Monitoring Oregon Coastal Harmful Algae: Observations and implications of a harmful algal bloom-monitoring project

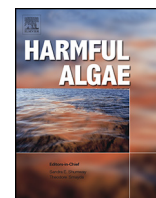# Monitoring Oregon Coastal Harmful Algae: Observations and implications of a harmful algal bloom-monitoring project

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A B S T R A C T

The accumulation of domoic acid (DA) and saxitoxins (STX), phycotoxins produced by some species of Pseudo-nitzschia and Alexandrium, respectively, in coastal food webs are a focus of research on the West Coast of the United States due to the deleterious effects they have on coastal ecosystems and economies. Results are presented from the 2007–2012 Monitoring Oregon Coastal Harmful Algae (MOCHA) project, the Oregon coast's first HAB monitoring and research program. Both historical toxin databases and more detailed case-study observations of individual HAB events are compiled to provide the first detailed overview of HAB occurrence in this region. These results are also presented in the context of informing future HAB monitoring in this and other upwelling regimes affected by STX and DA. A 2009–2010 warming event was associated with the greatest HAB activity during the MOCHA project, including anomalously high sea surface temperatures and shellfish harvesting closures due to STX and DA in 2009 and 2010, respectively. In regards to HAB monitoring, it is shown that (1) razor clams are a more sensitive indicator of DA than mussels; (2) water column concentrations of particulate domoic acid greater than 10^3 ng L^{-1} can be used as a threshold for early-warning of shellfish DA toxicity and (3) approximately bi-weekly, or shorter, monitoring of Alexandrium in the surf zone and/or offshore can provide advance notice of STX contamination of shellfish. Both of the latter two metrics gain added value when coupled with local wind stress, a proxy of downwelling/relaxation events that facilitate greater interaction between offshore blooms and shellfish.

1. Introduction

Globally, harmful algal blooms (HAB) are increasing in their frequency, persistence, toxicity, and regional coverage (Anderson et al., 2008; Hallegraeff, 1993; Van Dolah, 2000). Toxigenic HAB events along the West Coast of the United States are no exception and have been a topic of extensive HAB research and monitoring due to the threats they impose on coastal economies, ecosystems, and public health. Two of the major phycotoxins of interest in this region are the water-soluble amino acid domoic acid (DA), produced by some species of the diatom genus Pseudo-nitzschia, and a suite of heterocyclic guanidines collectively called saxitoxins (STX) that are produced by certain dinoflagellates, including some species of Alexandrium (Horner et al., 1997; Horner, 2001; Van Dolah, 2000). Both STX and DA can accumulate in the marine food web, potentially threatening living marine resources and public health. Human consumption of DA- or STX-contaminated shellfish in sufficient quantities can lead to Amnesic Shellfish Poisoning (ASP) or Paralytic Shellfish Poisoning (PSP), respectively (Picot et al., 2011). Symptoms of these illnesses range from gastrointestinal

distress to neurological dysfunction and, in rare cases, death. Horner et al. (1997) note that 'it is evident from early records, local native customs and the apparent ability of some native marine animals to distinguish toxic prey items, that PSP has been present on the West Coast for hundreds of years, perhaps longer.' Fryxell et al. (1997) found historical accounts of *Pseudo-nitzschia* on the West Coast, including reports of *Pseudo-nitzschia* in Oregon as early as 1920. Globally, DA and ASP first became a public health concern in 1987 when an outbreak of food-related illness, including three deaths, in Prince Edward Island, Canada were traced to DA in mussels (Bates et al., 1989). On the West Coast of the United States, the first recorded DA event occurred in 1991 when cormorant and pelican deaths were traced to DA in diatoms (Buck et al., 1992). Subsequent research revealed both DA in razor clams on the West Coast of the U.S. (Drum et al., 1993) and the production of DA by *Pseudo-nitzschia* strains isolated from Monterey Bay, California and Coos Bay, Oregon (Garrison et al., 1992; Villac et al., 1993).

The Oregon coast, a key transition zone in West Coast oceanography, has been understudied compared to other regions (Lewitus et al., 2012); although there have been several Master's theses on HAB species in Oregon (Cziesla, 1999; Hughes, 1997; Ohana-Richardson, 2007; Scott, 2007) and a West Coast summit on DA was held at the Oregon Institute of Marine Biology (Wood et al., 1994). In 2007 a collaborative research program termed MOCHA, Monitoring Oregon Coastal Harmful Algae, was the first long-term project (5 years) funded by the National Oceanic and Atmospheric Administration to explore HAB events in this region. The MOCHA project's primary goals included collection of the scientific data necessary to describe both HAB occurrence in Oregon and the ecological mechanisms underlying them and then to use these findings to inform future HAB monitoring.

Harvest restrictions for commercial and recreational harvest of razor clams are costly to the coastal economy of Oregon. In the first known estimate for Oregon, Nosho (1999) determined that full closures in 1991 along the Washington and Oregon coasts resulted in a loss of $23–28 million in combined revenue to these states. Due to the popularity of these fisheries, the accumulation of phycotoxins in shellfish poses serious risks for both human health and local economies (Hoagland et al., 2002; Hoagland and Scatasta, 2006; Picot et al., 2011). As a result, the Oregon Department of Agriculture (ODA) has been routinely monitoring STX and DA concentrations in shellfish since 1979 and 1992, respectively. When thresholds of 80 μg 100 g^{-1} for STX or 20 ppm for DA are exceeded, shellfish harvesting is suspended. Until the MOCHA project (2007–2012), the ODA's shellfish toxin data (Lewitus et al., 2012) were the only time-series record of HAB events in Oregon, and few data regarding the spatial or temporal variability of HAB forming species were available.

High primary productivity along the Oregon coast occurs from late spring through early fall when net northerly wind stress brings nutrient-rich waters to the surface through Ekman transport. Variability in net northerly and southerly winds occurs on the order of 3–10 days (Hickey and Banas, 2003), driving fluctuations in surface currents and water properties. Phytoplankton blooms are initiated by upwelling-favorable (northerly) winds and, as measured by in situ chlorophyll-*a*, vary at similar scales (McKibben et al., 2012). Relaxation of these upwelling winds can transport blooms to the shore (Shanks et al., 2014). Du and Peterson (2014) have shown that the patterns of phytoplankton community structure during upwelling season in coastal Oregon follow the classic paradigm of diatom dominance in spring/summer during the early/mid upwelling season and dinoflagellate dominance in autumn/late upwelling season, as the water column warms and stratifies. The trends in species composition (e.g. which diatoms bloom in summer), however, are unpredictable. Given that diatoms and dinoflagellates are favored under different environmental conditions (Smayda and Trainer, 2010), STX-(dinoflagellate) and DA-related (diatom) HAB events do not regularly co-occur. Prediction of specific HAB events is a goal for coastal managers, but is not currently possible due to the high biophysical variability inherent in coastal upwelling regions (Shanks and McCulloch, 2003). Even so, long-term (years to decades) HAB datasets can be used to determine regions and seasons with the greatest probability of a HAB event; HAB-specific parameters associated with shellfish tissues should be useful as early warning proxies of future HAB events.

The 5-year MOCHA project collected the first extensive time series database of the Oregon coast's biological, chemical, and physical variables in both the surf zone and offshore habitat over a variety of sampling scales. "HAB events" are defined here as DA or STX levels in coastal shellfish tissue that exceed the threshold values that trigger a closure decision. In order to provide a comprehensive overview of HAB occurrence in Oregon and to inform future HAB monitoring efforts the following are presented: (1) a retrospective analysis of long-term (decades) historical shellfish toxin levels; (2) synoptic, coastwide analysis of HAB events and phytoplankton counts during the MOCHA project and (3) case studies of two major HAB events that occurred during the MOCHA project, including a combined view of shipboard, surf zone, and environmental data.

2. Data & methods

2.1. Surf zone monitoring

Coastal HAB monitoring was conducted via (1) monitoring of STX and DA levels (1979–present and 1992–present, respectively) in tissue samples from mussels and razor clams and (2) collection of surface water from the surf zone for phytoplankton cell counts (2007–2012). For the former, the ODA collects shellfish at intertidal sites along the Oregon coast (Fig. 1) every 2–4 weeks. Shellfish sampled include predominantly mussels (*Mytilus californianus*, *Mytilus edulis*) and razor clams (*Siliqua patula*). Concentration of STX is measured using the standard mouse bioassay method (AOAC, 1990) and DA concentrations are measured using high performance liquid chromatography (HPLC) methods recommended by the Canadian Food Inspection Agency's Shellfish Sanitation Program[1]. Detection limits for STX and DA are approximately 38 μg 100 g^{-1} and 1 part per million (ppm), respectively. Closure thresholds for STX and DA in shellfish tissue are 80 μg 100 g^{-1} and 20 ppm, respectively.

The second type of coastal HAB monitoring, phytoplankton counts in the surf zone, was conducted coastwide (Fig. 1) from 2007 to 2012. These samples were collected and analyzed by the Oregon Department of Fish and Wildlife (ODFW) every 2–4 weeks for the MOCHA project. Water was collected in the surf zone using a bucket and gently swirled to provide a well-mixed sample. The water was poured into a 125 mL glass jar and fixed with 5 mL of 37% formaldehyde solution buffered with sodium acetate for a final concentration of 1.5% formalin.

