A springtime source of toxic *Pseudo-nitzschia* cells on razor clam beaches in the Pacific Northwest

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A R T I C L E   I N F O

A B S T R A C T

Concentrations of domoic acid (DA) above the regulatory limit in Washington coast razor clams are usually higher on northern beaches from summer to fall. Recent field studies have confirmed that the primary source of toxic *Pseudo-nitzschia* (*PN*) cells in those seasons is a semi-retentive topographically trapped seasonal eddy located offshore and north of the clamming beaches. Another semi-retentive coastal feature, Heceta Bank, that has been shown to support toxic *PN* cells in summer, is located south of Washington's clamming beaches. In this paper we present evidence to demonstrate that Heceta Bank, although not a likely source of toxic cells to Washington in summer due to the prevailing southward seasonal currents, may be a source of cells in springtime before the southward currents develop. In contrast to summer and fall seasons, concentrations of DA in razor clams are typically higher at southern beaches in spring. The likelihood of a southern source is explored using biological and transport data surrounding a period of toxic razor clams in April 2005. In particular, satellite-derived chlorophyll data confirm that a bloom occurred over Heceta Bank in March of that year, just prior to a period of strong storm-driven northward transport. *PN* cells of the same species observed in the April bloom on Washington beaches and in offshore waters were documented in Oregon offshore waters on the northern edge of Heceta Bank. That species, *P. australis*, has been shown to be highly toxic in this region; shore-based data show that razor clams on Oregon beaches were also toxic at the time when *P. australis* was observed offshore. Both measured and modeled currents show that transport was more than sufficient to move cells from the vicinity of Heceta Bank, Oregon to southern Washington beaches by the time the toxic cells were observed on those beaches. The rapid transport was due in part to the presence of the buoyant plume from the Columbia River, a common feature in winter and spring in nearshore waters of the U.S. Pacific Northwest.

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1. Introduction

Accurate risk assessment for the arrival of a harmful algal bloom (HAB) at a coastal beach depends on a detailed understanding of the ecology of the toxigenic organism producing a toxin, the triggers for toxin production, and transport from the toxic bloom development site to the beach. The ecology of organisms responsible for toxic blooms, including several species of *Pseudo-nitzschia* (*PN*) that can produce the neurotoxin, domoic acid (DA), as well as triggers for cellular toxicity in situ are still poorly understood. A complement to detailed information about species ecology and toxin triggers is knowledge of bloom development sites ("hotspots") in combination with robust transport and biological models that incorporate the variable conditions occurring along *PN* transport pathways.

The Pacific Northwest shelf and slope are set within an eastern boundary upwelling system, the California Current System (CCS) (Hickey, 1979, 1998). Isopycnals begin to tilt upward toward the coast following the transition from winter wind conditions to spring/summer wind conditions (Huyer et al., 1979; Huyer, 1983; Strub and James, 1988) resulting in the upward movement of deeper, nutrient-rich water. Although seasonal oceanographic properties in this region generally have large alongshore scales

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(>500 km) (Hickey, 1989; Hickey and Banas, 2003), smaller scale (~10–50 km) features such as capes and banks may have a controlling influence on regions of HAB initiation. A whole-coast map of particulate domoic acid (pDA) concentrations collected during summer 1998 shows high concentrations of toxin *only* near the several mesoscale features where the typical upwelling circulation patterns are known to be interrupted (Fig. 1) (Hickey and Banas, 2003; Trainer et al., 2001). Recirculating current patterns form over banks such as offshore of the entrance to Juan de Fuca Strait in the feature known as the Juan de Fuca eddy (Freeland and Denman, 1982; Foreman et al., 2008), and, to a lesser extent, on Heceta Bank, off central Oregon (Kosro, 2005; Barth et al., 2005; Gan and Allen, 2005). These features tend to be retentive; i.e., they retain phytoplankton and other particles for longer time periods than an open, straight coastline (e.g., MacFadyen and Hickey, 2010 for the Juan de Fuca eddy; Venegas et al., 2008 for Heceta Bank). Due to the greater retention of phytoplankton in these regions, and low grazing rates relative to growth rates (Olson et al., 2006, 2008, for the Juan de Fuca eddy), phytoplankton can accumulate to high densities (Spitz et al., 2005 for Heceta Bank; MacFadyen et al., 2008 for the Juan de Fuca eddy region). They may also be subjected to both macro- and micro-nutrient stress in these regions (Trainer et al., 2009a,b), potential contributors to toxin production by PN (e.g., Bates et al., 1991; Pan et al., 1996; Maldonado et al., 2002; Wells et al., 2005; Schnetzer et al., 2007).

On six 3-week summer/fall interdisciplinary surveys of the Juan de Fuca eddy and coast region over a 4-year period, pDA was found in and downstream of the eddy in every case, but was rarely measured near the coast (Trainer et al., 2002, 2009a). Seasonal currents over the mid shelf to the upper slope are southward during the summer–fall season in the northern CCS and continuous over distances of a few hundred kilometers (MacFadyen et al., 2005, 2008), suggesting that the eddy is the likely source of toxic cells for Washington razor clam beaches, all of which are located south of the eddy. Recent research shows that the eddy is more retentive during and just following periods of downwelling-favorable (northward) winds; whereas escape from the eddy and travel downcoast occurs following periods of upwelling-favorable (southward) winds (MacFadyen et al., 2005; MacFadyen and Hickey, 2010). If a transition to downwelling-favorable winds (a summer storm) occurs during the period that the toxic cells are transiting down the coast, frictional surface currents move algae shoreward and onto coastal beaches, where razor clams and other crustaceans are impacted (Trainer et al., 2002; MacFadyen et al., 2005; MacFadyen and Hickey, 2010).

Like the Juan de Fuca eddy, Heceta Bank can readily be identified as a local maximum in chlorophyll concentration (e.g., Fig. 2) (also see Landry et al., 1989; Venegas et al., 2008 for the seasonal mean). Its circulation is retentive (Kosro, 2005; Barth et al., 2005), although not as retentive as the Juan de Fuca eddy. During summer, modification of the southward coastal jet by the bank introduces an alongshore pressure gradient that enhances northward velocity over the inner shelf onshore of the bank during downwelling-favorable winds, thus making the region more
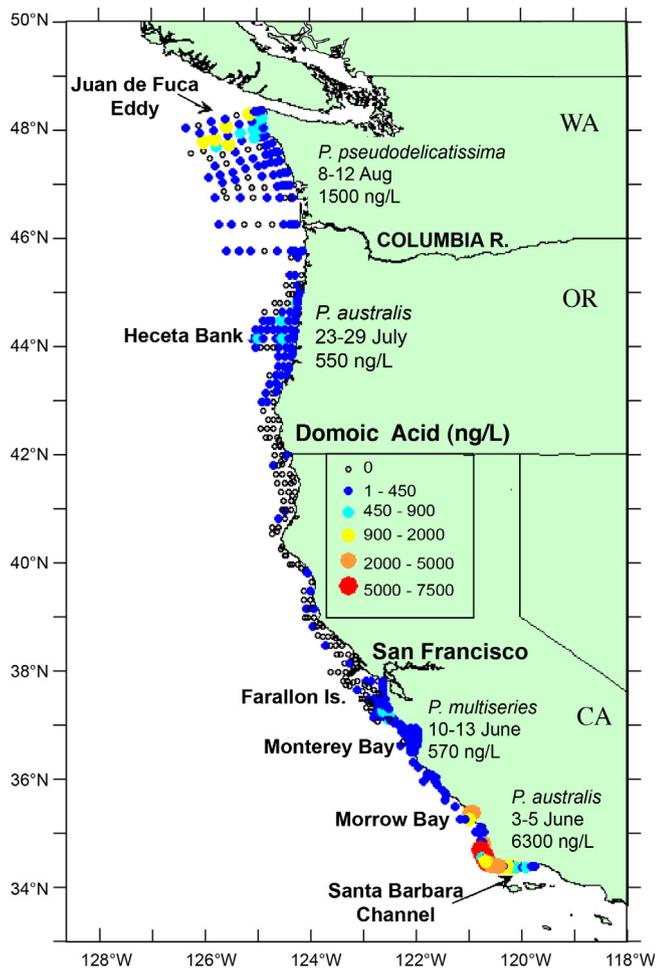
Fig. 1. Particulate DA along the whole U.S. west coast in summer 1998. Note regions of high pDA near recirculating topographic features.
Adapted from Springer Fig. 7, p. 1016, Hickey and Banas, 2003, original copyright; with kind permission from Springer Science and Business Media. Original data and maps in Trainer et al. (2000, 2001).
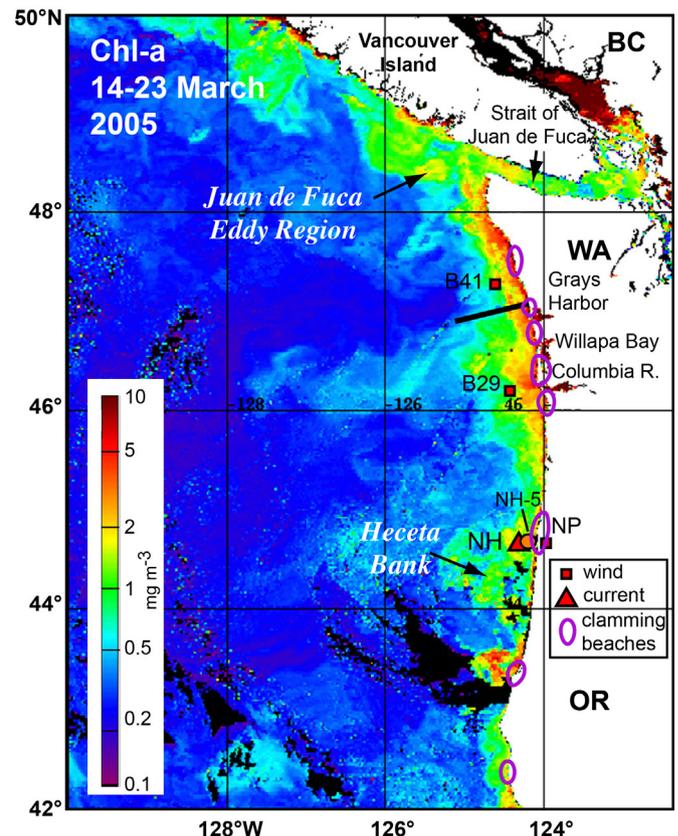
Fig. 2. MODIS satellite-derived chlorophyll image, averaged over 14–23 March 2005 (Kudela, Pers. Comm.). Physical features of interest are labeled and razor clam beaches are identified. The offshore sampling transect is denoted by a black line. Locations of wind buoys (B41, B29, and NP), a moored current profiler (NH) and a PN sampling station (NH-5) are also shown. Note higher chlorophyll concentrations near Heceta Bank, Oregon and along the Washington coast/British Columbia.

retentive than the straight open coast (Kirincich and Barth, 2009). Much less is known about circulation patterns over the bank during other seasons. Because of the tendency of currents over much of the region to be strongly southward during the primary phytoplankton growth season, Heceta Bank has not previously been considered as a source of toxic blooms for the Washington coast.

