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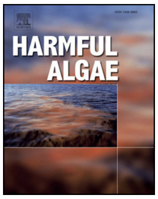

A decade and a half of *Pseudo-nitzschia* spp. and domoic acid along the coast of southern California

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ABSTRACT

Blooms of the marine diatom genus *Pseudo-nitzschia* that produce the neurotoxin domoic acid have been documented with regularity along the coast of southern California since 2003, with the occurrence of the toxin in shellfish tissue predating information on domoic acid in the particulate fraction in this region. Domoic acid concentrations in the phytoplankton inhabiting waters off southern California during 2003, 2006, 2007, 2011 and 2017 were comparable to some of the highest values that have been recorded in the literature. Blooms of *Pseudo-nitzschia* have exhibited strong seasonality, with toxin appearing predominantly in the spring. Year-to-year variability of particulate toxin has been considerable, and observations during 2003, 2006, 2007, 2011 and again in 2017 linked domoic acid in the diets of marine mammals and seabirds to mass mortality events among these animals. This work reviews information collected during the past 15 years documenting the phenology and magnitude of *Pseudo-nitzschia* abundances and domoic acid within the Southern California Bight. The general oceanographic factors leading to blooms of *Pseudo-nitzschia* and outbreaks of domoic acid in this region are clear, but subtle factors controlling spatial and interannual variability in bloom magnitude and toxin production remain elusive.

1. Introduction

The Southern California Bight (SCB) is a major portion of the western boundary of North America and the U.S. west coast. The feature is generally defined as an approximately 700 km coastline extending from Point Conception, California south to beyond the U.S. border (Fig. 1) (Hickey, 1992). The physical oceanography of the Bight is complex, and is distinct from the coastal ocean to the north of Point Conception, and the California Current to the west; yet, this region shares a degree of continuity with, and influence from these features. The Channel Islands throughout the Bight act to buffer the southern California coast from much of the direct impact of the otherwise oceanic California Current, as well as moderate meteorological effects along the coast. The curved orientation of the SCB, compared to the north-south trending coastline of the rest of the west coast, also acts to buffer the southern coast of California to prevailing winds.

A Mediterranean-type climate dominates throughout the SCB. Annual average daily highs in air temperatures in the Los Angeles area are ≈20-26 °C, while annual sea surface temperatures generally range ≈14-21 °C. Wind events, rainfall and river discharges are highly seasonal. The majority of the rainfall in the region occurs during winter months, and strong wind and upwelling events are dominant during winter and spring. Within seasons, these events are episodic and short-lived, generally lasting a few days. Average annual rainfall in the region is historically low (< 40 cm) but interannual variability in rainfall can be great. An ‘extreme-to-exceptional’ drought during 2012–2016 was

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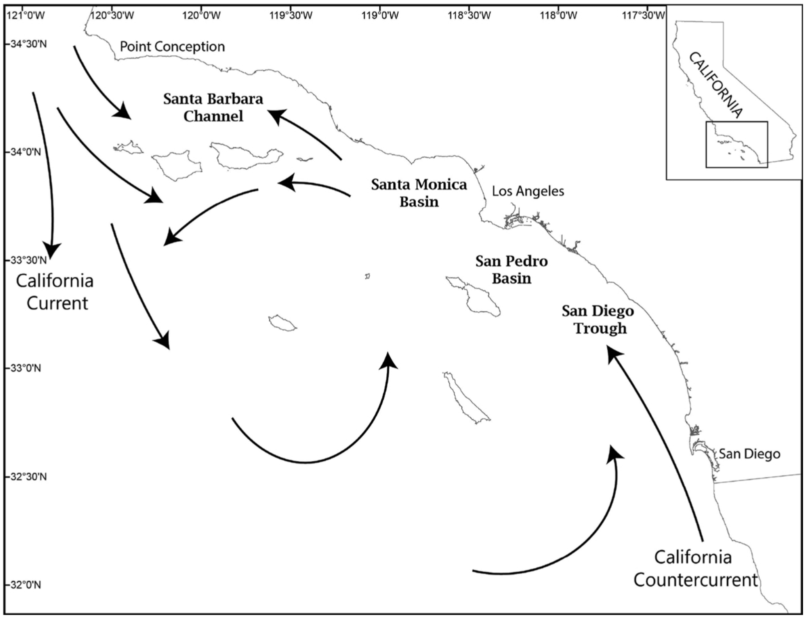

Fig. 1. Map of the Southern California Bight (Point Conception to San Diego) indicating the general circulation pattern within the region. Modified from Hickey (1992). Inset shows the location of the Bight along the California coast.

followed by the highest average rainfall in the state in 122 years during the winter of 2016–2017 (http://www.latimes.com/local/lanow/la-me-g-california-drought-map-htmlstory.html) (Griffin and Anchukaitis, 2014).

The SCB is a coastal ocean region of extensive economic, environmental and cultural importance as well as increasing human impact. The population of the Los Angeles-Long Beach area alone was estimated at > 18 million people in 2015 (Annual Estimates of the Resident Population: April 1, 2010 to July 1, 2015; Source: U.S. Census Bureau, Population Division; Release Date: March 2016). Beach visitations in the SCB a decade ago averaged approximately 129 million per year (Dwight et al., 2007), and have almost certainly increased concurrently with the population over the last decade. Coastal property development throughout most of the region is extensive, as are commercial and other activities. The ports of Los Angeles and Long Beach are the two busiest ports in the U.S. and together handle over 400 billion USD in trade annually (http://labusinessjournal.com/news/2017/jul/17/june-imports-surge-l-long-beach-ports/). Additionally, some coastal areas in the SCB have significant agricultural activities.

Nutrient loading within the SCB differs greatly throughout the region and these differences have potentially important impacts on algal blooms. Land use varies significantly within the SCB, from largely undeveloped land (e.g. from San Clemente to Oceanside, San Diego County) to areas draining a mixture of agricultural and urban landscape (e.g. Ventura County) to highly urbanized regions (Los Angeles and Orange Counties). This mosaic of land use results in variability in the magnitude and type of nutrient loading to the coastal ocean, but anthropogenic nutrients appear to constitute significant sources of growth-stimulating nutrients for coastal phytoplankton in some regions (Howard et al., 2014; Kudela et al., 2008; Reifel et al., 2013). Recent studies suggest these inputs may have ramifications for the resilience of coastal ecosystems (Capone and Hutchins, 2013) and have significantly affected near-shore waters in these urban areas. For example, Howard et al. (2014) reported that wastewater discharge from Publicly Owned Treatment Works (POTW) in highly urbanized areas of the SCB contributed similar amounts of nitrogen to nearshore coastal ecosystems as wind-driven upwelling events, which was the most significant source of nitrogen. Additionally, nitrification of ammonium from wastewater effluent has been shown to provide a significant source of nitrogen utilized by the biological community (McLaughlin et al., 2017). Increased anthropogenic input to ocean ecosystems is not unique to the SCB or the impact of POTW, but rather appears to be a growing problem globally (Ren et al., 2017). The full impact of increased anthropogenic input on phytoplankton communities in the Bight has been difficult to characterize because there are no phytoplankton biomass data that predate POTW discharges in the region. The findings of Howard et al. (2014) and McLaughlin et al. (2017) along the southern California coast are consistent with the observations of Nezlin et al. (2012) that algal bloom 'hot spots' along the coast were co-located with POTW outfalls. Additionally, on small spatial scales, wastewater effluent and terrestrial runoff have been shown to increase phytoplankton biomass and affect patterns of phytoplankton productivity and community composition (Corcoran et al., 2010; Reifel et al., 2013). Furthermore, studies in the SCB have concluded that patterns of chlorophyll variability and productivity in the nearshore coastal waters are not always attributed to classical coastal upwelling (Corcoran et al., 2010; Kim et al., 2009; Nezlin et al., 2012).

2. *Pseudo-nitzschia* blooms and domoic acid along the west coast of North America

The west coast of North America has been the site of a few well-documented harmful algal bloom (HAB) issues, as well as some emerging ones (Lewitus et al., 2012). These issues include a long history of paralytic shellfish poisoning (PSP; caused by saxitoxin contamination) along the northwestern U.S. coast and Canada dating to the 1700s, while outbreaks of amnesic shellfish poisoning (ASP; caused by domoic acid) have only been documented more recently along the west coast. Considerable environmental and seafood monitoring has been, and continues to be conducted along the western coast of North America due to the threat that these toxins pose to human and animal health.

Extensive field studies to understand the environmental factors leading to *Pseudo-nitzschia* blooms and domoic acid events along the northern sector of the west coast have been conducted off Washington state (Trainer et al., 2007, 2003), and to a lesser extent off Oregon (Du et al., 2016; McKibben et al., 2015) during the past few decades. Studies in coastal waters off Washington have characterized the Juan de Fuca eddy, located offshore from the mouth of the Juan de Fuca Straight, as a 'hot spot' for the development of toxic *Pseudo-nitzschia* blooms (Trainer et al., 2002, 2009). Contamination of beaches and inlets along the

Olympic Peninsula of Washington and Vancouver Island, British Columbia results when toxic waters from the eddy are transported onshore by prevailing weather and oceanographic conditions (Trainer et al., 2009).

Mexican coastal waters south of California have been less well-characterized with respect to *Pseudo-nitzschia* blooms and toxic events attributable to domoic acid, in contrast to findings along the U.S. and Canadian coasts. Multiple *Pseudo-nitzschia* species, including some toxic ones, have been reported from the coast of Baja California (García-Mendoza et al., 2009; Hernández-Becerril, 1998), and at least one published report to date has linked an animal mortality event in the region to the toxin (Sierra Beltrán et al., 1997).

Phytoplankton blooms along the coast of California have historically included a number of potentially harmful algae, including toxin-producing diatom species within the genus *Pseudo-nitzschia* (Buck et al., 1992; Fryxell et al., 1997; Lange et al., 1994). Other harmful species known to live along the California coast include numerous dinoflagellates (*Lingulodinium polyedrum* (Howard et al., 2008; Torrey, 1902), *Akashiwo sanguinea* (Jessup et al., 2009), *Prorocentrum micans* (Gregorio and Pieper, 2000), *Cochlodinium fulvescens* (Howard et al., 2012; Kudela and Gobler, 2012), *Alexandrium catenella* (Garneau et al., 2011; Jester et al., 2009) and *Dinophysis* spp.), and the raphidophytes *Heterosigma akashiwo*, *Chattonella marina* and *Fibrocapsa japonica* (Caron et al., 2010; Gregorio and Connell, 2000; Herndon et al., 2003; O'Halloran et al., 2006).

Paralytic shellfish poisoning along the California coast has been a long-standing health concern (Meyer et al., 1928), as it has farther north along the California coastline and in the Pacific Northwest (PNW); however, awareness of toxic events attributable to domoic acid is a more recent concern that has been documented along the California coast only within the last two decades. A seabird mortality event caused by domoic acid poisoning along the California coast was first linked to a *Pseudo-nitzschia* bloom in 1991 off central California (Work et al., 1993), and subsequently to a marine mammal mass mortality event in that region (Scholin et al., 2000). Circumstantial evidence exists that toxic *Pseudo-nitzschia* blooms, and mass mortality events resulting from these blooms, may have occurred for years prior to that date in and around Monterey Bay (Buck et al., 1992; Fritz et al., 1992; Greig et al., 2005; Walz et al., 1994). Kudela et al. (2003) identified four major blooms of *Pseudo-nitzschia* off central California during 1991, 1998, 2000, and 2002. Regardless of its role prior to the 1990s, domoic acid poisoning has been documented since then as a recurring threat along the entire coastline of California. Data collected by the California Department of Public Health indicate that domoic acid has been detected in shellfish tissue in virtually all years from 2003 to 2016, although the magnitude and geographic extent of the toxin has varied considerably by year and county (Fig. 2). In particular, counties in central California (north of the SCB) and the northern counties within the SCB (Santa Barbara and Ventura counties) have experienced the highest concentrations and most frequent occurrences of domoic acid contamination of shellfish (Fig. 2B,C).

3. *Pseudo-nitzschia* blooms and domoic acid in the Southern California Bight

Reports implicating toxic *Pseudo-nitzschia* blooms in large mortality events for seabirds and marine mammals off central California (Scholin et al., 2000; Work et al., 1993) and seabirds off Baja California (Sierra Beltrán et al., 1997) during the 1990s were followed by an unusual marine mammal mortality event in the SCB during 2002 that was eventually attributed to domoic acid poisoning (Torres de la Riva et al., 2009). These reports linked domoic acid in the particulate fraction of the plankton to animal mortality events, but they were by no means the first documentation of *Pseudo-nitzschia* blooms in the region. Lange et al. (1994) analyzed historical data of phytoplankton communities collected off Scripps Pier in La Jolla, located in San Diego County. Lange et al. (1994) reported high abundances of '*Nitzschia seriata'* (later recognized as a member of the genus *Pseudo-nitzschia*) present in the plankton throughout the 1930s, and sporadically through subsequent years, although no toxic episodes attributable to these diatoms were documented. Species of '*Nitzschia'* were also a common occurrence in Monterey Bay decades before toxin events there were attributed to this diatom group (Bolin and Abbott, 1962). An analysis of *Pseudo-nitzschia* frustules and domoic acid in a collection of sediment trap samples from the Santa Barbara Channel dating back to 1993 also demonstrated that the toxin was present in the region prior to the 2002 toxic event (Sekula-Wood et al., 2011). Barron et al. (2010) reported on analyses of sediment cores that revealed increased abundances of *P. australis* in the Santa Barbara Basin beginning around 1985.

3.1. Interannual variability in domoic acid in the SCB since 2002

Several studies since the 2002 mortality event have documented the presence and concentrations of particulate domoic acid in coastal waters of the Southern California Bight. A summary of that information (≈4500 measurements) indicates that domoic acid was present in all years, although there was significant year-to-year variability in maximal particulate concentrations observed (Fig. 3, Supplemental Fig. S1), as well as considerable spatial variability in the distribution of toxin in shellfish samples along the length of the SCB coastline (Fig. 2C,D). Domoic acid was documented throughout the Bight in 2003, undoubtedly a result of the increased awareness and monitoring efforts following the 2002 mortality event. High concentrations ($> 10\,\mu g\,L^{-1}$) of particulate domoic acid were observed during spring 2003 in the San Pedro Basin around and within the mouth of Los Angeles Harbor (Schnetzer et al., 2007), with lower concentrations documented to the north in the Santa Barbara Channel (Anderson et al., 2006) and to the south off San Diego (Busse et al., 2006).

In contrast to 2002 and 2003, relatively low concentrations of particulate domoic acid (generally $\leq 2\,\mu g\,L^{-1}$) were observed Bight-wide during 2004 for those regions that were studied (Anderson et al., 2009; Busse et al., 2006; Schnetzer et al., 2007). Domoic acid concentrations were also generally low during 2005 in most of the Southern California Bight. Coincidentally, a massive summer-fall bloom of the dinoflagellate, *Lingulodinium polyedrum* occurred along the entire coastline of the SCB during 2005 (Howard et al., 2008). Only the Santa Barbara Channel exhibited significant concentrations of particulate domoic acid during that year, with two exceptionally high values for the SCB, ≈18 and $\approx 50\,\mu g\,L^{-1}$ observed (Anderson et al., 2009). Toxin concentrations in Santa Monica Bay and the San Pedro Basin were generally extremely low or below the limit of detection ($0.01\,\mu g\,L^{-1}$ or $0.02\,\mu g\,L^{-1}$, depending on methodology) for the methods used at that time (Anderson et al., 2009; Schnetzer et al., 2013; Shipe et al., 2008).

Substantial amounts of particulate toxin reappeared during 2006 and 2007 in both the Santa Barbara Channel and the San Pedro Basin (Anderson et al., 2009; Schnetzer et al., 2013), and massive mortality/stranding events involving large numbers of marine mammals and seabirds were associated with the appearance of particulate domoic acid during both years in the SCB (see Section 5 below). The years between 2008 and 2016 did not experience toxin-related mortality events of the magnitude observed during 2006 and 2007, but measurable quantities of domoic acid occurred in all years through 2013 (Fig. 3), and animal mortalities attributable to the toxin were recorded.

Concentrations of particulate domoic acid during the following three years (2014–2016) remained remarkably and consistently low, given the constancy with which the toxin occurred during the previous decade (Fig. 3), and given the unprecedented *Pseudo-nitzschia* bloom and domoic acid event that occurred during 2015 along the west coast of North America from just north of the Southern California Bight to Alaska (McCabe et al., 2016; Ryan et al., 2017). Interestingly, 2014–2016 corresponded to an unprecedented drought across southern California and much of the southwestern U.S. (Flint et al., 2018).