Surf zone data were separated into 3 latitudinal bins: north (45–46.5°N), central (43–45°N), and south (42–43°N) (Fig. 1). Bins partition the data according to distinct hydrographic features: the Columbia River Plume in the north, a retentive feature that is a source of freshwater (and buoyancy); Heceta Bank, a retentive central coast shelf feature (Fig. 1); and Cape Blanco, a region characterized by a strong coastal jet that both transports water offshore north of Cape Blanco (Fig. 1; ~43°N) but causes also retention to the south between ~42 and 43°N (Tweddle et al.,

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[1] Method disseminated at the 1992 Washington Sea Grant Program, Workshop on Domoic Acid, Seattle, WA.
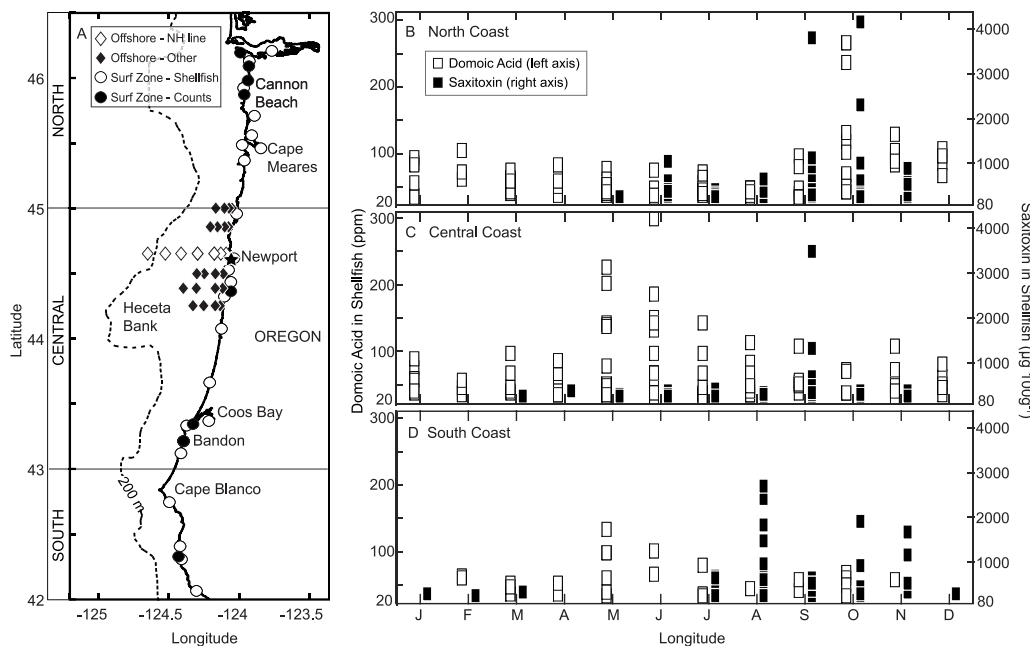
Fig. 1. (a) Area of study. Area to the right of solid black line is land (Oregon). Dashed line shows the continental shelf break at the 200-m isobath. Diamond symbols show offshore locations sampled aboard research vessels. White diamonds highlight the Newport Hydrographic (NH) line at 44.65°N. Wind data were collected at Newport, Oregon (star symbol). Circles on coast represent surf zone sampling locations for shellfish DA and STX (white) or *Alexandrium* and *Pseudo-nitzschia* cell counts (black). Surf zone data are binned into north (45–46.5°N), central (43–45°N), and south (42–43°N) regions. (b–d) Monthly STX and DA are shown as black squares (right axis) and white squares respectively for (b) north, (c) central, and (d) south coast locations defined in (a). Only values above the 80 µg 100 g^{-1} and 20 ppm harvesting closure thresholds for STX and DA, respectively, are shown, i.e. y axes start at closure thresholds.

2010; Venegas et al., 2008). Binning of surf zone samples by region also allows for comparison of surf zone data to offshore shipboard sampling.

2.2. Shipboard sampling

The central Oregon coast was routinely sampled aboard the R/V Elakha on cruises of 8–12 h duration from 2007 to 2012. Cruises covered either the Newport Hydrographic (NH) line only (44.65°N; Fig. 1) year-round at bi-weekly to monthly intervals, or surveyed six hydrographic lines including the NH-line (Fig. 1) every 4–6 weeks between March and October. During the latter, up to 28 stations were sampled between 44.2°N and 45°N at isobaths from 20 to 100 meters (m) deep. The number of stations sampled per cruise and cruises per year varied according to weather conditions and ship availability. Regional surveys also occurred once or twice per year aboard larger research vessels. Data from four of these surveys are included: an August 10–18, 2009 Pacific Coast Ocean Observing System (PaCOOS) cruise aboard the R/V McArthur II; an August 29–September 10 Center for Coastal Margin Observation (CMOP) cruise aboard the R/V New Horizon; a May 24–June 4 2010 PaCOOS cruise aboard the R/V Miller Freeman; and a May 21–May 26 CMOP cruise aboard the R/V Wecoma. Broadly, these cruises covered on- and off-shelf locations off the Oregon, California, and Washington coasts. Data include surface water samples of total phytoplankton cell counts and community composition, as well as coincident concentrations of particulate and dissolved DA (pDA and dDA, respectively).

2.3. Shipboard particulate and dissolved domoic acid

Several methods are available for measuring pDA and dDA, including high performance liquid chromatography (HPLC) and various ELISA methods. During the 2003–2006 NOAA's Oceans and Human Health (OHH) project between the University of Oregon

and Oregon State University it was decided the indirect competitive enzyme-linked assay kit (PNW-ELISA) already in use by Washington researchers would be used for the MOCHA project. The similarity in methods ensured that data collected by these groups could be compared directly.

For particulate DA (pDA), 1 L of seawater was filtered onto a 0.45 µm 47-mm diameter nitrocellulose membrane filter (Millipore HAWP04700), which was folded and wrapped in foil. Dissolved DA (dDA) was measured by filtering seawater through a 25-mm 0.45 µm nitrocellulose membrane filter (Millipore HAWP02500) into a cryovial. Filters and cryovials were frozen and stored at −80 °C for weeks up to 26 months prior to DA analysis. Both pDA and dDA in unknown samples were quantified using an indirect competitive enzyme-linked assay (PNW-ELISA) developed at the NOAA/Northwest Fisheries Science Center (Eberhart et al., 2012). Briefly, pDA samples were prepared by placing a filter into a centrifuge tube containing 4 mL of deionized water. The filter was then ground using a metal spatula and sonicated for 2 h, with vortexing after every hour. Samples were then stored at 4 °C overnight to settle any filter paper. Samples for dDA required 10 fold dilution in deionized–distilled water prior to analysis to eliminate sample matrix. Diluted dDA or pDA samples were then distributed into a 96 well plate for ELISA analysis (Eberhart et al., 2012). Note the differences in units for DA levels in coastal shellfish tissue discussed in Section 2.1 (ppm) and shipboard pDA and dDA samples (ng L^{-1}) discussed here. These units were not converted to a common unit to emphasize the two different DA data types and sources.

Shipboard samples collected in 2010 of pDA and dDA were were linearly regressed against coincident counts of *Pseudo-nitzschia* for two time frames: all 2010 shipboard data; and May 2010 only, when a DA event was observed. These data were log$_{10}$ transformed and reduced to only non-zero values from on-shelf (0–200 m depth) locations between 42 and 46.5°N. Count data were subdivided into four categories: total *Pseudo-nitzschia* as well as three size-delineated subclasses (see Section 2.4).

2.4. Phytoplankton cell enumeration

For both shipboard and surf zone cell counts, preserved whole water samples were concentrated prior to counting by chilling samples at 4 °C overnight and allowing all plankton to settle in the 125 mL jars in which they were collected. Details are described in White et al. (2014). Briefly, samples were concentrated 10 fold, settled on a Palmer–Maloney slide, and then counted using a compound microscope at 200× magnification (20× objective, 10× ocular). The limit of detection for this method is <1000 cells L^{-1}. All diatoms and dinoflagellates were identified to the genus level using Tomas (1997). Counts of *Pseudo-nitzschia* spp. were further subdivided into three categories based on size and morphology: wide (4–8 μm wide); medium (2–4 μm wide); and thin (<2 μm wide). While these size categories are not intended to substitute for species-level identification using cleaned material and/or scanning electron microscopy, three species clusters can be attributed to the categories above: wide, *Pseudo-nitzschia australis*, *Pseudo-nitzschia fraudulenta*, *Pseudo-nitzschia heimii*; medium, *Pseudo-nitzschia pungens* and *Pseudo-nitzschia multiseries*; and thin, *Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia pseudodelicatissima* (Trainer and Suddleson, 2005).

2.5. Wind stress and seasonal upwelling

Seasonality in this region is defined by a productive spring/summer upwelling season, with net movement of water offshore through Ekman transport. During fall/winter a more turbulent downwelling season is defined by strong southerly (from the south) wind stress and net movement of water towards the shore. Daily net northerly and southerly wind stress was calculated from wind speed and direction data from NOAA station NWP03 in Newport, OR (Fig. 1) using the methods of Large and Pond (1981).

The cumulative upwelling index (CUI) is a measure of wind stress energy input into coastal waters during upwelling season. The annual CUI is calculated by integrating the daily wind stress observed at Newport, Oregon from January 1st. The first day of the year when integrated wind stress is negative defines day one of both the CUI and upwelling season. The negative value of the CUI is a directional indicator of northerly wind stress and offshore (westward) movement of water due to Ekman transport. A shift to cumulative positive wind stress signifies the end of the annual CUI and day one of downwelling season. Data were obtained from http://damp.coas.oregonstate.edu/windstress/index.html.

2.6. Satellite sea surface temperature anomaly

Daily Level-3 (L3) 4-kilometer (km) Moderate Resolution Imaging Spectroradiometer (MODIS) nighttime SST (nSST) standard products (processing version R2012.1) were downloaded for each year that had complete MODIS coverage (2003–2012) from http://oceancolor.gsfc.nasa.gov/cms/. Daily climatology was calculated by composite-averaging imagery for each day of the year (day 1–365) from 2003 to 2012, resulting in 365 images that describe the average nSST observed over a 9-year period. This daily climatology was then subtracted from the corresponding daily L3 nSST product in 2009 and 2010 to yield a daily anomaly product. A Hovmöller map was then compiled by averaging 48 km (12 pixel), the approximate average width of the continental shelf along the Oregon coast, due west of the coast for each day of the year and each pixel of latitude from 42°N to 46.5°N. Seasonally, satellite coverage is best and potential bias due to cloud cover is least during upwelling season (McKibben et al., 2012).

3. Results

3.1. Retrospective shellfish toxin analysis

Coastwide, more mussels than razor clams are sampled for monitoring of STX and DA. For all shellfish and toxin types, the north coast is the most and the south is the least sampled (Table 1). Central coast mussel sampling is also relatively high. Razor clams are sampled less frequently than mussels and the number of samples collected decreases from north to south coast regions (Table 1).

Levels of STX are greater in mussel versus razor clam tissue; depending on the region, mussel tissue exceeded STX closure levels in 49–108 instances whereas high STX was less frequently observed in razor clams with 0–115 closures (Table 1). 107 of the 115 instances in the north were due to sustained high STX values in razor clams during a single event that spanned late 1992–1994 (ODA unpublished data). Aside from this event, STX in mussels surpassed closure levels 8 times in the north. The maximum STX concentrations in mussels were 10–58% greater than in razor clams (Table 1). Conversely, DA levels are higher in razor clam versus mussel tissue: coastwide, 5 mussel samples had DA levels above closure threshold while 27–107 razor clam samples surpassed threshold (Table 1). Maximum DA levels in razor clams were 10–42% higher than maximum DA in mussels (Table 1).

