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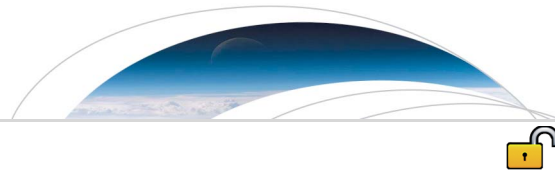
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## Special Section:

Midlatitude Marine Heatwaves:  
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## Key Points:

- The 2015 U.S. West Coast wide toxic *Pseudo-nitzschia australis* bloom was facilitated by anomalous ocean conditions
- The seasonal transition to upwelling provided nutrients for the bloom, and spring storms delivered toxic cells to the nearshore environment
- West Coast toxic *Pseudo-nitzschia* events are triggered by warm anomalies associated with El Niño and the Pacific Decadal Oscillation

## Supporting Information:

- Supporting Information S1

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## An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions

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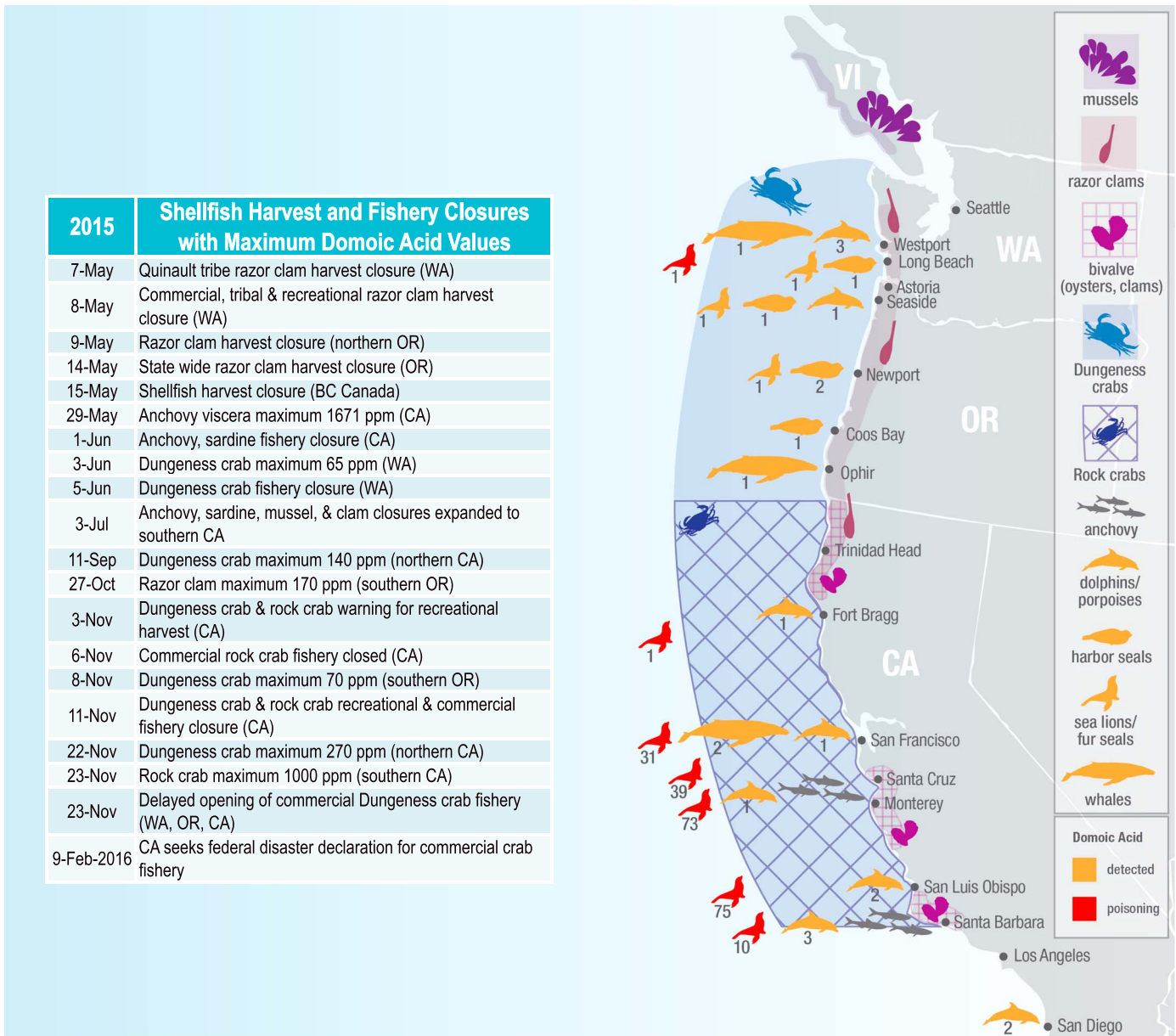
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**Abstract** A coastwide bloom of the toxigenic diatom *Pseudo-nitzschia* in spring 2015 resulted in the largest recorded outbreak of the neurotoxin, domoic acid, along the North American west coast. Elevated toxins were measured in numerous stranded marine mammals and resulted in geographically extensive and prolonged closures of razor clam, rock crab, and Dungeness crab fisheries. We demonstrate that this outbreak was initiated by anomalously warm ocean conditions. *Pseudo-nitzschia australis* thrived north of its typical range in the warm, nutrient-poor water that spanned the northeast Pacific in early 2015. The seasonal transition to upwelling provided the nutrients necessary for a large-scale bloom; a series of spring storms delivered the bloom to the coast. Laboratory and field experiments confirming maximum growth rates with elevated temperatures and enhanced toxin production with nutrient enrichment, together with a retrospective analysis of toxic events, demonstrate the potential for similarly devastating ecological and economic disruptions in the future.