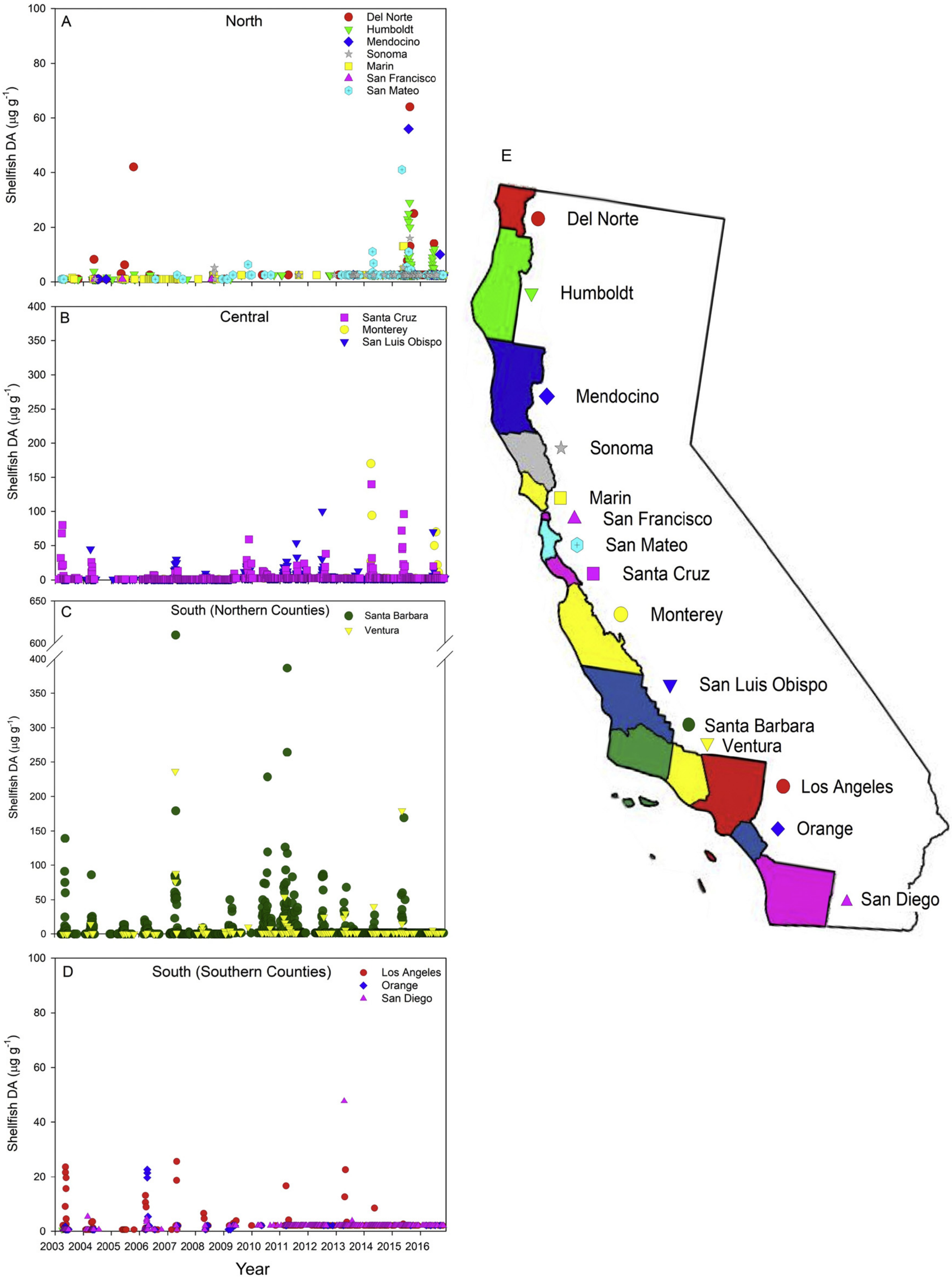

Fig. 2. Scatter plots of domoic acid concentrations measured in shellfish tissue (mussels and oysters) over the period of 2003 to 2016 in each coastal county of California (total number of samples, n = 4528). Individual counties are color-coded on the map, and correspond to the same colors on each scatter plot. Panel (A) shows samples collected in northern California (n = 620), (B) shows samples collected in central California (n = 1966), (C) shows samples collected in the northern counties of the Southern California Bight (n = 1335), and (D) shows samples collected in the southern counties of Southern California Bight (n = 607). Data summarized from California Department of Public Health Center for Environmental Health (2014).

Particulate domoic acid concentrations of the Southern California Bight returned to substantial levels during spring 2017 (> 5 µg L^{-1}) within both southern and northern regions (Fig. 3). The bloom resulted in significant marine mammal and seabird mortality events whose impacts are still being investigated.

An ongoing weekly plankton-monitoring program established at several piers within the SCB in 2008 has provided uninterrupted documentation since that time of *Pseudo-nitzschia* abundances and the occurrence of domoic acid (http://www.sccoos.org/data/habs/). This time-series, and a number of ship-based studies conducted throughout

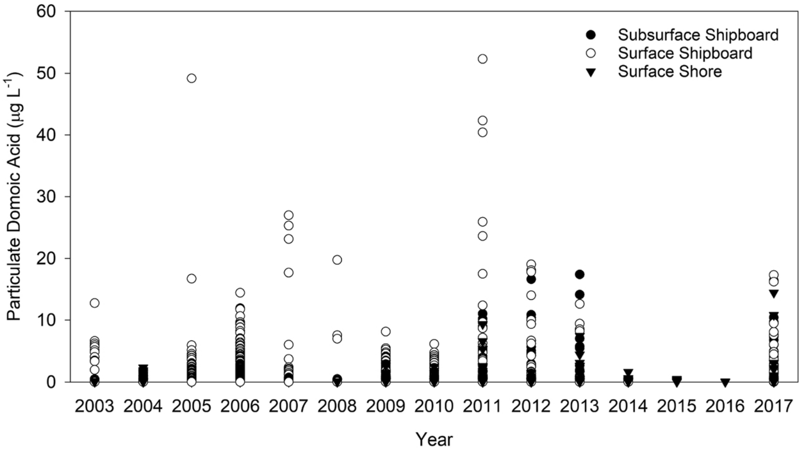

Fig. 3. Summary of ≈4500 particulate domoic acid measurements for plankton samples collected and analyzed during the last 15 years from the Southern California Bight (see Supplemental Table S2 for complete dataset of samples that yielded values of domoic acid above the methodological limit of detection). Symbols indicate samples collected shipboard at the surface, defined as < 2 m depth, (open circles) or subsurface, defined as a depth of > 2 m depth, (filled circles), or by bucket from pier stations (inverted filled triangles).

the past decade, have documented substantial and sporadically exceptional concentrations of particulate domoic acid in the SCB. The highest values to date of particulate domoic acid in the Bight were reported during 2011 by Stauffer et al. (2012) from a small number of samples collected in the central San Pedro Channel. A few of the values exceeded 50 μg L^{-1}, rivaling some of the highest values of particulate domoic acid ever recorded from natural plankton communities. The bloom was very short-lived and was not implicated in significant numbers of animal mortalities.

Shipboard studies during the past decade have also shed light on the complexity of *Pseudo-nitzschia* blooms and domoic acid events in the region. Seegers et al. (2015) documented the potential importance of subsurface populations of *Pseudo-nitzschia* during 2010, suggesting that populations were maintained in the subsurface chlorophyll maxima. The authors reported results indicating a role for these subsurface populations of *Pseudo-nitzschia* along the San Pedro Shelf (Fig. 1) in 'seeding' surface blooms during coastal upwelling events. Advection of subsurface populations may also contribute to rapid increases in domoic acid concentrations during these events as toxin-producing cells are upwelled into surface waters (see Section 3.3 below). Most recently, Smith et al. (2018) conducted extensive sampling on and off the San Pedro Shelf near the city of Newport Beach during 2013 and 2014. Similar bloom abundances of *Pseudo-nitzschia* cells were observed in both years during that study, yet particulate domoic acid concentrations in the two years differed by two orders of magnitude. The authors presented evidence that differences in species/strain composition among potential bloom-forming *Pseudo-nitzschia* species was an important determinant of particulate domoic acid concentrations during the spring along the San Pedro Shelf.

Analyses of these time-series and shipboard datasets, and others from Santa Monica Bay and the San Pedro Shelf (Anderson et al., 2011, 2009; Schnetzer et al., 2013, 2007; Seubert et al., 2013; Smith et al., 2018) have yielded only weak correlations between physical-chemical parameters or chlorophyll, and the abundances of *Pseudo-nitzschia* and domoic acid concentration (see Section 4 below). Thus, the specific factors that might preferentially stimulate the growth of toxic *Pseudo-nitzschia* species that occur in the region remain enigmatic. A variety of species in this genus have been identified (or implicated) in the appearance of domoic acid in the particulate fraction of the plankton and marine food webs in the Southern California Bight during the past 15 years. These include *P. australis*, *P. pungens*, *P. multiseries* and *P. pseudodelicatissima* (Horner et al., 1997), although *P. australis* has been implicated most often in major toxic events. Nevertheless, it appears that toxic events in the region may be attributable to a number of toxic species rather than a single reoccurring species, and the specific factors leading to the growth of these different species are poorly understood. Such mixed assemblages of *Pseudo-nitzschia* appear to be the rule rather than the exception, and may explain the significant year-to-year variability in toxin concentrations that have been observed in multi-year monitoring datasets. Similar findings (multiple *Pseudo-nitzschia* species and year-to-year variability in toxin concentrations) have been reported from a decade of monitoring off New Zealand by Rhodes et al. (2013).

3.2. Seasonality of domoic acid in the SCB

A synthesis of monthly averages and maxima for domoic acid concentration in shellfish tissue along the entire coast of California during the past 15 years (Fig. 4) indicates that domoic acid has occurred in all seasons statewide, although highest averages and maximal tissue concentrations tended to occur during spring and lowest values in winter (Fig. 4A). The seasonal pattern for the northern counties within the Southern California Bight (Santa Barbara and Ventura Counties) exhibited an overall pattern for both monthly averages and maximal values of domoic acid in shellfish tissue that were similar to the overall seasonal pattern statewide (Fig. 4B). Monthly averages in the northern counties of the SCB, however, were generally greater than averages determined across the entire state, and the highest monthly maxima statewide tended to occur within the northern counties of the SCB.

The seasonal pattern of domoic acid in shellfish tissue observed in Santa Barbara and Ventura Counties was reflected in the monthly distribution of maximal particulate domoic acid concentrations observed during each year since 2003 (numbers and colored arrows in Fig. 4B). Maximal particulate domoic acid concentrations for most years occurred during April for 7 of 15 annual maxima (Anderson et al., 2006) but maximal annual particulate domoic acid concentrations also occurred at least once in all months except February, March, October, and December. Data for particulate domoic acid concentrations (colored arrows in Fig. 4) were based on ≈4500 data points (the distribution of samples by month is shown in (Fig. S2; Supplemental), and maximal values for each month in the datasets from the northern and southern counties are given in Table S1 (Supplemental).

In contrast, the seasonal occurrence of domoic acid in the particulate fraction of the plankton and in shellfish tissue along the coast of the southern counties (Los Angeles, Orange, and San Diego counties; Fig. 4C) within the SCB during the past 15 years was strikingly different than the statewide pattern, or the pattern observed in the northern counties of the SCB. First, the southern counties generally experienced substantially lower maximal concentrations of domoic acid in shellfish tissue relative to the rest of the state, particularly compared to values observed in the northern counties of the SCB (note different ranges on the Y axes in Fig. 4A,B versus C). Second, substantive values of shellfish contamination were largely associated with spring months in the southern counties (March-May) indicating much stronger seasonality in the appearance of the toxin along the coast of those counties.

Strong seasonality in the southern counties of the SCB is

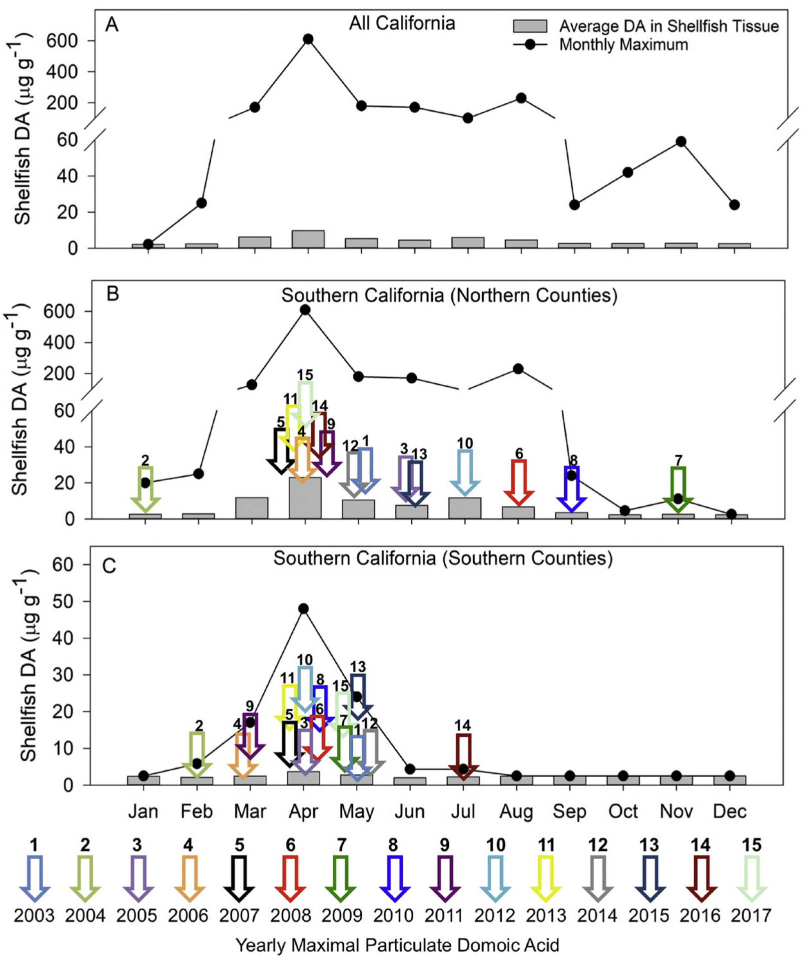

Fig. 4. Average and maximal concentrations of domoic acid in shellfish tissue. Grey bars show the average domoic acid concentrations in shellfish tissue samples in each month for the period of 2003 to 2016. The black line indicates the maximal domoic acid concentration measured in each month during the same period. (A) data from all coastal counties in California; (B) data from the northern counties of the Southern California Bight only (Santa Barbara and Ventura); (C) data from the southern counties of the Southern California Bight only (Los Angeles, Orange and San Diego). Arrows and numbers indicate the month in which the maximal particulate domoic acid concentrations were observed during each year, with the color of the arrow and number indicating the year. Shellfish data obtained from California Department of Public Health Center for Environmental Health (2014).

substantiated by examination of the month in each year that experienced the maximal concentration of particulate domoic acid along the coast of the southern counties (colored arrows in Fig. 4C). Maximal particulate domoic acid was observed in March, April or May in 13 of 15 years since 2003 in the southern counties of the SCB. Only two years had maxima that occurred in other months, and those were years that experienced relatively moderate or very low overall particulate domoic acid concentrations. A maximal value of ≈2 μg L^{-1} was observed in February 2004, and a maximal value of 0.05 μg L^{-1} was observed in July of 2016 in the southern counties (the latter year exhibited exceptionally low concentrations of domoic acid throughout the SCB). These differences between the northern and southern counties of the SCB in the timing of toxic blooms of *Pseudo-nitzschia*, and the magnitude and timing of the appearance of toxin in shellfish, indicate somewhat different factors controlling toxic blooms of diatoms in these two sub-regions of the Bight.

3.3. Anatomy of a domoic acid event in the SCB: the role(s) of upwelling

A close relationship between coastal upwelling events along the California coast and the appearance of phytoplankton blooms, specifically blooms of *Pseudo-nitzschia* and the occurrence of domoic acid, has been documented for many years (Brzezinski and Washburn, 2011; Lange et al., 1994; Trainer et al., 2000). More than two decades ago Lange et al. (1994) documented a correlation between the appearance of *Pseudo-nitzschia* off the coast of La Jolla and the intrusion of cold, presumably upwelled water at the coast (albeit no major toxic episodes were reported in that study). Blooms typically occurred between February and August, a seasonality that is consistent with upwelling-favorable, down-coast winds peaking during winter-spring (Hickey, 1992; Nezlin et al., 2012).

