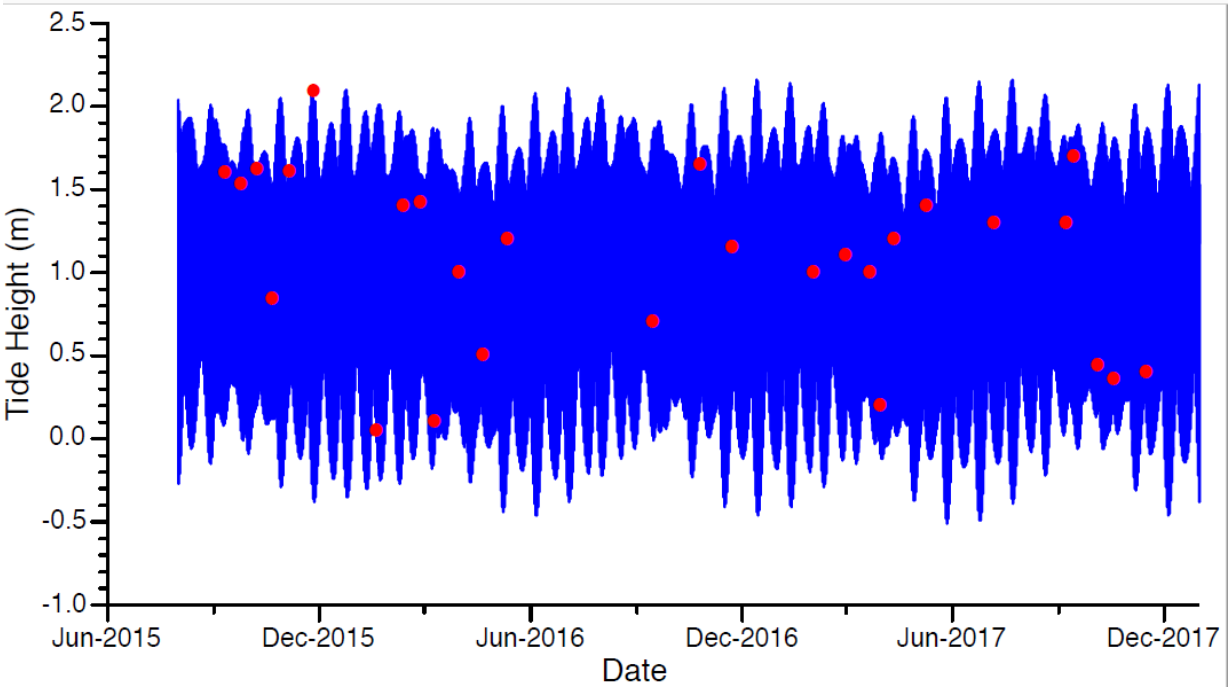

Figure 23. Tidal cycle at the Golden Gate Strait (mouth of San Francisco Bay) from August 2015 through January 2018. Sample dates indicated with red symbols.

Statistics

Non-metric multidimensional scaling (NMDS) analyses allowed for a comparison of the community composition across the different sampling dates. When relative abundance data were used in the ordination, several distinct clusters were formed (Figure 24). These clusters appeared to be based on season. Of the four seasons, which were determined prior to NMDS analysis and based off of rainfall patterns, fall assemblages formed the tightest cluster (Figure 24). Spring samples also formed a cluster, while winter sampling dates were more spread out. There were insufficient sampling dates during the summer season to determine whether this season formed a cluster.