Seasonal scale currents during winter and early spring, in contrast to those during summer, are generally northward over the shelf and slope in the northern CCS (Hickey, 1989). In this paper, we explore the possibility that Heceta Bank is a source of toxic blooms on beaches along the Washington coast in the seasons with northward prevailing flow. After describing our methods, we show that razor clams can become toxic in the spring season (Section 3.1). Selecting one spring "event", we next describe the spatial structure and time horizon for a bloom of toxic PN observed on coastal beaches in spring 2005 (Section 3.2). We then demonstrate that transport of cells from the vicinity of Heceta Bank was likely responsible for the Washington coast bloom (Sections 3.3 and 3.4).

2. Methods

As will be shown in this paper, events in which DA in razor clams exceed regulatory limits are relatively rare and difficult to predict in the Pacific Northwest. Thus, studies of specific events must rely on a synthesis of data collected for reasons other than a focused study. For the 2005 event, for example, it was only fortuitous that offshore sampling by the Olympic Region Harmful Algal Bloom (ORHAB) partnership occurred during a DA event on the coastal beaches. Model results were provided using the MoSSea modeling framework (Modeling the Salish Sea) which was developed through the Puget Sound Regional Synthesis Model (PRISM) study at the University of Washington and the Pacific Northwest Toxin (PNWTOX) project. Data used in this paper came from these and a variety of other sources and programs, including the Washington State Department of Health (WDOH), the Oregon Department of Agriculture (ODA), the National Data Buoy Center (NDBC), a study of Global Ocean Ecosystem Dynamics (GLOBEC), and a study of the Ecology and Oceanography of Harmful Algal Blooms in the Pacific Northwest (ECOHAB PNW). Details are given below.

2.1. Hydrographic data

As a component of the ORHAB program, hydrographic data were obtained across the Washington shelf on 19 April 2005 from the fishing vessel Karelia (see transect location in Fig. 2). The data were collected on downcasts using a Sea-Bird Electronics SBE 19 Conductivity, Temperature, and Depth (CTD) system. The data were averaged into 1 m bins. Quality control consisted of removing spikes that created density inversions >0.02 kg m^{-3}. Conductivity values causing such inversions were removed and the resulting gaps (if less than 2–3 m) were filled using linear interpolation. The CTD data were used to compute geostrophic velocities normal to the transect referenced to 200 m, using the method of Reid and Mantyla (1976) to extrapolate data to depths shallower than 200 m.

2.2. Pseudo-nitzschia quantification and size groups

Water samples were obtained both on several beaches in Washington and Oregon and on the ORHAB cross-shelf transect. At each CTD station or beach site, water samples were collected at the sea surface using a bucket. Samples for PN abundance and size were preserved in sodium acetate buffered formalin (<1% final concentration). Pseudo-nitzschia cell numbers were quantified

microscopically (Zeiss Axiovert 135 inverted light microscope) from whole water samples using a Palmer-Maloney counting chamber after 12–24 h of settling. All cells were enumerated at 400x magnification with a limit of detection of 700 cells L^{-1} (Trainer and Suddleson, 2005; www.orhab.org). Because of recent changes in PN species identification, species were grouped into two size categories (in order of increasing size) of *pseudodelicatissima/ delicatissima/cuspidata* ("small"), and *australis/fraudulenta/heimii/ pungens/multiseries* ("large"). The efficacy of these categorizations in relation to species identification was established using scanning electron microscopy (SEM) analyses on ~1% (>10) of the surface samples (Simonsen, 1974; Round et al., 1990; Miller and Scholin, 1998). In brief, samples were prepared using a modified KMnO$_4$/ HCl oxidation method. Filter membranes with processed samples were bonded to aluminum stubs, air-dried, coated with gold–palladium and examined with an AMRAY 1000 SEM.

Washington beach sites were generally sampled twice per week from March through November and once a week from December through February. For a more detailed schedule see http://www.orhab.org/plan/sampling/sampling.html. Beach site salinity was measured using a YSI C30 SCT handheld sensor.

2.3. Domoic acid analysis

To determine pDA in seawater at each sample site, one liter of seawater from each station was filtered onto a 47-mm diameter nitrocellulose filter (HAWP04700 Millipore MF^{TM}-Membrane filter; 0.45 μm pore-size). The filter was mascerated and sonicated to ensure the release of intracellular DA, and analyzed using the receptor binding assay method as outlined by Bill et al. (2006). Standards were prepared with a certified DA standard (DACs-1B, Certified Reference Materials Program, National Research Council, Canada). The limit of detection was 0.1 nM with an overall precision of ~5% coefficient of variation.

Concentration of DA in razor clams on selected beaches was determined by the WDOH and the ODA utilizing a methanol/water extraction and analysis by High Performance Liquid Chromatography (Hatfield et al., 1994). These samples were obtained at multiple sites on each beach for analysis of DA in a composite sample. WDOH data was used to create a multi-decadal time series. For the present analysis, when several analyses were performed on clams from the same beach, the highest value was selected in order to emphasize toxic events. Concentrations of DA in clams at or above the current regulatory limit, 20 ppm, are considered unsafe for human consumption.

2.4. Currents and winds

A time series of water velocity was obtained from data collected by the GLOBEC program including an upward looking Sontek 500 kHz Acoustic Doppler Current Profiler (ADCP) moored on the central Oregon coast (44° 38.8′ N, 124° 18.4′ W) a few meters off the bottom in a water depth of 81 m (labeled "NH" in Fig. 2; Kosro, 2002, 2003). Data were sampled in 34 s averages at 3 min intervals, and averaged to hourly values. These data were low-pass filtered to remove higher frequency signals such as diurnal and semi-diurnal tides using a cosine-lanczos filter with a half power point of 46 h, and decimated to 6 h values.

Eleven SeaSonde HF radar surface current mapping systems (five at ~12 MHz and six at ~5 MHz) collected hourly radial current data between ~42°N (northern California) and ~46.4°N (southern Washington), which were mapped to two-dimensional surface current vectors on a 6 km grid, and low-pass filtered after screening for regions of low geometrical accuracy (Kosro, 2005). To obtain an estimate of alongshelf transport during the April 2005 period of interest, "virtual drifters" were released from three

locations on Heceta Bank into the time-varying field of HF surface currents, beginning 20 March 2005. The drifters were tracked until they reached latitude 46.5°N. HF measurements did not extend all the way to the coast, and did not extend north of about 46.4°N. When the currents at the virtual drifter location would have carried the drifter inshore of the HF coverage, the location was nudged offshore in small increments until the locally measured currents would carry it to a new location within HF coverage.

Hourly wind speed and direction was obtained from NDBC for the Cape Elizabeth buoy (B46041, "B41"), the Columbia River buoy (B46029, "B29"), and from the Newport, Oregon land-based station (NWPO3, "NP"). Locations are shown in Fig. 2. Wind data were low-pass filtered in a manner similar to the velocity data discussed above.

2.5. Satellite imagery

Satellite-derived estimates of chlorophyll-*a* concentrations were obtained from Level 2 MODIS data provided by the NASA Ocean Biology Processing Group (http://oceancolor.gsfc.nasa.gov/). Data from 14 to 23 March were composited to improve coverage; the remaining black regions in the image were persistently cloudy.

2.6. Columbia plume model

Results from a Regional Ocean Modeling System (ROMS, Rutgers version 3-based) simulation using realistic forcing from river flow, tides, wind stress and surface heat flux are used to illustrate time-variable surface currents as well as the location of the plume from the Columbia River during spring 2005 (Sutherland

et al., 2011). The model is configured in a similar manner to previous simulations of the Columbia River plume (MacCready et al., 2009; Liu et al., 2009a,b), and is embedded in a larger area regional modeling system (NCOM), which uses data assimilation to improve results. The ROMS model domain includes Puget Sound and the Strait of Georgia, and extends from 45°N to 50°N with an offshore open boundary at 127°W. Grid cell spacing ranges from 280 m in Puget Sound to a maximum of 3.1 km over the shelf, with <1 km resolution near the mouth of the Columbia River.

3. Results

3.1. Seasonal patterns in multi-decadal time series of DA in razor clams

During the period from 1991 to 2009, the majority of the 10 clamming beach closures along the Washington coast occurred in summer and fall (8 of 10 closures) (Fig. 3). In summer and fall, higher DA concentrations are observed on the more northern beaches. Both modeling and observational studies of the Washington coast suggest that the source of summer/fall toxic cells is the Juan de Fuca eddy (Marchetti et al., 2004; MacFadyen et al., 2005; MacFadyen and Hickey, 2010; Trainer et al., 2009a). This pattern is consistent with the occurrence of higher clam toxicity at more northern beaches, and with the persistent and large scale southward flow that occurs in near surface waters over the shelf and slope in these seasons (MacFadyen et al., 2005, 2008).