Nutrient delivery to coastal surface waters via upwelling is believed to be an important stimulus for *Pseudo-nitzschia* growth and toxin production along the entire U.S. west coast (Kudela et al., 2010), although other sources of nutrients may also contribute. McPhee-Shaw et al. (2007) compared the importance of upwelling, storm runoff and diurnal motions for the delivery of nutrients to the nearshore community in the Santa Barbara Channel. Seasonally, storm runoff contributed most significantly to nutrient loading during winter, diurnal motions contributed strongly during the summer, but upwelling was the dominant source of nutrients between March and May (i.e. coinciding with the timing of most domoic acid events in the SCB). Additionally, attention in recent years has focused on the potential for anthropogenic nutrient sources to contribute to coastal phytoplankton blooms in the SCB (Nezlin et al., 2012). As noted above (Section 1), nutrients discharged by large POTW in the central Bight may contribute as much as half of the annual nitrogen to coastal waters in the region, but those nutrient discharges are not highly seasonal. Therefore, the recurrence of toxic blooms of *Pseudo-nitzschia* during the spring in the SCB, as observed over the last 15 years, is consistent with nutrient loading due to upwelling as a primary driver of toxic blooms of *Pseudo-nitzschia* in the region. The timing of these events has been strongly linked to the timing of spring upwelling for the southern counties of the SCB (Fig. 4C), as well as the northern counties, although the pattern has been less dramatic along the latter coasts (Fig. 4B).

The classical pattern emerging from plankton studies within the region implicates nutrient delivery into surface waters via upwelling during the spring when other conditions are concurrently favorable for phytoplankton growth (Nezlin et al., 2012; Schnetzer et al., 2013; Smith et al., 2018). Rapid decreases in surface water temperature at

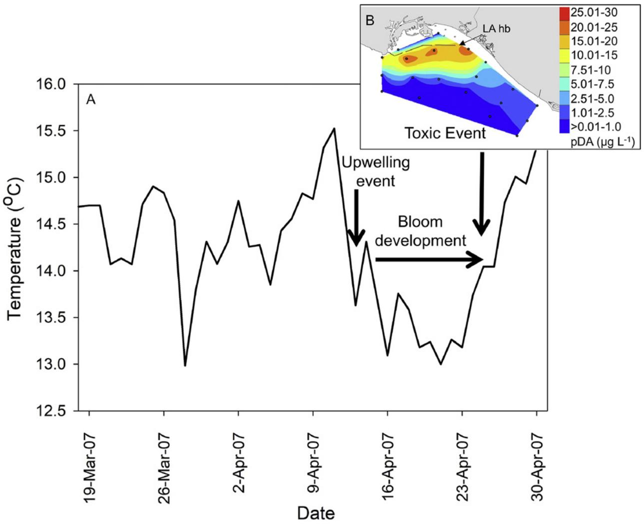

Fig. 5. Typical relationship between the timing of spring coastal upwelling, resulting in a decrease in temperature of surface waters at the coastline, followed by subsequent population growth and toxin production by *Pseudo-nitzschia* species in the central Southern California Bight. Temperature information (A) was obtained from the NOAA weather buoy (Station 46,222 – San Pedro, California (092), 33.618 °N, 118.317 °W). Inset (B) shows the distribution of particulate domoic acid in the plankton community at the surface on 27 April 2007, approximately one week after the minimum in water temperature. LA hb indicates the Los Angeles harbor, black dots show the shipboard sampling stations, the legend indicates particulate domoic acid concentrations. Note that inset (B) also appears in Fig. 10, which demonstrates the temporal relationship between particulate domoic acid concentrations and marine mammal and seabird poisoning events resulting from food web contamination.

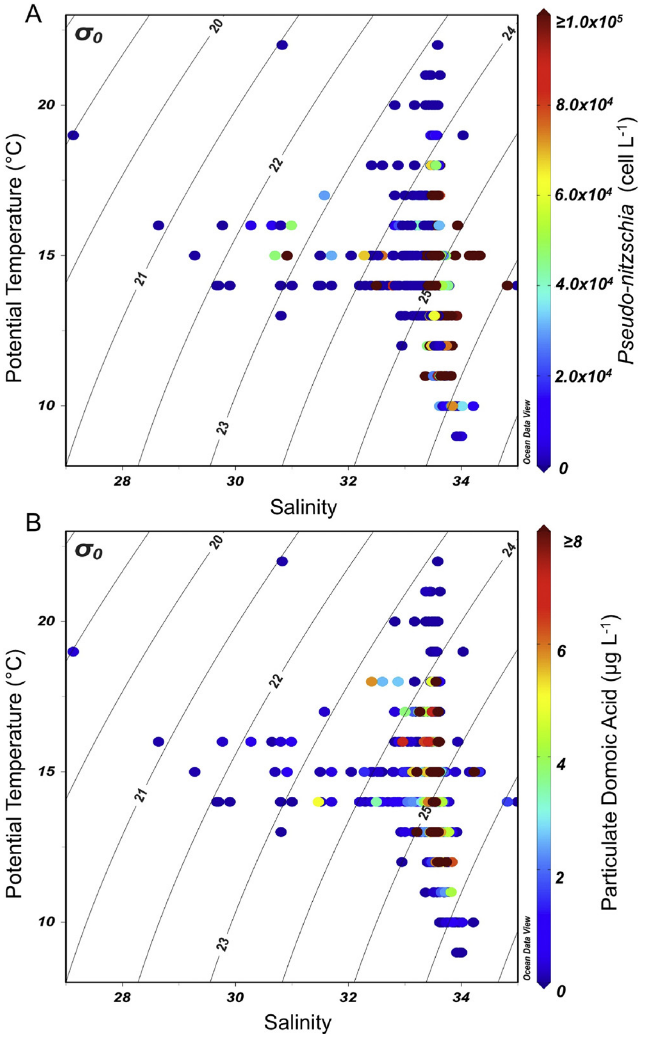

Fig. 6. *Pseudo-nitzschia* abundances (A) and particulate domoic acid concentrations (B) from the Southern California Bight plotted on temperature-salinity diagrams. 649 values were plotted for each parameter. Lowest toxin concentrations were plotted first, followed by successively higher concentrations, in order to allow higher values (which are rarer) to be visible. *Pseudo-nitzschia* abundances were plotted in order of lowest associated domoic acid concentrations to highest.

moored buoys or at pier monitoring stations along the coast of the SCB have recorded the transport of deep, nutrient-rich waters to the ocean surface (Fig. 5). Pulses of upwelled water, followed by periods of wind relaxation, typically result in rapid population growth of the endemic phytoplankton assemblage, including *Pseudo-nitzschia* cells if present. Given sufficient 'seed' populations and time for growth, the response of toxin-producing species of *Pseudo-nitzschia* can result in substantial toxic events 1–2 weeks following the upwelling event (Fig. 5B). Seubert et al. (2013) noted this temporal progression at the Newport Beach Pier in Orange County, where a significant relationship was observed between elevated *Pseudo-nitzschia* abundances two weeks after upwelling events.

A general relationship between upwelling and outbreaks of domoic acid, as depicted in Fig. 5 during 2007, was also described by Schnetzer et al. (2013) and is further substantiated by an examination of water temperature and salinity across the 15-year study period (Fig. 6). Patterns of the abundances of *Pseudo-nitzschia* and concentrations of domoic acid in the water column plotted on T-S diagrams reveal that highest abundances and toxin concentrations were consistently observed in cooler, saltier waters of this region (warmer colors in Fig. 6), characteristics consistent with upwelled water and elevated nutrient concentrations (see Fig. 2 in (Seegers et al., 2015)). In particular, substantial toxin concentrations were only occasionally observed at salinities < 33, and never at temperatures > 19 °C (Fig. 6B).

The scenario described above (Fig. 6) of nutrient loading of surface waters by upwelling implies a significant amount of time between the upwelling event and the subsequent development of a *Pseudo-nitzschia* bloom and appearance of toxin (typically 1–2 weeks following the upwelling event). Domoic acid, however, can also appear in surface waters of the central SCB during or immediately after an upwelling event, giving rise to an 'instant' domoic acid event (Fig. 7). Evidence presented by Seegers et al. (2015) implicated the uplifting of a subsurface chlorophyll maximum containing toxic *Pseudo-nitzschia* cells into surface waters by upwelling as a probable explanation for these observations. An Environmental Sample Processor (Greenfield et al., 2006) deployed just above the subsurface chlorophyll maximum on the San Pedro Shelf in that study exhibited higher abundances of *Pseudo-nitzschia* cells immediately following shoaling of the subsurface chlorophyll feature (Figs. 3–5 in (Seegers et al., 2015); Fig. 7A). Uplifting of the subsurface chlorophyll feature was documented using an autonomous underwater vehicle, and surface manifestations of the uplifted chlorophyll layer were apparent in Moderate Resolution Imaging Spectroradiometer (MODIS) images (Figs. 4 and 5 in (Seegers et al., 2015); Fig. 7B). Additionally, the authors reported that barnacles that grew on the autonomous underwater vehicle during deployment contained significant concentrations of domoic acid prior to the appearance of measurable concentrations of domoic acid in surface water samples, implying that toxin contamination was attributable to phytoplankton not present in surface water assemblages.

The scenario described above of an immediate or nearly immediate appearance of particulate domoic acid at the time of an upwelling event constitutes an interesting corollary to the classical 1–2-week temporal progression from upwelling event to the appearance of domoic acid in

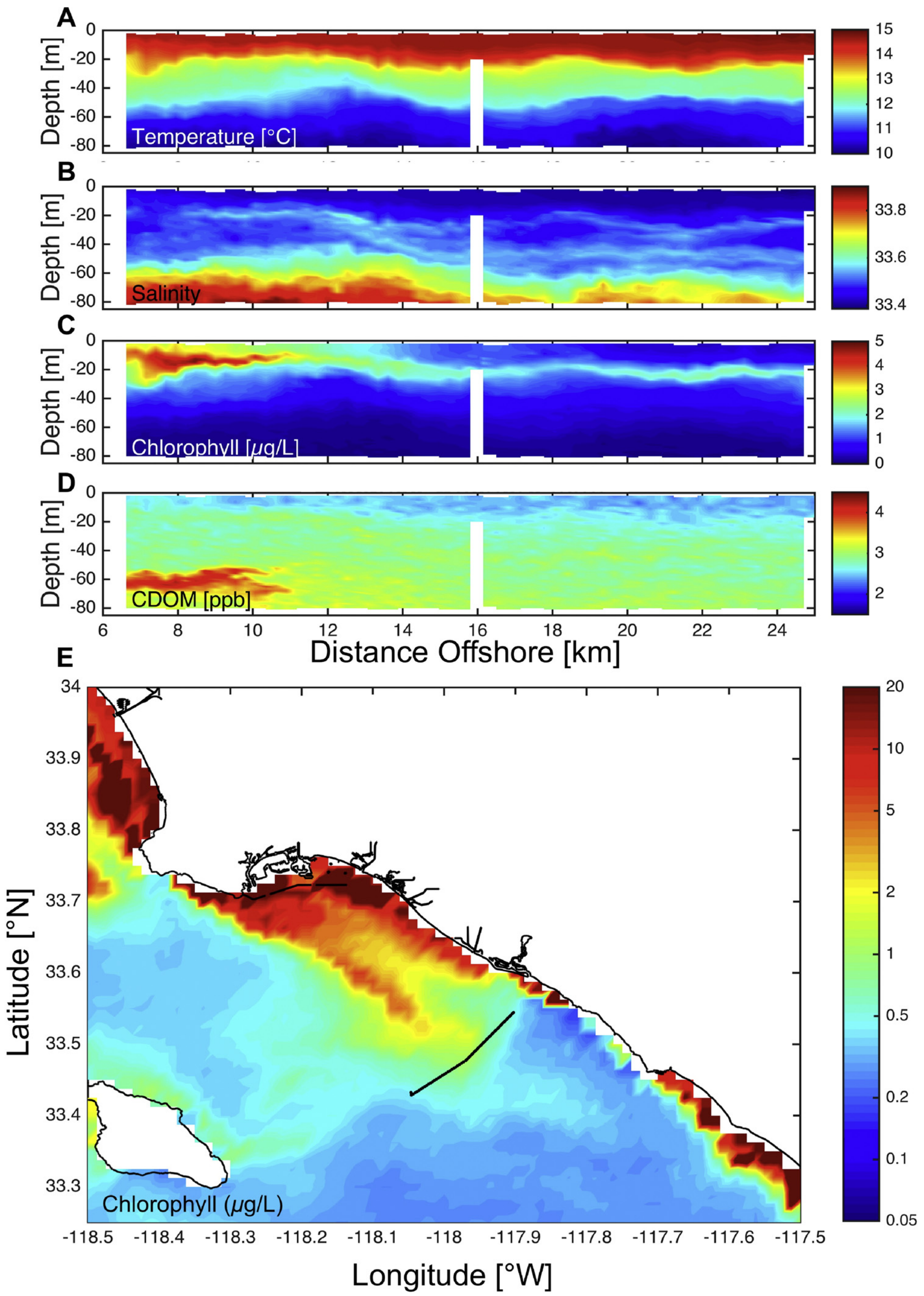

Fig. 7. Two-dimensional depictions (water depth and distance from shore) of temperature (A), salinity (B), chlorophyll fluorescence (C) and colored dissolved organic matter (CDOM) along an onshore-offshore transect off Newport Beach, Orange County, April 3, 2009 obtained using an autonomous underwater vehicle (Slocum Glider). A surface manifestation of a phytoplankton bloom is apparent as elevated chlorophyll fluorescence near the shore (left side of panel C), which extends offshore as a subsurface chlorophyll maximum. The maximum in CDOM in panel (D) is due to effluent discharge of a nearby sewage treatment plant. A MODIS image obtained on the same day (E) indicates the nearshore surface-associated phytoplankton bloom (as indicated by elevated chlorophyll fluorescence. The black line in (E) indicates the onshore-offshore track of the glider for parameters depicted in A–D.

surface waters. Subsurface chlorophyll maxima and 'thin layers' are known to act as retention areas in the water column for some phytoplankton species (Durham and Stocker, 2012; Ryan et al., 2010; Velo-Suárez et al., 2008). The association of *Pseudo-nitzschia* populations with subsurface chlorophyll maxima and thin layers have been documented along the California coast and elsewhere (Rines et al., 2002, 2010; Seegers et al., 2015; Timmerman et al., 2014), and has been hypothesized as a missing link explaining the existence of 'cryptic blooms'; that is, the appearance of toxin at higher trophic levels in the absence of the bloom in surface waters (McManus et al., 2008). These subsurface features are cooler and contain higher concentrations of nutrients than surface waters (conditions that may favor the growth of *Pseudo-nitzschia*). Uplifting of these population into low nutrient, high light surface waters should dramatically affect cellular physiology and may increase toxin production (Terseleer et al., 2013).

It is likely that the impact of subsurface populations of toxic *Pseudo-nitzschia* on the timing and magnitude of toxin appearance in surface waters following an upwelling event may depend not only on the amount of toxic *Pseudo-nitzschia* cells in the subsurface layer, but also on the magnitude and duration of the upwelling event. Events that are too weak to bring the subsurface *Pseudo-nitzschia* assemblage to the surface will be insufficient to affect conditions in surface waters, while very strong upwelling events may result in surfacing and seaward advection of the subsurface assemblage, limiting the nearshore manifestation or magnitude of an 'instant' domoic acid event.

4. Other factors affecting blooms in the Southern California Bight

General nutrient loading into surface waters as a consequence of coastal upwelling is unquestionably a primary factor affecting *Pseudo-*

nitzschia blooms and the production of domoic acid in the Southern California Bight, but it is not the sole explanation for the observed pattern of toxic events over the past 15 years. Blooms of *Pseudo-nitzschia* did not occur in every year in the region, nor have they occurred in response to every upwelling event. Additionally, when *Pseudo-nitzschia* blooms have occurred, the blooms have not always resulted in domoic acid production. That result is exemplified by the situation in 2013 and 2014, where peak spring abundances of *Pseudo-nitzschia* in the central SCB were similar, yet maximal particulate domoic acid concentrations differed by approximately two orders of magnitude (Smith et al., 2018). A somewhat variable relationship between upwelling and domoic acid events is also supported by studies that have not always reported strong correlations between domoic acid concentrations and either abundances of *Pseudo-nitzschia* or total chlorophyll concentrations (Seubert et al., 2013; Smith et al., 2018). Therefore, other factors appear to play secondary but important roles in determining whether individual *Pseudo-nitzschia* blooms, or specific years, will result in toxic events.

It is also apparent from this summary of the last 15 years that the details and magnitudes of *Pseudo-nitzschia* blooms and domoic acid outbreaks in much of the SCB often have been different from the situation in central and northern California as well as in the PNW. Rather than a simple seasonal progression of blooms beginning in southern California and moving north as spring progresses, conditions within the SCB have often been distinct from the fate of the coastline to the north. For example, a massive domoic acid event in 2015 occurred along the west coast of North America from central California to Alaska (McCabe et al., 2016). Only minor concentrations of particulate toxin appeared in the northern counties of the SCB during that year, while the central and southern Bight was virtually devoid of elevated concentrations of particulate domoic acid. These varied outcomes presumably indicate subtle physical and chemical differences in the coastal waters of southern California, resulting in differences in the ability of these ecosystems to support the growth of *Pseudo-nitzschia* species and stimulate domoic acid production by toxigenic species. In short, upwelling appears to be fundamentally important, but other factors also contribute to toxic *Pseudo-nitzschia* blooms in the region.