### 1. An Unprecedented Coastwide Toxic Algal Bloom

Record-breaking concentrations of the marine neurotoxin, domoic acid (DA) in 2015 caused unprecedented widespread closures of commercial and recreational shellfish and finfish fisheries and contributed to the stranding of numerous marine mammals along the U.S. West Coast (Figure 1). Several species of the marine diatom, *Pseudo-nitzschia*, many of which produce DA, have been responsible for toxic blooms around the world [Lelong et al., 2012; Trainer et al., 2012]. The toxin is transferred through marine food webs by ingestion of live, dying, or dead *Pseudo-nitzschia* cells by pelagic and benthic organisms and sickens or kills marine mammals and sea birds, as well as humans who ingest contaminated fish, shellfish, or crustaceans [Lefebvre et al., 2002]. Seafood contaminated with DA cause symptoms in humans ranging from mild gastrointestinal distress to seizures, coma, permanent short-term memory loss, and death [Perl et al., 1990].

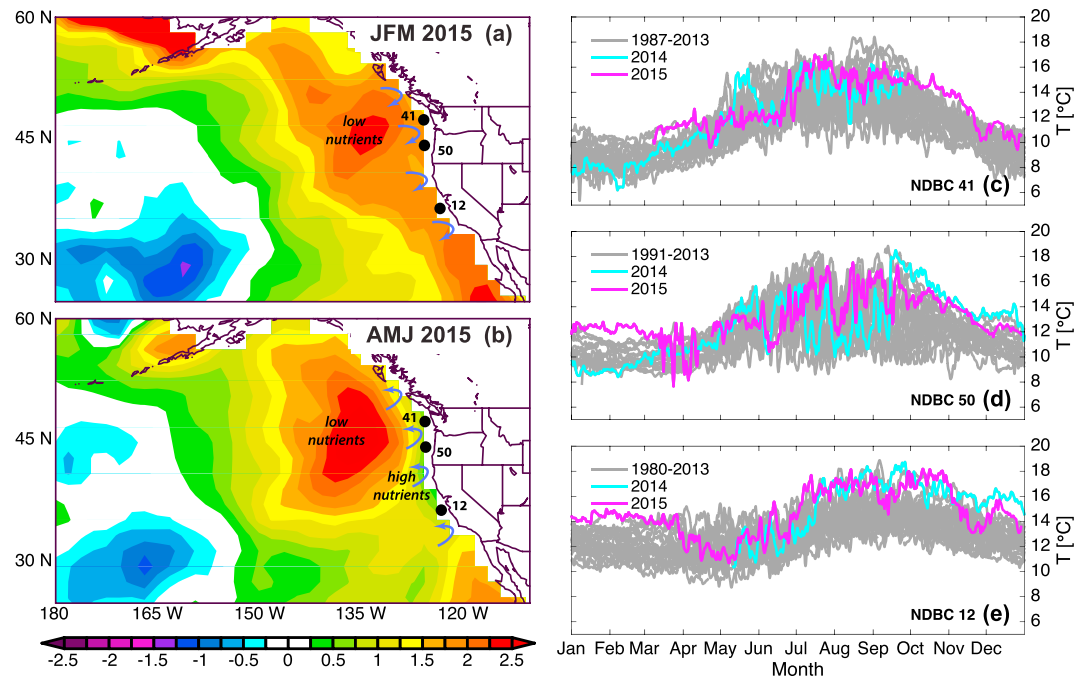
Seasonal blooms of *Pseudo-nitzschia* are common along the U.S. West Coast. Past toxic events have been attributed to a number of different species of this genus [Trainer et al., 2012]. Analyses of DA outbreaks over the last two decades have identified regional initiation “hotspots” where blooms either develop or become concentrated. These source zones tend to coincide with retentive flow patterns, such as those associated with seasonal eddies [Trainer et al., 2002], over submarine banks [Hickey et al., 2013], or in the lee of coastal capes [Graham et al., 1992; Trainer et al., 2000]. Toxic blooms off central and southern California are generally due to *P. australis* [Scholin et al., 2000; Sekula-Wood et al., 2011] whereas toxic spring blooms off Washington and Oregon are rarely caused by *P. australis* and, instead, are attributed to several different species [Trainer and Suddleson, 2005; Trainer et al., 2009]. Here we show that the highly toxic species, *P. australis*, bloomed simultaneously along the west coast of the U.S. and Canada in spring 2015. This extensive bloom was a consequence of three sequential factors: the onset of seasonal upwelling, followed by a series of late spring storms and the northward transport of the toxin-producing *P. australis* at a time of anomalously high surface temperatures throughout the northeast Pacific. Refer to the supporting information for a description of data analysis methods used herein.



**Figure 1.** Impacts of domoic acid (DA) on fisheries and marine mammals in 2015. Shaded areas with shellfish symbols on land denote shellfish closures. Fish symbols indicate northern anchovy closures at designated landing sites. Shaded or hatched areas offshore (Dungeness crab and rock crab) correspond to the closures listed on the left. Stranded marine mammals with detectable DA (orange) and California sea lions diagnosed with DA poisoning (red) are pictured with the number of individuals indicated. DA poisoning is defined as the presentation of at least two of the following: neurologic signs (seizures, head weaving, ataxia), detectable DA, histopathologic lesions, and/or blood chemistry changes.