Out of the 35-year record of STX levels in shellfish, 20 (57%), 7 (20%), and 14 (40%) of the years had at least one STX sample above

Table 1

Statistical values for coastal shellfish toxin records. Columns 1–2 represent the total number of mussel samples collected throughout the entire saxitoxin (STX; 1958–2014) and domoic acid (DA; 1992–2014) coastal shellfish toxin monitoring datasets. Columns 3–4 represent the same totals, except for razor clams only. Columns 5–8 display the total number of samples collected that surpassed the closure threshold values (80 μg 100 g for STX and 20 ppm for DA). Values in parenthesis in columns 5–8 are the percent of samples above closure threshold relative to total samples collected (Columns 1–4). Columns 9–12 show the maximum toxin value detected for STX and DA records, separated by shellfish type. Columns 13–14 show the interannual closure frequency, or total number of years in the STX and DA records that had at least one sample above closure threshold (number in parenthesis), relative to the total number of years in the record (35 for STX, 22 for DA). All data are binned by region, with rows 1–3 corresponding with the north, central, and south coastal regions (Fig. 1a).

| | N mussel samples | | N razor clam samples | | N Samples above closure threshold (% of total) | | | | Maximum STX (μg 100 g^{-1}) | | Maximum DA (ppm) | | Interannual Closure Frequency (n years) | |
| | | | | | Mussels | | Razor clams | | | | | | | |
	STX	DA	STX	DA	STX	DA	STX	DA	Mussels	Razor clams	Mussels	Razor clams	STX	DA
North	1928	1117	959	894	108 (6%)	2 (0.2%)	115 (12%)	107 (12%)	3983	415	128	308	57% (20)	45% (10)
Central	3066	1650	340	427	49 (2%)	3 (0.2%)	2 (0.01%)	122 (29%)	3308	200	53	287	20% (7)	27% (6)
South	987	594	62	68	55 (6%)	0 (0%)	0 (0%)	27 (40%)	2520	43	13	120	40% (14)	27% (6)

closure threshold at north, central, and south coast regions, respectively (Table 1). In the 35-year record, from June through November coastwide, 201 total mussel samples had STX levels above closure (Fig. 1b–d) and 11 in December through May (Fig. 1b–d). Out of the 22-year record of DA levels in shellfish, 10 (45%), 6 (27%), and 6 (27%) of the years had at least one DA sample above closure threshold at north, central, and south coast regions, respectively (Table 1). In the 22-year record, from April through November coastwide, 295 total razor clam samples had DA levels above closure (Fig. 1b–d) and 42 in December through March (Fig. 1b–d).

3.2. HAB events during MOCHA monitoring time frame

Between 2007 and 2012, STX levels in shellfish tissue samples annually exceeded the closure threshold of 80 µg 100 g^{-1} (Fig. 2a). Elevated STX was most prevalent in 2008 (27/271, i.e. 27 of 271 total samples for the year were above closure threshold) and 2009 (37/390) with samples above closure level 6 and 7 months out of each year, respectively (Fig. 2a). From a coastwide perspective, surf zone concentrations of *Alexandrium* spp. corresponded to STX levels in shellfish (Fig. 2a and b), although not at a statistically significant level (*t*-test, *p* > 0.05). In contrast, 6 samples of 163 total exceeded the DA closure threshold during just 4 months of the 5-year study period (Fig. 2c), and changes in total *Pseudo-nitzschia* spp. were not synchronous with DA (Fig. 2c and d).

North coast *Alexandrium* counts (Fig. 2b) ranged from <1000 to 23,000 cells L^{-1} while central and south coast *Alexandrium* spp. had a lower range, from <1000 to 3000 cells L^{-1} (Fig. 2b). Counts of *Alexandrium* were typically below the limit of detection (Fig. 2b). In contrast, total *Pseudo-nitzschia* spp. showed marked seasonality, with one to three separate count maxima of 10^5–10^6 cells L^{-1} occurring each year during upwelling season (Fig. 2d). Successional

patterns of the *Pseudo-nitzschia* subgroups varied considerably from year-to-year, showing no consistent pattern; there was also no clear successional pattern when the time series was separated by region (not shown).

Based on cell count maxima, toxin maxima, and closure frequency, the greatest HAB activity during 2007–2012 occurred in 2009 and 2010 (Fig. 2). During the first event shellfish harvesting was closed from August through December of 2009 along the entire Oregon coast. Concentrations of *Alexandrium* spp. in the surf zone (23,000 cells L^{-1}, 8 August; Fig. 2b) and STX levels (948 µg 100 g^{-1}, 1 September; Fig. 2a) both reached their highest levels observed during the study period. This event also yielded the third-highest STX value observed since 1979. The second HAB event occurred in mid-2010 when central Oregon coast shellfish harvesting was closed due to elevated DA up to 55 ppm in shellfish tissue (Fig. 2c). This was the only DA-related HAB event during the MOCHA study period. These two events were selected for case studies to examine the associated environmental forcing of these HAB events.

3.2.1. 2009–2010 Physical conditions

As indicated by positive Pacific Decadal Oscillation (PDO) indices and a strong El Niño event, the eastern Pacific Ocean was anomalously warm from August 2009 through May 2010 (Fig. 3). This basin-scale warming is also observed in local SST observations, which were warmer than average from August 2009 through mid-June 2010 (Fig. 3a). Positive temperature anomalies were greatest in August and September 2009, up to +4–5 °C, and persisted through spring 2010 (Fig. 3a). Negative, or "cool favorable," PDO and La Niña conditions began in June 2010.

The 2009 upwelling season began on 14 May 2009 (Fig. 3b; average is 29 April ± 24 days) and ended on 12 October 2009. Five downwelling/relaxation events occurred during this upwelling season (Fig. 3b). In 2010, upwelling season was delayed, and began
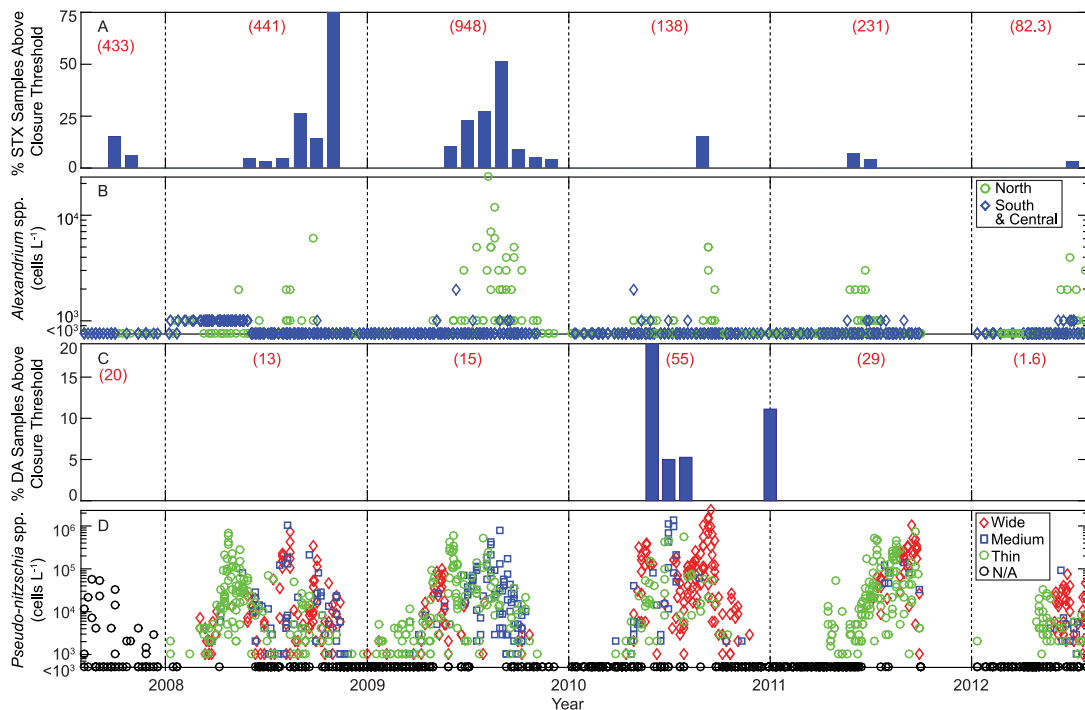

Fig. 2. Shellfish closure and cell count data from surf zone locations (Fig. 1, circles) during the MOCHA project, August 1, 2007–July 31, 2012. (a) and (c) show the coastwide percentage of shellfish samples collected each month that surpassed closure levels for saxitoxin (closure threshold 80 µg 100 g^{-1}) and domoic acid (closure threshold 20 ppm), respectively. Maximum toxin value reached for each year indicated by red numbers in parenthesis. (b) Surf zone cell counts for *Alexandrium* spp. at north (green circle) and central and south (blue diamond) regions. (d) Surf zone total *Pseudo-nitzschia* spp. counts colored to show whether the wide (red diamond), medium (green circle), or thin (blue square) subclass comprised >50% of total *Pseudo-nitzschia*. Black circles are data collected prior to 2008 or counts below detectable limits that did not include distinction of subclasses.
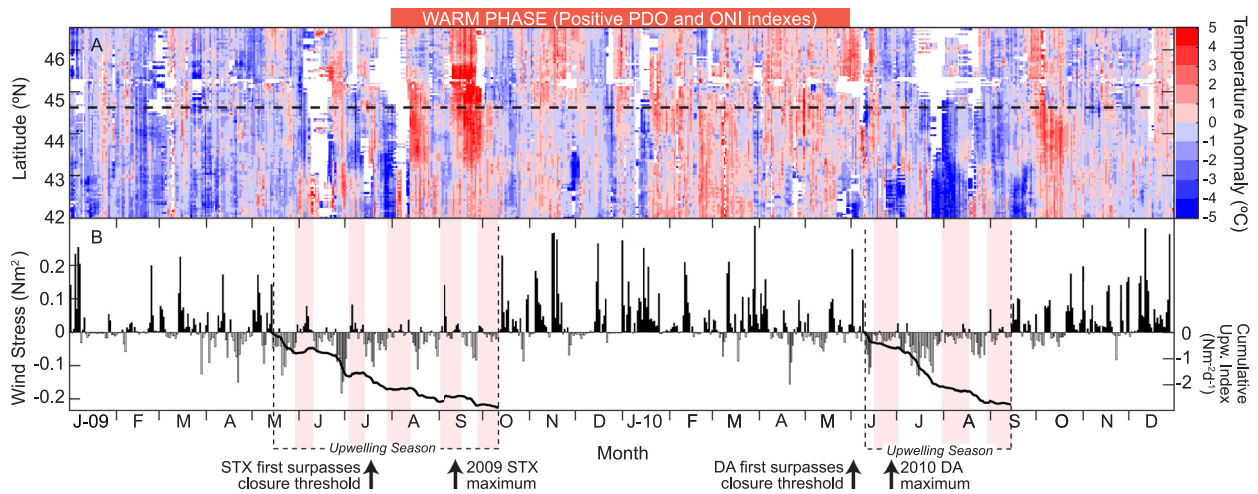
Fig. 3. 2009–2010 physical conditions. (a) Coastwide sea surface temperature (SST) anomaly (MODIS nighttime SST) for the Oregon coastline (42–46.5°N). Dashed line shows latitude of the NH hydrographic line (Fig. 1a). (b) Positive (downwelling-favorable) and negative (upwelling-favorable) wind stress conditions at Newport, OR. Right axis on panel (b) and black lines represent the cumulative upwelling index (CUI), a measure of net-upwelling favorable conditions. Consistently negative CUI indicates stronger, more persistent upwelling and net transport of waters offshore. Values that remain steady or become less negative represent weakening or reversal in upwelling conditions. Dashed vertical lines indicate the start dates of up- and downwelling seasons as determined by the beginning and end of the CUI. Timing of the basin-scale warming event highlighted by red bar at top. Arrows below x-axis correspond to peaks in toxin levels in central coast shellfish (Figs. 4b and 6b).