4.1. *Influence of timing, chemistry, and physics*

Factors that might influence phytoplankton community activity, beyond the general nutrient loading that occurs during upwelling events, include physical changes such as light and temperature, and chemical modifications such as specific nutrient enrichment or depletion, or changes in nutrient ratios. These changes may affect *Pseudo-nitzschia* dominance within the phytoplankton, species composition within the assemblage, and the induction of toxin production. These factors presumably act synergistically, which has complicated the process of attributing toxic events to any specific factor(s).

4.1.1. *Water temperature*

Temperature appears to be an important factor constraining blooms of *Pseudo-nitzschia* and toxin production in the SCB (Fig. 6: Fig. S3 Supplemental). Upwelling in the SCB can decrease surface water temperatures in the coastal ocean to 13–14 °C, a condition that may favor the growth of some *Pseudo-nitzschia* species (Lelong et al., 2012). Interestingly, high abundances of *Pseudo-nitzschia* have not been reported in the region at temperatures exceeding 20 °C, and virtually no substantive values of particulate domoic acid in plankton samples have been recorded above ≈19 °C (Fig. 6, and Supplemental Fig. S3A and B, respectively).

These findings imply that the timing (and/or magnitude) of seasonal upwelling events (i.e. nutrient loading of surface waters), and specifically the surface water temperatures attained during and immediately following these events, may strongly influence whether *Pseudo-nitzschia* species will dominate the phytoplankton assemblage and produce toxin. The timing of seasonal upwelling in northern California was examined by Schwing et al. (2006), whose results are in accordance with this speculation. The authors noted a 2–3 month delay in the spring upwelling season in northern California during 2005 relative to other years (no information was provided for southern California). Concurrently, abundances of *Pseudo-nitzschia* and particulate domoic acid concentrations were very low in the central and southern SCB during spring 2005, although values in the previous year (2004) and following two years (2006–2007) were substantial (Schnetzer et al., 2013, 2007). It is possible that the delayed seasonal upwelling during 2005, and warmer water temperatures at the time of the onset of upwelling, may explain the lack of a significant domoic acid event in the central and southern SCB during that year.

The empirical observation that water temperature above 19 °C did not result in *Pseudo-nitzschia* dominance or domoic acid production in the SCB (Fig. 6, Supplemental Fig. S3B) implies that nutrient loading, by itself, might not necessarily result in toxic events if the receiving surface waters are too warm. This speculation is in agreement with observations during 2015, an anomalously warm year that witnessed a massive domoic acid event extending from central California to Alaska but little to no toxin produced in the SCB (McCabe et al., 2016).

It is also in accordance with the results of two recent, large-scale discharges of sewage effluent into nearshore waters. The Orange County Sanitation District (OCSD) off Newport Beach on the San Pedro Shelf, and the Hyperion Treatment Plant (HTP) of the City of Los Angeles off El Segundo in Santa Monica Bay, conducted diversions from their offshore outfall pipes (discharging below the euphotic zone ≈8 km from shore) to pipes ≈1.6 km from shore to enact repairs on the longer pipes during the fall of 2012 and 2015, respectively. Massive nutrient loading into nearshore surface waters resulting from these discharges ($\sim 12 \times 10^6\ \mathrm{m}^3$ of treated wastewater discharged during the OCSD diversion and $\sim 39 \times 10^7\ \mathrm{m}^3$ of treated wastewater discharged during the HTP diversion, containing inorganic nitrogen at concentrations approximately three orders of magnitude above ambient concentrations) was expected to result in dramatic responses of the phytoplankton community and potentially the development of a HAB event (Howard et al., 2017; *J.* Smith unpublished data).

In contrast to anticipated outcomes, the OCSD diversion resulted in only a modest increase in phytoplankton biomass, where *Pseudo-nitzschia* was not a significant component of the community and domoic acid was near or below detection throughout the 3-week diversion (Caron et al., 2017). The 6-week HTP diversion resulted in three taxonomically distinct and substantive phytoplankton blooms (diatoms, euglenids, raphidophytes) within Santa Monica Bay, but none of them contained significant abundances of *Pseudo-nitzschia* or measurable concentrations of domoic acid (*J.* Smith unpublished data). Cruises conducted following the 2015 diversion (November 2015), however, did reveal some low concentrations of toxin and increased abundances of *Pseudo-nitzschia* cells in the plankton – potentially a result of seasonal cooling of surface water temperature. A similar but shorter diversion (< 3 days) from HTP during fall 2006 resulted in a significant stimulation of dinoflagellates within the phytoplankton assemblage, but no significant response of the *Pseudo-nitzschia* assemblage (Reifel et al., 2013). These surprising results seem to be a consequence, at least in part, of effluent release during a season not conducive to growth and toxin production by potentially toxic *Pseudo-nitzschia* species in the Southern California Bight (presumably due to supraoptimal temperatures of > 19 °C).

4.1.2. *River discharge and composition*

Much of the river discharge to the coastal ocean in the SCB is seasonal and enters the ocean through a relatively small number of large rivers. The potential impacts of these discharges are therefore somewhat localized within the Bight and their contributions to blooms and domoic acid are complicated by the fact that the season of strongest river discharge typically co-occurs with the season of upwelling events.

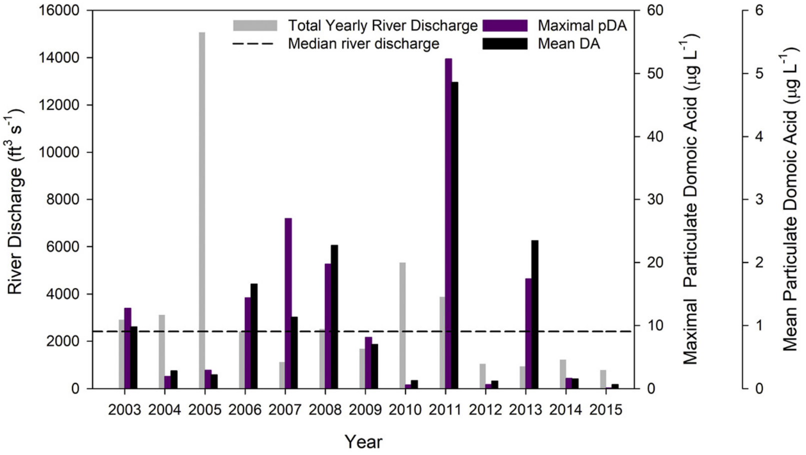

Fig. 8. Yearly river discharge of three major rivers (summed discharge of Los Angeles, Santa Ana, San Gabriel Rivers) along the coast in the southern counties of the Southern California Bight (grey bars) for the years 2003–2015 plotted with yearly maximal detectable particulate domoic acid (purple bars), and annual average particulate domoic acid (black bars). Median river discharge for the entire period is shown as a black dashed line.

Additionally, interannual variability in total discharge volume can be significant, and that variability has been very high since 2003 (> 20-fold; gray bars in Fig. 8).

River discharge in central California has been proposed as a factor that may play a stimulatory role in *Pseudo-nitzschia* blooms and domoic acid production due to nitrogenous compounds contained in agricultural runoff that are a significant component of the discharge in that region (Kudela et al., 2008). Such anthropogenic point sources of nutrients comprise a significant amount of the terrestrial nutrient loads to the SCB; > 90% of total nitrogen and > 75% total phosphorus (Sengupta et al., 2013). Nevertheless, a direct relationship between river discharge and *Pseudo-nitzschia* growth or toxin production is much less clear for the SCB (Schnetzer et al., 2013), perhaps due to the fact that rivers in the Bight receive runoff from a wide spectrum of land use ranging from agriculture in the north to highly urbanized and industrialized sectors in the central Bight.

Howard et al. (2014) characterized river discharge in the SCB as a significant component of total nitrogen delivery to the coastal ocean, but minor in comparison to nitrogen delivered via upwelling, or discharge from large POTW in the region. Rivers were, however, a major percentage of the organic nitrogen compounds entering the coastal ocean. Nevertheless, data compiled for the period 2003–2015 comparing discharge from the major river systems in the southern counties of the SCB with maximal or average concentrations of domoic acid in coastal waters near those discharges did not reveal a relationship (Fig. 8). In fact, high average and maximal concentrations of particulate domoic acid have been observed during ‘wet’ years (e.g. 2011), ‘dry’ years (e.g. 2007, 2013), and years with median river discharge (e.g. 2003, 2006, 2008). The two years with the largest river discharges depicted in Fig. 8 (2005, 2010) exhibited very low concentrations of domoic acid in the SCB, while 2017 (a very wet year) witnessed a large domoic acid event in the Bight (total discharge data not yet available for 2017).

4.1.3. Macro/micronutrients, nutrient depletion, and nutrient ratios

Generalized relationships between nutrient availability and toxic blooms in the SCB, beyond the relationships to upwelling and temperature noted above, have not been dramatic when examined across the entire available data set (~2330 data points) (Fig. S4, Supplemental) or for the spring months of March, April and May (~1900 data points, data not shown) when *Pseudo-nitzschia* blooms occur most regularly. These loose relationships tend to fit ‘standard’ expectations reported in the literature for the stimulation of *Pseudo-nitzschia* blooms and domoic acid events (Lelong et al., 2012). Nutrient limitation during bloom formation, in particular silicate and/or phosphorus limitation, or low ratios between those elements and other nutrient elements (e.g. low Si:N) have yielded the most consistent correlations with domoic acid in the Bight (Anderson et al., 2009; Schnetzer et al., 2013, 2007; Smith et al., 2018). Similar relationships have been observed for *Pseudo-nitzschia* blooms north of the SCB in Monterey Bay (Lane et al., 2009; Ryan et al., 2017). These correlations confirm a well-documented effect of nutrient status of the water on toxin production as a *Pseudo-nitzschia* bloom progresses, although this effect is presumably secondary to the factors described above.

Less-well-characterized relationships between water chemistry and *Pseudo-nitzschia* species composition and/or toxin production remain to be examined in the SCB. The form of nitrogen (NH_4^+, NO_3^- and urea) has been shown to affect growth and toxicity of *Pseudo-nitzschia* species (Howard et al., 2007; Kudela et al., 2008; Thessen et al., 2009), but to date, this effect is largely unexamined in field studies conducted in the Bight. Synergistic effects are also poorly understood. For example, high CO_2, phosphate limitation, and silicate limitation have been shown to act synergistically to increase the toxicity of some *Pseudo-nitzschia* species (Sun et al., 2011; Tatters et al., 2012). These complex interactions are exceedingly difficult to identify in field datasets, but they may be fundamental in determining which *Pseudo-nitzschia* species will dominate a bloom or whether toxin production will be stimulated among toxigenic species. Likewise, there is little information with respect to how domoic acid production by *Pseudo-nitzschia* species in the SCB may be affected by trace metal or vitamin status, although correlations in laboratory cultures and some field studies have indicated that they can play a role (reviewed in Lelong et al., 2012).

4.2. Long-term relationships and drivers

Climatic variability and its effects on oceanographic conditions unquestionably play a role in the year-to-year variability of coastal phytoplankton blooms, *Pseudo-nitzschia* abundances and maximal particulate domoic acid concentrations in the SCB. Climate indices such as the Pacific Decadal Oscillation (PDO) (Mantua and Hare, 2002; Mantua et al., 1997), North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008) and the Multivariate El Niño Southern Oscillation (ENSO) Index (MEI: indicative of ENSO dynamics) (Wolter and Timlin, 1993, 1998) have been correlated to low-frequency patterns in oceanographic conditions which in turn impact biological communities, such as zooplankton abundances and fish stocks, in the northeast Pacific (Lavaniegos and Ohman, 2007; Lynn et al., 1998; McGowan et al., 1998). These large-scale climatic patterns vary on timescales ranging from months and years (ENSO) to decades (NPGO and PDO) (Alexander, 2010).

The influence of ENSO can be linked to the decadal dynamics of the PDO and NPGO, and the manifestations of the three climatic patterns result in definable changes in the oceanography of the California Current (Di Lorenzo et al., 2013). The PDO is the first dominant mode of variation in sea surface temperature anomalies (SSTa) and sea surface height anomalies (SSHa) in the northeast Pacific. The positive phase of the PDO index generally results in increased biological productivity along the Alaskan coast and muted productivity along the more southern regions of the North American west coast, including parts of California (Mantua and Hare, 2002; Mantua et al., 1997). The negative phase of the PDO is marked by the opposite trend with increased biological productivity along the North American west coast. In either phase, the PDO generally exerts a greater influence on regions north of 38 °N (approximately the latitude of San Francisco, California) (Chhak and Di Lorenzo, 2007; King et al., 2011).

The NPGO is the second dominant mode of SSHa variability in the northeast Pacific and also captures the second mode of north Pacific SSTa variations. Prominent low-frequency changes in salinity, nutrients, sea level and chlorophyll across the Pacific region have been attributed to phase changes in the NPGO index (Di Lorenzo et al., 2008), particularly in regions south of 38 °N (Chhak and Di Lorenzo, 2007; King et al., 2011). The positive phase of NPGO represents the strengthening of the geostrophic circulation of the North Pacific Gyre and manifests as increased southward transport of the California Current System (CCS) and intensification of upwelling favorable wind patterns (Di Lorenzo et al., 2008).

The activity of ENSO in the equatorial Pacific, as indicated by MEI (Wolter and Timlin, 1993, 1998) is characterized by variations between El Niño warm phases and La Niña cold phases (indicated by positive and negative MEI phases, respectively). El Niño events have been shown to impact the CCS, generally resulting in weaker coastal upwelling and fresher, warmer and shallower source waters; conversely, La Niña typically manifests with the opposite trend (Jacox et al., 2015).

Long-term trends in particulate domoic acid concentrations from the present data set were examined in relation to climatic indices, demonstrating significant relationships with NPGO and MEI but not PDO (Table 1). Particulate domoic acid concentrations above the limit of detection (0.01 $\mu g\ L^{-1}$ or 0.02 $\mu g\ L^{-1}$, depending on data source) were matched by month to respective index values, and then separated into two groups based on whether the respective climatic index was in the positive or negative phase. The same analysis was also conducted with a 1-month lag (the index and toxin concentration in the water one month later), assuming that bloom development and toxin production require time to respond to climatic shifts. A bulk comparison was conducted between the two groups of particulate domoic acid concentrations using the Mann-Whitney Rank Sum Test. Significance was determined at $p < 0.05$ (Table 1).

The PDO showed no significant relationship to the median concentration of particulate domoic acid observed during the negative or positive phase, with or without a time lag. This implies, to the extent that the available data can determine, that PDO has not exerted a clear influence on overall particulate domoic acid concentrations in the SCB during the past decade and a half. This result may reflect the fact that previous studies have noted that the PDO exerts a greater influence on regions north of 38 °N; i.e., north of central California (Chhak and Di Lorenzo, 2007; King et al., 2011), and that the influence of the PDO within the SCB is moderated or subdued by other factors.

Median particulate domoic acid concentrations were higher during the negative phase of NPGO than in the positive phase with both lagged and un-lagged data (Table 1), indicating that the negative phase of the NPGO may enhance toxigenic *Pseudo-nitzschia* events in the SCB. This result is surprising given that the positive phase of the NPGO is characterized by conditions that favor coastal upwelling (Di Lorenzo et al., 2008), which has generally been shown to play an important role in toxigenic bloom development in the Bight (Fig. 6). The majority of data points in the present analysis, however, were collected during the positive phase of the NPGO (Table 1), potentially skewing the results of this analysis.

A significant difference between median concentrations of particulate domoic acid measured during the negative and positive phases of ENSO (MEI) was shown, with higher median particulate domoic acid concentrations occurring during the negative phase of the MEI (Table 1). The negative phase of MEI is associated with decreased sea surface temperatures (SST) which, as noted above (Fig. 6; Supplemental Fig. S3), appear to favor toxigenic *Pseudo-nitzschia* blooms in the SCB.