A map of satellite-derived chlorophyll-*a* shows high chlorophyll along the Washington coast (5–10 mg m^{-3}), in the Juan de Fuca eddy region ($\sim$1–2 mg m^{-3}) and offshore of Heceta Bank
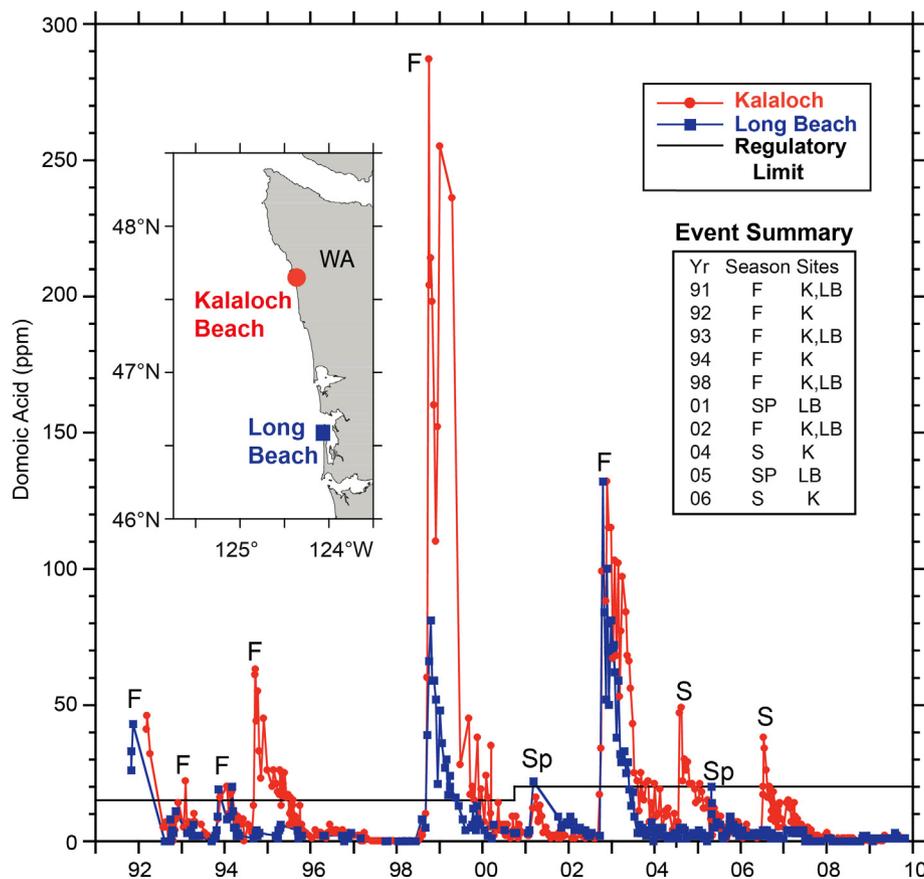
Fig. 3. Multi-year time series of DA concentration in razor clams at two beaches off the Washington coast. Periods when DA exceeded the regulatory limit (20 ppm at present; 15 ppm prior to late 2000) are labeled F, Sp and S, denoting fall, spring and summer events, respectively. Event seasons are labeled according to the season where the increase began, rather than where maximum DA was observed.

($\sim$1 mg m^{-3}) during late March 2005 (Fig. 2). Two periods of razor clam toxicity have been observed in spring over the past two decades, one in 2001 and the other in 2005 (Fig. 3). During both these events, in contrast to the summer and fall events, DA concentrations were higher on the southern beaches, and toxicity of the clams was similar on northern and southern beaches rather than higher toward the north. In the following sections we present data from spring 2005 to show that the source of toxic *PN* cells observed in spring on the Washington coast is likely Heceta Bank, the semi-retentive feature located $\sim$200 km south of the Washington coast that generally supports the highest chlorophyll concentrations on the Oregon coast (e.g., Figs. 1 and 2; see also Landry et al., 1989). Data include pDA in seawater (defined as the DA associated with the >0.45 μm filtered size fraction); *PN* abundance on both Oregon and Washington beaches, and in Washington offshore waters; and both observed and modeled surface currents.
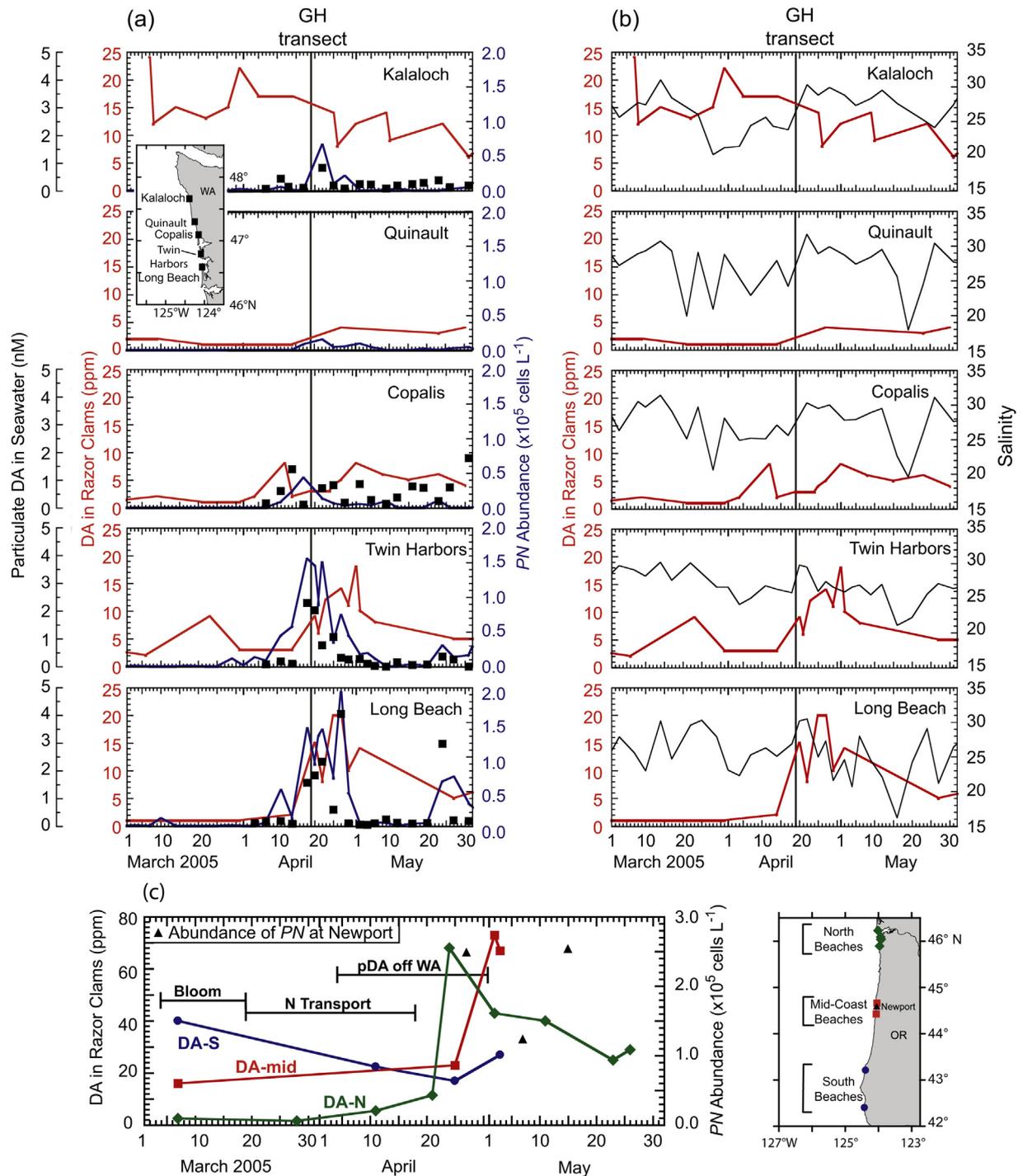
Fig. 4. Time series of razor clam and seawater properties on Washington and Oregon beaches in spring 2005: (a) DA in razor clams (red), pDA in seawater (black squares) and abundance of *PN* cells (blue); (b) DA in razor clams (red) and salinity (black), where salinity <31.5 indicates water within the plume from the Columbia River; (c) time series of DA in razor clams for three regions on the Oregon coast including the southern (DA-S), middle (DA-mid), and northern (DA-N) beaches and *PN* abundance on the beach at Newport, Oregon. Horizontal bars indicate periods of the bloom, northward transport of *PN* cells, and detection of pDA in cells off the Washington coast, as discussed in the text. Abundance of "large" (a/f/h/p/m) *PN* cells at Newport, Oregon on selected dates is also shown.

3.2. Details of the April 2005 toxic bloom

3.2.1. Washington beach samples

An expanded view of data in the period March–May 2005 illustrates the relationship between changes in *PN* cell abundance and both DA in razor clams and pDA in seawater on razor clam beaches spanning the entire Washington coast (Fig. 4a). In particular, cell abundance (blue lines) increased rapidly from near zero to $1.5–2 \times 10^5$ cells L^{-1} beginning around 7 April at the two southernmost stations. Cell abundance decreased rapidly to near zero by about 1 May. The sudden onset of the bloom suggests an origin due to transport rather than due to in situ growth.

A slight increase ($\sim 0.5 \times 10^5$ cells L^{-1}) during this period was observed at two of the northern beaches (Kalaloch and Copalis), but the duration of the increase (elevated abundance on only one sample day) was much shorter than on the southern beaches. Particulate DA in seawater (black squares) rose and fell roughly in concert with the number of *PN* cells, consistent with the fact that the sampled cells contained toxin. At Copalis Beach, the increase in toxin was not coincident with the increase in *PN* abundance and the data there exhibited a higher degree of variability over time; the reasons for this behavior are presently unknown. In general, higher concentrations of pDA in seawater were observed toward the south along the Washington coast.

Domoic acid in razor clams (red lines) increased from early to late April at all beaches except Kalaloch, and was generally higher at southern beaches. The increase at Long Beach, the most southern beach, occurred more rapidly than at beaches to the north, almost in concert with the increase in pDA in seawater. At the next beach northward (Twin Harbors), maximum DA in razor clams lagged the maximum pDA in seawater by several days. Maximum DA

concentration in razor clams occurred later to the north (from south to north, 25 April at Long Beach and 1 May at Twin Harbors) (Fig. 4a). DA in razor clams generally decreased after 1 May except at Kalaloch, the most northern beach. The high values of DA in razor clams at Kalaloch Beach, which generally decreased from March to May, are likely the signature of slow depuration of DA from clam tissue following the toxic event that began in the preceding summer, in July 2004 (Fig. 3). Concentrations of DA remained quantifiable until at least the end of May at all open coast beaches, although values were below the regulatory limit of 20 ppm by the end of April.

Comparison of *PN* abundance and alongshelf wind (Fig. 5a) shows that abundance began to increase on about 7 April following a ~ 3 week period of predominantly downwelling-favorable winds (storms) that began near 20 March. Downwelling-favorable winds cause onshore transport in the surface layer, a result of Ekman layer dynamics, and have been shown to cause onshore transport of particles (MacFadyen and Hickey, 2010). Cell abundance increased more rapidly following storms beginning 14–16 April. Thus, variability in *PN* abundance is consistent with onshore transport during storms/downwelling winds as discussed previously in Trainer et al. (2002) and MacFadyen et al. (2005).

Cells identified in ORHAB beach samples during April 2005 were the large type of *PN*: 95–100% from 11 April through at least 2 May at all locations where any *PN* cells were observed; and 80% and 64% large cells on 6 May at the two southernmost stations. Analysis via SEM confirmed that the large *PN* species was *Pseudo-nitzschia australis* a species that, to date, has consistently produced DA in the Pacific Northwest (e.g., Stehr et al., 2002; Baugh et al., 2006).