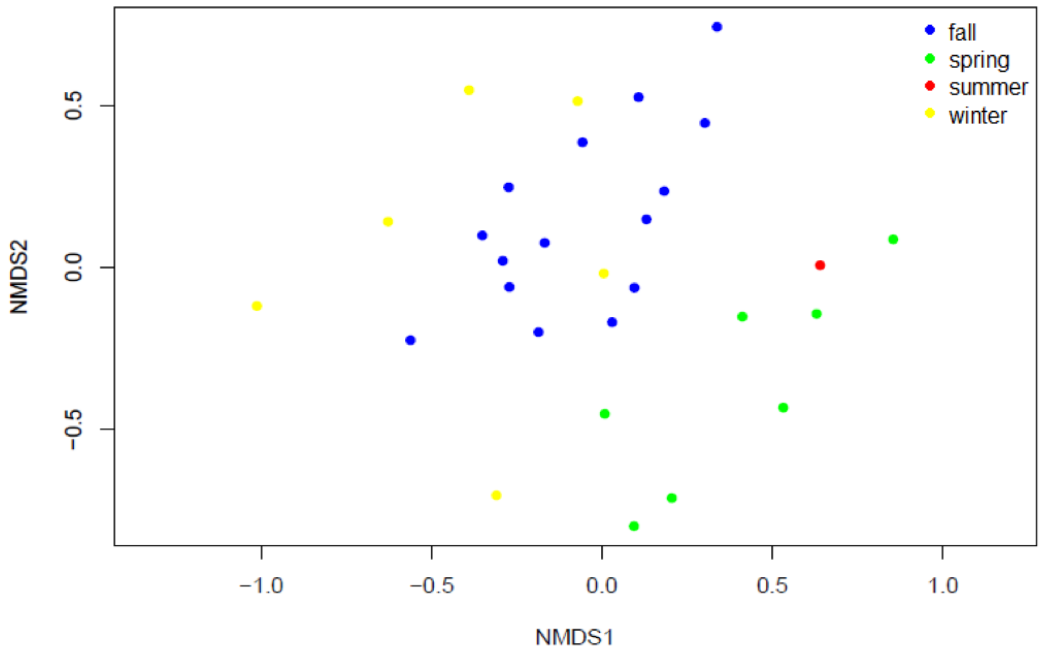

Figure 24. NMDS ordination of samples based on relative abundance of diatom species in San Francisco Bay, color-coded by season.

When biovolume data was used in the ordination, similar clusters were formed as seen with relative abundance (Figure 25). Fall samples clustered most tightly, spring assemblages formed a cluster, and winter dates were more spread out. High-volume species were plotted on NMDS ordination using biovolume data, showing which species were important contributors to biovolume within seasonal clusters (Figure 26). The taxa *Tropidoneis antarctica*, *Biddulphia mobiliensis*, *Lithmodesmium undulatum*, *Streptotheca tamensis*, *Pleurosigma* sp. 1, *Rhizosolenia setigera*, and the Centrics all occur within the fall cluster; while *Skeletonema costatum*, *Chaetoceros curvisetus*, and *Thalassiosira* spp. appear to align within the spring cluster.