on 10 June, one standard deviation later than the mean (30 April); two upwelling phases in late July and August 2010 alternated with three major relaxation events (Fig. 3b). The 2010 upwelling season was 54 days shorter than in 2009, but upwelling wind stress was stronger and more persistent.

3.2.2. 2009 STX event

In 2009, STX concentrations in shellfish first surpassed the closure threshold in late June, late July, and late October at north, central, and south coast regions, respectively (Fig. 4a–c). North

coast surf zone *Alexandrium* spp. counts reached their maximum value for the year (23,000 cells L^{-1}, 8 August; Fig. 4a) before the maximum STX value (948 µg 100 g^{-1}, 1 September; Fig. 4a) for the region. Central coast surf zone *Alexandrium* spp. counts remained low, reaching a maximum of 1000 cells L^{-1} once each in May, July, and September (Fig. 4b). Offshore central coast *Alexandrium* spp. counts increased from May through September 2009, reaching a maximum of 47,000 cells L^{-1} (10 September, Fig. 4b). Surf zone STX in this region surpassed closure levels in July through September, with a maximum of 532 µg 100 g^{-1} (15 September,
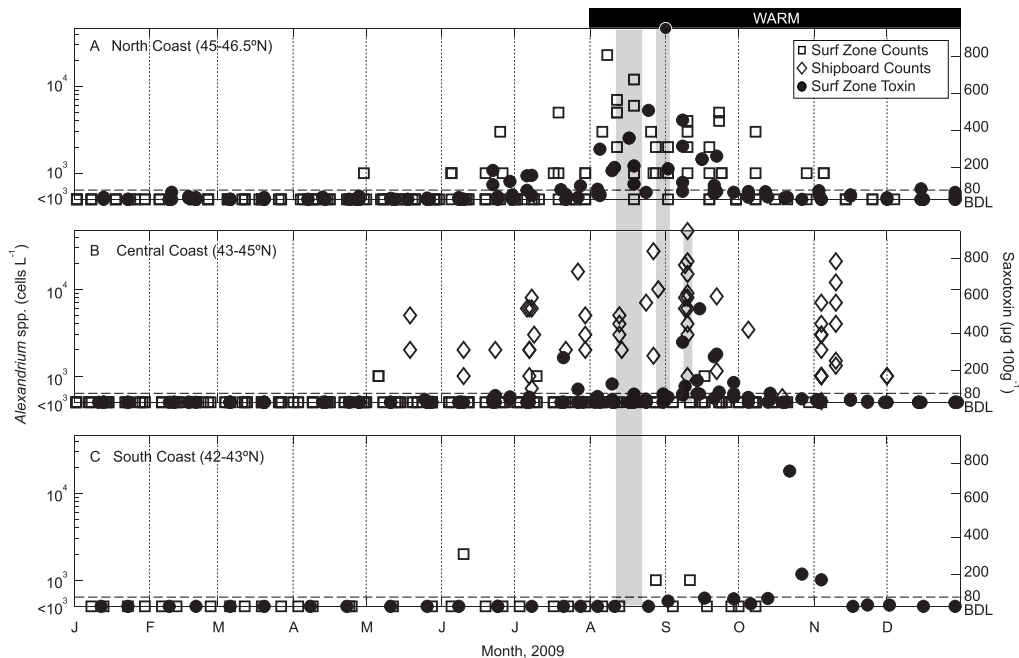

Fig. 4. 2009 Concentrations of saxitoxin (STX) in intertidal, or "surf zone," shellfish (circles, right y-axis) and abundance of surf zone *Alexandrium* spp. (squares, left y-axis) for a) north (45–46.5°N), (b) central (43–45°N), and (c) south (42–43°N) coast sampling locations (Fig. 1). Horizontal dashed line indicates the 80 µg 100 g^{-1} threshold for shellfish harvesting closure. Diamonds (panel b only) indicate central coast offshore *Alexandrium* spp. obtained during research cruises. Gray shaded regions show coincidence in time and space with offshore sampling efforts featured in Fig. 5. The duration of the 2009 warming event described in section 3.2.1 is highlighted by a black bar at the top of the figure. All y-axes are set to the minimum and maximum cell count or STX values for 2009; Below Detectible Levels (BDL) is the minimum for STX levels (right axes).

Fig. 4b). South coast *Alexandrium* spp. surf zone counts were low, reaching high values of 5000 cells L^{-1} once in June and 1000 cells L^{-1} in August and September (Fig. 4c). South coast STX exceeded the closure threshold in late October and early November, with a high of 757 µg 100 g^{-1} (22 October, Fig. 4c). In August the ODA closed mussel harvesting over the full Oregon coast. In September all bays and estuaries were closed to the harvest of scallops, oysters, razor clams, and bay clams. Bay clam harvesting was reopened in mid-October, mussels in late December, and razor clams in January of 2010.

Surf zone STX and *Alexandrium* spp. maxima at the north and central coasts in August and September (Fig. 4a,b) coincided with regional-scale sampling efforts during two 2009 cruises (10–18 August, Fig. 5a; 29 August–3 September and 9–10 September, Fig. 5b and c). Shipboard sampling occurred during a downwelling phase coincident with periods of high SST (August and September, Figs. 3b and 5a–c). During these sampling efforts, surface *Alexandrium* spp cell concentrations reached a maximum of 56,000 cells L^{-1} with the highest concentrations (up to 10^4 cells L^{-1}) north of roughly 45°N (Fig. 5a and b) off the Oregon and Washington coasts.

3.2.3. 2010 DA event

From May through September 2010, *Pseudo-nitzschia* spp. was commonly present coastwide in surf zone water samples at concentrations up to 10^5, and occasionally up to 10^6, cells L^{-1} (Fig. 6). Central coast DA levels in shellfish tissue surpassed the closure threshold (20 ppm) from June through August, reaching a maximum of 55 ppm (28 June). In central coast surf zone counts (Fig. 6b), the wide, medium, and thin subclasses dominated (comprised >50%) the *Pseudo-nitzschia* community 70%, 19%, and 10% of the time, respectively (n = 67); coastwide, the wide subclass was dominant prior to closures in June (Fig. 2d). From June through late October 2010 the ODA closed razor clam harvesting from Cape Meares to Bandon, OR (see Fig. 1 for locations). By late August 2010, DA returned to sub-closure levels; DA remained sub-closure in the north and south coasts throughout 2010 (Fig. 6a and c).

Three day cruises (Fig. 7a and d) and two larger-scale cruises (Fig. 7b, e and c, f) provided snapshots of the offshore spatial distribution of surface pDA and dDA just prior to the DA-related shellfish harvesting closures in mid and late June (Fig. 6b). In early May, surface pDA levels were mostly low (~10^1 ng L^{-1}, Fig. 7a) with dDA being comparatively elevated (up to 10^3 ng L^{-1}, Fig. 7d). The highest pDA and dDA values were recorded south of 45°N after mid-May 2010 (Fig. 7b, c, e and f), reaching maximum values of 40,400 ng L^{-1} and 10,300 ng L^{-1}, respectively. In May through June, central coast shipboard total *Pseudo-nitzschia* spp. counts typically ranged from 10^4 to 10^5 cells L^{-1}; 2010 shipboard counts surpassed 10^6 in September four times, with 3,000,000 cells L^{-1} being the highest value (9 September). In May 2010, the only
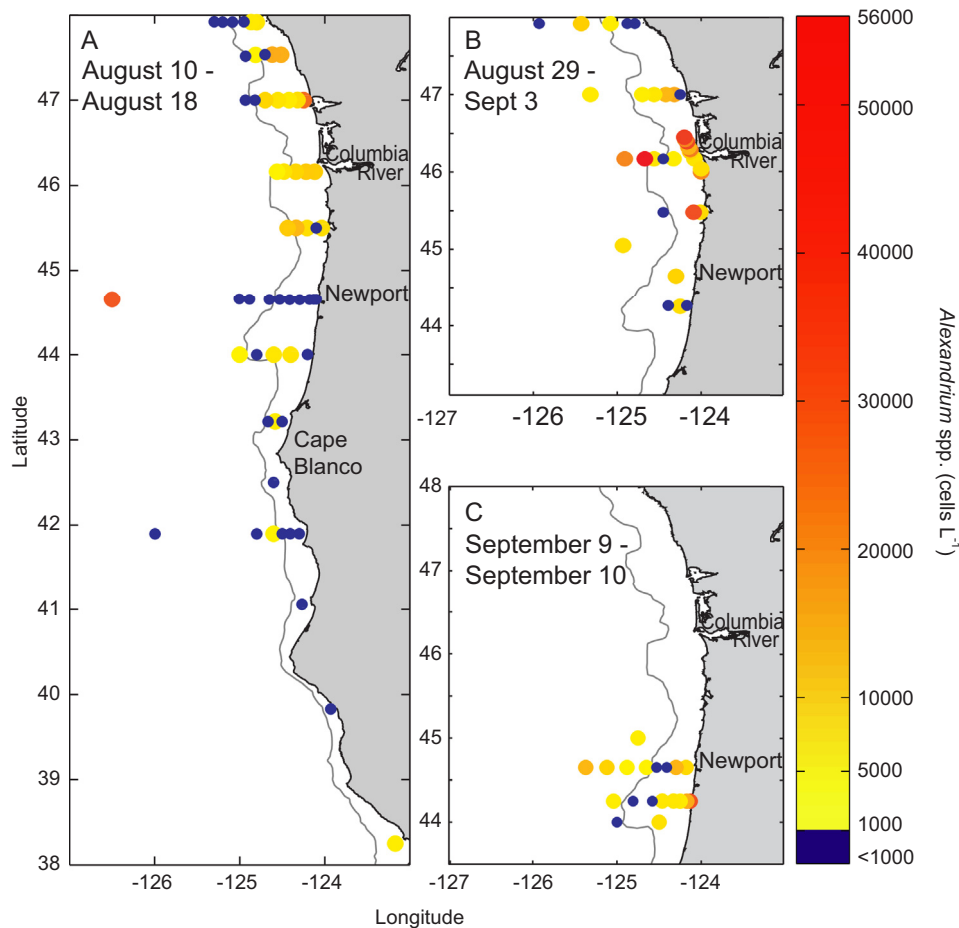