## 2. The North Pacific Ocean Warm Anomaly

A ~500 km wide and ~100 m deep body of anomalously warm, relatively fresh, and nutrient-poor water (hereafter referred to as the warm anomaly) developed in fall 2013 in the northeast Pacific Ocean and persisted throughout 2014 and 2015 [Freeland and Whitney, 2014; Bond et al., 2015; Whitney, 2015a, 2015b; Peña and Nemcek, 2016; Di Lorenzo and Mantua, 2016] (Figure 2). Water in this region was more than 2.5°C warmer at the sea surface than the long-term mean temperature. The anomaly was caused by an expansion of the North Pacific atmospheric high-pressure cell to the north, which led to reduced ocean cooling and enhanced northward surface ocean transport by anomalous easterly winds [Freeland and Whitney, 2014; Bond et al., 2015; Peterson et al., 2015a].



**Figure 2.** Anomalously warm surface water in the North Pacific Ocean. Sea surface temperature anomalies ( $^{\circ}\text{C}$ ) from the NCEP/NCAR Reanalysis for the 3 month period of (a) January, February, March (JFM) 2015 and (b) April, May, June (AMJ) 2015, relative to the 1981–2010 composite average. Blue arrows indicate (Figure 2a) downwelling and (Figure 2b) upwelling. (c–e) Multiyear near-surface temperature records from three National Data Buoy Center (NDBC) buoys off the U.S. West Coast (numbered locations shown in left panels). Temperature records from 2014 and 2015 are colored cyan and magenta, respectively, whereas data from all other years are colored gray.

At the end of the upwelling season in September 2014, the warm anomaly expanded to waters adjacent to the continental margin, as was apparent from the exceedingly warm surface temperatures measured at continental shelf buoys (Figures 2c–2e). Coincident with this encroachment of warm water into the coastal zone, the copepod community off central Oregon transitioned from a “cold water” to a “warm water” assemblage that included southern species, such as *Rhincalanus nasutus* and *Clausocalanus furcatus*, not seen since the 1998 El Niño [Peterson *et al.*, 2015a]. Numerous observations of other southern species well north of their typical habitats have been linked to the warm anomaly [Bond *et al.*, 2015; Peterson *et al.*, 2015a, 2015b]. In early 2015, the warm anomaly extended along the entire west coasts of the U.S. and Canada (Figure 2a). On 10 March 2015, DA was detected in preserved zooplankton net tow samples collected in the warm water off Trinidad, California ( $41^{\circ}\text{N}$ ). Similar samples collected 1 month later off Newport, Oregon ( $44.6^{\circ}\text{N}$ ), also contained DA. Both samples confirm the presence of a toxic species of *Pseudo-nitzschia* within the anomalously warm water prior to spring 2015.

In spring 2015, the warm anomaly moved well offshore (Figure 2b) and by summer had diminished in size and strength and remained isolated from the coast (with the exception of southern California). The summertime offshore movement of the warm anomaly was controlled by the alongshore, southward winds, which move surface water to the right of the wind vector as a result of Earth’s rotation. Onshore movement of the water mass was critical to whether any associated biotoxin-producing species were able to reach the coast where they could then be fueled by nutrients from coastal upwelling. As long as the anomalously warm water remained separated from the coast, it would have lacked sufficient macronutrients to fuel a significant phytoplankton bloom.

### 3. Springtime Shelf Conditions and Nutrient Supply

Northward winds over the continental shelf during storms cause onshore flow in the upper water column and downwelling and mixing at the coast. The switch to prevailing southward winds along the coast in late spring and summer leads to offshore transport of near-surface waters and to upwelling of deep nutrient-rich water within a few tens of kilometers of the coast (Figure 2). This seasonal change, termed the “spring transition”

[Huyer *et al.*, 1975], occurs almost simultaneously along the entire coast [Strub *et al.*, 1987; Strub and James, 1988] and provides the macronutrients that drive the rich biological ecosystem characteristic of North American west coast waters.