The relationships noted above between particulate domoic acid within the SCB and large-scale climate variability indices are somewhat at odds with the general patterns reported in the literature pertaining to toxic events along the U.S. west coast. Admittedly, these patterns are difficult to assess from a dataset that is 15 years long, particularly for climate patterns that span ~10 years. Another factor that appears significant, however, is that previous reports have largely focused on the coastline from Santa Barbara county northward, and have not specifically addressed the southern regions of the SCB, as in this analysis. McCabe et al. (2016) and McKibben et al. (2017) suggested that domoic acid events (i.e. shellfish contamination) occurring from central California to Washington State were related to warm phases of the PDO and El Niño periods. A significant relationship between particulate domoic acid concentrations and PDO was not detected for the SCB; rather, results suggest La Niña periods are related to higher particulate domoic acid concentrations in the Bight (Table 1). Sekula-Wood et al., (2011) reported a relationship between the positive phase of the NPGO and elevated domoic acid concentrations measured from sediment trap samples from the Santa Barbara Basin at the northern end of the SCB from 1993 to 2008. Yet the present analysis, which included data from across the entire Southern California Bight, detected the opposite trend between 2003 and 2017. It is possible that toxic blooms within the more southern regions of the SCB have been influenced by somewhat different dynamics than those acting in the northern counties of the Bight, and that the northern counties appear to be more in agreement

Table 1
Fifteen year medians (2003–2017) in domoic acid concentrations ($\mu g\ L^{-1}$) and chlorophyll *a* concentrations ($\mu g\ L^{-1}$) in relation to the positive or negative phase of the Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO) and Multivariate ENSO Index (MEI). Analyses were conducted using the median of particulate domoic acid concentrations that were above the limit of detection and the corresponding chl a concentrations (where available). Bolded values are significantly different at $p \le 0.05$; n = number of measurements included in the comparisons.

Variable	Time Lag	Median pDA concentration	*n*	*p*	Median Chl *a* concentration	*n*	*p*
PDO (+)	None	0.177	841	0.845	**4.26**	606	< **0.001**
PDO (-)		0.183	807		**2.83**	630	
PDO (+)	1 month	0.167	939	0.569	**3.91**	692	< **0.001**
PDO (-)		0.170	767		**2.84**	599	
NPGO (+)	None	**0.136**	1216	< **0.001**	**2.78**	853	< **0.001**
NPGO (-)		**0.264**	457		**4.75**	438	
NPGO (+)	1 month	**0.130**	1188	< **0.001**	**2.76**	825	< **0.001**
NPGO (-)		**0.277**	492		**4.65**	466	
MEI (+)	None	**0.130**	959	< **0.001**	**2.74**	633	< **0.001**
MEI (-)		**0.260**	747		**3.99**	658	
MEI (+)	1 month	**0.114**	826	< **0.001**	**2.73**	602	< **0.001**
MEI (-)		**0.262**	880		**3.82**	689	

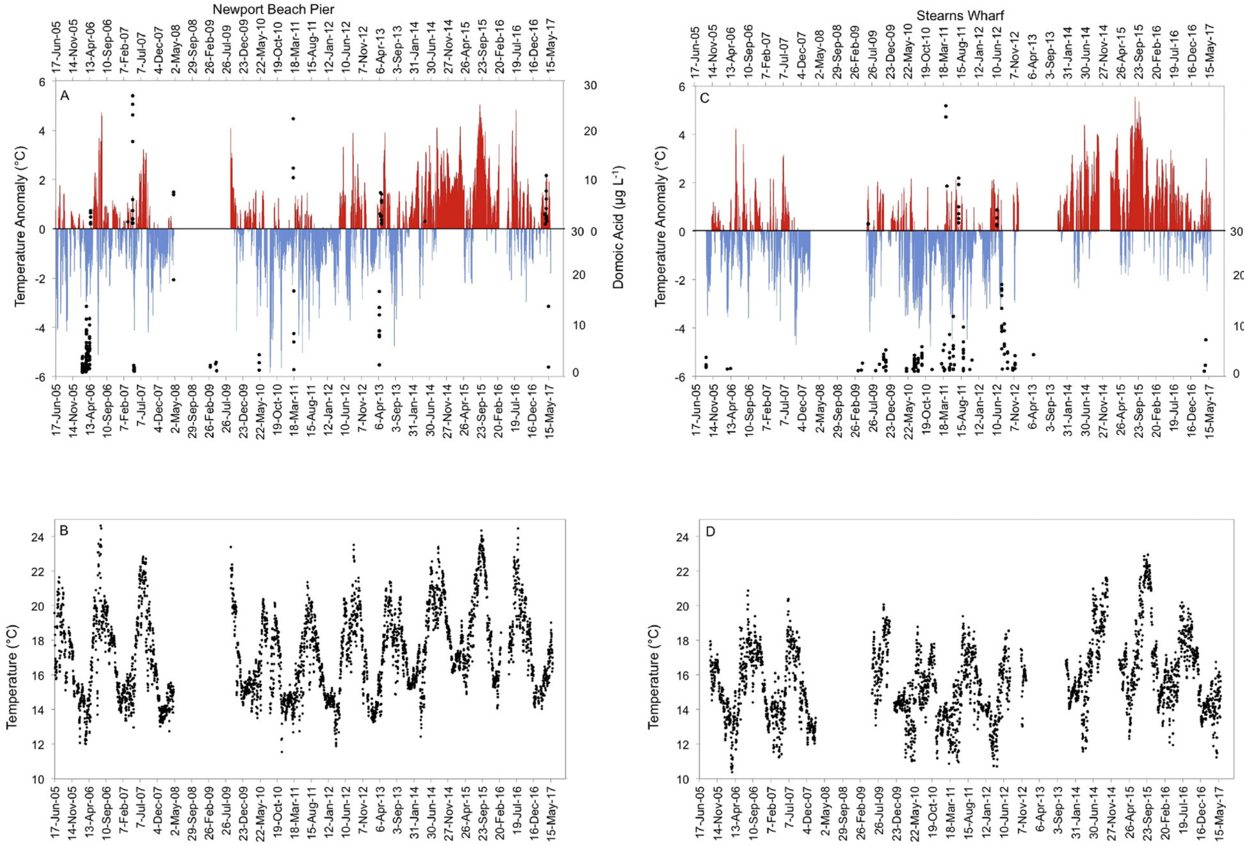

Fig. 9. Daily temperature anomaly and absolute temperature time-series for the period 2005-2017. Time-series data were collected from shore station sensors located at Newport Beach Pier, City of Newport Beach, Orange County (representative of the southern region of the SCB: two panels on left), and Stearns Wharf, Santa Barbara, Santa Barbara County (representative of the northern region of the SCB: two panels on right). Temperature anomalies were calculated for each site from the time-series of temperature data collected from the shore station sensors. Particulate domoic acid concentrations from the entire southern and northern regions of the SCB (A,C, respectively) were temporally matched to positive or negative temperature anomalies, and are plotted accordingly on the figures (black dots). The righthand axes are duplicated above and below a temperature anomaly of zero to denote whether concentration data were matched to a positive or negative temperature anomaly. Only particulate domoic acid concentrations $\geq 1\ \mu g\ L^{-1}$ (representing substantive concentrations of particulate domoic acid) were plotted. Absolute surface water temperatures for the same period are shown for Newport Beach Pier (B) and Stearns Wharf (D). Note the differences in maximal absolute temperatures between the two sites.

with the central and northern Californian coast. This speculation seems to be consistent with observed differences in the magnitude of spring upwelling that can exist between the northern sector of the SCB relative to the central and southern sectors (Fig. S5, Supplemental). Additionally, this speculation is supported by differences in the magnitude and frequency of domoic acid in shellfish of the northern vs. southern counties of California observed in the present synthesis (Fig. 2).

It also appears that during the past 15 years, surface water temperature has been an overriding factor controlling the production of domoic acid in the SCB. A strong relationship between surface water temperature ≤19 °C and domoic acid was observed, as noted above (Section 4.1.1; Fig. 6; Fig. S3 Supplemental). In accordance with that finding, an analysis of two SSTa time series from Newport Pier (located in Orange County) and Stearns Wharf (located in Santa Barbara County) indicate that elevated domoic acid concentrations generally do not occur during periods of sustained positive temperature anomalies (Fig. 9A, C). Conversely, McCabe et al. (2016) postulated that the large toxigenic *Pseudo-nitzschia* bloom that occurred from central California northward during 2015 was related to positive temperature anomalies. These anomalies resulted in SSTs of ≤19 °C throughout the region affected by the toxic bloom (see Fig. 2 in McCabe et al., 2016), while surface water temperatures during this period in southern California were ≥19 °C (Fig. 9B, D). Generally, mean absolute SSTs are higher in the Bight (particularly in the southern regions of the SCB), than along the west coast to the north of the SCB. These observations are consistent with the conclusion that processes that increase temperatures along the U.S. west coast (such as El Niño) may stimulate the growth of *Pseudo-nitzschia* in more northern regions, but appear to have a negative effect on *Pseudo-nitzschia* populations in the SCB. These results suggest that temperatures above 19 °C in the Bight will suppress the growth and buildup of toxigenic *Pseudo-nitzschia* cell populations, thereby also resulting in lower particulate toxin concentrations at higher temperatures. The effect of temperature on toxin production on a per cell basis, however, is less clear.

Beyond latitudinal differences along the coast and their effects on water temperature, two other features may help explain differences in the response of the phytoplankton community within the SCB from communities to the north. Firstly, the orientation of the coastline of the Southern California Bight to prevailing wind patterns along the coast is different than the coastline to the north, affecting the magnitude of upwelling events and heterogeneity associated with their geographic distribution within the Bight. Secondly, the Channel Islands, which are located throughout the Bight, result in a complicated pattern of coastal circulation (Fig. 1) that may temper the applicability of relationships derived from observations farther north along the coast. The islands also impact retention time, which has shown to be important by Nezlin et al. (2012).

4.3. Implications for modeling and prediction

A long-term goal of the work conducted in the SCB is the development of an operational forecasting model for toxigenic *Pseudo-nitzschia* bloom events. The development of operational HAB models for predicting blooms, including toxigenic *Pseudo-nitzschia*, is a central objective of NOAA's Ecological Forecasting Roadmap (Anderson et al., 2016). At the time of this writing, operational models of this type exist for *Karenia brevis* blooms in the Gulf of Mexico (Stumpf et al., 2009), and for cyanobacterial blooms in Lake Erie (Wynne et al., 2010). These efforts are the joint work of NOAA National Ocean Service's (NOS) National Centers for Coastal Ocean Sciences (NCCOS), government agencies, researchers, and regional associations of the U.S. Integrated Ocean Observing System (IOOS) to develop NOAA's HAB Operation Forecasting System (HAB-OFS; https://tidesandcurrents.noaa.gov/hab/). Pilot HAB forecast models are being developed with the goal of becoming operational for *Alexandrium* in the Gulf of Maine (He et al., 2008; McGillicuddy et al., 2005; Stock et al., 2005), *Alexandrium* and *Pseudo-nitzschia* in the PNW (Trainer and Suddleson, 2005), and *Pseudo-nitzschia* along the California coast (Anderson et al., 2016).

Predictive modeling of *Pseudo-nitzschia* related HAB events requires the determination of pertinent variables and their measurement on appropriate temporal and spatial scales (Jochens et al., 2010). There are currently few environmental factors that have been unequivocally linked to increases in *Pseudo-nitzschia* cell abundances or the initiation of domoic acid production *in situ*. As noted above, the conditions related to increases in *Pseudo-nitzschia* abundances can differ from the conditions related to domoic acid production, creating an additional challenge. Several studies have identified variables that might be used to help model toxigenic *Pseudo-nitzschia* blooms (Anderson et al., 2011, 2016; Anderson et al., 2009; Blum et al., 2006; Lane et al., 2009). Limiting macronutrient concentrations, most often silicate, have emerged as an important factor in DA-producing blooms from several of these studies (Anderson et al., 2011, 2009; Blum et al., 2006; Lane et al., 2009). Another challenge to predictive modeling is the need for substantial and sustained data input into the model. Remotely sensed information, particularly satellite imagery, has provided the most extensive temporal and spatial coverage, making it useful for current and forecast models. A major challenge to this approach, however, is the lack of a novel optical signal for domoic acid or *Pseudo-nitzschia* abundances from the currently available multi-spectral ocean color satellite sensors (Anderson et al., 2016). Approaches using chlorophyll anomalies from satellite observations have yet to be successfully applied to predict *Pseudo-nitzschia* or domoic acid events with high accuracy, as they have with other forecast models such as those for *Karenia brevis* blooms (Stumpf et al., 2009).

The majority of *Pseudo-nitzschia* and domoic acid modeling studies in the SCB have focused on the Santa Barbara Channel region to central California. Anderson et al. (2009) utilized a stepwise linear regression approach to identify *in situ* biological and physiochemical factors, as well as remotely sensed data, that contributed to *Pseudo-nitzschia* blooms and DA over a 1.5-year period. Remote sensing reflectance ratio (R_{rs}) (510/555), Si:P, SST and sea surface salinity (SSS) were the strongest predictors of particulate domoic acid concentrations. The model performed well at estimating the presence or absence of particulate domoic acid (e.g. thresholds), but was less skilled at estimating the absolute concentration of the toxin and, overall, performed better at predicting *Pseudo-nitzschia* cell thresholds than domoic acid thresholds. Unsurprisingly, the conditions related to elevated *Pseudo-nitzschia* abundances differed from those related to elevated particulate domoic acid. Conditions related to *Pseudo-nitzschia* abundances above a bloom threshold were found to be R_{rs}(412/555), ln(Si:N), R_{rs}(555), particulate absorption (A_p)(490), and R_{rs}(510/555).

Anderson et al. (2011) expanded upon the work reported in Anderson et al. (2009) and employed satellite-derived ocean color data and the Regional Ocean Modeling System (ROMS) (Shcehpetkin and McWilliams, 2005) to estimate circulation patterns, sea surface temperature and sea surface salinity, and an updated empirical HAB model that utilized a generalized linear model approach with a larger data set. A 'full model' that included all available data and 'remote-sensing' model that included only variables from remote platforms were produced. The predictors of the 'full model' generally agreed with previous *Pseudo-nitzschia* and DA modeling studies (Anderson et al., 2009; Lane et al., 2009), identifying R_{rs} (510/555), Si:N, Si:P, SST and SSS as significant predictors of DA. The 'full model' demonstrated greater predictive skill than the 'remote-sensing' model; however, nowcasts and forecasts are currently only possible using remotely sensed data due to its higher temporal and spatial coverage compared to *in situ* measurements.

The California Harmful Algal Risk Mapping (C-HARM) system (Anderson et al., 2016), (http://www.cencoos.org/data/models/habs) is a pre-operational model that provides a risk map of particulate domoic acid, cellular domoic acid, and *Pseudo-nitzschia*. C-HARM has been in operation since February 2014 and is built upon the efforts of Anderson et al. (2011; 2009). The system utilizes ROMS to estimate circulation patterns, sea surface temperature, and salinity, MODIS Aqua (MODISA) to derive ocean color data, and the previously developed empirical models for toxigenic *Pseudo-nitzschia* blooms noted above. This model also utilizes Data Interpolating Empirical Orthogonal Function (DINEOF), a data interpolating technique, to fill gaps in satellite coverage to enhance the nowcast and forecast abilities of the model. Currently, C-HARM has been shown to be more skilled at the estimation of particulate domoic acid than *Pseudo-nitzschia* cell abundance thresholds. Anderson et al. (2016) reported that the model correctly predicted more than 50% of the domoic acid events observed above a designated event threshold at the Santa Cruz Municipal Wharf as well as some of the shore stations maintained by California Harmful Algal Bloom Monitoring and Alert Program (CalHABMAP) and Southern California Coastal Ocean Observing System (SCCOOS) during the validation study. The bulk of the validation study was conducted with data collected at Santa Cruz Municipal Wharf in central California and in Santa Barbara County of the SCB at Stearns Wharf. Lower predictive ability was reported at some of the shore stations, particularly at the shore stations in San Diego County (Scripps Pier) and in San Luis Obispo county (Cal Poly Pier), again indicating potential regional disconnections between sites in the SCB as noted above.

The approach of merging data from various platforms in C-HARM has proven useful, and model skill will undoubtedly improve as the data coverage and resolution from remote sensing and ROMS platforms increases. Additionally, the development of a regional biogeochemical model capable of estimating nutrient concentrations would likely enhance the skill of C-HARM as indicated by the results of Anderson et al. (2011; 2009), where models that included nutrient data were generally more skilled than those with remotely sensed data alone.

5. Food web consequences of toxic blooms in the Southern California Bight

The consequences of domoic acid events along the U.S. west coast, and within the SCB, have stimulated awareness of the risk that the toxin poses to human health (and safeguards to prevent exposure). These events have resulted in mass animal mortality events and losses in fishery revenue due to contamination of pelagic and benthic food webs. Documentation of domoic acid within coastal marine food webs, and animal mortalities attributable to the toxin in the SCB followed the first reports of mass mortality events from central California in the late 1990s.