Fig. 5. Total *Alexandrium* spp. counts at the surface (plots a–c) obtained during regional-scale sampling cruises that coincided with the saxitoxin closure events in 2009 (see gray vertical bars on Fig. 4). The first cruise covered (a) northern California to Washington from August 10–18, 2009. The second cruise covered (b) the central Oregon coast north to Washington from August 29 to September 3, 2009 and then the (c) central Oregon coast on September 9–10, 2009. Gray line is the 200-m isobath. Colors represent the total number of *Alexandrium* spp. (cells L^{-1}); smaller blue dots are indicative of counts below detectible levels (<1000 cells L^{-1}). Color axis is set to minimum (<1000 cells L^{-1}) and maximum (56,000 cells L^{-1}) for these cruises.
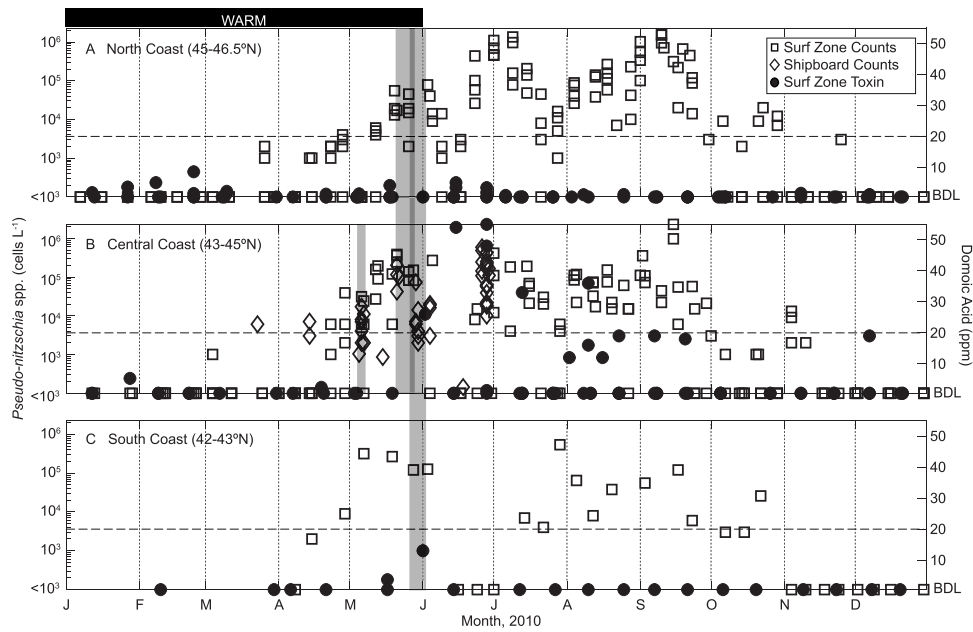
Fig. 6. 2010 Concentrations of domoic acid (DA) in intertidal, or "surf zone," shellfish tissue (circles, right y-axis) and surf zone *Pseudo-nitzschia* spp. abundance (squares, left y-axis) for (a) north (45–46.5°N), (b) central (43–45°N), and (c) south (42–43°N) coast sampling locations (Fig. 1). Horizontal dashed line indicates the 20-ppm threshold for shellfish harvesting closure. Diamonds (panel b only) indicate offshore central coast *Pseudo-nitzschia* spp. counts obtained during research cruises. Gray shaded regions show coincidence in time and space with offshore sampling efforts featured in Fig. 7. Warming event highlighted by black bar at the top. y-Axes are set to the minimum and maximum cell count or DA values for 2010; Below Detectible Levels (BDL) is the minimum value for DA (right axes).

month offshore pDA and dDA were greater than 10^3 ng L^{-1}, a significant relationship was seen between total *Pseudo-nitzschia* and the wide and thin subclasses versus both pDA and dDA (Table 2). When all of the 2010 shipboard data were considered, there were no significant relationships between total *Pseudo-nitzschia* or any of the size subclasses and pDA or dDA (Table 2).

4. Discussion

4.1. Retrospective analysis of STX and DA levels in shellfish

Historical shellfish toxin levels were analyzed with respect to two questions: (1) when and where are HAB events most likely to occur, i.e. what is the seasonal, interannual, and regional variability in toxin sampling and concentrations; and (2) are mussels versus razor clams better indicators of STX or DA events? The north coast was both more heavily sampled and had the highest occurrence of DA and STX events from year to year compared to other regions.

This region is also where the greatest commercial and recreational shellfish harvesting occurs. Even though it is sampled less often, the south coast also had relatively frequent STX events while the central coast had relatively few. Overall, STX events are most likely to occur later in the year from June through November. DA events occur most frequently between April and November, which encompasses all of upwelling season. Due to the slow depuration rate of razor clams (discussed below), DA persists longer in razor clam tissue than STX.

Levels of STX and DA differ over time in mussel versus razor clam tissues at similar locations. Mussels are more heavily sampled coastwide than razor clams as they are considered the sentinel indicator species for the Oregon coast's STX and DA events due to their far greater abundances and less labor- and skill-intensive harvesting methods. This assumption holds when analyzing mussel tissue for STX; however, if only mussel tissue were sampled, most DA events would be missed entirely due to the low DA levels in mussel tissue. Similarly, razor clams were shown

Table 2

Shipboard particulate and dissolved domoic acid values (y) versus shipboard *Pseudo-nitzschia* counts (x). Cell counts are reported for total *Pseudo-nitzschia*, as well as for the wide, medium, and thin size classes. *p*-Values are reported to the 95% confidence interval. Bolded rows are significant relationships.

|	log$_{10}$(Wide) P. fraudulenta P. australis			log$_{10}$(Medium) P. multiseries P. pungens			log$_{10}$(Thin) P. pseudodelicatissima P. delicatissima			log$_{10}$(Total Pseudo-nitzschia)		
	n	r²	p	n	r²	p	n	r²	p	n	r²	p
May 2010												
log$_{10}$(pDA)	**28**	**0.65**	**<0.0001**	11	0.25	0.12	**18**	**0.46**	**0.0021**	**41**	**0.63**	**<0.0001**
log$_{10}$(dDA)	**25**	**0.37**	**0.0013**	10	0.16	0.24	**15**	**0.46**	**0.0052**	**34**	**0.40**	**<0.0001**
All of 2010												
log$_{10}$(pDA)	112	0.0094	0.31	73	0.0073	0.47	66	0.0006	0.85	153	0.014	0.15
log$_{10}$(dDA)	64	0.00018	0.92	32	0.21	0.008	34	0.023	0.39	80	0.000001	0.99
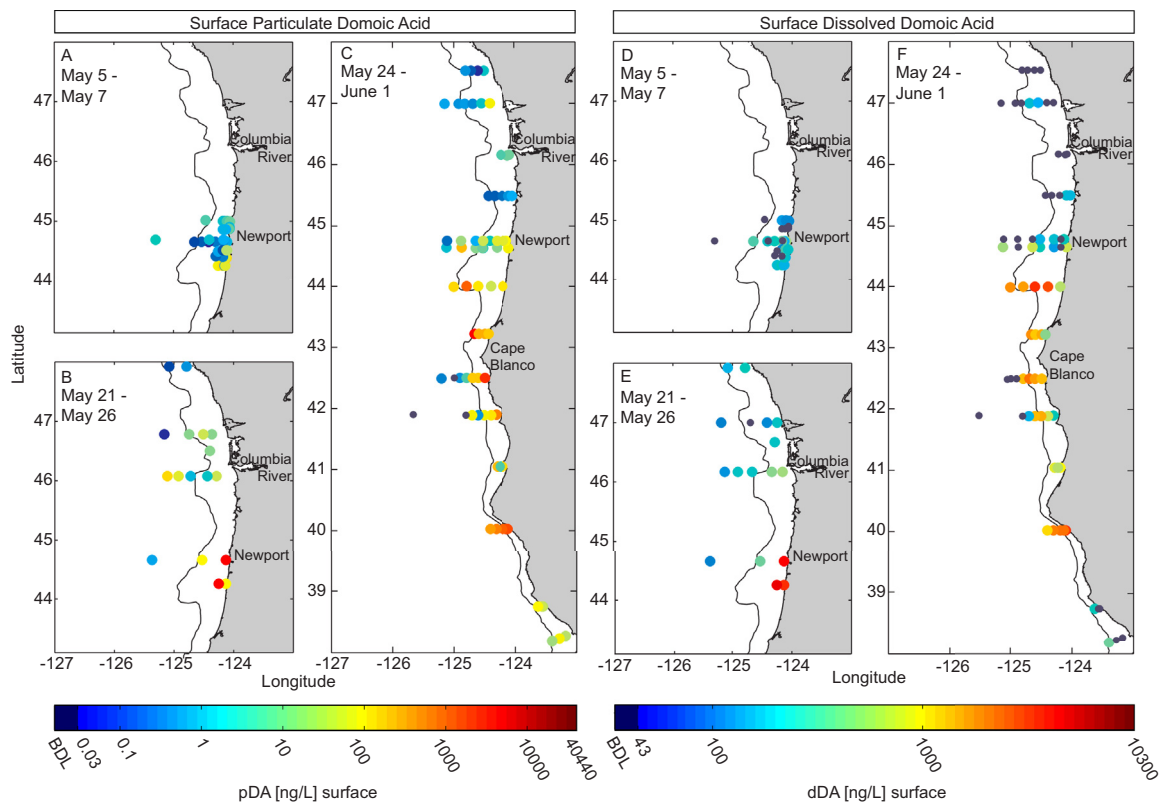
Fig. 7. Surface particulate (panels a–c) and dissolved (panels d–f) domoic acid (pDA and dDA, respectively) concentrations obtained during sampling cruises just before the coastwide domoic acid (DA) induced shellfish closures in 2010 (see gray bars on Fig. 6). Panels (a) and (d) include three separate day-long cruise efforts at the central coast (May 5: NH-line only; May 6: 3 southern lines; May 7: 3 NH-line and 2 northern lines; see diamonds on Fig. 1 for station locations). Regional-scale cruises span (b and e) the central Oregon coast north to Washington from May 21–26, 2010, and (c and f) northern California to Washington from May 24–June 1, 2010. Colors indicate the concentration of pDA or dDA at a particular sampling location; smaller blue dots are indicative of DA below detectible levels (BDL). Color axis set to minimum (BDL) and maximum values (see color bars for maximum pDA and dDA values) observed during these cruises. Black line is the 200-meter isobath.

to be poor indicators of STX events relative to mussels, with STX levels in razor clams rarely exceeding closure threshold levels.