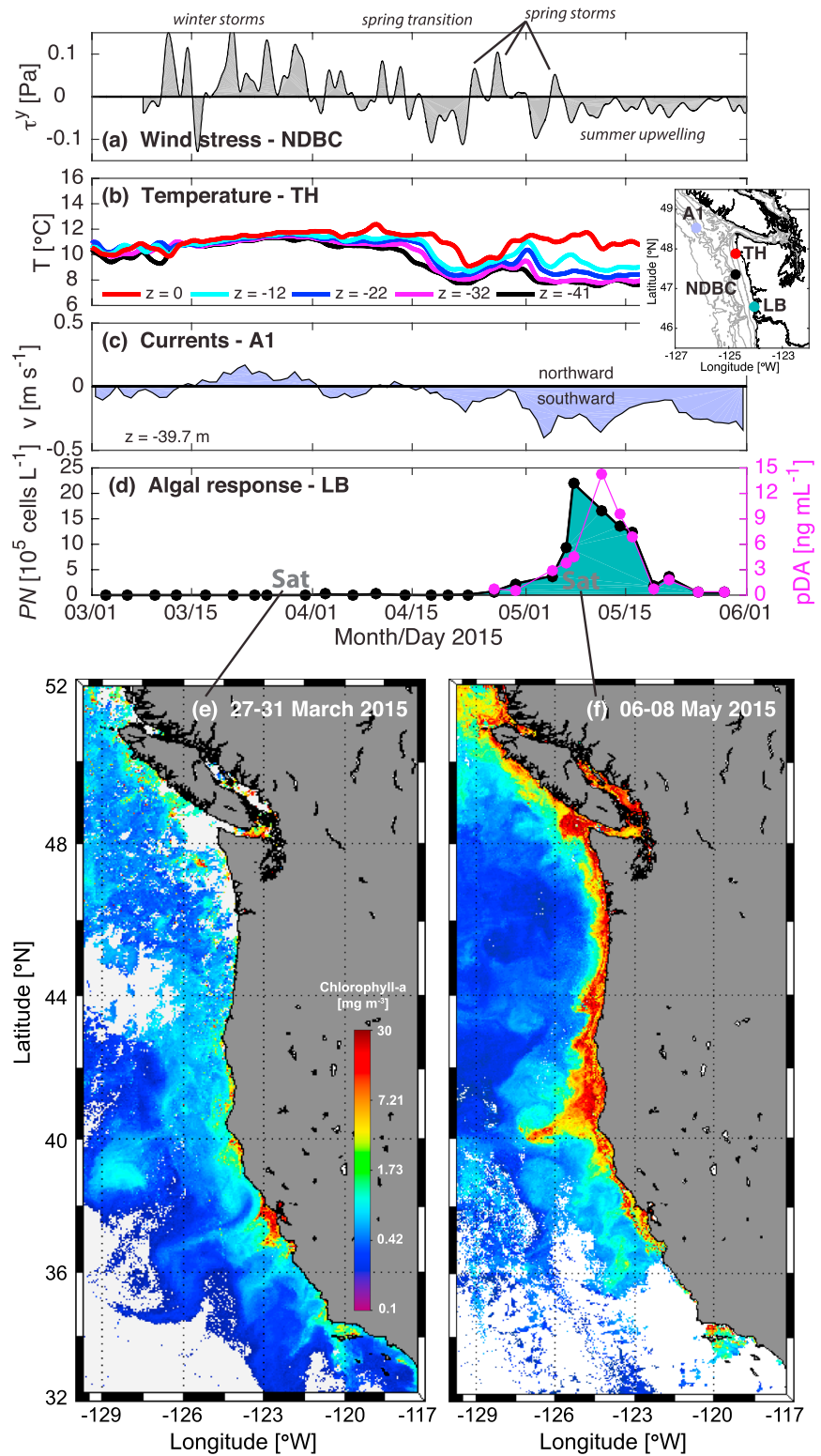
Nutrient-depleted water does not generally support a dense phytoplankton bloom. Indeed, no evidence of enhanced chlorophyll *a* (a proxy for phytoplankton biomass) was observed in the winter or early spring satellite images in the central North Pacific (Figure 3e), although brief upwelling favorable winds did result in a few short-lived phytoplankton blooms very near the coast. However, with the return to seasonal upwelling favorable conditions in mid April 2015 (the mean transition period observed in this region for the past two decades [Thomson *et al.*, 2014]), satellite-derived chlorophyll *a* increased along the continental margin of the western U.S. (Figure 3f). Off Washington, winds switched to a predominantly southward direction (Figure 3a), with the upwelling response clearly captured by a moored chain of thermistors as a rapid cooling and increased stratification beginning in mid April (Figure 3b). Near-surface currents at a site on the southern British Columbia continental slope changed from weak (and often northward) prior to the transition, to strongly southward following the mid April switch to upwelling (Figure 3c). After the spring transition, surface waters all along the continental margin cooled as the anomalously warm water was advected offshore (Figures 2b–2e).

#### 4. The Phytoplankton Bloom and Its Toxin

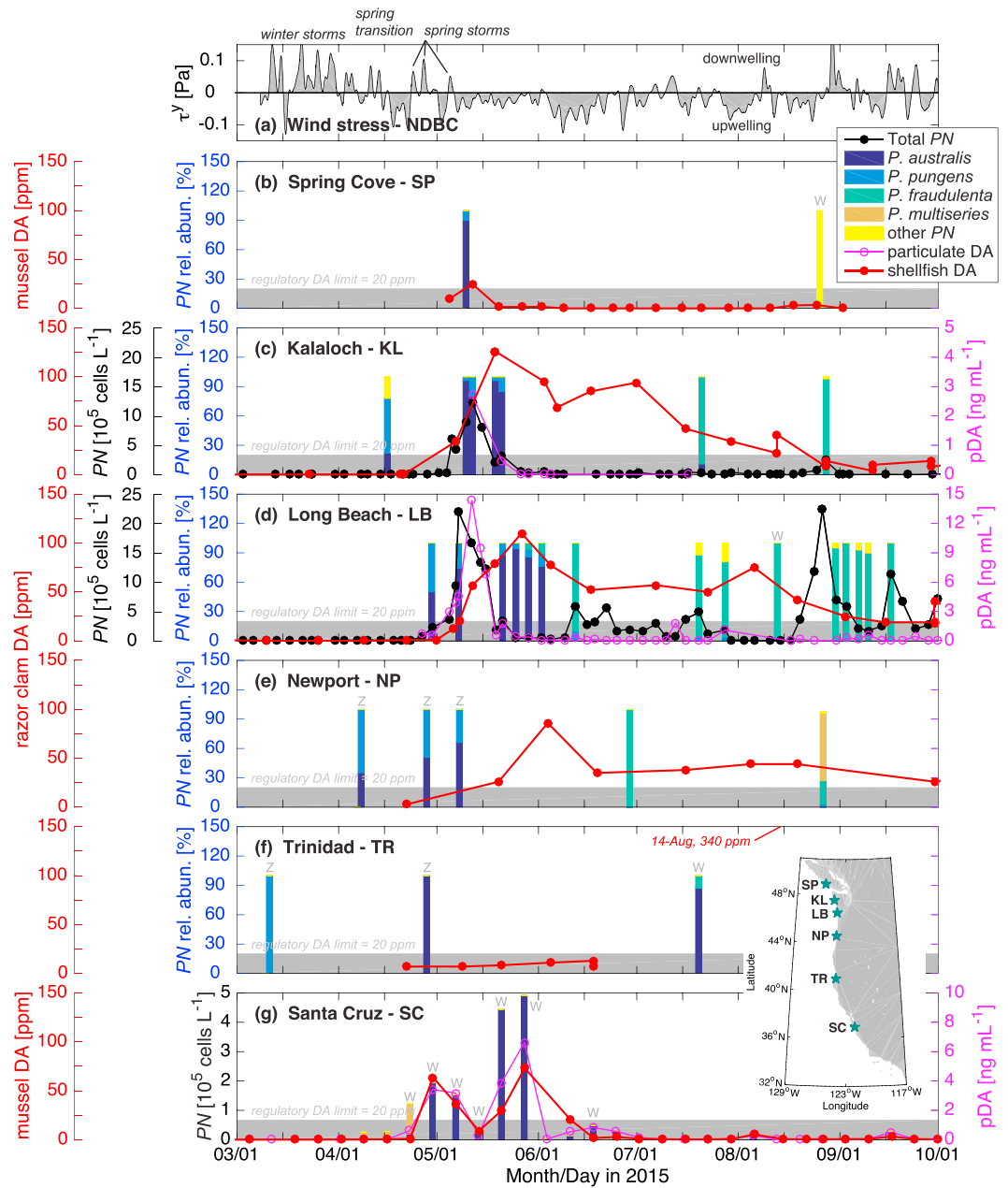
With the transition to upwelling of cold, nutrient-rich water to the euphotic zone, spring blooms of phytoplankton are observed annually over the continental shelf of the northeast Pacific [Thomas and Strub, 1989; Landry *et al.*, 1989; Lynn *et al.*, 2003; Jackson *et al.*, 2015]. Such blooms contain many phytoplankton species but are primarily composed of centric diatoms, which are not toxic.