Note that a second persistently stormy period occurred during 12–24 May 2005 and this storm was also associated with an
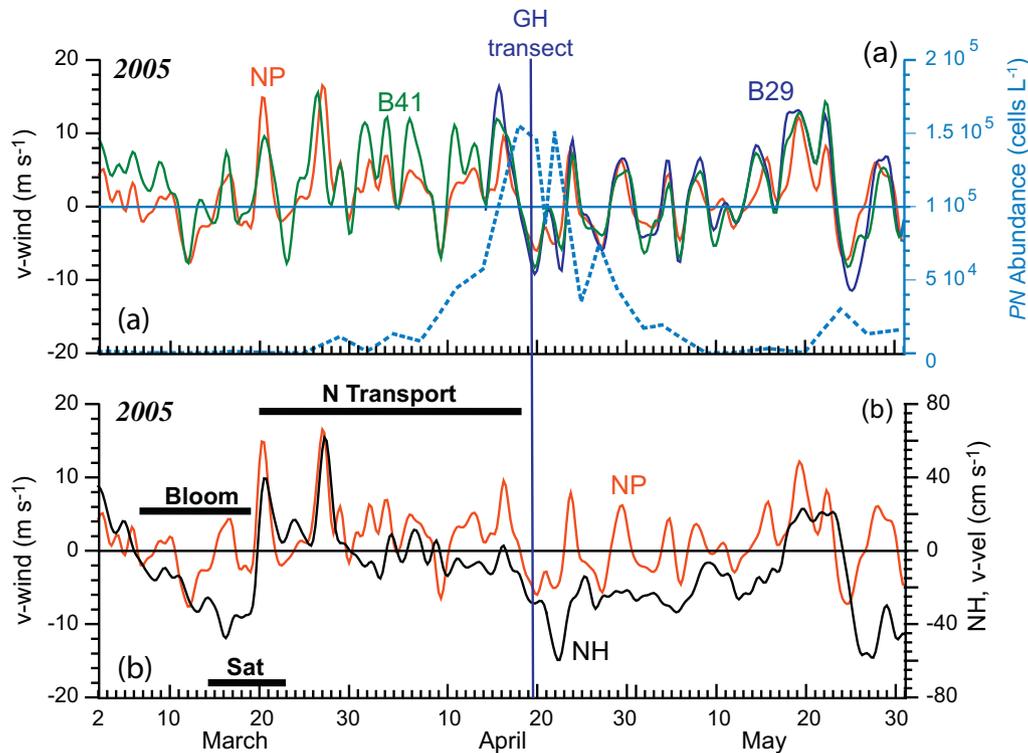
Fig. 5. Timing of *PN* cell arrival on coastal beaches relative to winds and currents in spring 2005. Periods of blooms on Heceta Bank and northward transport as discussed in the text are marked with horizontal black bars. The timing of the offshore transect (GH), marked with a vertical blue line, and the date of satellite imagery (Sat) shown with a horizontal black bar, are also shown. (a) Time series of alongshelf wind (positive northward) off the Washington (B41 and B29) and Oregon coasts (NP). Station locations are shown in Fig. 2. *PN* abundance off the Washington coast at Twin Harbors is shown with a blue dashed line (see station location in Fig. 4). (b) Alongshelf wind (positive northward) at Newport, Oregon (NP) and 10 m alongshelf velocity (positive northward) at mid shelf off Oregon (NH).

increase in *PN* abundance at the three southernmost beaches (Fig. 4a). However, the type of cells was more than 50% small *PN* (ORHAB database; data not shown), rather than the large *PN* cells seen almost exclusively during the earlier storm period. No simultaneous increase in toxicity was measured in razor clams during this period.

Salinity data collected at the beaches for the same period in April 2005 demonstrate that all the cell and toxin samples during this period were obtained in relatively fresh water (Fig. 4b). Note that this is an important difference from results during the summer and fall seasons (Trainer et al., 2009a), when toxic cells were rarely observed in plume-influenced water. At all beaches salinities were generally less than 31.5, which is considered a signature of plume water over the Washington shelf (Hickey et al., 2005, 2010). Effects of the Columbia plume will be described in detail in Section 3.4.

3.2.2. Washington offshore samples

Fortuitously, on 19 April 2005, around the time of the peak in *PN* abundance on the Washington coast, abundance and pDA data as well as water property profiles were obtained on a transect (GH) across the shelf just offshore of the coastal beaches where maximum pDA was observed (Fig. 6). Abundance of *PN* in the surface samples along the offshore transect generally decreased in number from the shore to the open ocean (Fig. 6a). The highest abundance and the maximum pDA concentrations were observed in water influenced by the Columbia River plume (blue contoured region on the shoreward side of the transect). 100% of the cells over the inner and mid shelf were the large type of *PN*; 84% of the cells on the outer shelf were the large type of *PN* (see numbers along the top axis of Fig. 6a). The dominant species *Pseudo-nitzschia australis*, as confirmed by SEM, was the same as the dominant species at the beach, with the exception of the station farthest from the coast. At that station the presence of *Pseudo-nitzschia pseudodelicatissima* and *Pseudo-nitzschia delicatissima* was confirmed by SEM. Toxin was measurable at most transect stations (see numbers along the top axis of Fig. 6a) although an order of magnitude lower than observed in water near the beach (Fig. 4a). The lower toxin concentrations observed along the transect are consistent with lower *PN* abundance on the transect than at the neighboring Twin Harbors Beach (average ~50,000 cells L^{-1} vs. ~150,000 cells L^{-1}).

3.2.3. Oregon beach samples

Oregon razor clams were already highly toxic at southern Oregon beaches and slightly less toxic at mid Oregon beaches at the onset of the early March 2005 upwelling period (Fig. 4c). The high toxicity was likely due to a period of higher toxicity in prior years (not shown). However, toxin was negligible at northern Oregon beaches during March 2005. DA declined at southern Oregon beaches and rose at middle and northern Oregon beaches over the following month, when wind conditions were primarily downwelling-favorable. Large *PN* cells dominated the Oregon seawater samples collected by ORHAB personnel on the beach near Newport in late April/early May. Analysis by SEM for the 7 May samples confirmed that the cells were primarily (>90%) *Pseudo-nitzschia australis*, the same species observed off Washington beaches in mid to late April 2005. The abundance of *PN* observed at Newport, Oregon in May was roughly the same as that observed off Washington beaches the preceding month.

In addition to an increase in cell number in early May on Oregon beaches, toxicity in razor clams on middle Oregon beaches (DA-mid in Fig. 4c) increased three-fold between 25 April and 3 May and was much higher than in razor clams on Washington beaches. As will be shown in Section 3.4 the increase over time in both cell numbers and razor clam toxin is consistent with southward recirculation of toxic cells that were previously in waters off northern Oregon (DA-N in Fig. 4c) and the Washington coast.

3.2.4. Oregon offshore samples

Offshore samples were collected at a station in 50 m water on the northern edge of the Heceta Bank complex at roughly monthly intervals throughout 2005 (data from B. Peterson, not shown; see location in Fig. 2). *PN* cells of the "large" group were present on 18 March, just following the bloom period, along with some cells of the "small" *PN* group. By 14 April, the number of large cells had increased and the number of small cells had decreased. On 27 April, large cells numbered over 250,000 cells L^{-1}, similar to the numbers observed on Oregon beaches at that time, which were shown by SEM to be primarily *Pseudo-nitzschia australis* (Fig. 4c). Although no DA data are available for these offshore samples, we note that *P. australis* is almost never observed without some toxin. The estimated minimum toxicity of *P. australis* in coastal waters is 11.5 pg per cell (Baugh et al., 2006).

Fig. 6. (a) Salinity along the GH transect off southern Washington on 19 April 2005 (location shown in Fig. 2), with stations shown as vertical lines. *PN* abundance, percentage of *PN* in the "large" (*a/f/h/p/m*) category, and pDA are shown along the top of the section. Note the freshwater feature next to the coast, the signature of a plume from the Columbia River. (b) Geostrophic alongshelf velocity (positive northward) relative to 200 db on 19 April 2005.

3.3. Transport of toxic cells from Oregon to Washington

In this section we address the origin of the toxic *PN* observed both offshore of and on the Washington coast in spring 2005. The analysis includes satellite-derived chlorophyll, estimates of flow across the Washington coast transect, surface currents from a coastal HF radar surface current mapping system maintained along the Oregon coast, and velocity time series from an ADCP profiler moored at mid shelf off central Oregon (see location in Fig. 2). Note that because *PN* are found primarily in the upper few meters of the water column in this region, with a maximum at 1–5 m from the sea surface (Trainer et al., 2009a), transport is estimated only for the upper 10 m of the water column.

Possible sources for toxic cells off the Washington coast in April 2005 include an in situ origin of cells and toxin, and northward or southward transport of toxic cells from remote locations. Although we cannot prove that in situ production did not occur, we will demonstrate below that cells, toxic or not, residing on the Oregon inner shelf in mid March 2005 would have been transported northward to southern Washington by mid April; while cells residing on the southern Washington inner shelf would have been transported northward to the British Columbia coast or into the Strait of Juan de Fuca (e.g., Hickey et al., 1991) during that period.

Time series of alongshelf wind and mid shelf currents off the central Oregon coast illustrate that two periods of persistent upwelling-favorable winds and southward currents occurred in spring 2005; one in mid March, the other in the second half of April extending through mid-May (Fig. 5b). Satellite-derived chlorophyll imagery averaged over the interval from 14 to 23 March illustrates that during the March upwelling period a chlorophyll bloom developed over Heceta Bank in central Oregon as well as along most of the Oregon and Washington coast, a typical pattern during periods of coastal upwelling (Fig. 2).