Most studies of marine animal poisoning have focused primarily on the California sea lion population (*Zalophus californianus*) in central California north of the SCB, but have also included events within the Bight (Bargu et al., 2012, 2010; Torres de la Riva et al., 2009). A substantial body of work on sea lions followed the mass mortality event of 1998 (north of the Bight) and events in the SCB during 2002, 2006 and 2007. These studies have brought attention to the role of domoic acid in sea lion strandings along the west coast (Scholin et al., 2000), and provided possible explanations for mass mortality events of other species. Since that time, domoic acid poisoning in sea lions has been linked to premature parturition and abortion, disruption of hippocampal-thalamic brain networks and other neurological problems (Cook et al., 2015; Goldstein et al., 2008, 2009; Silvagni et al., 2005). Significant mortality events of seabirds attributable to domoic acid have also been documented in the region, including brown pelicans (*Pelecanus occidentalis*) and other birds off Baja (Sierra Beltrán et al., 1997) and central California (Fritz et al., 1992; Work et al., 1993).

Losses to marine animal populations attributable to domoic acid have been significant. During the period of 2001–2009, nearly 27,000 marine mammal strandings were recorded along the coast of California (http://www.nmfs.noaa.gov/pr/health/prescott/: ≈94% pinnipeds, ≈6% cetaceans; 40% of animals were dead). In recent years, marine animal deaths have occurred with considerable frequency (http://www.whoi.edu/redtide/page.do?pid = 18103&tid = 542&cid = 47892&c = 3). Strandings have many causes, including injury, disease, even unusual oceanographic conditions (Melin et al., 2010) but published reports also indicate a strong link between some of these mass mortality events and algal toxins (particularly domoic acid) in marine food webs (Gulland, 2006). Other marine mammals along the California coast for which domoic acid poisoning has been demonstrated include Pacific harbor seals (McHuron et al., 2013), northern fur seals (Lefebvre et al., 2010) and southern sea otters (Kreuder et al., 2003). As a consequence of this work, biotoxins are increasingly recognized as a major cause of mass mortality events for marine mammal populations, and the overall number of events in the U.S. southwest region has increased markedly during the past few decades (Gulland, 2006).

Data collected during mortality events in 2006 and 2007 documented the pattern and impact that toxic *Pseudo-nitzschia* blooms have on marine animal populations in the SCB (Fig. 10). Both years witnessed massive toxic blooms of domoic acid on the San Pedro Shelf near the mouth of the Los Angeles Harbor in the central Southern California Bight. Maximal concentrations of particulate domoic acid of approximately 15 and 25 $\mu g\ L^{-1}$ during 2006 and 2007, respectively, were observed in the particulate domoic acid fraction (Fig. 10A, B). Concentrations of domoic acid averaged across 20 sampling stations on the Shelf were also high, and the timing of the appearance of particulate toxin coincided with the appearance of domoic acid in marine mammals and seabirds stranding at that time (Fig. 10C, D). Peaks in the number of animals testing positive for domoic acid co-occurred with the time of seasonal peaks in the number of stranding animals, and at or just before the time of peak particulate toxin concentrations were observed (Fig. 10C, D). Species affected in the 2006–2007 mortality events included several bird species of concern in California, including common loon, double-crested cormorant, rhinoceros auklet and California gull.

Studies beyond charismatic macrofauna along the U.S. west coast have documented that domoic acid is pervasive throughout the marine food web during toxic events (Lefebvre et al., 2002). The accumulation of domoic acid in sardines, anchovies, and krill during toxic blooms is well documented because these species constitute ‘vectors’ for the trophic transfer to species that prey on them (Bargu et al., 2002; Costa and Garrido, 2004; Lefebvre et al., 1999). Contamination and/or death of a wide variety of species, however, has been demonstrated including several pelagic and benthic fish, Humboldt squid and at least one Minke whale in the SCB (Busse et al., 2006; Fire et al., 2010; Mazzillo et al., 2011).

Contamination of benthic ecosystems and biological communities with domoic acid due to the potential for rapid sinking of toxic diatom cells and other particulate material in the SCB has also been demonstrated (Busse et al., 2006; Powell et al., 2002; Schnetzer et al., 2007; Sekula-Wood et al., 2009). Recent years have witnessed numerous closures of razor clam (and other bivalve mollusks), rock crab and Dungeness crab fisheries. The considerable magnitude and consequences of the contamination of benthic food webs were well-documented during the extensive domoic acid event along much of the U.S. west coast north of the SCB in 2015 (McCabe et al., 2016).

Continuing problems for marine animal health in the Southern California Bight include the re-occurrence of toxic *Pseudo-nitzschia* blooms (and resulting animal mortality events) such as the event that emerged in spring 2017 (http://www.ocregister.com/2017/04/10/are-toxic-algae-blooms-sickening-a-record-number-of-sea-lions/). Emerging issues include the potential for multiple toxins and other stressors to impact animal populations (Fire et al., 2010; Gulland, 2007), the transport of freshwater toxins from freshwater environments where they are produced into marine food webs (e.g. otter deaths in central California; (Miller et al., 2010)), and exposure to several algal and/or cyanobacterial toxins in an environment (Tatters et al., 2017).

6. Conclusions and future efforts

Much attention has been garnered recently regarding ocean warming and its realized and anticipated impact on the global distribution of HAB events. Concern within the scientific community is particularly acute for the development of freshwater cyanobacterial blooms and their associated toxins (Paerl, 2014; Paerl and Huisman, 2009; Paerl and Paul, 2012), but similar concerns surround the intensity and frequency of well-documented marine HABs (Gobler et al., 2017). These concerns include blooms and events along the west coast of North America produced by species of *Pseudo-nitzschia* (McCabe et al., 2016; McKibben et al., 2017), *Alexandrium* and *Dinophysis* (Jester et al., 2009), as well as HAB issues only recently documented in the region (Caron et al., 2010; Howard et al., 2008, 2012; Jessup et al., 2009; Reifel et al., 2013; *J.* Smith unpublished data). McCabe et al. (2016), for example, speculated that the massive domoic acid outbreak along the west coast from central California to Alaska was in part a consequence of a northern expansion of the range of *P. australis* enabled by anomalously warm ocean temperature throughout the region in that year.

Paradoxically, while ocean warming may expand the northern distributions of some HAB species, it is possible that ocean warming may actually reduce the occurrence of domoic acid in the Southern California Bight, based on information summarized here. Overall, the last 15 years have witnessed recurrent toxic events, but the recent exceptional drought years in the U.S. southwest (2014–2016) witnessed very low concentrations of particulate domoic acid in the Bight (Fig. 3). Moreover, the SCB experienced extremely low domoic acid concentrations during 2015, completely anomalous to the massive toxic event that occurred along the entire North American coast north of the Bight. Rising water temperatures might shrink the seasonal ‘window of opportunity’ for *Pseudo-nitzschia* species (i.e. the period of cooler surface water temperatures with sufficient light for population growth; Fig. 4C), particularly in the central and southern regions of the SCB, thereby reducing their competitive ability. Future domoic acid events are anticipated in the Bight due to year-to-year and decadal-scale climatic variability, but a general trend towards higher surface water temperatures in the region may act to limit or even prevent these toxic events.

The speculation above must be tempered, of course, by the possibility that warm-adapted, toxigenic species of *Pseudo-nitzschia* may eventually dominate in the region. The present dataset strongly indicated blooms of *Pseudo-nitzschia* and domoic acid production did not occur at surface water temperatures above 19 °C (Fig. 6, Supplemental Fig. S3). There is no *a priori* reason, however, to believe that warm-adapted toxigenic species of *Pseudo-nitzschia* will not become established in the region as ocean water warms, and continue to cause domoic acid events in future years. Indeed, Zhu et al. (2017) documented a *P. australis* strain isolated from the SCB that showed increased toxin

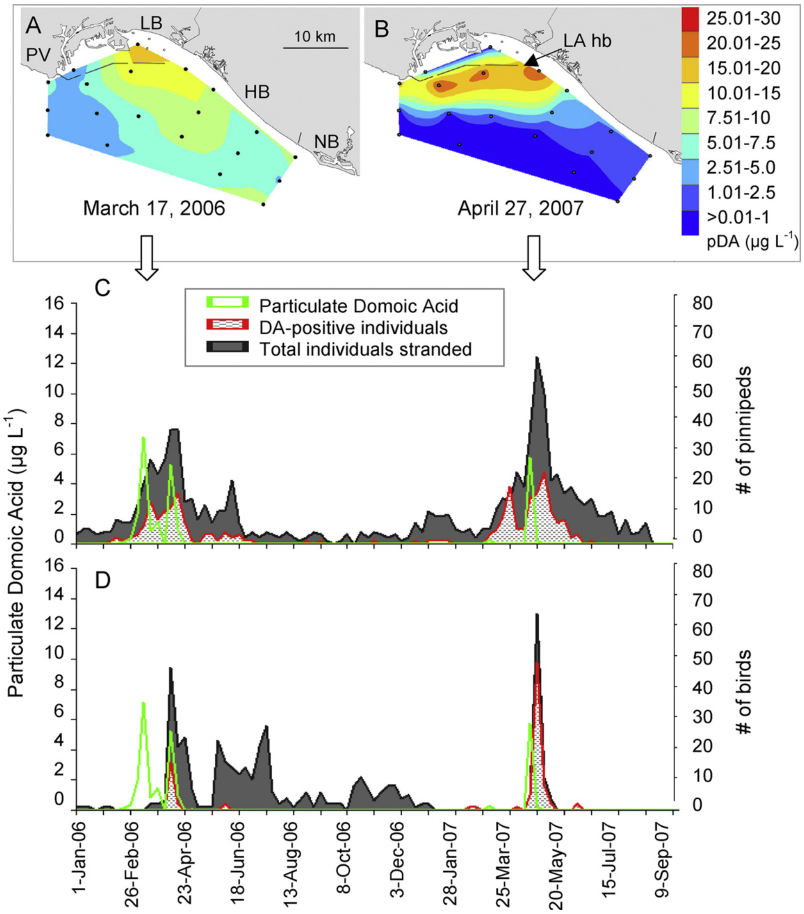

Fig. 10. Two examples of toxic *Pseudo-nitzschia* blooms on the San Pedro Shelf during 2006 and 2007, showing concentrations of particulate domoic acid, and their correspondence to domoic acid concentrations in the fluids and excreta of animals stranding during the same period. (A,B) Maximal concentrations and geographical distribution in the study area during blooms in the two years (black dots indicate sampling stations; particulate domoic acid concentrations in μg L^{-1}). LA hb indicates the Los Angeles harbor, PV indicates Palos Verdes, LB indicates Long Beach, HB indicates Huntington Beach, NB indicates Newport Beach; black lines show the breakwater. Data for marine mammals are shown in (C) and seabirds are shown in (D). Concentrations of particulate domoic acid (green lines: values are averages for 20 samples per cruise), total numbers of stranded or dead animals (black lines with gray fill) and animals testing positive for domoic acid (red lines with stippled fill) along the SCB during 2006 and 2007.

production and growth at 23 °C in culture, suggesting that some toxigenic strains of *Pseudo-nitzschia* exist in the region.

Perhaps more significantly, the role of subsurface chlorophyll maxima (including ‘thin layers’) as reservoirs of toxic populations of *Pseudo-nitzschia* is poorly understood. Evidence exists for the presence of toxic cells in subsurface layers within the SCB, but there is only cursory information on the extent to which these cells/toxins might seed surface blooms along the coast, explain the rapid emergence of toxic events due to uplifting of these layers during upwelling events, or contribute to animal strandings/mortalities when no surface manifestation of domoic acid is apparent (i.e. ‘cryptic blooms’). Establishing the significance of these phenomena should be a topic for future study and clarification.

Additionally, there is a poor understanding of blooms originating or taking place offshore within the Southern California Bight. The contribution of offshore blooms in the SCB to animal strandings and mortalities events is also poorly documented at this time. The potential for onshore advection of offshore toxic blooms to contribute to domoic acid in surface waters along the coast is understudied in large part because offshore monitoring and surveillance is generally sparse and/or ad hoc. Additional research is needed to gain a better understanding of the potentially important impact of offshore *Pseudo-nitzschia* dynamics and the level of connectivity to the onshore regions of the Bight.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.hal.2018.07.007.

References

Alexander, M., 2010. Extratropical air-sea interaction, sea surface temperature variability, and the Pacific Decadal Oscillation. In: Sun, D.-Z., Bryan, F. (Eds.), Climate Dynamics: Why Does Climate Vary? American Geophysical Union, Washington, D.C, pp. 123–148.

Anderson, C.R., Brzezinski, M.A., Washburn, L., Kudela, R., 2006. Circulation and environmental conditions during a toxigenic *Pseudo-nitzschia australis* bloom in the Santa Barbara Channel, California. Mar. Ecol. Prog. Ser. 327, 119–133.

Anderson, C.R., Siegel, D.A., Kudela, R.M., Brzezinski, M.A., 2009. Empirical models of toxigenic *Pseudo-nitzschia* blooms: potential use as a remote detection tool in the Santa Barbara Channel. Harmful Algae 8 (3), 478–492.

Anderson, C.R., Kudela, R.M., Benitez-Nelson, C., Sekula-Wood, E., Burrell, C.T., Chao, Y., Langlois, G., Goodman, J., Siegel, D.A., 2011. Detecting toxic diatom blooms from ocean color and a regional ocean model. Geophys. Res. Lett. 38 (4). https://doi.org/10.1029/2010GL045858.

Anderson, C.R., Kudela, R.M., Kahru, M., Chao, Y., Rosenfeld, L.K., Bahr, F.L., Anderson, D.M., Norris, T.A., 2016. Initial skill assessment of the California harmful algae risk mapping (C-HARM) system. Harmful Algae 59, 1–18.

Bargu, S., Powell, C.L., Coale, S.L., Busman, M., Doucette, G.J., Silver, M.W., 2002. Krill: a potential vector for domoic acid in marine food webs. Mar. Ecol. Prog. Ser. 237, 209–216.

Bargu, S., Silver, M., Goldstein, T., Roberts, K., Gulland, F., 2010. Complexity of domoic acid-related sea lion strandings in Monterey Bay, California: foraging patterns, climate events, and toxic blooms. Mar. Ecol. Prog. Ser. 418, 213–222.

Bargu, S., Goldstein, T., Roberts, K., Li, C., Gulland, F., 2012. *Pseudo-nitzschia* blooms, domoic acid, and related California sea lion strandings in Monterey Bay, California. Mar. Mammal Sci. 28, 237–253.

Barron, J.A., Bukry, D., Field, D., 2010. Santa Barbara Basin diatom and silicoflagellate response to global climate anomalies during the past 2200 years. Quat. Int. 15, 34–44.

Blum, I., Rao, D.S., Pan, Y., Swaminathan, S., Adams, N., 2006. Development of Statistical Models for Prediction of the Neurotoxin Domoic Acid Levels in the Pennate Diatom *Pseudo-nitzschia multiseries* Utilizing Data From Cultures and Natural Blooms, Algal Cultures: Analogues of Blooms and Applications. Science Publishers Inc., New Hampshire, pp. 891–925.

Bolin, R.L., Abbott, D.P., 1962. Studies on the marine climate and phytoplankton of the central coastal area of California, 1954-1960. Calif. Coop. Ocean. Fish. Invest. Rep. IX, 23–45 1 July 1960 to 30 June 1962.

Brzezinski, M.A., Washburn, L., 2011. Phytoplankton primary productivity in the Santa Barbara Channel: effects of wind-driven upwelling and mesoscale eddies. J. Geophys. Res. Oceans 116 (C12), C12013.

Buck, K.R., Uttal-Cooke, L., Pilskaln, C.H., Roelke, D.L., Villac, M.C., Fryxell, G.A., Cifuentes, L., Chavez, F.P., 1992. Autecology of the diatom *Pseudo-nitzschia australis*, a domoic acid producer, from Monterey Bay, California. Mar. Ecol. Prog. Ser. 84 (3), 293–302.

Busse, L., Venrick, E., Antrobus, R., Miller, P., Vigilant, V., Silver, M., Mengelt, C., Mydlarz, L., Prézelin, B., 2006. Domoic acid in phytoplankton and fish in San Diego, CA, USA. Harmful Algae 5, 91–101.

Capone, D.G., Hutchins, D.A., 2013. Microbial biogeochemistry of coastal upwelling regimes in a changing ocean. Nat. Geosci. 6 (9), 711–717.

Caron, D.A., Garneau, M.É., Seubert, E., Howard, M.D.A., Darjany, L., Schnetzer, A., Cetinic, I., Filteau, G., Lauri, P., Jones, B., Trussell, S., 2010. Harmful algae and their potential impacts on desalination operations off southern California. Water Res. 44 (2), 385–416.

Caron, D.A., Gellene, A.G., Smith, J., Seubert, E.L., Campbell, V., Sukhatme, G.S., Seegers, B., Jones, B.H., Lie, A.A.Y., Terrado, R., Howard, M.D.A., Kudela, R.M., Hayashi, K., Ryan, J., Birch, J., Demir-Hilton, E., Yamahara, K., Scholin, C., Mengel, M., Robertson, G., 2017. Response of phytoplankton and bacterial biomass during a wastewater effluent diversion into nearshore coastal waters. Estuar. Coast. Shelf Sci. 186 (Part B), 223–236.