Details of the timing between coastal winds and currents, the spring transition, the rise of total *Pseudo-nitzschia* abundance, and toxin concentration in seawater are shown in Figure 3 for Long Beach, Washington. Results for this station are representative of other U.S. West Coast locations north of central California (Figure 4). The spring transition to upwelling began with weak southward winds on 7 April, culminating in strong upwelling winds on 16 April (Figure 3a). Phytoplankton near the coast began to increase in abundance (i.e., bloom) when nutrients from depth were supplied to the euphotic zone on the inner shelf. Once the upwelled water mixed with the overlying and adjacent waters of the warm anomaly, phytoplankton, including *P. australis*, bloomed (Figures 3 and 4) and moved seaward in the offshore flowing surface layers. Scanning electron microscope analysis of a zooplankton net tow sample (integrated 0–100 m, 202  $\mu\text{m}$  mesh) collected  $\sim 9$  km offshore of Newport, Oregon, on 7 April reveal an assemblage of *Pseudo-nitzschia* chains containing 65% *P. pungens* and 35% *P. australis* (Figure 4e). On 15 April, a phytoplankton net tow (20  $\mu\text{m}$  mesh) off Kalaloch, Washington, documented a similar assemblage (56% *P. pungens*, 22% *P. australis*, and 22% *P. cf. heimii*; Figure 4c). By 22 April *Pseudo-nitzschia* abundance estimates were  $10^4$  cells  $\text{L}^{-1}$  at Washington beaches, and on 26 April cell densities had increased by an order of magnitude immediately following the first of a series of spring storms that moved toxic cells shoreward. Two additional storms occurred in early May, transporting the surface bloom back toward shore while mixing near-surface and middepth water with recently upwelled water. As *Pseudo-nitzschia* abundances peaked in early May (Figure 3d), *P. australis* emerged as the dominant species from central California to southern British Columbia (Figure 4). In late May, upwelling was more persistent and *P. australis* abundance decreased dramatically as newly upwelled water likely transported more regionally typical species from deeper depths. By June 2015, the more endemic and less toxic diatom *P. fraudulenta* had replaced *P. australis* in the northern waters off Washington and Oregon (Figure 4).

Concentrations of water column particulate DA (pDA) also peaked in late April and early May, coincident with peaks in *P. australis* abundance (Figures 3d and 4). DA concentrations in razor clams (*Siliqua patula*) and mussels (*Mytilus* spp.) began to rise in early May north of central California (Figure 4). As expected, the timing of maximum DA in razor clams lagged the periods of both maximum pDA and *Pseudo-nitzschia* abundance [Hickey *et al.*, 2013]. Laboratory analysis of DA concentrations in mussels (*M. californianus*) indicated that the regulatory limit of 20 ppm was first exceeded on 29 April off Santa Cruz, California. Following this, shellfish samples collected from beaches throughout Oregon, Washington, and British Columbia, exceeded the regulatory limit, resulting in the closures of tribal, commercial, and recreational shellfish harvests (Figure 1). In Washington,  $\sim 1950$  kg of clams harvested 1 day prior to the closure were ordered to be discarded. Although mussels depurate DA relatively quickly (days to weeks), razor clams retain DA for months [Horner