To evaluate transport during the period between the observation of the chlorophyll bloom on Heceta Bank and the observation of toxic cells off southern Washington, we first present geostrophic velocities (velocities derived from density gradients) on the Washington coast transect on 19 April 2005 (Fig. 6b). Development of large scale jets are a seasonal, baroclinic feature of the regional circulation and vary on time scales of months rather than days; hence a snapshot gives a reasonable view of the presence or absence of large scale seasonal features like the summertime shelf break upwelling jet (southward-flowing) or the wintertime Davidson Current (northward-flowing). Results demonstrate that flow relative to 200 db was northward across the entire southern Washington shelf and slope on 19 April, typical of winter rather
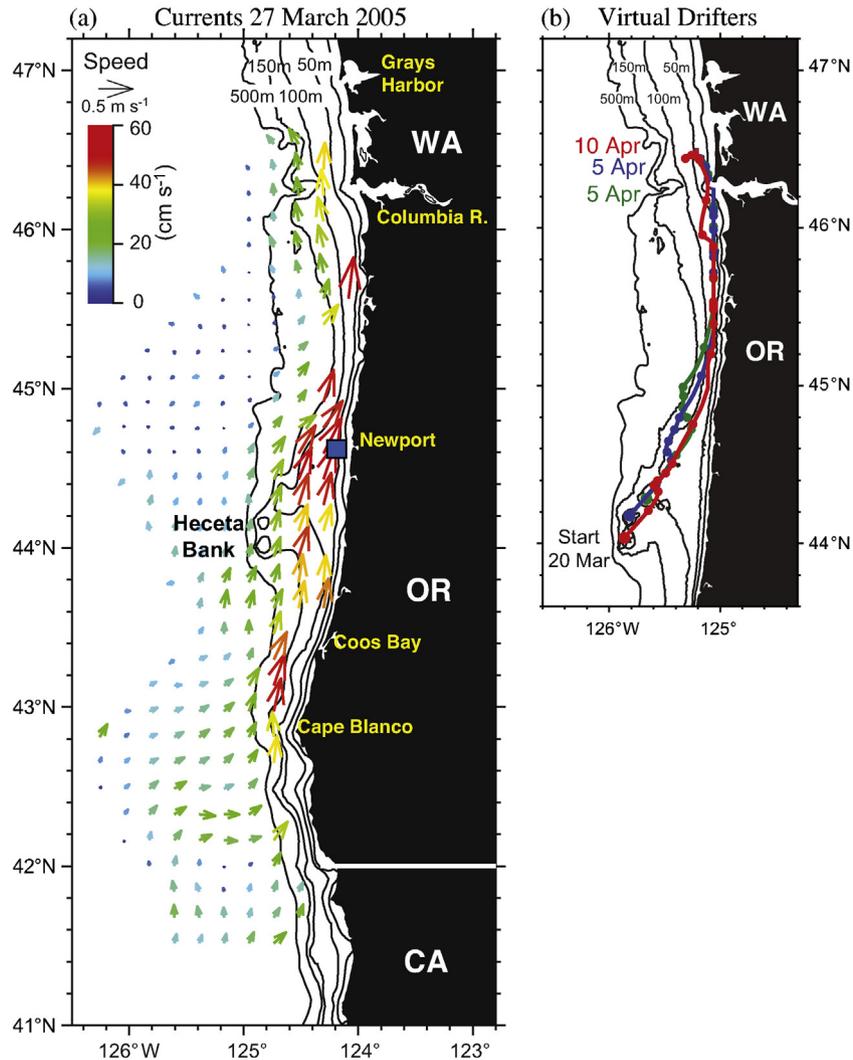
Fig. 7. (a) Daily averaged surface currents from a coastal HF Radar for the Oregon and southern Washington coasts on 27 March 2005 during a storm period (see NH time series in Fig. 5b for setting). The location of the NH mooring is shown with a blue square. (b) Virtual drifters released from 3 locations on Heceta Bank into the time-varying field of HF surface currents, starting on 20 March 2005. The drifters were tracked until they reached latitude 46.5° N—on 5 April for the blue and green tracks and on 10 April for the red track. Solid dots indicate daily progress.

than summertime flow patterns (Hickey, 1989). The weak northward flow across the shelf and slope is an indication that the spring transition to large scale upwelling and a southward current pattern has not yet occurred. The spring transition was delayed by about a month in 2005, occurring on 24 May (Kosro et al., 2006; Hickey et al., 2006).

Near-surface currents farther south obtained from coastal HF radar on 27 March during a period of strong downwelling-favorable winds (storms) (Fig. 7) confirm that currents over the southern Washington and central Oregon inner shelves were strongly northward over the entire region during the storm (Fig. 7a). Spatially coherent alongshore-directed currents over this entire region are consistent with prior research (Hickey, 1981; Kosro, 2005).

Coastal HF radar surface current data are available off Oregon and southern Washington on an hourly basis throughout the analysis time period. To estimate whether particles originating on Heceta Bank could be transported to the southern Washington coast by early April when toxic cells first appeared off the southern Washington coast, "virtual drifters" were embedded in the observed velocity fields to derive particle pathways between 20 March and when the drifters passed out of the HF radar data domain to the north (Fig. 7b). Because the winds are downwelling-favorable (causing onshore near surface transport), the trajectories moved toward shore and thus out of true radar coverage. Note that "real" drifters frequently move alongshore on the inner shelf rather than beaching—this is because Ekman layers shut down on the inner shelf during storms when the inner shelf is well mixed (Austin and Barth, 2002). However the Ekman layers are not expected to shut down under stratified conditions (Lentz, 2001) such as would occur if Columbia plume water is present and wind strength is insufficient to vertically mix plume and ocean waters. The technique used tests whether the next point on the trajectory lies within radar coverage; if not, the drifter is moved ~0.5 km west and is tested iteratively until its destination point remains within radar coverage. In this way, the northward/southward translation is not modified, but the east/west translation is modified near the coast. Results indicate that particles originating on Heceta Bank, Oregon, could reach southern Washington by 5–10 April. Thus, the observed increase in pDA and PN abundance off southern Washington (Fig. 4a) is consistent with the source of the cells being on or near Heceta Bank.

3.4. Influence of the plume from the Columbia River on transport from Oregon to Washington and vice versa

Samples of cell numbers and pDA collected on beaches along the Washington coast (Fig. 4a,b) and in offshore waters (Fig. 6) in spring 2005 were mostly situated in low salinity water (<31.5) throughout the study period of March through May. Salinity maps from a numerical model confirm that a low salinity plume from the Columbia River extended along the Washington coast throughout this period (Fig. 8). A plume frequently occurred at the same time off the Oregon coast. In general, plumes from the Columbia River tend northward during periods of downwelling-favorable winds and/or northward regional flow; southwest during periods of upwelling-favorable winds and southward regional flow; and in both directions if winds fluctuate from northward to southward, as occurred during the period studied here (Hickey et al., 2005).

On 15 March, model results show remnants of an Oregon branch of the plume, likely generated during the upwelling period that resulted in the phytoplankton bloom over Heceta Bank (Fig. 8). By 20 March both plume branches have been moved close to shore by onshore flow in the surface Ekman layer, similar to flow patterns observed on 27 March (Fig. 7a). Beginning 19 April, after winds turned to upwelling-favorable, the Washington branch of

the plume began to spread seaward across the shelf. At the same time a new southwest-tending plume began to develop. The southwest plume can develop more easily once the regional currents transition to primarily southward, as occurred in mid April in 2005 (see observed Oregon currents in Fig. 5b).

Recent research shows that the new southwest-tending plume, such as that seen on 25 April, consists primarily of water that originated off the Washington shelf—the new plume water (purple color) pushes out into aged plume water, which folds around the new plume (Fig. 8; see example in Hickey et al., 2009). The mixed new and aged plume continues southward down the coast throughout most of May, although periods of downwelling winds keep the plume somewhat trapped to the coast. This result provides a likely explanation for the increase in DA in razor clams, and high numbers of PN cells off central Oregon in May—water containing toxic PN cells flows back down the coast, removing the cells from Washington beaches, and once again providing them to Oregon beaches.

4. Discussion and summary

In this paper we demonstrate that the topographically constrained, biologically rich, semi-retentive region, Heceta Bank, Oregon is a likely source of toxic PN cells that impact beaches and razor clams on Washington beaches in the early spring season (i.e., before the "spring transition"). Because seasonal regional currents have two primary directions: southward in summer and fall, northward in winter and early spring, the Washington coast has two likely sources of toxic cells, one north and one south of the clamming beaches. Details are summarized in a cartoon illustrating seasonal flow patterns and likely sources of toxic cells in each season (Fig. 9a–c). The cartoon also illustrates the role of the buoyant plume from the Columbia River as primarily a barrier (at some locations, e.g., in summer/fall) and primarily a conduit (e.g., winter/early spring).

It is not uncommon for phytoplankton blooms to occur in late winter and early spring in the northern CCS (Landry et al., 1989). Seasonally averaged wintertime values of chlorophyll, while lower than in summer and fall seasons, are about 1 mg m^{-3} (Landry et al., 1989; see also Fig. 17a in Huyer et al., 2007). Wetz et al. (2006) report that blooms offshore of the Oregon coast were observed in February–March in every year sampled during the GLOBEC study (1998–2003). During week-long periods of clear weather that occur at ~monthly time scales from February through March, surface layers receive sufficient light to trigger phytoplankton growth, and, at times, blooms. Blooms occur well before the transition to the summer upwelling season when deep nutrient-rich water upwells to the surface to fuel blooms. Nitrate and other macronutrients in winter and spring are adequately supplied (e.g., nitrate, ~5–10 μg), by riverine input from the Columbia River (Landry et al., 1989) and also from the numerous smaller rivers along the coasts of both Oregon and Washington (Wetz et al., 2006). Iron is plentiful in these sources (Bruland et al., 2008). Stratification is also high due to the freshwater input, increasing the likelihood of dense plankton blooms.