Chhak, K., Di Lorenzo, E., 2007. Decanal variations in the California current upwelling cells. Geophys. Res. Lett. 34. https://doi.org/10.1029/2007GL03020.

Cook, P.F., Reichmuth, C., Rouse, A.A., Libby, L.A., Dennison, S.E., Carmichael, O.T., Kruse-Elliott, K.T., Bloom, J., Singh, B., Fravel, V.A., Barbosa, L., Stuppino, J.J., Van Bonn, W.G., Gulland, F.M.D., Ranganath, C., 2015. Algal toxin impairs sea lion memory and hippocampal connectivity, with implications for strandings. Science 350 (6267), 1545–1547.

Corcoran, A.A., Reifel, K.M., Jones, B.H., Shipe, R.F., 2010. Spatiotemporal development of physical, chemical, and biological characteristics of stormwater plumes in Santa Monica Bay, California (USA). J. Sea Res. 63, 129–142.

Costa, P.R., Garrido, S., 2004. Domoic acid accumulation in the sardine *Sardina pilchardus* and its relationship to *Pseudo-nitzschia* diatom ingestion. Mar. Ecol. Prog. Ser. 284, 261–268.

Di Lorenzo, E., Schneider, N., Cobb, K., Franks, P., Chhak, K., Miller, A., Mcwilliams, J., Bograd, S., Arango, H., Curchitser, E., 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. Geophys. Res. Lett. 35. https://doi.org/10.1029/2007GL032838.

Di Lorenzo, E., Combes, V., Keister, J.E., Strub, P.T., Thomas, A.C., Franks, P.J., Ohman, M.D., Furtado, J.C., Bracco, A., Bograd, S.J., 2013. Synthesis of Pacific Ocean climate and ecosystem dynamics. Oceanography 26, 68–81.

Du, X., Peterson, W., Fisher, J., Hunter, M., Peterson, J., 2016. Initiation and development of a toxic and persistent *Pseudo-nitzschia* bloom off the Oregon coast in spring/summer 2015. PLoS One 11 (10) e0163977.

Durham, W.M., Stocker, R., 2012. Thin phytoplankton layers: characteristics, mechanisms, and consequences. Ann. Rev. Mar. Sci. 4 (1), 177–207.

Dwight, R.H., Brinks, M.V., SharavanaKumar, G., Semenza, J.C., 2007. Beach attendance and bathing rates for Southern California beaches. Ocean Coast. Manage. 50 (10), 847–858.

Fire, S.E., Wang, Z., Berman, M., Langlois, G.W., Morton, S.L., Sekula-Wood, E., Benitez-Nelson, C.R., 2010. Trophic transfer of the harmful algal toxin domoic acid as a cause of death in a minke whale (*Balaenoptera acutorostrata*) stranding in southern California. Lat. Am. J. Aquat. Mamm. 36, 342–350.

Flint, L.E., Flint, A.L., Mendoza, J., Kalansky, J., Ralph, F., 2018. Characterizing drought in California: new drought indices and scenario-testing in support of resource management. Ecol. Processes 7 (1), 1.

Fritz, L., Quilliam, M.A., Wright, J.L.C., Beale, A.M., Work, T.M., 1992. An outbreak of domoic acid poisoning attributed to the pennate diatom Pseudonitzschia australis. J. Phycol. 28 (4), 439–442.

Fryxell, G.A., Villac, M.C., Shapiro, L.P., 1997. The occurrence of the toxic diatom genus *Pseudo-nitzschia* (Bacillariophyceae) on the West Coast of the USA, 1920-1996: a review. Phycologia 36 (6), 419–437.

García-Mendoza, E., Rivas, D., Olivos-Ortiz, A., Almazán-Becerril, A., Castañeda-Vega, C., Peña_Manjarrez, J.L., 2009. A toxic *Pseudo-nitzschia* bloom in Todos Santos Bay, northwestern Baja California, Mexico. Harmful Algae 8, 493–503.

Garneau, M.-E., Schnetzer, A., Countway, P.D., Jones, A.C., Seubert, E.L., Caron, D.A., 2011. Examination of the seasonal dynamics of the toxic dinoflagellate *Alexandrium catenella* at Redondo Beach, California, by quantitative PCR. Appl. Environ. Microbiol. 77, 7669–7680.

Gobler, C.J., Doherty, O.M., Hattenrath-Lehmann, T.K., Griffith, A.W., Kang, Y., Litaker, R.W., 2017. Ocean warming since 1982 has expanded the niche of toxic algal blooms in the North Atlantic and North Pacific oceans. Proc. Nat. Acad. Sci. https://doi.org/10.1073/pnas.1619575114.

Goldstein, T., Mazet, J.A.K., Zabka, T.S., Langlois, G., Colegrove, K.M., Silver, M., Bargu, S., Van Dolah, F., Leighfield, T., Conrad, P.A., Barakos, J., Williams, D.C., Dennison, S., Haulena, M., Gulland, F.M.D., 2008. Novel symptomatology and changing epidemiology of domoic acid toxicosis in California sea lions (*Zalophus californianus*): an increasing risk to marine mammal health. Proc. R. Soc. Lond. B: Biol. Sci. 275 (1632), 267–276.

Goldstein, T., Zabka, T.S., DeLong, R.L., Wheeler, E.A., Ylitalo, G., Bargu, S., Silver, M., Leighfield, T., Van Dolah, F., Langlois, G., Sidor, I., Dunn, J.L., Gulland, F.M.D., 2009. The role of domoic acid in abortion and premature parturition of California sea lions (*Zalophus californianus*) on San Miguel Island, California. J. Wildl. Dis. 45, 91–108.

Greenfield, D.I., Marin, R., Jensen, S., Massion, E., Roman, B., Feldman, J., Scholin, C., 2006. Application of the Environmental Sample Processor (ESP) methodology for quantifying *Pseudo-nitzschia australis* using ribosomal RNA-targeted probes in sandwich and fluorescent in situ hybridization. Limnol. Oceanogr. 4, 426–435.

Gregorio, D.E., Connell, L., 2000. Range of *Heterosigma akashiwo* expanded to include California, USA. In: Hallegraeff, G.M., Blackburn, S.I., Bolch, C.J., Lewis, R.J. (Eds.), Harmful Algae Blooms 2000. UNESCO, Hobart, Australia, pp. 86–88.

Gregorio, D.E., Pieper, R.E., 2000. Investigations of red tides along the southern California coast. Bull. Soc. Cal. Acad. Sci. 99, 147–160.

Greig, D.J., Gulland, F.M.D., Kreuder, C., 2005. A decade of live California sea Lion (*Zalophus californianus*) strandings along the central California coast: causes and trends, 1991-2000. J. Wildl. Dis. 31, 11–22.

Griffin, D., Anchukaitis, K., 2014. How unusual is the 2012-2014 California drought? Geophys. Res. Lett. 41, 9017–9023.

Gulland, F.M.D., 2006. Review of the Marine Mammal Unusual Mortality Event Response Program of the National Marine Fisheries Service. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service p. 37.

He, R., McGillicuddy, D.J., Keafer, B.A., Anderson, D.M., 2008. Historic 2005 toxic bloom of *Alexandrium fundyense* in the western Gulf of Maine: 2. Coupled biophysical numerical modeling. J. Geophys. Res. Oceans 113 (C7). https://doi.org/10.1029/2007JC004602.

Hernández-Becerril, D.U., 1998. Species of the planktonic diatom genus *Pseudo-nitzschia* of the Pacific coasts of Mexico. Hydrobiologia 379 (1), 77–84.

Herndon, J., Cochlan, W.P., Horner, R., 2003. *Heterosigma akashiwo* blooms in San Francisco Bay. Interagency Ecol. Prog. San Francisco Estuary Newslett. 16, 46–48.

Hickey, B.M., 1992. Circulation over the Santa Monica - San Pedro basin and shelf. Prog. Oceanogr. 30, 37–115.

Horner, R.A., Garrison, D.L., Plumley, F.G., 1997. Harmful algal blooms and red tide problems on the U.S. West coast. Limnol. Oceanogr. 42, 1076–1088.

Howard, M.D.A., Cochlan, W.P., Ladizinsky, N., Kudela, R.M., 2007. Nitrogenous preference of toxigenic Pseudo-nitzschia australis (Bacillariophyceae) from field and laboratory experiments. Harmful Algae 6 (2), 206–217.

Howard, M.D., Silver, M., Kudela, R., 2008. Yessotoxin detected in mussel (*Mytilus californicus*) and phytoplankton samples from the US west coast. Harmful Algae 7, 646–652.

Howard, M.D.A., Jones, A.C., Schnetzer, A., Countway, P.D., Tomas, C.R., Kudela, R.M., Hayashi, K., Chia, P., Caron, D.A., 2012. Quantitative real-time PCR for *Cochlodinium fulvescens* (Dinophyceae), a potentially harmful dinoflagellate from California coastal waters. J. Phycol. 48, 384–393.

Howard, M.D.A., Sutula, M., Caron, D.A., Chao, Y., Farrara, J.D., Frenzel, H., Jones, B., Robertson, G., McLaughlin, K., Sengupta, A., 2014. Anthropogenic nutrient sources rival natural sources on small scales in the coastal waters of the Southern California bight. Limnol. Oceanogr. 59, 285–297.

Howard, M.D.A., Kudela, R.M., McLaughlin, K., 2017. New insights into impacts of anthropogenic nutrients on urban ecosystem processes on the Southern California coastal shelf: introduction and synthesis. Estuar. Coast. Shelf Sci. 186 (Part B), 163–170.

Jacox, M.G., Fiechter, J., Moore, A.M., Edwards, C.A., 2015. ENSO and the California current coastal upwelling response. J. Geophys. Res. Oceans 120, 1691–1702.

Jessup, D.A., Miller, M.A., Ryan, J.P., Nevins, H.M., Kerkering, H.A., Mekebri, A., Crane, D.B., Johnson, T.A., Kudela, R.M., 2009. Mass stranding of marine birds caused by a surfactant-producing red tide. PLoS One 4 (2), e4550.

Jester, R., Lefebvre, K., Langlois, G., Vigilant, V., Baugh, K., Silver, M.W., 2009. A shift in the dominant toxin-producing algal species in central California alters phycotoxins in food webs. Harmful Algae 8 (2), 291–298.

Jochens, A.E., Malone, T.C., Stumpf, R.P., Hickey, B.M., Carter, M., Morrison, R., Dyble, J., Jones, B., Trainer, V.L., 2010. Integrated ocean observing system in support of forecasting harmful algal blooms. Mar. Technol. Soc. J. 44, 99–121.

Kim, H.-J., Miller, A.J., McGowan, J., Carter, M.L., 2009. Coastal phytoplankton blooms in the Southern California bight. Prog. Oceanogr. 82 (2), 137–147.

King, J.R., Agostini, V.N., Harvey, C.J., Mcfarlane, G.A., Foreman, M.G., Overland, J.E., Di Lorenzo, E., Bond, N.A., Aydin, K.Y., 2011. Climate forcing and the California current ecosystem. ICES J. Mar. Sci. 68, 1199–1216.

Kreuder, C., Miller, M.A., Jessup, D.A., Lowenstine, L.J., Harris, M.D., Ames, J.A., Carpenter, T.E., Conrad, P.A., Mazet, J.A.K., 2003. Patterns of mortality in southern sea otters (*Enhydra lutris nereis*) from 1998–2001. J. Wildl. Dis. 39 (3), 495–509.

Kudela, R.M., Gobler, C.J., 2012. Harmful dinoflagellate blooms caused by *Cochlodinium* sp.: global expansion and ecological strategies facilitating bloom formation. Harmful Algae 14 (0), 71–86.

Kudela, R., Cochlan, W., Roberts, A., 2003. Spatial and temporal patterns of *pseudo-nitzschia* spp. in central California related to regional oceanography. In: Steidinger, K.A., Landsberg, J.H., Tomas, C.R., Vargo, G.A. (Eds.), Harmful Algal Blooms 2002. Florida Fish and Wildlife Conservation Commission and Intergovernmental Oceanographic Commission of UNESCO, Proceedings of the X International Conference on Harmful Algae, pp. 347–349.

Kudela, R.M., Lane, J.Q., Cochlan, W.P., 2008. The potential role of anthropogenically derived nitrogen in the growth of harmful algae in California, USA. Harmful Algae 8, 103–110.

Kudela, R.M., Seeyave, S., Cochlan, W.P., 2010. The role of nutrients in regulation and promotion of harmful algal blooms in upwelling systems. Prog. Oceanogr. 85, 122–135.

Lane, J.Q., Raimondi, P.T., Kudela, R.M., 2009. Development of a logistic regression model for the prediction of toxigenic *Pseudo-nitzschia* blooms in Monterey Bay, California. Mar. Ecol. Prog. Ser. 383, 37–51.

Lange, C.B., Reid, F.M.H., Vernet, M., 1994. Temporal distribution of the potentially toxic diatom *Pseudonitzschia australis* at a coastal site in Southern California. Mar. Ecol. Prog. Ser. 104 (3), 309–312.

Lavaniegos, B.E., Ohman, M.D., 2007. Coherence of long-term variations of zooplankton in two sectors of the California current System. Prog. Oceanogr. 75 (1), 42–69.

Lefebvre, K.A., Powell, C.L., Busman, M., Doucette, G.J., Moeller, P.D.R., Silver, J.B., Miller, P.E., Hughes, M.P., Singaram, S., Silver, M.W., Tjeerdema, R.S., 1999. Detection of domoic acid in northern anchovies and california sea lions associated with an unusual mortality event. Nat. Toxins 7 (3), 85–92.

Lefebvre, K.A., Bargu, S., Kieckhefer, T., Silver, M.W., 2002. From sanddabs to blue whales: the pervasiveness of domoic acid. Toxicon 40 (7), 971–977.

Lefebvre, K.A., Robertson, A., Frame, E.R., Colegrove, K.M., Nance, S., Baugh, K.A., Wiedenhoft, H., Gulland, F.M.D., 2010. Clinical signs and histopathology associated with domoic acid poisoning in northern fur seals (*Callorhinus ursinus*) and comparison of toxin detection methods. Harmful Algae 9 (4), 374–383.

Lelong, A., Hégaret, H., Soudant, P., Bates, S.S., 2012. *Pseudo-nitzschia* (Bacillariophyceae) species, domoic acid and amnesic shellfish poisoning: revisiting previous paradigms. Phycologia 51 (2), 168–216.

Lewitus, A.J., Horner, R.A., Caron, D.A., Garcia-Mendoza, E., Hickey, B.M., Hunter, M., Huppert, D.D., Kelly, D., Kudela, R.M., Langlois, G.W., Largier, J.L., Lessard, E.J., RaLonde, R., Rensell, J.E., Strutton, P.G., Trainer, V.L., Tweddle, J.F., 2012. Harmful algal blooms in the North American west coast region: history, trends, causes, and impacts. Harmful Algae 19, 133–159.

Lynn, R.J., Collins, C.A., Mantyla, A.W., Schwing, F.B., Baumgartner, T., Hayward, T.L., Murphree, T., Sakuma, K.M., Garcia, J., Hyrenbach, K.D., 1998. The state of the California current, 1997–1998: transition to El Niño conditions. Calif. Coop. Oceanic Fish. Invest. Rep. 39, 25–49.

Mantua, N.J., Hare, S.R., 2002. The Pacific decadal oscillation. J. Oceanogr. 58, 35–44.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C., 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meterol. Soc. 78, 1069–1079.

Mazzillo, F.M., Staaf, D.J., Field, J.C., Carter, M.L., Ohman, M.D., 2011. A note on the detection of the neurotoxin domoic acid in beach-stranded *Dosidicus gigas* in the Southern California bight. CalCOFI Report 52, 109–115.

McCabe, R.M., Hickey, B.M., Kudela, R.M., Lefebvre, K.A., Adams, N.G., Bill, B.D., Gulland, F.M.D., Thomson, R.E., Cochlan, W.P., Trainer, V.L., 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. Geophys. Res. Lett. 43 (19), 10366–10376.

McGillicuddy, D.J., Anderson, D.M., Lynch, D.R., Townsend, D.W., 2005. Mechanisms regulating large-scale seasonal fluctuations in *Alexandrium fundyense* populations in the Gulf of Maine: results from a physical–biological model. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 2698–2714.

McGowan, J.A., Cayan, D.R., Dorman, L.M., 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science 281, 210–217.

McHuron, E.A., Greig, D.J., Colegrove, K.M., Fleetwood, M., Spraker, T.R., Gulland, F.M.D., Harvey, J.T., Lefebvre, K.A., Frame, E.R., 2013. Domoic acid exposure and associated clinical signs and histopathology in Pacific harbor seals (*Phoca vitulina richardii*). Harmful Algae 23, 28–33.