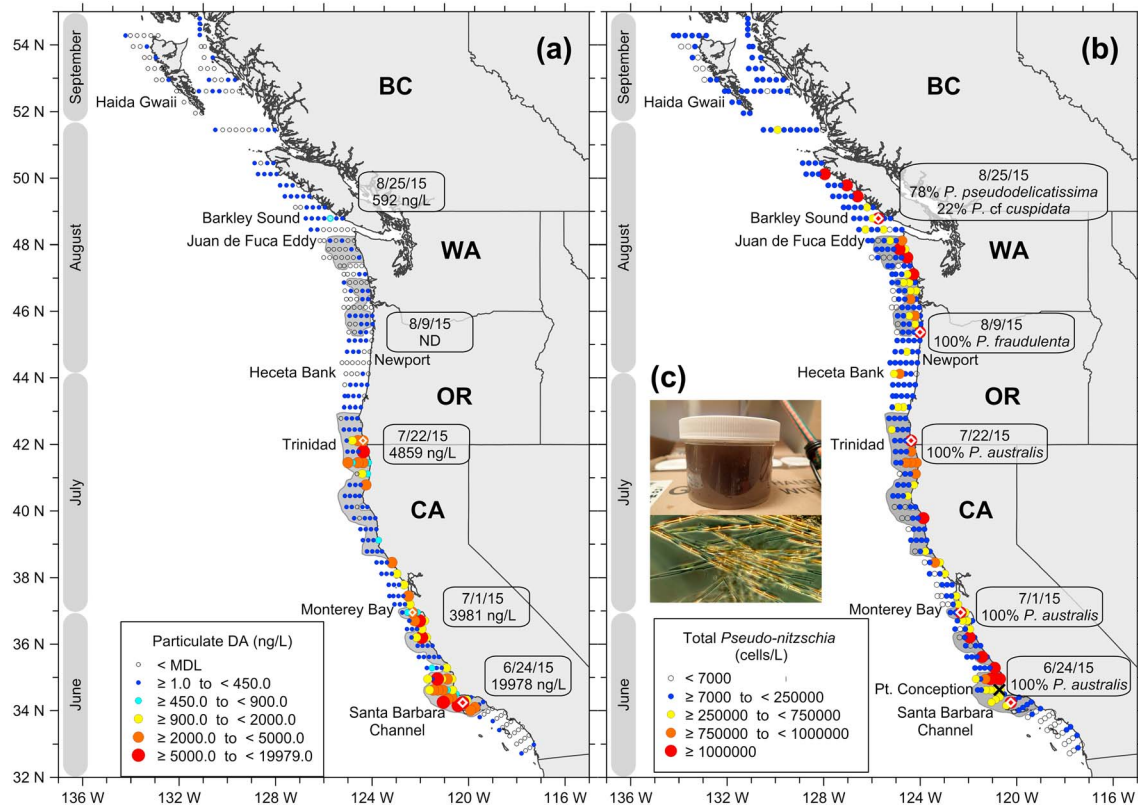
**Figure 3.** Relationship between physical environmental conditions and the toxic spring *Pseudo-nitzschia* bloom. (a) North-south wind stress off Washington (site NDBC). (b) Water column temperature at five depths at a site on the 42 m isobath off Teahwhit Head, Washington (site TH). (c) Along-slope near-surface currents off the southern British Columbia-northern Washington continental slope (site A1). (d) Total *Pseudo-nitzschia* abundance (black line with green shading) and pDA (magenta line) off Long Beach, Washington (site LB). Site locations are shown in the inset. Satellite chlorophyll a estimates are averaged over the periods of (e) 27–31 March 2015, and (f) 06–08 May 2015.



**Figure 4.** DA in mussels or razor clams (red line) and *Pseudo-nitzschia* abundance at six locations along the North American west coast (see lower inset). (a) North-south wind stress off Washington. *Pseudo-nitzschia* species abundance (colored bars) quantified as (b–f) percentage or as (g) cells L<sup>-1</sup>. Text labels indicate sample type, including phytoplankton net (not labeled), Z = zooplankton net, W = whole water. The regulatory shellfish DA limit of 20 ppm is shown (horizontal gray band). Figures 4c and 4d include total *Pseudo-nitzschia* abundance (black line). Figures 4c, 4d, and 4g include water column pDA (magenta line with open circles).

et al., 1993]. Razor clam DA concentrations began decreasing in late May off Washington and Oregon, but harvest closures continued at one Washington beach through June 2016.

Domoic acid outbreaks often continue to impact benthic organisms long after the toxin-producing species have dissipated [Horner et al., 1993]. Following the 2015 spring bloom and the mussel and razor clam fishery closures, Washington closed the coastal Dungeness crab fishery on 5 June (Figure 1), ~4.5 months earlier than scheduled and were forced to delay the December reopening. In California, the commercial and recreational Dungeness and rock crab fisheries did not open as expected at the beginning of November and the



**Figure 5.** (a) Particulate DA and (b) *Pseudo-nitzschia* abundance in surface (3 m) seawater samples collected aboard the NOAA Ship *Bell M. Shimada* from June through September (months shown in shaded boxes, left side of both panels). Red “targets” in Figure 5b are locations where representative pDA and *Pseudo-nitzschia* abundances are shown on select dates in adjacent boxes. Gray shading along the coast indicates regions where *Pseudo-nitzschia* was the dominant phytoplankton. (c) A Bongo net tow sample off Point Conception on 24 June (concentrated sample, top panel; microscopic image of ~100X diluted sample at 200X magnification, bottom panel). ND = not detected.

Dungeness crab fishery was not reopened along the entire U.S. coast until May 2016. Given that Dungeness crab are the single most valuable fishery on the U.S. West Coast, with an estimated ex-vessel value of ~\$170 million [*Pacific States Marine Fisheries Commission Dungeness Crab Report*, 2014], it is not surprising that the State of California requested a federal fishery disaster declaration from the U.S. Department of Commerce.

A research cruise aboard the National Oceanic and Atmospheric Administration (NOAA) Ship *Bell M. Shimada* from 20 June to 7 September sampled phytoplankton abundance and pDA from southern California to northern British Columbia (Figure 5). Elevated concentrations of pDA and *P. australis* were measured at the majority of stations south of central Oregon, and the pDA concentrations at many of the California stations exceeded previously reported maximum values, reaching 19,978 ng mL<sup>-1</sup>. *Pseudo-nitzschia* was the dominant phytoplankton genus at approximately half of the stations sampled off California (Figure 5b). At times, the densities of *Pseudo-nitzschia* cells were so high that even zooplankton net tows were clogged with long chains (Figure 5c). Live samples collected near Point Conception, California, commonly included chains of 20–30 cells with large, bulging chloroplasts. The research vessel arrived off Oregon and Washington after the initial bloom and after the *Pseudo-nitzschia* community shifted to *P. fraudulenta* in that region. Thus, pDA concentrations were low or undetectable in waters where either *P. fraudulenta* or *P. pseudodelicatissima* were prevalent (Figure 5).