Such springtime blooms usually contain toxigenic PN species, a common member of the local ecosystem (Frame and Lessard, 2009) and the multi-decadal time series of DA in razor clams presented herein illustrates that such blooms can become toxic. Off the Oregon coast, phytoplankton densities are generally highest over the region known as Heceta Bank (e.g., Fig. 2; also see Venegas et al., 2008) and a whole-coast survey of pDA demonstrated that this semi-retentive area was the one region of Oregon where cells were toxic (Fig. 1). In this paper we provide details of a toxic phytoplankton bloom off the Washington coast in April 2005, illustrating that the most likely source of cells observed on
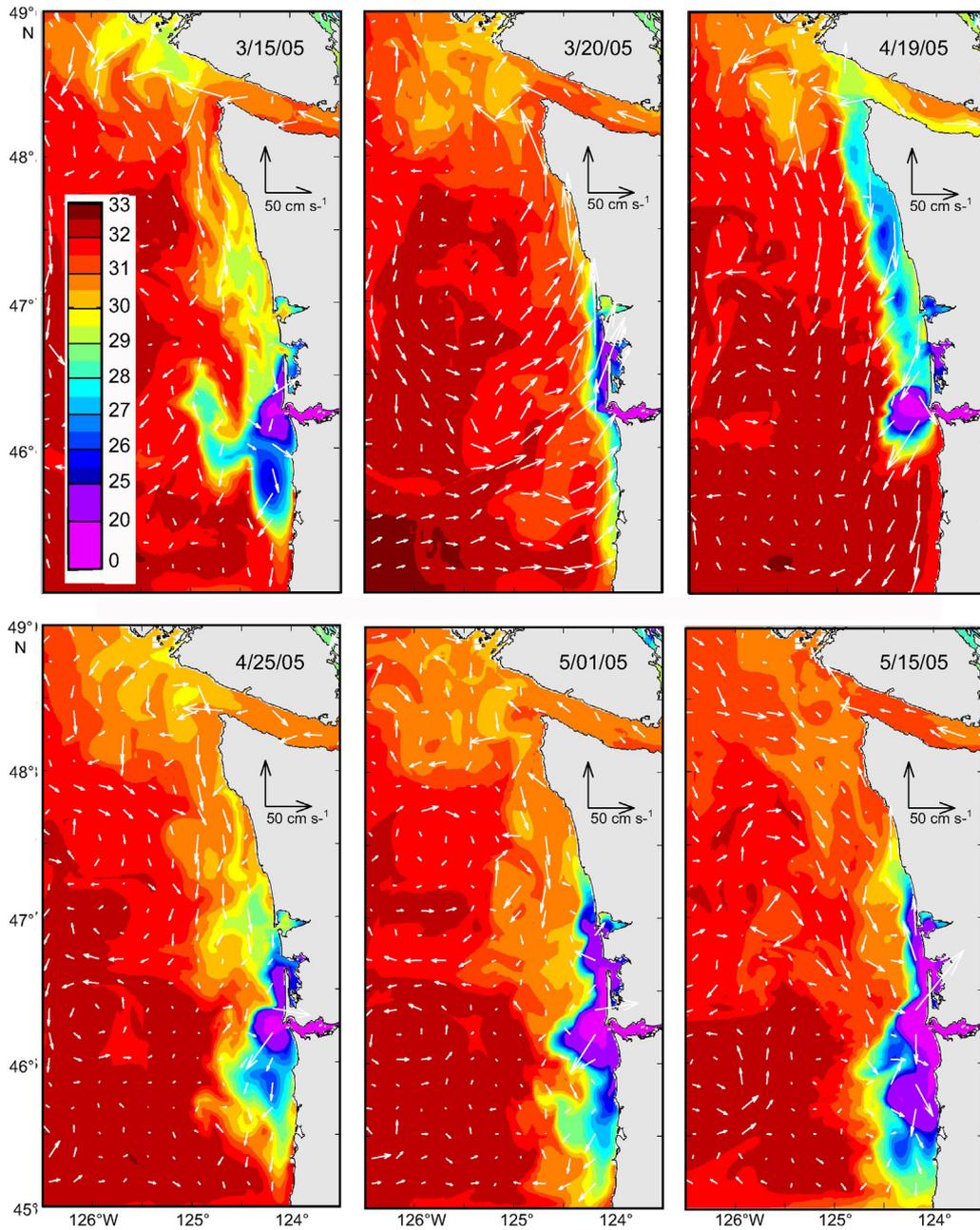
Fig. 8. Plan view maps of daily-averaged surface salinity from a numerical model of the Columbia plume and coastal waters for selected dates in 2005 (model data, MacCready Pers. Comm.; see details in Sutherland et al., 2011). Surface velocity vectors (linearly interpolated to an evenly spaced 15 km grid) are also shown.

southwest Washington beaches was from the vicinity of Heceta Bank, some 200 km south of the affected beaches. In support of this hypothesis, satellite-derived chlorophyll data showed a bloom concentrated over Heceta Bank just 2–3 weeks prior to the increase in toxic *PN* cell numbers and the increase in razor clam toxicity documented off the southern Washington coast. Transport measurements as well as numerical model results illustrate that northward displacement in a single storm can be more than sufficient to move water and accompanying phytoplankton northward from the vicinity of Heceta Bank to the southern Washington coast. If the phytoplankton assemblage includes toxigenic *PN*, they will be ingested together with other associated phytoplankton by razor clams on Washington beaches. Thus phytoplankton that originate near Heceta Bank are likely transported to the southern Washington coast during these spring downwelling-favorable periods; and any plankton that resided off

the Washington coast at the onset of the storm are transported many tens of kilometers northward, into the Strait of Juan de Fuca or along the Vancouver Island coast, with negligible impact on the coastal beaches.

Toxin in razor clams increased on northern (first), and central (a week later) Oregon beaches following the April DA event on the Washington beaches. The transport maps demonstrate that water from the Heceta Bank region moved shoreward and northward over both the Oregon and Washington shelves during the storm of 25–28 March 2005. Toxic cells off Oregon were thus transported northward for several days, mixing into water from the Columbia River plume along the transport route and causing the pDA and cell number increase on the southern Washington beaches beginning about 10 April. However when upwelling-favorable winds subsequently returned around 20 April, transport (as seen in model results) reversed to southward so that the toxic cells likely
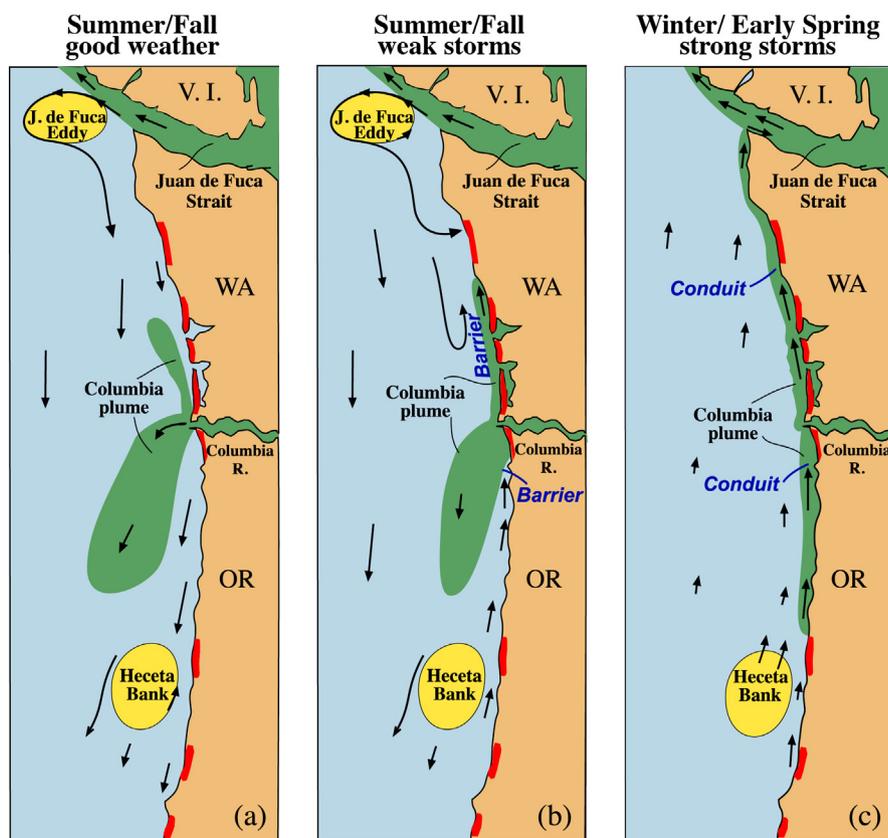
Fig. 9. Conceptual framework for environmental conditions that transport toxic *PN* cells southward from northern (the Juan de Fuca eddy) and southern (Heceta Bank) sources (shown in yellow) in summer/fall in the Pacific Northwest under (a) prevailing upwelling-favorable winds; (b) during a reversal to weak downwelling-favorable winds; and (c) in late winter/spring, prior to the spring transition. Surface currents are shown with arrows. Clamming beaches are shown in red. Green indicates freshwater plumes from the Columbia River and from the Strait of Juan de Fuca. Notations "Barrier" and "Conduit" refer to the role of the Columbia plume (see text for details).

returned to the Oregon shelf, causing the increasing toxicity in razor clams and cell numbers on central and northern Oregon beaches.

Whether phytoplankton can escape from a retentive region, can be transported along a shelf in a relatively intact patch, and whether/how they also can maintain their toxicity during transit is not presently well known. In the Juan de Fuca region tendrils of higher chlorophyll concentrations have been observed "leaking" from the Juan de Fuca eddy region (Trainer et al., 2009a). High values of pDA and per cell toxicity have been observed in the eddy region, and, several days later, on the Washington outer shelf in the filament region (Baugh et al., 2006). The issue is far from trivial—nutrient supply and other environmental conditions can be significantly different between the source region and the region through which the cells are being transported. For example, nitrate at the sea surface is usually over 20 μm near the Juan de Fuca eddy, but is frequently near zero on the outer shelf south of the eddy, due to assimilation by phytoplankton (Fig. 14 in MacFadyen et al., 2008). Maintenance of toxicity outside the Juan de Fuca eddy initiation site was addressed specifically by a study in September 2004, in which three surface drifters deployed in regions where cells were known to be highly toxic were followed for periods up to two weeks (Lessard et al., in preparation). The data illustrate that high concentrations of pDA (>15 nM) were maintained over periods exceeding the two weeks that the drifters were tracked, both within the source region and outside the source region during transit southward along the coast. No such data are available to directly test maintenance of toxicity during transit for the Oregon coastal region.

It is impossible to distinguish a source of water originating from Heceta Bank from a source nearshore on the inner Oregon shelf with the transport models and data presently available. If toxic cells were located in the upwelling zone nearshore prior to a storm, they would be transported toward the coast and northward, and, if a plume from the Columbia was present offshore at the onset of a storm, those cells could be entrained into plume waters as they move onshore and northward during the storm. Their arrival at the Washington coast might even precede the arrival of cells that originated on the offshore bank. However, detailed studies of the preferred location of toxic *PN* cells in both active upwelling, plume and Juan de Fuca eddy waters on the Washington coast on six separate cruises illustrated that toxic cells were never found in active upwelling zones (Trainer et al., 2009a). The preponderance of evidence—documented higher phytoplankton densities and the idea that development of toxin is favored in retentive areas—suggests that Heceta Bank is more likely to be source of toxic cells transported from Oregon to Washington than the nearshore Oregon region.

Prior research has hypothesized that in summer and fall seasons, strong alongcoast-oriented density fronts associated with the plume from the Columbia River may prevent toxic cells from reaching coastal beaches by providing a barrier to onshore transport (see cartoon panels Fig. 9b) (Hickey and Banas, 2003; Banas et al., 2009). Indeed, data collected on the Washington shelf during six summer and fall surveys found pDA in Columbia-influenced water on only one occasion, which occurred one day after a storm (Trainer et al., 2009a). In the present data, however, all the toxic *PN* cells offshore of the Washington coast in April 2005

resided in Columbia plume-affected coastal waters. Thus it is appropriate to ask under what conditions the Columbia plume is a "barrier" and under what conditions it is more likely to be a "conduit" to transport of a toxic bloom.