Depuration of phycotoxins in shellfish can be modulated by a range of factors, leading to variability in DA or STX observations according to shellfish species tested. These factors include, but are not limited to: storage location of toxin in organism, organism's response to toxin, environmental factors, and size or age of the shellfish sampled (Mons et al., 1998; Van Egmond et al., 2004). In mussels, toxins accumulate in the digestive glands and are rapidly depurated (Novaczek et al., 1992). Relative to other shellfish, mussels accumulate STX faster than other toxins (Mons et al., 1998). Mussels also eliminate STX, as well as other toxins, relatively quickly (Costa et al., 2009; Mons et al., 1998). A study by Stewart et al. (1998) found bacterial metabolization is a potential mechanism of further DA elimination in blue mussels. Together these factors may explain the high STX, but much lower DA, values in mussels. In contrast, razor clams accumulate DA into body tissues such as the foot and mantle, slowing depuration rates (Wekell et al., 1994). Razor clams are among the slowest at depurating DA compared to other shellfish (Blanco et al., 2002). This combination of factors means that both intense blooms and low, persistent levels of toxin-producing *Pseudo-nitzschia* in the water can induce high DA levels in razor clams (Van Egmond et al., 2004). Due to these differences, and likely others as well, razor clams and mussels record the same DA and STX events differently over time, with mussels being more sensitive to STX events and razor clams to DA events in this region.

4.2. 2007–2012: HAB events during the MOCHA project

Coastal toxin and phytoplankton counts were combined to provide a synoptic overview of HAB events during the MOCHA project (Figs. 1 and 2). Following on these findings, an event-scale analysis of the most significant STX and DA events during MOCHA was conducted (Figs. 3–7). The MOCHA project's coastal and shipboard HAB observations were combined with coincident proxies of wind and SST to yield a detailed view of HAB formation, offshore extent, and movement onshore. Using these rich datasets, the following questions were investigated: (1) how informative are HAB cell counts at the coast as a proxy of HAB events; (2) what was the spatial extent of these HAB events offshore; (3) what can be learned regarding HAB initiation and movement from pairing time series wind and SST proxies with HAB observations?

4.2.1. 2009 Case study: STX event

Phytoplankton of the genus *Alexandrium* are the only STX-producing dinoflagellates known to occur regularly in the Oregon coastal regime. Like other dinoflagellates, *Alexandrium* spp. tend to bloom during the late upwelling season when waters warm in response to weakening of upwelling-favorable winds and stratification of the water column (Du and Peterson, 2014). Previous work relating remote sensing data with the ODA STX record has also shown that STX events occur most frequently during upwelling events at the end of the summer off of Oregon (Tweddle et al., 2010). Regular annual closures of shellfish harvests are recorded in Oregon due to STX contamination; these closures vary in their

spatial extent and persistence. In 2009 and 2010, a strong El Niño event occurred and the Pacific Decadal Oscillation (PDO) shifted to positive, or warm, values. Local SST was anomalously warm, up to +4–5 °C (Fig. 3a). A strong downwelling/relaxation event in early-mid September 2009 (Fig. 3b) and a peak in central coast STX levels in shellfish (Fig. 4b) coincided with the highest SST values observed along the Oregon coast, including the central coast, in 2009–2010 (Fig. 3a). This combination of events suggests onshore transport of warmer, and apparently HAB-rich, waters. Offshore counts for the central coast became elevated throughout the summer and fall, peaking coincident with the region's highest STX levels in shellfish for 2009 (Fig. 4b). During this warm phase in the fall of 2009, just as winds became downwelling-favorable and the water column presumably became more stratified, intense dinoflagellate blooms formed. In 2009, STX closures coincided with historical highs in *Alexandrium* cell concentrations, as well as the first recorded occurrence of seabird mortality due to the dinoflagellate *Akashiwo sanguinea* (Du et al., 2011; Phillips et al., 2011; White et al., 2014) in this region. The STX closures were not limited to the Oregon coast. Elevated STX levels up to 191 $\mu g\,L^{-1}$ were also recorded in Washington State in September 2009 (A. Odell, Olympic Region HAB Monitoring program, personal communication) and in California from mid-August through mid-October, with an early September high of 916 $\mu g\,L^{-1}$ (CDPH, 2009).

Anomalously high, latitudinally extensive SST driven by large-scale climactic forcing are hypothesized to have promoted this STX event (Fig. 3a). The optimal temperature for vegetative growth of *Alexandrium* spp. ranges from 15 to 20 °C, depending on the species and environment (Anderson, 1998; Laabir et al., 2011; Laanaia et al., 2013), hence warming may simply have led to an increase in net growth rates. This is not to say that the complexities of *Alexandrium* blooms in this dynamic coastal regime can be constrained by a single forcing term. The coupling between physical forcing (e.g. circulation and transport, water column stratification, temperature, salinity), behavior (e.g. migration), and physiological adaptation to these conditions ultimately regulates cell abundance and toxicity (Anderson, 1998). While these observations are limited, it appears as if the combination of high temperatures, low winds (relaxation events), and water column stratification promote regular *Alexandrium* blooms in this region towards the end of upwelling season. The 2009 warming event presumably amplified these effects, leading to anomalously high SST and record high levels of both *Alexandrium* and STX compared to the other years in the study period.

Cell counts of *Alexandrium* equal to and above 1000 cells L^{-1} generally coincide with STX closures (Fig. 2a and b). This temporal coherence is largely driven by samples collected in the northern region (Table 1, Fig. 2b and Fig. 4). In 2009, 92% of the northern region STX samples that exceeded closure levels (n = 24 of 26, Fig. 4a, circles) corresponded within a two week window to *Alexandrium* cell counts at or above 1000 cells L^{-1}. In the central region, offshore *Alexandrium* counts exceeded 1000 cells L^{-1} during all STX closures (July–September; Fig. 4b). Surf zone counts, however, were consistently below this threshold, suggesting a lack of onshore transport to the surf zone of *Alexandrium* from offshore waters. There were only three closure-level STX samples in the south, and no cell count data were available for comparison during these events. In all regions, particularly for offshore data collected in the central region, there were instances when cell counts exceeded a threshold of 1000 cells L^{-1} and no STX events were detected within a 2-week window (e.g. false positives).

While surf zone cell count thresholds in the north were an indicator of shellfish toxicity in the region, this was not the case in the central or southern regions. At the central coast, surf zone counts remained low while offshore counts, and ultimately STX, continually increased. This lack of coherence between cell counts

and the absolute concentration of STX in shellfish tissue is not unexpected given the variability in toxin accumulation and depuration rates in shellfish, inherent patchiness of phytoplankton populations, and temporal and spatial offsets between the collection of surf zone shellfish tissue and cell count samples. Despite these caveats, *Alexandrium* cell counts >1000 cells L^{-1} are found to be effective predictors of STX contamination of shellfish in the north. This strong relationship in the north may be due to the combination of greater sampling frequency and/or greater retention in the north (described below), which may have increased the probability of capturing the short-lived blooms.

Along-shelf variability in local circulation patterns may also explain the regional variability in both the 5-year (Fig. 2a and b) and 2009 STX records (Fig. 4). The highest *Alexandrium* concentrations observed in 2009 were on the shelf north of 45.5°N (Fig. 5), near the influence of the Columbia River. Under upwelling conditions, the Columbia River normally acts as a strong barrier to cross-shelf transport (Banas et al., 2009; Giddings et al., 2014). Conversely, during the transition to downwelling favorable winds, the predominant flow of surface currents is northward and onshore, pushing the Columbia River plume along the Washington coast and inducing bloom retention. Under these conditions, cells generated in local, productive 'hot spots' like Heceta Bank (~44°N; Fig. 1) may be transported onshore. Heceta Bank has been identified as a local incubator for phytoplankton growth due to the fact that it is a region of high nutrient supply and retentive circulation (Hickey and Banas, 2003; Trainer et al., 2001). Giddings et al. (2014) have used a particle tracking approach to show that particles produced in Heceta Bank would rapidly be transported north, with beachings occurring from the site of origin to north of the Oregon border in less than two weeks. Our surf zone and offshore cell counts are consistent with the hypothesis that *Alexandrium* concentrations during downwelling/relaxation events are elevated at latitudes north of Heceta Bank. Additional characterization of the seasonal patterns of phytoplankton community structure in Heceta Bank is necessary to evaluate whether this region acts as an incubator for *Alexandrium* blooms at certain times of the year.

4.2.2. 2010 Case study: DA event

During the five-year MOCHA study, a single DA closure event was observed in the summer of 2010. While this event was not particularly toxic or prolonged relative to past DA events in the region, it was the only DA-related shellfish closure after a four-year closure hiatus. It was also the only DA event captured by both on- and offshore monitoring during MOCHA. This event coincided with the beginning of a delayed upwelling season that immediately followed, and was likely delayed by, a basin-scale warming event. Anomalously high SST and strong downwelling-favorable winds persisted from winter 2009 into mid-2010. Reversal to a cool phase conducive to cooler, upwelling-favorable conditions coincided with the beginning of a delayed upwelling season in June 2010. Elevated pDA and dDA levels offshore of the central and southern Oregon coast corresponded to closures at the central coast three weeks later, after strong upwelling winds relaxed during early upwelling season. The relaxation event, and subsequent onshore flow, would have allowed interaction between the toxigenic bloom and shellfish in the surf zone.