### 5. Toxins and the Food Chain

The impact of this toxic diatom bloom propagated up the food chain to include many species of marine mammals. In 2015, DA was detected in whales, dolphins, porpoises, seals, and sea lions ranging from southern California to northern Washington between March and November (Figure 1). This was the largest geographic extent of DA detection in marine mammals ever recorded globally. DA was first recognized as a threat to marine mammal health in 1998 when hundreds of California sea lions (*Zalophus californianus*)



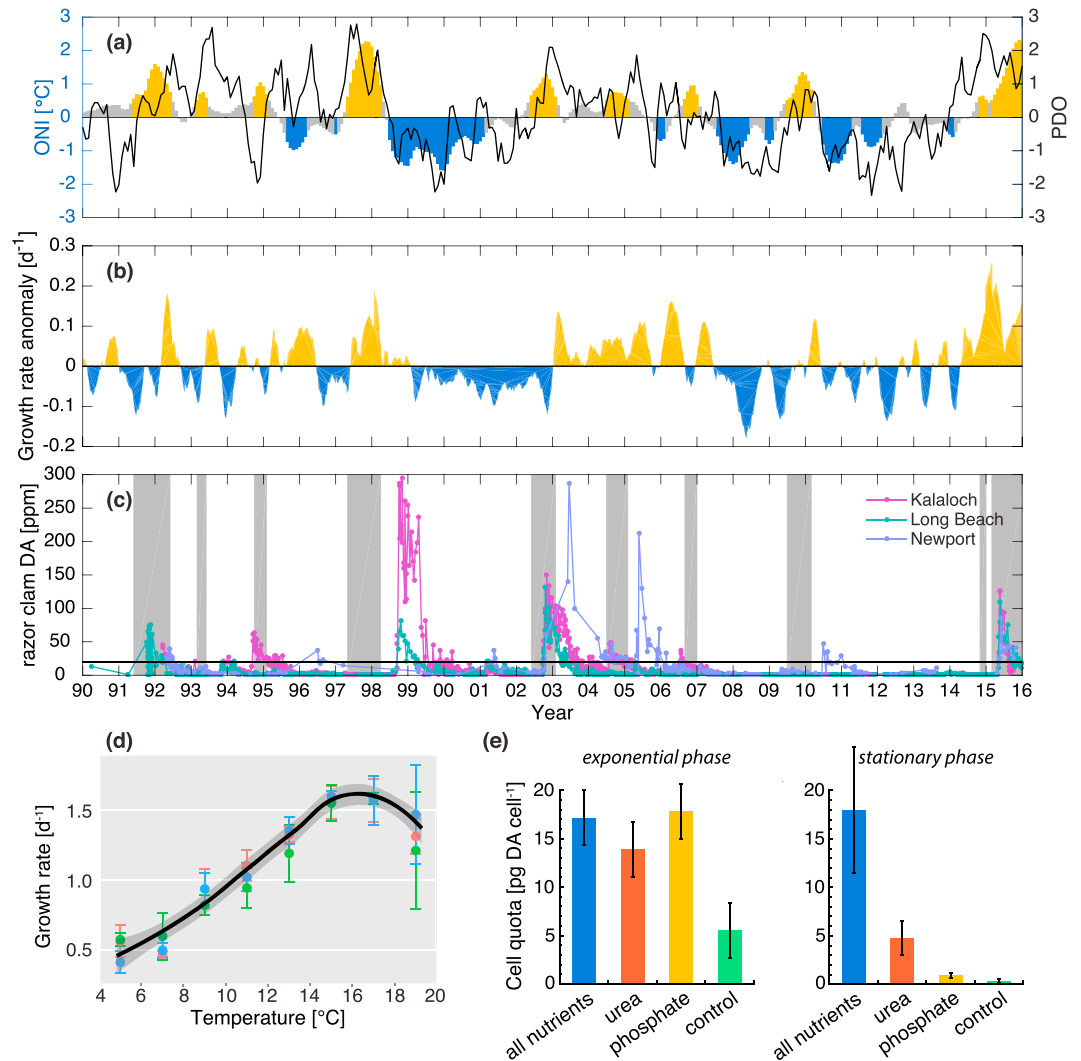
stranded along beaches in central California exhibiting signs of neuroexcitotoxicity including seizures, head weaving, and ataxia [Scholin *et al.*, 2000]. As sea lions are highly visible on public beaches and have been impacted every year in California since 1998 [Bejarano *et al.*, 2008], the animals examined at veterinary research hospitals serve as relatively robust indicators of the severity of toxic blooms. From 2010 to 2013, the numbers of live sea lions stranding on the central California coastline with suspected DA toxicosis and admitted to The Marine Mammal Center in Sausalito, California, averaged  $64 \pm 21$  animals per year. Beginning in 2014 and through 2015, the number of stranded sea lions from the same region diagnosed with suspected DA toxicosis rose to over 200 per year with 229 cases documented in 2015 (Figure 1). On 21 May 2015, DA-related seizures and high levels of DA in feces ( $1014 \text{ ng g}^{-1}$ ) were confirmed for a sea lion found on Long Beach, Washington, making this the first documented case of DA toxicosis in a sea lion this far north on the U.S. West Coast. Although DA was detected in several other stranded marine mammals in Washington and Oregon, DA-associated lesions were not confirmed in those animals as they were not examined histologically. Sea lions commonly feed on planktivorous fish such as northern anchovies (*Engraulis mordax*) that can be found in schools as deep as 100 m and several meters thick. During the *Shimada* cruise, anchovies collected with net hauls to depths of  $\sim 30$  m contained DA concentrations between  $1\text{--}505 \mu\text{g DA g}^{-1}$  (whole fish) and  $1\text{--}3239 \mu\text{g DA g}^{-1}$  (viscera). It is probable that stranded mammals with measurable DA in March 2015 acquired the toxin from these deep diving anchovies that fed on short-lived blooms of toxic *Pseudo-nitzschia* residing near the base of the nutrient-depleted waters of the warm anomaly.