In summer/fall, when the primary plume from the Columbia lies to the southwest and the source of toxic cells lies well offshore of any nearshore plume waters on the Washington coast (Fig. 9a), the plume likely functions primarily as a barrier during downwelling wind events (Fig. 9b). However, Adams et al. (2006) found toxic *PN* cells in Columbia plume water on the southern Washington shelf in fall following a series of storms, suggesting that the duration and frequency of storms also plays a role in determining whether or not cells become entrained in plume water, even during the fall season. When winds transition from upwelling to downwelling-favorable, cells originating from the northern source are rapidly transported onshore and may impact northern beaches prior to the arrival of the new branch of the Columbia plume that is generated by the downwelling conditions (Fig. 9b). Mixing into plume waters across the frontal boundaries is minimized by the fact that the coastally trapped plume itself is usually highly stratified and the winds are relatively weak in summer/earlyfall (Hickey et al., 2005, 2010). Thus southern Washington beaches are likely afforded some protection from the HAB event, consistent with the observations that razor clams on those beaches are usually less toxic than those on northern beaches (e.g., 1998, Fig. 3) or are not toxic at all when northern beaches are impacted (e.g., 1995, Fig. 3). During wind reversals by summer storms, cells originating on Heceta Bank may also be transported shoreward and northward on the inner shelf by the wind-generated currents; however in this case, the Columbia River likely forms a barrier between regions offshore and Washington coast beaches (Fig. 9b).

In early spring, as illustrated by the example in April 2005, on the other hand, the plume is likely present nearshore along the entire Pacific Northwest coast during downwelling winds (Fig. 9c) due to the frequency of storms during this season. Cells are likely transported onshore and mixed into plume waters by the relatively large winds that occur during this period. In this case, the plume becomes a conduit for northward transport, enhancing the speed of cell transport toward the Washington coast by as much as a factor of two (Hickey et al., 1998) (Fig. 9c). If upwelling-favorable winds are sufficiently persistent during spring and outflow from the Columbia is sufficiently large, the plume may extend well past Heceta Bank; but this plume would be located *offshore* of the bank. In this case, the onset of a storm would move cells from Heceta Bank onshore and into the northward wind-driven jet prior to the arrival of the plume itself from its offshore location. The cells would likely encounter the plume at some location farther north along the coast. Whether the cells would be entrained into the plume by the intense mixing that occurs near the river mouth (Nash et al., 2009) or be repelled by the plume frontal barrier would depend on the relative strength of the winds and the stratification at that time.

Domoic acid in razor clams only exceeded regulatory limits twice during spring in the 19-year record shown. We may ask "How frequently is Heceta Bank a source of cells for the Washington coast?" The year 2005 was anomalous in that the "transition" from winter to late spring upwelling conditions was late that year in the Pacific Northwest (Kosro et al., 2006). The transition occurred 24 May, ~one month later than is typical (Kosro et al., 2006). Thus the period during which regional currents were weak or even northward was much longer than would typically be the case. The second springtime event in which razor clam toxicity reached the regulatory limit (Fig. 3) took place 20 February–5 March 2001. In that year the spring transition occurred on 10 March, a month *earlier* than usual (Yamada and Kosro, 2010).

As in 2005, the increase in toxic *PN* cells and toxin in the razor clams occurred simultaneously on Washington southern beaches, and primarily on those beaches. A phytoplankton bloom on Heceta Bank documented in satellite data (not shown) occurred 6–15 February during a prolonged period of upwelling-favorable winds (not shown). Northward transport, documented with measured currents, followed the February bloom and occurred prior to the arrival of toxic cells on the southern Washington beaches. Because blooms on Heceta Bank have been observed in late winter/spring in most years, and because storms occur every 2–5 days during the spring period, it seems prudent to conclude that Heceta Bank could be a source of toxic cells in any year, especially prior to the spring transition. The risk of a spring toxic event on the Washington coast would increase the later the spring transition in that year.

In summary, the research presented herein emphasizes the role of HAB "hot spots" that occur in upwelling regions with a tendency for retention times of several days to weeks, and the ability to produce high density phytoplankton "blooms". Longer retention times are generally associated with complex topographies such as banks or headlands—in the present case we focus on Heceta Bank, Oregon and the Juan de Fuca eddy (overlying Swiftsure Bank), Washington/British Columbia. We show that the search for potential "hot spots" for toxic blooms must take into account seasonal changes in the direction of prevailing currents. In upwelling systems changes in current patterns generally differ between the upwelling and downwelling seasons, with a transition between the two states in spring and fall. Results presented here also suggest the importance of buoyant plumes in the upwelling regions: such plumes may at times function as barriers, at other times, as conduits for toxic cells. The presence and variability of the plume from the Columbia River may be an important factor in addressing why toxic blooms rarely arrive on Washington beaches, in comparison to the documented presence of toxic blooms in offshore waters. Details on the specific role of the Columbia and other plumes on HAB transport under a variety of conditions are the subject of ongoing research.

References

Adams, N.G., MacFadyen, A., Hickey, B.M., Trainer, V.L., 2006. The nearshore advection of a toxigenic *Pseudo-nitzschia* bloom and subsequent domoic acid contamination of intertidal bivalves. African Journal of Marine Science 28 (2), 271–276.

Austin, J.A., Barth, J.A., 2002. Drifter behavior on the Oregon–Washington shelf during downwelling-favorable winds. Journal of Physical Oceanography 32, 3132–3144.

Banas, N.S., MacCready, P., Hickey, B.M., 2009. The Columbia River plume as cross-shelf exporter and along-coast barrier. Continental Shelf Research 29 (1), 292–301, http://dx.doi.org/10.1016/j.csr.2008.03.011.

Barth, J.A., Pierce, S.D., Casteleo, R.M., 2005. Time-dependent, wind-driven flow over a shallow midshelf submarine bank. Journal of Geophysical Research 110, C10S05, http://dx.doi.org/10.1029/2004JC002761.

Bates, S.S., Defreitas, A.S.W., Milley, J.E., Pocklington, R., Quilliam, M.A., Smith, J.C., Worms, J., 1991. Controls on domoic acid production by the diatom *Nitzschia pungens f. multiseries* in culture: nutrients and irradiance. Canadian Journal of Fisheries and Aquatic Sciences 41, 1136–1144.

Baugh, K.A., Bush, J.M., Bill, B.D., Lefebvre, K.A., Trainer, V.L., 2006. Estimates of specific toxicity in several *Pseudo-nitzschia* species from the Washington coast, based on culture and field studies. African Journal of Marine Science 28 (2), 403–407.

Bill, B.D., Cox, F.H., Horner, R.A., Borchert, J.A., Trainer, V.L., 2006. The first closure of shellfish harvesting owing to domoic acid in Puget Sound, Washington, USA. African Journal of Marine Science 28 (2), 435–440.

Bruland, K.W., Lohan, M.C., Aguilar-Islas, A.M., Smith, G.J., Sohst, B., Baptista, A., 2008. Factors influencing the chemistry of the near-field Columbia River plume: nitrate, silicic acid, and dissolved Mn. Journal of Geophysical Research 113, C00B02, http://dx.doi.org/10.1029/2007JC004702.

Foreman, M.G.G., Callendar, W., MacFadyen, A., Hickey, B.M., Thomson, R.E., Di Lorenzo, E., 2008. Modeling the generation of the Juan de Fuca eddy. Journal of Geophysical Research 113, C03006, http://dx.doi.org/10.1029/2006JC004082.

Freeland, H.J., Denman, K.L., 1982. A topographically controlled upwelling center off southern Vancouver Island. Journal of Marine Research 40 (4), 1069–1093.

Frame, E.R., Lessard, E.J., 2009. Does the Columbia River Plume influence phytoplankton community structure along the Washington and Oregon coasts? Journal of Geophysical Research 114, C00B09, http://dx.doi.org/10.1029/2008JC004999.

Gan, J., Allen, J.S., 2005. Modeling upwelling circulation off the Oregon coast. Journal of Geophysical Research 110, C10S07, http://dx.doi.org/10.1029/2004JC002692.

Hatfield, C.L., Wekell Jr., J.C., Gauglitz, E.J., Barnett, H.J., 1994. Salt clean-up procedure for the determination of domoic acid by HPLC. Natural Toxins 2, 206–211.

Hickey, B.M., 1979. The California current system—hypotheses and facts. Progress in Oceanography 8, 191–279.

Hickey, B.M., 1981. Alongshore coherence on the Pacific Northwest continental shelf (January–April, 1975). Journal of Physical Oceanography 11, 822–835.

Hickey, B.M., 1989. Patterns and processes of circulation over the shelf and slope. In: Landry, M.R., Hickey, B.M. (Eds.), Coastal Oceanography of Washington and Oregon. Elsevier Science Publishers B.V., Amsterdam, pp. 41–115.

Hickey, B.M., 1998. Coastal oceanography of Western North America from the tip of Baja California to Vancouver Island. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea: Ideas and Observations on Progress in the Study of the Seas, vol. 11 Wiley and Sons, Inc, NY, NY, pp. 345–393 (chapter 12).

Hickey, B.M., Banas, N.S., 2003. Oceanography of the Pacific Northwest coastal ocean and estuaries with application to coastal ecosystems. Estuaries 26, 1010–1031.

Hickey, B.M., Thomson, R.E., Yih, H., LeBlond, P.H., 1991. Velocity and temperature fluctuations in a buoyancy-driven current off Vancouver Island. Journal of Geophysical Research 96 (C6), 10507–10538.

Hickey, B.M., Pietrafesa, L.J., Jay, D.A., Boicourt, W.C., 1998. The Columbia River plume study: subtidal variability in the velocity and salinity fields. Journal of Geophysical Research 103, 10339–10368.

Hickey, B.M., Geier, S., Kachel, N., MacFadyen, A., 2005. A bi-directional river plume: the Columbia in summer. Continental Shelf Research 25, 1631–1656.

Hickey, B.M., MacFadyen, A., Cochlan, W.P., Kudela, R.M., Bruland, K.W., Trick, C.G., 2006. Evolution of biological, chemical and physical water properties in the Pacific Northwest in 2005: remote or local wind forcing? Geophysical Research Letters 33, L22S02.

Hickey, B., McCabe, R., Geier, S., Dever, E., Kachel, N., 2009. Three interacting freshwater plumes in the Northern California Current System. Journal of Geophysical Research 114, C00B03, http://dx.doi.org/10.1029/2008JC004907.