McKibben, S.M., Watkins-Brandt, K.S., Wood, A.M., Hunter, M., Forster, Z., Hopkins, A., Du, X., Eberhart, B.T., Peterson, W.T., White, A.E., 2015. Monitoring Oregon coastal harmful algae: observations and implications of a harmful algal bloom-monitoring project. Harmful Algae 31, 32–44.

McKibben, S.M., Peterson, W., Wood, A.M., Trainer, V.L., Hunter, M., White, A.E., 2017. Climatic regulation of the neurotoxin domoic acid. Proc. Natl. Acad. Sci. U. S. A. https://doi.org/10.1073/pnas.1606798114.

McLaughlin, K., Nezlin, N., Howard, M.D.A., Beck, C.D.A., Kudela, R.M., Mengel, M.J., Robertson, G., 2017. Rapid nitrification of wastewater ammonium near coastal ocean outfalls, Southern California, USA. Estuar. Coast. Shelf Sci. 186, 263–275.

McManus, M.A., Kudela, R.M., Silver, M.W., Steward, G.F., Donaghay, P.L., Sullivan, J.M., 2008. Cryptic blooms: are thin layers the missing connection? Estuaries Coast. 31 (2), 396–401.

McPhee-Shaw, E.E., Siegel, D.A., Washburn, L., Brzezinski, M.A., Jones, J.L., Leydecker, A., Melack, J., 2007. Mechanisms for nutrient delivery to the inner shelf: observations from the Santa Barbara Channel. Limnol. Oceanogr. 52, 1748–1766.

Melin, S.R., Orr, A.J., Harris, J.D., Laake, J.L., DeLong, R.L., Gulland, F.M.D., Stoudt, S., 2010. Unprecedented mortality of California sea lion pups associated with anomalous oceanographic conditions along the central California coast in 2009. Calif. Cooperat. Ocean. Fish. Investig. Rep. 51, 182–194.

Meyer, K.F., Sommer, H., Schoenholz, P., 1928. Mussel poisoning. J. Prevent. Med. 2, 365–394.

Miller, M.A., Kudela, R.M., Mekebri, A., Crane, D., Oates, S.C., Tinker, M.T., Staedler, M., Miller, W.A., Toy-Choutka, S., Dominik, C., Hardin, D., Langlois, G., Murray, M., Ward, K., Jessup, D.A., 2010. Evidence for a novel marine harmful algal bloom: cyanotoxin (microcystin) transfer from land to sea otters. PLoS ONE 5 (9), e12576.

Nezlin, N.P., Sutula, M.A., Stumpf, R.P., Sengupta, A., 2012. Phytoplankton blooms detected by SeaWiFS along the central and southern California coast. J. Geophys. Res. Oceans 117 (C7). https://doi.org/10.1029/2011jc007773.

O'Halloran, C., Silver, M., Holman, T., Scholin, C., 2006. *Heterosigma akashiwo* in central California waters. Harmful Algae 5, 124–132.

Paerl, H.W., 2014. Mitigating harmful cyanobacterial blooms in a human- and climatically-impacted world. Life 4 (4), 988–1012.

Paerl, H.W., Huisman, J., 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ. Microbiol. Rep. 1 (1), 27–37.

Paerl, H.W., Paul, V.J., 2012. Climate change: links to global expansion of harmful cyanobacteria. Water Res. 46 (5), 1349–1363.

Powell, C.L., Ferdin, M.E., Busman, M., Kvitek, R.G., Doucette, G.J., 2002. Development of a protocol for determination of domoic acid in the sand crab (*Emerita analoga*): a possible new indicator species. Toxicon 40, 485–492.

Reifel, K.M., Corcoran, A.A., Cash, C., Shipe, R., Jones, B.H., 2013. Effects of a surfacing effluent plume on a coastal phytoplankton community. Cont. Shelf Res. 60, 38–50.

Ren, H., Chen, Y.-C., Wang, X.T., Wong, G.T.F., Cohen, A.L., DeCarlo, T.M., Weigand, M.A., Mii, H.-S., Sigman, D.M., 2017. 21st-century rise in anthropogenic nitrogen deposition on a remote coral reef. Science 356 (6339), 749–752.

Rhodes, L., Jiang, W., Knight, B., Adamson, J., Smith, K., Langi, V., Edgar, M., 2013. The genus *Pseudo-nitzschia* (Bacillariophyceae) in New Zealand: analysis of the last decade's monitoring data. New Zeal. J. Mar. Freshw. Res. 47 (4), 490–503.

Rines, J.E.B., Donaghay, P.L., Dekshenieks, M.M., Sullivan, J.M., Twardowski, M.S., 2002. Thin layers and camouflage: hidden *Pseudo-nitzschia* spp. (Bacillariophyceae) populations in a fjord in the San Juan Island, Washington, USA. Mar. Ecol. Prog. Ser. 225, 123–137.

Rines, J.E.B., McFarland, M.N., Donaghay, P.L., Sullivan, J.M., 2010. Thin layers and species-specific characterization of the phytoplankton community in Monterey Bay, California, USA. Cont. Shelf Res. 30 (1), 66–80.

Ryan, J.P., McManus, M.A., Sullivan, J.M., 2010. Interacting physical, chemical and biological forcing of phytoplankton thin-layer variability in Monterey Bay, California. Cont. Shelf Res. 30, 7–16.

Ryan, J.P., Kudela, R.M., Birch, J.M., Blum, M., Bowers, H.A., Chavez, F.P., Doucette, G.J., Hayashi, K., Marin, R., Mikulski, C.M., Pennington, J.T., Scholin, C.A., Smith, G.J., Woods, A., Zhang, Y., 2017. Causality of an extreme harmful algal bloom in Monterey Bay, California, during the 2014–2016 northeast Pacific warm anomaly. Geophys. Res. Lett. 44 (11), 5571–5579.

Schnetzer, A., Miller, P.E., Schnaffner, R.A., Stauffer, B.A., Jones, B.H., Weisberg, S.B., DiGiacomo, P.M., Berelson, W.M., Caron, D.A., 2007. Blooms of *Pseudo-nitzschia* and domoic acid in the San Pedro Channel and Los Angeles harbor areas of the Southern California bight, 2003-2004. Harmful Algae 6, 372–387.

Schnetzer, A., Jones, B.H., Schaffner, R.A., Cetinic, I., Fitzpatrick, E., Miller, P.E., Seubert, E.L., Caron, D.A., 2013. Coastal upwelling linked to toxic *Pseudo-nitzschia australis* blooms in Los Angeles coastal waters, 2005-2007. J. Plankton Res. 35, 1080–1092.

Scholin, C.A., Gulland, F., Doucette, G.J., Benson, S., Busman, M., Chavez, F.P., Cordaro, J., DeLong, R., De Vogelaere, A., Harvey, J., Haulena, M., Lefebvre, K., Lipscomb, T., Loscutoff, S., Lowenstine, L.J., Marin, R., Miller, P.E., McLellan, W.A., Moeller, P.D.R., Powell, C.L., Rowles, T., Silvagni, P., Silver, M., Spraker, T., Trainer, V., Van Dolah, F.M., 2000. Mortality of sea lions along the central California coast linked to a toxic diatom bloom. Nature 403 (6765), 80–84.

Schwing, F.B., Bond, N.A., Bograd, S.J., Mitchell, T., Alexander, M.A., Mantua, N., 2006. Delayed coastal upwelling along the U.S. West Coast in 2005: a historical perspective. Geophys. Res. Lett. 33 (22) L22S01.

Seegers, B.N., Birch, J.M., Marin, R., Scholin, C.A., Caron, D.A., Seubert, E.L., Howard, M.D.A., Robertson, G.L., Jones, B.H., 2015. Subsurface seeding of surface harmful algal blooms observed through the integration of autonomous gliders, moored environmental sample processors, and satellite remote sensing in southern California. Limnol. Oceanogr. 60 (3), 754–764.

Sekula-Wood, E., Schnetzer, A., Benitez-Nelson, C.R., Anderson, C., Berelson, W., Brzezinksi, M., Burns, J., Caron, D.A., Cetinic, I., Ferry, J., Fitzpatrick, E., Jones, B., Miller, P.E., Morton, S.L., Schaffner, R., Siegel, D., Thunell, R., 2009. Rapid downward transport of the neurotoxin domoic acid in coastal waters. Nat. Geosci. 2, 272–275.

Sekula-Wood, E., Benitez-Nelson, C., Morton, S., Anderson, C., Burrell, C., Thunell, R., 2011. *Pseudo-nitzschia* and domoic acid fluxes in Santa Barbara Basin (CA) from 1993 to 2008. Harmful Algae 10 (6), 567–575.

Sengupta, A., Sutula, M.A., McLaughlin, K., Howard, M., Tiefenthaler, L., Von Bitner, T., 2013. Terrestrial Nutrient Loads and Fluxes to the Southern California bight, USA, Southern California coastal Water Research Project Annual Report, Costa mesa. pp. 245–258.

Seubert, E.L., Gellene, A.G., Howard, M.D.A., Connell, P., Ragan, M., Jones, B.H., Runyan, J., Caron, D.A., 2013. Seasonal and annual dynamics of harmful algae and algal toxins revealed through weekly monitoring at two coastal ocean sites off southern California, USA. Environ. Sci. Pollut. Res. 20, 6878–6895.

Shcehpetkin, A., McWilliams, J.C., 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model. (Oxf) 9, 347–404.

Shipe, R.F., Leinweber, A., Gruber, N., 2008. Abiotic controls of potentially harmful algal blooms in Santa Monica Bay, California. Cont. Shelf Res. 28 (18), 2584–2593.

Sierra Beltrán, A., Palafox-Uribe, M., Grajales-Montiel, J., Cruz-Villacorta, A., Ochoa, J.L.,

1997. Sea bird mortality at Cabo San Lucas, Mexico: evidence that toxic diatom blooms are spreading. Toxicon 35 (3), 447–453.

Silvagni, P.A., Lowenstine, L.J., Spraker, T., Lipscomb, T.P., Gulland, F.M.D., 2005. Pathology of domoic acid toxicity in California sea lions (*Zalophus californianus*). Vet. Pathol. Online 42 (2), 184–191.

Smith, J., Gellene, A.G., Hubbard, K.A., Bowers, H.A., Kudela, R.M., Hayashi, K., Caron, D.A., 2018. Pseudo-nitzschia species composition varies concurrently with domoic acid concentrations during two different bloom events in the Southern California bight. J. Plankton Res. 40 (1), 29–45.

Stauffer, B.A., Gellene, A., Schnetzer, A., Seubert, E.L., Oberg, C., Sukhatme, G.S., Caron, D.A., 2012. An oceanographic, meterological and biological ‘perfect storm’ yields a massive fish kill. Mar. Ecol. Prog. Ser. 468, 231–243.

Stock, C.A., McGillicuddy, D.J., Solow, A.R., Anderson, D.M., 2005. Evaluating hypotheses for the initiation and development of *Alexandrium fundyense* blooms in the western Gulf of Maine using a coupled physical–biological model. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 2715–2744.

Stumpf, R.P., Tomlinson, M.C., Calkins, J.A., Kirkpatrick, B., Fisher, K., Nierenberg, K., Currier, R., Wynne, T.T., 2009. Skill assessment for an operational algal bloom forecast system. J. Mar. Syst. 76, 151–161.

Sun, J., Hutchins, D.A., Feng, Y., Seubert, E.L., Caron, D.A., Fu, F.-X., 2011. Effects of changing $p\mathrm{CO}_2$ and phosphate availability on domoic acid production and physiology of the marine harmful bloom diatom *Pseudo-nitzschia multiseries*. Limnol. Oceanogr. 56, 829–840.

Tatters, A.O., Fu, F.-X., Hutchins, D.A., 2012. High CO2 and silicate limitation synergistically increase the toxicity of *Pseudo-nitzschia fraudulenta*. PLoS ONE 7 (2), e32116.

Tatters, A.O., Howard, M.D., Nagoda, C., Busse, L., Gellene, A.G., Caron, D.A., 2017. Multiple stressors at the land-sea interface: cyanotoxins at the Land-Sea Interface in the Southern California bight. Toxins 9 (3), 95.

Terseleer, N., Gypens, N., Lancelot, C., 2013. Factors controlling the production of domoic acid by *Pseudo-nitzschia* (Bacillariophyceae): a model study. Harmful Algae 24, 45–53.

Thessen, A.E., Bowers, H.A., Stoecker, D.K., 2009. Intra- and interspecies differences in growth and toxicity of *Pseudo-nitzschia* while using different nitrogen sources. Harmful Algae 8, 792–810.

Timmerman, A.H.V., McManus, M.A., Cheriton, O.M., Cowen, R.K., Greer, A.T., Kudela, R.M., Ruttenberg, K., Sevadjian, J., 2014. Hidden thin layers of toxic diatoms in a coastal bay. Deep Sea Res. Part II Top. Stud. Oceanogr. 101, 129–140.

Torres de la Riva, G., Johnson, C.K., Gulland, F.M.D., Langlois, G.W., Heyning, J.E., Rowles, T.K., Mazet, J.A.K., 2009. Association of an unusual marine mammal mortality event with *Pseudo-nitzschia* spp. Blooms along the southern California coastline. J. Wildl. Dis. 45 (1), 109–121.

Torrey, H.B., 1902. An unusual occurrence of Dinoflagellata on the California coast. Am. Nat. 36, 187–192.

Trainer, V.L., Suddleson, M., 2005. Monitoring approaches for early warning of domoic acid events in Washington State. Oceanography 18, 228–237.

Trainer, V.L., Adams, N.G., Bill, B.D., Stehr, C.M., Wekell, J.C., Moeller, P., Busman, M., Woodruff, D., 2000. Domoic acid production near California coastal upwelling zones, June 1998. Limnol. Oceanogr. 45 (8), 1818–1833.

Trainer, V.L., Hickey, B.M., Horner, R.A., 2002. Biological and physical dynamics of domoic acid production off the Washington coast. Limnol. Oceanogr. 47, 1438–1446.

Trainer, V.L., Eberhart, B.-T.L., Wekell, J.C., Adams, N.G., Hanson, L., Cox, F., Dowell, J., 2003. Paralytic shellfish toxins in Puget Sound, Washington state. J. Shellfish Res. 22, 213–223.

Trainer, V.L., Cochlan, W.P., Erickson, A., Bill, B.D., Cox, F.H., Borchert, J.A., Lefebvre, K.A., 2007. Recent domoic acid closures of shellfish harvest areas in Washington State inland waterways. Harmful Algae 6, 449–459.

Trainer, V.L., Hickey, B.M., Lessard, E.J., Cochlan, W.P., Trick, C.G., Wells, M.L., MacFadyen, A., Moore, S.K., 2009. Variability of *Pseudo-nitzschia* and domoic acid in the Juan de Fuca eddy region and its adjacent shelves. Limnol. Oceanogr. 54, 289–308.

Velo-Suárez, L., González-Gil, S., Gentien, P., Lunven, M., Bechemin, C., Fernand, L., Raine, R., Reguera, B., 2008. Thin layers of *Pseudo-nitzschia* spp. And the fate of *Dinophysis acuminata* during an upwelling-downwelling cycle in a Galician Ría. Limnol. Oceanogr. 53, 1816–1834.

Walz, P.M., Garrison, D.L., Graham, W.M., Cattey, M.A., Tjeerdema, R.S., Silver, M.W., 1994. Domoic acid-producing diatom blooms in Monterey Bay, California: 1991-1993. Nat. Toxins 2 (5), 271–279.

Wolter, K., Timlin, M.S., 1993. Monitoring ENSO in COADS with a seasonally adjusted principal component index. Proc. of the 17th Climate Diagnostics Workshop. Oklahoma Clim. Survey, CIMMS and the School of Meteor. 52–57.

Wolter, K., Timlin, M.S., 1998. Measuring the strength of ENSO events: how does 1997/98 rank? Weather 53, 315–324.

Work, T.M., Barr, B., Beale, A.M., Fritz, L., Quilliam, M.A., Wright, J.L.C., 1993. Epidemiology of domoic acid poisoning in Brown Pelicans (*Pelecanus occidentalis*) and Brandt's Cormorants (*Phalacrocorax penicillatus*) in California. J. Zoo Wildl. Med. 24 (1), 54–62.

Wynne, T.T., Stumpf, R.P., Tomlinson, M.C., Dyble, J., 2010. Characterizing a cyanobacterial bloom in Western Lake Erie using satellite imagery and meteorological data. Limnol. Oceanogr. 55, 2025–2036.

Zhu, Z., Qu, P., Fu, F., Tennenbaum, N., Tatters, A.O., Hutchins, D.A., 2017. Understanding the blob bloom: warming increases toxicity and abundance of the harmful bloom diatom *Pseudo-nitzschia* in California coastal waters. Harmful Algae 67, 36–43.