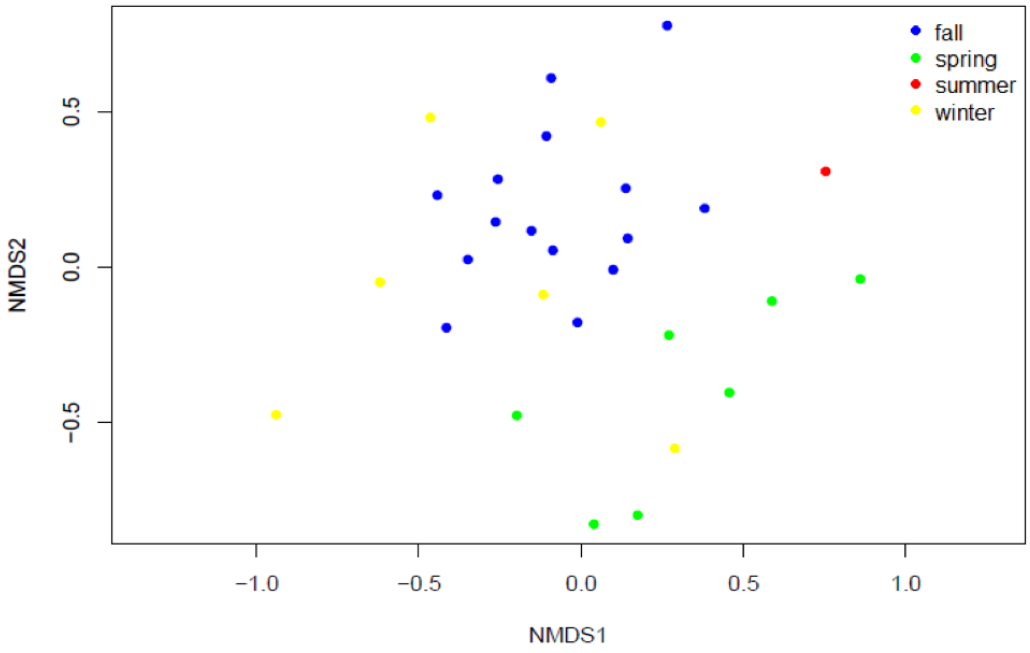

Figure 25. NMDS ordination of samples from San Francisco Bay based on biovolume of species, color-coded by season.

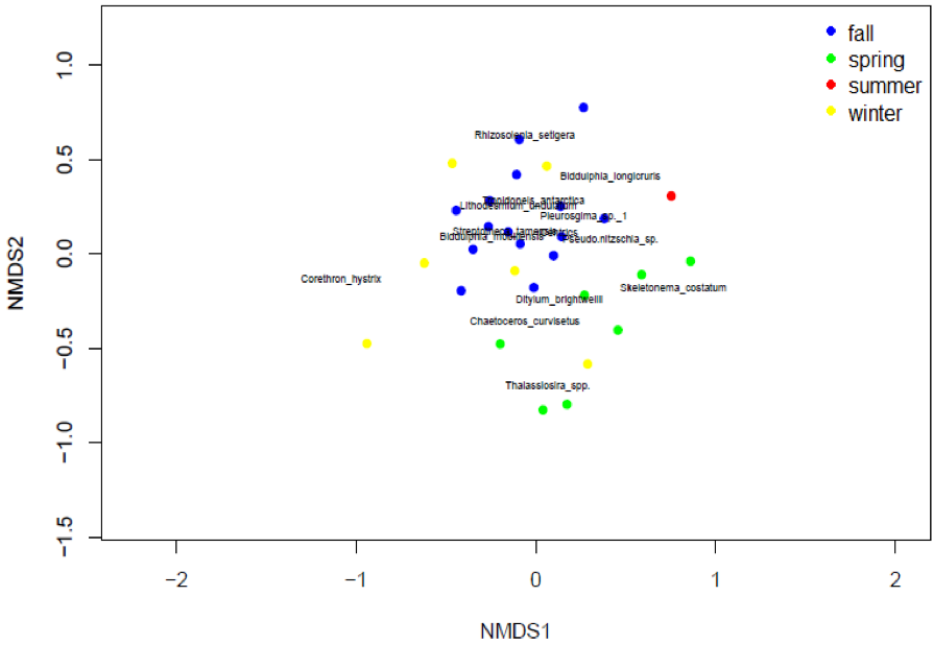

Figure 26. NMDS ordination of diatom taxa from San Francisco Bay based on biovolume, color-coded by season, with highest biovolume species indicated.

Analysis of the effect of the environment on community composition showed that temperature could be an important factor. A PERMANOVA evaluating the effect of temperature on community similarity

based on biovolumes per taxa indicated that temperature could predict 16-17% of the variation in community similarity based on biovolumes per taxa across samples ($p = 0.004$). Temperature could not significantly predict the variation in relative abundance. Salinity and transmittance were not significantly predictive of variation in either relative abundance or biovolume (PERMANOVA $p > 0.05$).

DISCUSSION

Hutchinson's (1961) fundamental question of how so many species can coexist in a seemingly unstructured habitat forms the basis for many studies of phytoplankton community composition. Studies of species succession address this question from a specific angle, by asking what changes in community composition occur over time and what could be driving those changes. We examined species succession in a unique area of San Francisco Bay over a 2-and-a-half-year period and our results confirm previous observations of the coexistence of a wide variety of species in San Francisco Bay and demonstrate seasonal patterns in the species of phytoplankton found in the Bay.