Hickey, B.M., Kudela, R.M., Nash, J.D., Bruland, K.W., Peterson, W.T., MacCready, P., Lessard, E.J., Jay, D.A., Banas, N.S., Baptista, A.M., Dever, E.P., Kosro, P.M., Kilcher, L.F., Horner-Devine, A.R., Zaron, E.D., McCabe, R.M., Peterson, J.O., Orton, P.M.,

Pan, J., Lohan, M.C., 2010. River influences on shelf ecosystems: introduction and synthesis. Journal of Geophysical Research 115, C00B17, http://dx.doi.org/10.1029/2009JC005452.

Huyer, A., 1983. Upwelling in the California Current System. Progress in Oceanography 12, 259–284.

Huyer, A., Sobey, E.J.C., Smith, R.L., 1979. The spring transition in currents over the Oregon continental shelf. Journal of Geophysical Research 84 (C11), 6995–7011.

Huyer, A., Wheeler, P., Strub, P.T., Smith, R.L., Letelier, R.M., Kosro, P.M., 2007. The Newport line off Oregon–Studies in the North East Pacific. Progress in Oceanography 75 (2), 126–160, http://dx.doi.org/10.1016/j.pocean.2007.08.003.

Kirincich, A.R., Barth, J.A., 2009. Alongshelf variability of inner-shelf circulation along the central Oregon coast during summer. Journal of Physical Oceanography 39, 1380–1398.

Kosro, P.M., 2002. A poleward jet and an equatorward undercurrent observed off Oregon and northern California, during the 1997–98 El Niño. Progress in Oceanography 54 (1–4), 343–360.

Kosro, P.M., 2003. Enhanced southward flow over the Oregon shelf in 2002: a conduit for subarctic water. Geophysical Research Letters 30 (15), 8023, http://dx.doi.org/10.1029/2003gl017436.

Kosro, P.M., 2005. On the spatial structure of coastal circulation off Newport, Oregon, during spring and summer 2001 in a region of varying shelf width. Journal of Geophysical Research 110 (C10), 16, http://dx.doi.org/10.1029/2004jc002769.

Kosro, P.M., Peterson, W.T., Hickey, B.M., Shearman, R.K., Price, S.D., 2006. Physical versus biological spring transition: 2005. Geophysical Research Letters 33, L22S03, http://dx.doi.org/10.1029/2006GL027072.

Landry, M.R., Postel, J.R., Peterson, W.K., Newman, J., 1989. Broad-scale patterns in the distribution of hydrographic variables. In: Landry, M.R., Hickey, B.M. (Eds.), Coastal Oceanography of Washington and Oregon. Elsevier Science Publishers B.V., Amsterdam, pp. 1–40.

Lentz, S.J., 2001. The influence of stratification on the wind-driven cross-shelf circulation over the North Carolina shelf. Journal of Physical Oceanography 31, 2749–2760.

Lessard, E.J., Hickey, B.M., Trainer, V.L., Olson, M.B., MacFadyen, A., Foy, J.S., Schatz, M., Cochlan, W.P., Trick, C.G., Wells, M.L., Evolution of an extensive toxic *Pseudo-nitzschia cuspidata* and Eutreptiella cf. gymnastica bloom originating in the Juan de Fuca Eddy: a Lagrangian study. Limnology and Oceanography, in preparation.

Liu, Y., MacCready, P., Hickey, B.M., 2009a. Columbia River plume patterns in summer 2004 as revealed by a hindcast coastal ocean circulation model. Geophysical Research Letters 36, L02601, http://dx.doi.org/10.1029/2008GL036447.

Liu, Y., MacCready, P., Hickey, B.M., Dever, E.P., Kosro, P.M., Banas, N.S., 2009b. Evaluation of a coastal ocean circulation model for the Columbia River plume in summer 2004. Journal of Geophysical Research 114, C00B04, http://dx.doi.org/10.1029/2008JC004929.

MacCready, P., Banas, N.S., Hickey, B.M., Dever, E.P., Liu, Y., 2009. A model study of tide- and wind-Induced mixing in the Columbia River estuary and plume. Continental Shelf Research 29 (1), 278–291, http://dx.doi.org/10.1016/j.csr.2008.03.015.

MacFadyen, A., Hickey, B.M., 2010. Generation and evolution of a topographically linked, mesoscale eddy under steady and variable wind-forcing. Continental Shelf Research 30, 1387–1402, http://dx.doi.org/10.1016/j.csr.2010.04.001.

MacFadyen, A., Hickey, B.M., Foreman, M.G.G., 2005. Transport of surface waters from the Juan de Fuca eddy region to the Washington coast. Continental Shelf Research 25, 2008–2021.

MacFadyen, A., Hickey, B.M., Cochlan, W.P., 2008. Influences of the Juan de Fuca Eddy on circulation, nutrients and phytoplankton production in the northern California Current System. Journal of Geophysical Research 113, C08008, http://dx.doi.org/10.1029/2007JC004412.

Maldonado, M.T., Hughes, M., Rue, E., Wells, M.L., 2002. The effect of Fe and Cu on the growth and domoic acid production of *Pseudo-nitzschia multiseries* and *Pseudo-nitzschia australis*. Limnology and Oceanography 47, 515–526.

Marchetti, A., Trainer, V.L., Harrison, P.J., 2004. Environmental conditions and phytoplankton dynamics associated with *Pseudo-nitzschia* abundance and domoic acid in the Juan de Fuca eddy. Marine Ecology: Progress Series 281, 1–12.

Miller, P.E., Scholin, C.A., 1998. Identification and enumeration of cultured and wild *Pseudo-nitzschia* (Bacillariophyceae) using species-specific LSU rRNA-targeted fluorescent probes and filter-based whole cell hybridization. Journal of Phycology 34, 371–382.

Nash, J.D., Kilcher, L.F., Moum, J.N., 2009. Structure and composition of a strongly stratified, tidally pulsed river plume. Journal of Geophysical Research 114, C00B12, http://dx.doi.org/10.1029/2008JC005036.

Olson, M.B., Lessard, E.J., Wong, C.H.J., Bernhardt, M.J., 2006. Copepod feeding selectivity on microplankton, including the toxigenic diatoms *Pseudo-nitzschia* spp., in the coastal Pacific Northwest. Marine Ecology Progress Series 326, 207–220.

Olson, M.B., Lessard, E.J., Cochlan, W.P., Trainer, V.L., 2008. Intrinsic growth and microzooplankton grazing on toxigenic *Pseudo-nitzschia* spp. diatoms from the coastal Northeast Pacific. Limnology and Oceanography 53, 1352–1368.

Pan, Y., Rao, D.V.S., Mann, K.H., 1996. Changes in domoic acid production and cellular chemical composition of the toxigenic diatom *Pseudo nitzschia multiseries* under phosphate limitation. Journal of Phycology 32, 371–381.

Reid, J.L., Mantyla, A.W., 1976. The effect of the geostrophic flow upon coastal sea elevation in the northern North Pacific Ocean. Journal of Geophysical Research 81, 3100–3110.

Round, F.E., Crawford, R.M., Mann, D.G., 1990. The Diatoms: Biology and Morphology of the Genera. Cambridge University Press, Cambridge 747 pp.

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

Simonsen, R., 1974. The diatom plankton of the Indian Ocean expedition of R/V Meteor 1964–5. Meteor Forschungsergebnisse. Reihe D: Biologie D 19, 1–107.

Spitz, Y.H., Allen, J.S., Gan, J., 2005. Modeling of ecosystem processes on the Oregon shelf during the 2001 summer upwelling. Journal of Geophysical Research 110, C10S17, http://dx.doi.org/10.1029/2005JC002870.

Stehr, C.M., Connell, L., Baugh, K.A., Bill, B.D., Adams, N.G., Trainer, V.L., 2002. Morphological, toxicological, and genetic differences among *Pseudo-nitzschia* (Bacillariophyceae) species in inland embayments and outer coastal waters of Washington State, USA. Journal of Phycology 38, 55–65.

Strub, P.T., James, C., 1988. Atmospheric conditions during the spring and fall transitions in the coastal ocean off western United States. Journal of Geophysical Research 93 (C12), 15561–15584.

Sutherland, D.A., MacCready, P.M., Banas, N.S., Smedstad, L.F., 2011. A model study of the Salish Sea estuarine circulation. Journal of Physical Oceanography 41, 1125–1143, http://dx.doi.org/10.1175/2011JPO4540.1.

Trainer, V.L., Suddleson, M., 2005. Monitoring approaches for early warning of domoic acid events in Washington State. Oceanography 18 (2), 228–237.

Trainer, V.L., Adams, N.G., Bill, B.D., Stehr, C.M., Wekell, J.C., Moeller, P., Busman, M., Woodruff, D., 2000. Domoic acid production near California upwelling zones, June 1998. Limnology and Oceanography 45 (8), 401–440.

Trainer, V.L., Adams, N.G., Wekell, J.C., 2001. Domoic acid-producing *Pseudo-nitzschia* species off the U.S. west coast associated with toxification events.

In: Hallegraeff, G.M., Blackburn, S.I., Bolch, C.J., Lewis, R.J. (Eds.), Proceedings of the Ninth International Conference on Harmful Algal Blooms. Intergovernmental Oceanographic Commission, UNESCO, pp. 46–48.

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

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

Trainer, V.L., Wells, M.L., Cochlan, W.P., Trick, C.G., Bill, B.D., Baugh, K.A., Beall, B.F., Herndon, J., Lundholm, N., 2009b. An ecological study of a massive toxigenic bloom of *Pseudo-nitzschia cuspidata* off the Washington State coast. Limnology and Oceanography 54 (5), 1461–1474.

Venegas, R.M., Strub, P.T., Beier, E., Letelier, R., Thomas, A.C., 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. Journal of Geophysical Research 113, C03015, http://dx.doi.org/10.1029/2007JC004481.

Wells, M.L., Trick, C.A., Cochlan, W.P., Hughes, M.P., Trainer, V.L., 2005. Domoic acid: the synergy of iron, copper, and the toxicity of diatoms. Limnology and Oceanography 50 (6), 1908–1917.

Wetz, M.S., Hales, B., Chase, Z., Wheeler, P.A., Whitney, M.M., 2006. Riverine input of macronutrients, iron, and organic matter to the coastal ocean off Oregon, U.S.A., during the winter. Limnology and Oceanography 51 (5), 2221–2231.

Yamada, S.B., Kosro, P.M., 2010. Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas*. Biological Invasions 12 (6), 1791–1804, http://dx.doi.org/10.1007/s10530-009-9589-y.