## 6. Prognosis

While DA reached unprecedented levels in water samples, planktivorous fish and marine mammals, field experiments suggest even greater toxicity had the bloom been provided with additional macronutrients [Kudela *et al.*, 2008]. Nutrient manipulation experiments conducted in Monterey Bay during 2015 demonstrated that cellular toxicity increased up to fivefold in experiments of exponentially and stationary-growing assemblages of *P. australis* (Figure 6e). Thus, the combination of warm ocean water and expected future increases in coastal nutrient loading from runoff (globally [Seitzinger *et al.*, 2010; Lee *et al.*, 2016] and locally [Bergamaschi *et al.*, 2012]) could potentially lead to yet larger toxic events.

Although 2015 was unusual in the spatial extent and magnitude of the warm anomaly, the west coast of North America experiences regular warm periods in response to approximately decadal forcing from El Niño and the Pacific Decadal Oscillation (PDO; Figure 6a), with concomitant biological responses [Chavez *et al.*, 2002; Mackas and Galbraith, 2002; Peterson and Schwing, 2003; Fisher *et al.*, 2015]. Previous studies suggest that *Pseudo-nitzschia* abundance in southern California is correlated with both the PDO and the North Pacific Gyre Oscillation [Sekula-Wood *et al.*, 2011]. Laboratory experiments conducted with *P. australis* strains isolated from Monterey Bay, California, in 2015 demonstrate that this toxic diatom reaches maximal growth rates at  $\sim 17\text{--}18^\circ\text{C}$  with specific growth rates increasing by  $\sim$ threefold from  $5$  to  $17^\circ\text{C}$  (Figure 6d). The resulting estimated growth rate anomalies (Figure 6b) exhibit a strong ( $r=0.36$ ,  $p < 0.001$ ) correlation between *P. australis* growth potential and the PDO with 1 month lag and to the Oceanic Niño Index (ONI) with a 3 month lag ( $r=0.34$ ,  $p < 0.001$ ). Toxin concentration in razor clams showed a strong relationship, with a 3 month lag to both growth potential ( $r=0.14$ ,  $p < 0.001$ ) and the ONI ( $r=0.20$ ,  $p < <0.001$ ), and with the PDO ( $r=0.16$ ,  $p < <0.001$ ) at zero lag (Figure 6c). Moreover, the historical DA events in Figure 6c also track regional anomalies in southern zooplankton species [Fisher *et al.*, 2015] (which, at times, peak in the year following an El Niño, similar to some DA events shown here; see their Figure 2), suggesting a relationship between toxic events and advectively driven ecosystem shifts [Bi *et al.*, 2011]. Thus, west coast wide toxic bloom events are directly related to warm anomalies associated with both El Niño and PDO cycles, leading to faster growth (and northward expansion of *P. australis* habitat as seen in 2015), followed by increased toxin accumulation in razor clams.

This paper documents the first *Pseudo-nitzschia* bloom to negatively impact both shellfish and fish harvest industries, as well as marine mammal health, along the entire U.S. and Canada west coasts. What led to such an unprecedented monospecific toxic bloom? Studies of *P. australis* isolated from coastal California waters show that this organism is well adapted to low-nutrient conditions and is capable of responding rapidly to excess nutrients during upwelling, as well as to a variety of nitrogen sources, making the conditions during 2015 particularly amenable to blooms of this species [Cochlan *et al.*, 2008; Kudela *et al.*, 2010]. Laboratory and field experiments conducted in 2015 with *P. australis* confirm that it responds positively to both warm



**Figure 6.** Variability of historical toxic events, biological response, and mechanisms. (a) The ONI (gold indicates El Niño, blue indicates La Niña, gray represents neutral conditions) and the PDO (black line). (b) *Pseudo-nitzschia* growth rate anomaly estimated using the temperature-growth relationship in Figure 6d. (c) Razor clam DA concentration at three beaches (sites in Figure 4). Periods of El Niño conditions (gray shading) and the 20 ppm regulatory DA limit (black line) are indicated. (d) Temperature-growth rate results from laboratory cultures for three strains of *P. australis* isolated by H. Bowers from Monterey Bay during spring 2015. (e) Effects of nutrient enrichment on cell toxicity. Error bars in Figures 6d and 6e represent the standard error of the mean.

temperatures and enhanced nutrient loading. We suggest that the physiological capabilities of *P. australis* to acquire nitrate [Cochlan et al., 2008], to utilize a variety of nitrogen sources for growth [Howard et al., 2007], and to complex trace metals [Wells et al., 2005] selected for this genus over all other phytoplankton in the natural assemblage. The survival of *P. australis* in the anomalously warm and nutrient-depleted waters, its unusual presence along the entire continental margin of the western U.S. prior to the upwelling season, and its rapid expansion following the injection of nutrients with the spring transition to upwelling conditions, resulted in the coastwide, high-impact bloom. We may anticipate similarly severe toxic algal blooms along the North American west coast in future years with enhanced northward transport and relatively warm ocean conditions, including but not limited to El Niño periods. Given the large-scale warming and potential increase in frequency of extreme events expected with climate change [Cai et al., 2014] coupled with documented links between increased temperature and increased *Pseudo-nitzschia* abundance [Hinder et al., 2012], both the warm anomaly and the massive 2015 toxic algal bloom serve as instructive examples for what future decades may hold in store.

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