Similar to previous studies in other areas (e.g., Karentz & McIntire 1977; Karentz & Smayda 1998; Watanabe et al. 2017) and in San Francisco Bay (Cloern et al. 1985; Cloern & Dufford 2005), we found that relative abundance and biovolume of the phytoplankton community differed across the seasons. The clusters seen in the NMDS plots indicate that both relative abundance and biovolume of samples were more similar to other samples collected during the same season than during a different season (Figures 24 and 25). In particular, the samples from the fall season cluster most tightly together, suggesting that the community composition during the fall months is more consistent from year to year than in other seasons. This is likely because there is less variation in environmental factors from year to year during the fall months.

The phytoplankton community in San Francisco Bay has been well documented by the USGS since 1992, and the taxa we observed matched closely with those observed by the USGS. Although not as many taxa were observed in this study as appear in the 25-year USGS dataset, almost all the taxa identified in this study overlapped with those observed by USGS. It is important to note that there was great variation in the taxa seen each year by USGS and not all of the species we observed occurred every year in the USGS study. Of the four additional species observed in this study, two were from genera (*Rhizosolenia* and *Chaetoceros*) that were well-represented in the USGS dataset. The similarity in species observations to the USGS dataset is interesting because of the difference in sampling sites. Sampling for the USGS study occurred on a transect from South Bay, through Central Bay, San Pablo Bay, and Suisun Bay, all the way to the mouth of the San Joaquin River (Cloern 2018). Our sample site was significantly different in that it was situated along the Golden Gate Strait in an area that receives much less fresh water than Suisun and San Pablo Bays. Despite these differences, similar species were seen, which could indicate that the Bay is well-mixed or that many of the species observed occur in multiple places and can tolerate a wide range of conditions.

Of the diversity measures used in this study, the clearest pattern was seen in species richness across sample dates. Samples with species richness of greater than about 15 grouped together while samples with lower species formed another group (Figure 3). It is clear that this higher group is almost entirely comprised of samples from September through January, and the lower group of February through July (Figure 3). There is a clear distinction between the fall/winter months and the spring/summer months. Although there is a general trend of higher species richness in the fall/winter and lower species richness in the spring/summer, the samples from 9 Mar 2016, 13 Sept 2017, and 11 Oct 2016 are exceptions to this trend. The high species richness (16) on 9 Mar 2016 may be explained by a drop in the number of

Centrics and an increase in other taxa present. Although this date marked the beginning of a bloom of *Skeletonema costatum*, it also marked a decline in the relative abundance of Centrics from 38.35% on the previous sampling date to 6.58% on this date. The decline of this group during this period of time most likely allowed for more rapid growth of less dominant taxa, which increased the species richness. The samples from 13 Sept 2017 and 11 Oct 2016 both had lower species richness than other samples from the fall months. In the September 13 sample, this appears to be because *Grammataphora marina* and *Rhizosolenia setigera* are very abundant, constituting over half of the relative abundance when taken together. Similarly, the October 11 sample was dominated by a bloom of the Centrics, which made up 81.62% of the sample. These blooms lowered the species richness of the sample that was collected.

Environmental patterns were also examined in this study, and the dataset was unique because it included data from three years of the drought and the period of extreme rainfall in the beginning of 2017 that ended the drought. This rainfall event, which lasted from approximately January to June of 2017, caused salinity at the sampling location to decrease far beyond what was seen in the previous three years (23-33 PSU). During this time, salinity varied between 7.24 PSU and approximately 30 PSU. Rainfall of greater than 2.5 cm did occur sporadically in 2014-2016 without causing large decreases in salinity. It appears that continuous periods of rainfall are necessary to cause sustained decreases in salinity in this area of the Bay. This period of time was a unique opportunity to observe which phytoplankton species persisted and dominated at low salinity.