Surf zone observations show that when shellfish DA became elevated in June, the wide subclass frequently comprised the majority of the *Pseudo-nitzschia* community in 2010, both before and after the closure event. Total *Pseudo-nitzschia* counts were abundant throughout the upwelling season. As such, there is no predictive relationship between DA in shellfish and total counts or subclasses of *Pseudo-nitzschia*. This finding may reflect the same issues caused by regional variability in sampling frequency and

hydrography discussed in Section 4.2.2 or 4.2.1, depending on how headers are renumbered for relating *Alexandrium* counts to STX, as well as the fact that toxigenic species of *Pseudo-nitzschia* do not always produce DA (e.g. Lelong et al., 2012; Trainer et al., 2012). It is also consistent with other studies in the region that note that *Pseudo-nitzschia* abundance does not always correspond to DA events (Giddings et al., 2014).

By restricting our analyses to May 2010, the only time pDA and dDA values exceeded 10^3 ng L^{-1} and spanned the broadest range (10^{-1}–10^4 ng L^{-1}), significant positive relationships were found between pDA or dDA and both wide and thin subclasses, as well as total *Pseudo-nitzschia* (Table 2). The wide cell type had the most significant relationship with pDA and was present in more samples than other classes. In May 2010, wide subclass abundances ranged 10^3–10^5 cells L^{-1} while the thin and medium ranged 10^3–10^4 cells L^{-1}. This morphotype also dominated *Pseudo-nitzschia* community structure in the surf zone samples collected during the early upwelling season, prior to the high DA levels in shellfish. These trends suggest the wide subclass was potentially responsible for the May–June 2010 DA event and shellfish closures, however the thin subclass and total *Pseudo-nitzschia* also had significant relationships with pDA and dDA in offshore waters. In Washington State, *P. australis* and *P. pseudodelicatissima* have been identified as the major toxigenic 'problem' species (Trainer and Suddleson, 2005). These species would be expected to fall into the wide and thin morphologies assessed here and either, or both, could have been responsible for the 2010 DA event although this would need to be confirmed by more formal methods of species identification.

The co-occurrence of toxigenic and non-toxigenic *Pseudo-nitzschia* species makes it impossible to determine the threat of shellfish contamination from total cell counts alone. For this reason, investigators have either identified cells to the species level, grouped cells according to size and morphology, or directly measured pDA. Previous studies have found positive relationships between abundances of toxigenic species of *Pseudo-nitzschia* and water column DA (e.g. Bargu et al., 2012; Busse et al., 2006; Trainer and Hickey, 2002) and determined the presence of particular toxigenic species of *Pseudo-nitzschia* to be a potentially robust early indicator of coastal DA toxicity (Trainer et al., 2001). These studies identified *Pseudo-nitzschia* to the species level, whereas this work instead tested the predictive ability of morphologically-grouped *Pseudo-nitzschia* cells, a practice adopted from resource management practices in Washington state (Trainer and Suddleson, 2005).

Nearly all pDA and dDA samples collected offshore during the 5 year study period yielded values below ~10^3 ng L^{-1}. The only exception was in May 2010 when pDA and dDA values both exceeded ~10^3 ng L^{-1} (Fig. 7). The possibility exists that the overall very low trends in our pDA and dDA data may be due in part to DA degradation during storage prior to sample analysis (Lane and Kudela, 2007). Even so, what is notable from our observations is that during the 5-year monitoring period the only high pDA and dDA values (>10^3 ng L^{-1}) observed in shipboard data (May 2010) occurred three weeks before the only DA-related shellfish harvesting closure in Oregon (June 2010). Based on these observations, an alert threshold value of 10^3 ng L^{-1} pDA is proposed as an early warning of shellfish toxicity in the Pacific Northwest region.

4.3. Monitoring implications

Concentrations of STX and DA are currently the only data used to guide management of shellfish harvests in Oregon. Ideally, resource managers and recreational and commercial harvesters could use earlier warning of HAB events to avoid human ingestion of contaminated shellfish or wastage of already-harvested shellfish. Monitoring observations reveal regions and seasons with the greatest likelihood of HAB events, as well as potential event-scale early warning metrics of HAB events.

North coast *Alexandrium* cell counts, where surf zone sampling efforts were greatest, closely track STX levels in shellfish. Accordingly, approximately bi-weekly cell counts are proposed as a low-cost, rapid, and effective means of early warning for potential shellfish closures due to STX. The concentration of total *Pseudo-nitzchia* cells and morphological subgroups were not correlated to either pDA, dDA, or concentrations of DA in shellfish tissue offshore or in the surf zone when the full dataset was evaluated. Based on shipboard data from May 2010 and the timing of subsequent DA closures in the surf zone, screening the intertidal zone for pDA levels exceeding a threshold of 10^3 ng L^{-1} during the upwelling season should provide early warning of shellfish contamination.

The north and south coast regions are most likely to have STX events from June through November. Initiation of a DA event is more likely during upwelling than downwelling seasons, but DA may persist in razor clams throughout the year. The north coast, and to a lesser extent the south coast, have the greatest occurrence of STX events. The south coast is comparatively under-sampled for STX in mussels, potentially contributing northern bias in these results. Relative to central or south coasts, the north coast also has the greatest occurrence of DA events. The decrease in razor clam sampling from north to south reflects their natural abundance along the coast. Over 90% of the razor clam population and harvesting effort occurs in the northernmost 18 miles of the Oregon coast (ODFW, 2000). South of this area, abundances are episodic and unpredictable due to infrequent recruitment success.

Mussels are currently considered the sentinel indicator of STX and DA events, but here mussels are shown to be a poor indicator of DA events. Razor clams represent the bulk of the commercial and recreational shellfish harvesting revenue in Oregon and also accumulate greater levels of DA that remain in edible parts of the clam for longer amounts of time compared to mussels. As such, ideally, razor clams instead of mussels should be considered sentinel indicators of DA events in this region and sampling increased; however this is not logistically feasible. Razor clams exist in numbers far lower than mussels and require greater skill and labor to harvest than mussels, which reside much higher in the intertidal at much greater and more consistent abundances. Nevertheless, knowledge that razor clams are more sensitive to DA events is critical to any DA monitoring or management program and evaluation of resulting data by researchers or managers.

The regional-scale survey cruises in 2009 and 2010 that fortuitously coincided with the region's major HAB events at the time reveal snapshots of both the STX and DA events and their regional-scale extent. The STX bloom spanned both the Washington and Oregon coasts and the DA event spanned the Oregon and California coasts. Due to the time and cost involved in oceanic data collection, shipboard views of HAB events of this scale are rare; however, they remind us that HAB events are often beyond the scope of data collection of most research projects, which are usually limited to a specific area of a specific coastline. As mentioned in previous work (Lewitus et al., 2012), these observations underscore the need for more regional-scale HAB research efforts to explore the potential causes of these events and how they move over time.

In this region and others, ecological and biogeochemical complexity complicate smaller-scale prediction of HAB events at a specific time or location. Nonetheless, this work has identified a number of terms related to HAB formation that can be utilized as precursors of an increased likelihood of HAB events: cell counts of HAB-forming dinoflagellates, pDA, and downwelling/relaxation events that facilitate onshore transport of HAB species or toxins detected offshore via ship or automated mooring. Additionally,

coincident MOCHA research has found warm phases of the PDO to be a reliable proxy of DA events (McKibben et al., in prep). All of these measurements should be considered in any STX- or DA-monitoring program aimed at early detection in the California Current regime. In order to more completely characterize the dynamics of HAB ecology in the region, further research is needed to understand two key unknowns: (1) what are the environmental conditions under which *Pseudo-nitzschia* become toxic and (2) there is a need to identify the regional sources of *Alexandrium* blooms (i.e. pelagic or benthic cyst beds).

Acknowledgements

References

Anderson, D.M., 1998. Physiology and bloom dynamics of toxic *Alexandrium* species, with emphasis on life cycle transitions. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), Physiological Ecology of Harmful Algal Blooms. Springer, Berlin, pp. 29–48.

Anderson, D.M., Burkholder, J.M., Cochlan, W.P., Glibert, P.M., Gobler, C.J., Heil, C.A., Kudela, R.M., Parsons, M.L., Rensel, J.E.J., Townsend, D.W., Trainer, V.L., Vargo, G.A., 2008. Harmful algal blooms and eutrophication: examining linkages from selected coastal regions of the United States. Harmful Algae 8, 39–53.

AOAC (Association of Official Analytical Chemists), 1990. Official Methods of Analysis of the Association of Official Analytical Chemists, 15th ed. AOAC, Arlington, VA.

Banas, N.S., Lessard, E.J., Kudela, R.M., MacCready, P., Peterson, T.D., Hickey, B., Frame, E., 2009. Planktonic growth and grazing in the Columbia River plume region: a biophysical model study. J. Geophys. Res. 114 (C2), C00B06.

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 (2), 237–253.

Bates, S., Bird, C.J., Freitas, A.d., Foxall, R., Gilgan, M., Hanic, L.A., Johnson, G.R., McCulloch, A., Odense, P., Pocklington, R., 1989. Pennate diatom *Nitzschia pungens* as the primary source of domoic acid, a toxin in shellfish from eastern Prince Edward Island, Canada. Can. J. Fish. Aquat. Sci. 46 (7), 1203–1215.

Blanco, J., Bermudez de la Puente, M., Arevalo, F., Salgado, C., Moroño, A., 2002. Depuration of mussels (*Mytilus galloprovincialis*) contaminated with domoic acid. Aquating Living Res. 15 (1), 53–60.

Buck, K., Uttal-Cooke, L., Pilskaln, C., Roelke, D., Villac, M., Fryxell, G., Cifuentes, L., Chavez, F., 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., Prezelin, B., 2006. Domoic acid in phytoplankton and fish in San Diego, CA, USA. Harmful Algae 5 (1), 91–101.

CDPH (California Department of Public Health), 2009. Monthly Marine Biotoxin Report, September 2009, No. 09-25, pp. 4.

Costa, P.R., Baugh, K.A., Wright, B., RaLonde, R., Nance, S.L., Tatarenkova, N., Etheridge, S.M., Lefebvre, K.A., 2009. Comparative determination of paralytic shellfish toxins (PSTs) using five different toxin detection methods in shellfish species collected in the Aleutian Islands, Alaska. Toxicon 54 (3), 313–320.