Several species that occurred prior to the period of sustained rainfall persisted during this period of low salinity at abundances that were not significantly different than at any other point. These included *Ditylum brightwellii, Asterionella japonica, Chaetoceros curvisetus, Chaetoceros decipiens,* and *Skeletonema costatum*. Although *Skeletonema costatum* was present throughout much of the study, one of its blooms occurred during the period of low salinity. This species also bloomed during the same month of the previous year, however, so this may or may not be strictly due to the unusually low salinity. There were several taxa that were much more abundant between January and June of 2017 than during the rest of the study. One of these was *Leptocylindrus danicus*, which made up 40% of the sample on two occasions (31 Jan 2017 and 28 Feb 2017) during this time period, but otherwise never exceeded 5.02%. *Chaetoceros debilis* and *Chaetoceros socialis* also made up significant percentages of the sample, as did *Thalassiosira* spp. It is interesting to note that the almost ubiquitous Centrics almost disappeared during this period, suggesting that they are less tolerant to lower salinities than the abovementioned taxa. In terms of biovolume, *Corethron hystrix*, *Thalassiosira* spp., and *Leptocylindrus danicus* all had greater relative biovolumes during this period than at other times in the study. *Ditylum brightwellii* maintained its high relative biovolume, but the Centrics accounted for only a small percent of total biovolume. These patterns suggest that there is a difference in salinity tolerance between different taxa, and that some thrive under drought conditions while others thrive during periods of heavy rainfall. As extreme weather events occur with increasing frequency, these data could be used to predict which species might become more prevalent in the Bay during these events.

In our analysis of environmental factors, temperature was the most useful factor in predicting variation in biovolume, although it was not a significant predictor of relative abundance. Temperature has been previously examined in relation to phytoplankton growth rate, both in the laboratory and the field (Edwards et al. 2016; Eppley 1972; Palmisano et al. 1987; Verity 1982). In his 1972 review, Eppley describes the major trends seen across many laboratory studies that phytoplankton growth rate increases gradually then exponentially with increases in temperature up to 40 C (Eppley 1972). Above 40 C growth rates decline rapidly. He also concluded that different plankton species have different optimum temperatures, based on a review of laboratory studies. Other studies have examined the interaction of

temperature and light (e.g., Edwards et al. 2016; Palmisano et al. 1987; Verity 1982) and temperature and nutrient supply on phytoplankton growth rates (Marañón et al 2014; López-Urrutia & Morán 2015). Growth rates continue to increase with temperature under optimal light conditions, but not when light is limited (Edwards et al. 2016; Palmisano et al. 1987; Verity 1982). Similar interactions can occur when nutrients are limited to varying degrees (López-Urrutia & Morán 2015). While previous studies (Cloern et al. 1985; Cloern & Dufford 2005) of San Francisco Bay have found light to be an important predictor of growth rate, our analyses did not show that light transmittance could significantly predict variation in relative abundance or biovolume. Others have studied the effect of increased temperature on community composition, and it is widely held that as temperature increases, large cells contribute relatively less and small cells contribute relatively more (López-Urrutia & Morán 2015; Mousing et al. 2015). As the ocean warms, understanding the effect of temperature on phytoplankton growth becomes increasingly important, since they are the basis of the marine food chain. Future studies of phytoplankton communities in San Francisco Bay may benefit from including temperature as a possible predictor of relative biovolumes.

In order to continue to better understand the community of phytoplankton in this area of San Francisco Bay, further investigation into the group of Centrics and other environmental variables should be conducted. Scanning electron microscopy can be used to distinguish at a species level those individuals placed in the Centrics group, and to determine their relative abundance. Since this group occurred on all sampling dates, it is important to understand which individual species make up this abundant group. Other environmental factors such as nutrient concentrations, water column mixing, and solar radiation should also be examined along with temperature and salinity in the future to understand how these processes individually and collectively drive changes in the phytoplankton community. Additionally, much can be learned from keeping clonal cultures of key species in the laboratory. These next steps will allow for a more complete understanding of the complexities of species succession of planktonic diatoms in San Francisco Bay.

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