Cziesla, C.A., 1999. The Transport and Distribution of the Toxic Diatom *Pseudo-nitzschia* spp. in the Coos Bay Estuary and the Adjacent Continental Shelf. University of Oregon, Eugene, OR.

Drum, A., Siebens, T., Crecelius, E., Elston, R., 1993. Domoic acid in the Pacific razor clam *Siliqua patula*. J. Shellfish Res. 12 (2), 443–450.

Du, X., Peterson, W., McCulloch, A., Liu, G., 2011. An unusual bloom of the dinoflagellate *Akashiwo sanguinea* off the central Oregon USA, coast in autumn 2009. Harmful Algae 10 (6), 784–793.

Du, X., Peterson, W.T., 2014. Seasonal cycle of phytoplankton community composition in the coastal upwelling system off central Oregon in 2009. Estuaries Coasts 37 (2), 299–311.

Eberhart, B., Bill, B., Trainer, V., 2012. Remote sampling of harmful algal blooms: a case study on the Washington State coast. Harmful Algae 19, 39–45.

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.

Garrison, D.L., Conrad, S.M., Eilers, P.P., Waldron, E.M., 1992. Confirmation of domoic acid production by *Pseudo-nitzschia australis* (*Bacillariophycea*) cultures. J. Phycol. 28 (5), 604–607.

Giddings, S., MacCready, P., Hickey, B., Banas, N., Davis, K., Siedlecki, S., Trainer, V., Kudela, R., Pelland, N., Connolly, T., 2014. Hindcasts of potential harmful algal bloom transport pathways on the Pacific Northwest coast. J. Geophys. Res. Oceans 119 (4), 2439–2461.

Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32 (2), 79–99.

Hickey, B.M., Banas, N.S., 2003. Oceanography of the US Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries Coasts 26 (4), 1010–1031.

Hoagland, P., Anderson, D., Kaoru, Y., White, A., 2002. The economic effects of harmful algal blooms in the United States: estimates, assessment issues, and information needs. Estuaries 25 (4), 819–837.

Hoagland, P., Scatasta, S., 2006. The economic effects of harmful algal blooms. In: Graneli, E., Turner, J.T. (Eds.), Ecology of Harmful Algae. Springer, Berlin, Heidelberg, pp. 391–402.

Horner, R., Garrison, D., Plumley, F., 1997. Harmful algal blooms and red tide problems on the US west coast. Limnol. Oceanogr. 42 (5), 1076–1088.

Horner, R.A., 2001. *Alexandriuum* and *Pseudo-nitzschia*: two of the genera responsible for harmful algal blooms on the U.S. west coast. In: RaLonde, R. (Ed.), Harmful Algal Blooms on the North American West Coast. University of Alaska Sea Grant, Fairbanks, AK, pp. 5–10.

Hughes, M.P., 1997. Temporal and Spatial Variability of Phytoplankton in Coastal and Estuarine Habitats in Coos Bay, Oregon. University of Oregon, Eugene, OR.

Laabir, M., Jauzein, C., Genovesi, B., Masseret, E., Grzebyk, D., Cecchi, P., Vaquer, A., Perrin, Y., Collos, Y., 2011. Influence of temperature, salinity and irradiance on the growth and cell yield of the harmful red tide dinoflagellate *Alexandrium catenella* colonizing Mediterranean waters. J. Plankton Res. 33 (10), 1550–1563.

Laanaia, N., Vaquer, A., Fiandrino, A., Genovesi, B., Pastoureaud, A., Cecchi, P., Collos, Y., 2013. Wind and temperature controls on *Alexandrium* blooms (2000–2007) in Thau lagoon (Western Mediterranean). Harmful Algae 28, 31–36.

Lane, J.Q., Kudela, R., 2007. Degradation of domoic acid under common storage conditions. In: Fourth Symposium on Harmful Algae in the US, Woods Hole, MA.

Large, W., Pond, S., 1981. Open ocean momentum flux measurements in moderate to strong winds. J. Phys. Oceanogr. 11 (3), 324–336.

Lelong, A., Hégaret, H., Soudant, P., Bates, 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., Kudela, R.M., Langlois, G.W., Largier, J.L., 2012. Harmful algal blooms along the North American west coast region: history, trends, causes, and impacts. Harmful Algae 19, 133–159.

McKibben, S.M., Strutton, P.G., Foley, D.G., Peterson, T.D., White, A.E., 2012. Satellite-based detection and monitoring of phytoplankton blooms along the Oregon coast. J. Geophys. Res. 117 (C12), C12002.

McKibben, S.M., White, A., Peterson, W., Trainer, V., in prep. Climactic Regulation of Domoic Acid Along the Oregon Coast.

Mons, M., Van Egmond, H., Speijers, G., 1998. Paralytic Shellfish Poisoning: A Review. National Institute of Public health and the Environment, Bilthoven, The Netherlands.

Nosho, T., 1999. In Western Regional Aquaculture Center. Waterlines 9 (Winter–Spring (1)), 3.

Novaczek, I., Madhyastha, M., Ablett, R., Donald, A., Johnson, G., Nijjar, M., Sims, D.E., 1992. Depuration of domoic acid from live blue mussels (*Mytilus edulis*). Can. J. Fish. Aquat. Sci. 49 (2), 312–318.

ODFW., 2000. Oregon Marine Fisheries: 2000 Status Report. Oregon Department of Fish and Wildlife, Marine Resources Program, Newport, OR.

Ohana-Richardson, A., 2007. Population ecology of the diatom genus *Pseudo-nitzschia* within the South Slough, Charleston, Oregon. University of Oregon, Eugene, OR.

Phillips, E.M., Zamon, J.E., Nevins, H.M., Gibble, C.M., Duerr, R.S., Kerr, L.H., 2011. Summary of birds killed by a harmful algal bloom along the south Washington and north Oregon coasts during October 2009. Northwest. Nat. 92 (2), 120–126.

Picot, C., Nguyen, T., Roudot, A., Parent-Massin, D., 2011. A preliminary risk assessment of human exposure to phycotoxins in shellfish: a review. Hum. Ecol. Risk Assess. 17 (2), 328–366.

Scott, B.A., 2007. The relationship between upwelling, shellfish toxicity, and the distribution of toxic cysts in Oregon. University of Oregon, Eugene, OR.

Shanks, A.L., McCulloch, A., 2003. Fornightly periodicity in the abundance of diatom and dinoflagellate taxa at a coastal study site. J. Exp. Mar. Biol. Ecol. 296, 113–126.

Shanks, A.L., Morgan, S.G., MacMahan, J., Reniers, A.J., Jarvis, M., Brown, J., Fujimura, A., Griesemer, C., 2014. Onshore transport of plankton by internal tides and upwelling-relaxation events. Mar. Ecol. Prog. Ser. 502, 39–51.

Smayda, T., Trainer, V., 2010. Dinoflagellate blooms in upwelling systems: seeding, variability, and contrasts with diatom bloom behaviour. Prog. Oceanogr. 85 (1), 92–107.

Stewart, J., Marks, L., Gilgan, M., Pfeiffer, E., Zwicker, B., 1998. Microbial utilization of the neurotoxin domoic acid: blue mussels (*Mytilus edulis*) and soft shell clams (*Mya arenaria*) as sources of the microorganisms. Can. J. Microbiol. 44 (5), 456–464.

Tomas, C.R., 1997. Identifying Marine Phytoplankton. Academic Press, San Diego, CA.

Trainer, V., Adams, N., Wekell, J., 2001. Domoic Acid-Producing *Pseudo-nitzschia* Species off the US West Coast Associated with Toxification Events. Intergovernmental Oceanographic Commission of UNESCO, Paris, France.

Trainer, V., Hickey, B., 2002. Biological and physical dynamics of domoic acid production off the Washington coast. Limnol. Oceanogr. 47 (5), 1438–1446.

Trainer, V.L., Bates, S.S., Lundholm, N., Thessen, A.E., Cochlan, W.P., Adams, N.G., Trick, C.G., 2012. *Pseudo-nitzschia* physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. Harmful Algae 14, 271–300.

Trainer, V.L., Suddleson, M., 2005. Monitoring approaches for early warning of domoic acid events in Washington State. Oceanography 18 (2), 228.

Tweddle, J.F., Strutton, P.G., Foley, D.G., O'Higgins, L., Wood, A.M., Scott, B., Everroad, R.C., Peterson, W.T., Cannon, D., Hunter, M., Forster, Z., 2010. Satellite phenology of coastal Oregon upwelling and phytoplankton blooms: relationship to phycotoxins in coastal shellfish. Mar. Ecol. Prog. Ser. 405, 131–145.

Van Dolah, F.M., 2000. Marine algal toxins: origins, health effects, and their increased occurrence. Environ. Health Perspect. 108 (Suppl. 1), 133–141.

Van Egmond, H., Van Apeldoorn, M., Speijers, G., 2004. Marine Biotoxins, Food and Nutrition Paper 80. Food and Agriculture Organization of the United Nations, Rome.

Venegas, R., Strub, P., Beier, E., Letelier, R., Thomas, A., Cowles, T., James, C., Soto-Mardones, L., Cabrera, C., 2008. Satellite-derived variability in chlorophyll wind stress, sea surface height, and temperature in the northern California Current System. J. Geophys. Res. 113 (C3), C03015.

Villac, M., Roelke, D., Chavez, F., Cifuentes, L., Fryxell, G., 1993. *Pseudo-nitzschia australis* Frenguelli and related species from the west coast of the U.S.A.: occurrence and domoic acid production. J. Shellfish Res. 12 (2), 457–465.

Wekell, J.C., Gauglitz, E.J., Bamett, H.J., Hatfield, C.L., Simons, D., Ayres, D., 1994. Occurrence of domoic acid in Washington state razor clams (*Siliqua patula*) during 1991–1993. Nat. Toxins 2 (4), 197–205.

White, A., Watkins-Brandt, K.S., McKibben, M., Wood, A.M., Hunter, M., Forster, Z., Du, X., Peterson, T.D., 2014. Large-scale bloom of *Akashiwo sanguinea* in the Northern California Current System in 2009. Harmful Algae 37, 38–46.

Wood, A.M., Shapiro, L.P., Bates, S.S., 1994. In: Domoic Acid: Final Report of the Workshop, February 21–23, 1992, Oregon Institute of Marine Biology, Oregon Sea. Grant ORESU-W-94-001, 22.