

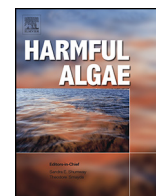


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# Large-scale bloom of *Akashiwo sanguinea* in the Northern California current system in 2009



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## ABSTRACT

Significant seabird mortality on the Oregon (OR) and Washington (WA) coast in 2009 has been attributed to a massive bloom of the dinoflagellate *Akashiwo sanguinea* (K. Hirasaka) G. Hansen & Ø. Moestrup. Initial, albeit limited, observations suggested this bloom began in WA and reached OR waters through southward transport. Here, we explore a combination of remote sensing products and an exceptional latitudinal dataset of plankton counts collected in the surfzone and offshore in OR and WA coastal waters. Records of satellite ocean color for this period support the new finding that blooms were concurrent in OR and WA waters, with no evidence for latitudinal propagation as had been previously suggested. Plankton analyses further indicate that there was a rapid and synchronized increase of *A. sanguinea* between late August and mid-September of 2009 along wide swaths of the OR and WA coasts. Bloom onset occurred during a prolonged quiescent and warm period in late August–early September, near the end of the March–October upwelling phase. An upwelling event in October likely contributed to foam production through vertical mixing of *A. sanguinea* rich waters. Bloom intensity peaked earlier and at higher levels in WA waters as compared to OR with cell concentrations exceeding  $1.5 \times 10^6$  cells  $L^{-1}$  (WA) and  $\sim 350,000$  cells  $L^{-1}$  (OR). In OR samples, *A. sanguinea* cells comprised upwards of 90% of dinoflagellate cell counts and  $\sim 30\%$  of total phytoplankton cells. At some locations, *A. sanguinea* persisted well into November–December of 2009, during which time satellite sea surface temperature records indicated anomalously warm surface waters (up to  $\sim 5^\circ C$  greater than climatological means). Taken together, the data reveal a HAB event of a magnitude unprecedented in over a decade of observations. We hypothesize that these blooms originated from either a cryptic cyst bed and/or a pelagic seed bank of viable vegetative cells.

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## 1. Introduction

The productive waters off the U.S. Pacific Northwest (PNW) coast are representative of a classic Eastern boundary current system: the region is characterized by strong, seasonal upwelling, rich biological productivity, rapid biogeochemical cycling and high perceived rates of carbon export to the open ocean and underlying

sediments (Barth and Wheeler, 2005; Hales et al., 2006). In this northern stretch of the California Current, winds predominantly blow equatorward alongshore from May to September, drawing dense, nutrient-rich, offshore subsurface waters shoreward and upward into the coastal euphotic zone. These intermittent upwelling events stimulate phytoplankton blooms that draw down surface water  $CO_2$  levels and ultimately sustain and fuel upper trophic levels (Chase et al., 2007; Hales et al., 2006; Kudela et al., 2008; Landry and Hickey, 1989). In contrast, from October to March, conditions in the PNW are predominantly downwelling favorable: the water column is well-stratified, the standing stock of primary producers is low (surface chlorophyll  $\leq 1 \mu g L^{-1}$ ), and

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productivity is presumed to be light or nutrient limited (Hales et al., 2006; Kudela and Peterson, 2009; Wetz et al., 2004). Clear shifts in phytoplankton community composition are observed over this seasonal progression: diatoms are favored during nutrient-rich upwelling phases, whereas the relative abundance of dinoflagellates increase in the nutrient-deplete and stratified summer periods and during the relaxation phases that interrupt upwelling events (Smayda and Trainer, 2010). These successional patterns are neither regular nor smooth; upwelling is of varying intensity and magnitude as are the duration of relaxation events. As a consequence, the relative composition of phytoplankton communities favored by these contrasting conditions (e.g. colder, nutrient-rich, and well-mixed versus warmer, nutrient-poor, and more stratified) can vary widely at sub-seasonal, seasonal and inter-annual scales.

Large scale shifts in climatic forcing can also impact phytoplankton community composition in upwelling regimes, at times in ways that favor harmful algal blooms (Hallegraeff, 1993; Smayda, 2000). In the California Current system in particular, unprecedented blooms of dinoflagellates have been observed in the last decade. Plankton sampling is inherently discontinuous and therefore limited in space and time, nonetheless these blooms have tentatively been linked to climate anomalies. Dinoflagellates commonly found in these coastal upwelling regions include toxigenic, cyst-forming species such as *Alexandrium catenella* as well as non-toxic species such as *Akashiwo sanguinea* (K. Hirasaka) G. Hansen & Ø. Moestrup (Kudela et al., 2005; Smayda, 2002; Trainer et al., 2010). In Monterey Bay, California, in situ data collected between 2000 and 2006 suggests that phytoplankton community structure shifted from a regime dominated by diatoms to one dominated by two genera of toxic dinoflagellates: *Alexandrium* and *Dinophysis* (Jester et al., 2009). Expanding on these data, Kudela et al. (2010a,b, 2011) report a strong correlation between dinoflagellate abundance and decadal climate indices favoring water column stratification, shallowing mixed layers, and weak upwelling.

Aperiodic climate anomalies have also led to blooms of what Smayda and Trainer (2010) call 'irregularly bloom-forming dinoflagellates', i.e. those organisms that aperiodically appear to dominate phytoplankton community structure. Specifically, blooms of *Akashiwo sanguinea* have been reported in the relatively well-monitored regions of the Pacific Northwest and the California coast (Cloern et al., 2005, 2007; Du et al., 2011; Jessup et al., 2009). In 2004, a large *A. sanguinea* bloom was observed in San Francisco Bay and attributed to an upper-atmosphere high-pressure anomaly following a summer of weak coastal upwelling; this species had not been detected at such levels in nearly three decades of observation in the region (Cloern et al., 2005). *A. sanguinea* cells are large (40–75 µm long), highly motile, and capable of vertical migration. The species is tolerant to a wide range of temperatures and salinities and characterized by relatively high growth rates (maximum growth rate of 1.13 divisions day<sup>-1</sup>) (Burkholder et al., 2008; Kudela et al., 2010a,b; Matsubara et al., 2007; Smayda, 2000; Tomas, 1997). While not directly toxic, this organism is detrimental to seabirds and other animals (Botes et al., 2003; Jessup et al., 2009; Nightingale, 1936).

In November of 2007 in Monterey Bay, discolored (yellow-green) sea foam concentrated on the coastal shorelines was linked to strong physical mixing following an *Akashiwo sanguinea* bloom. When analyzed via spectrometry this proteinaceous foam demonstrated mycosporine-like amino acids (MAA) absorption features (Jessup et al., 2009). Seabirds coated in this foam were found to be severely hypothermic. *A. sanguinea* blooms and sea foam have been described elsewhere in the region (e.g. San Francisco Bay, inlets of the Juan de Fuca Strait and more recently off Newport, Oregon (Cardwell et al., 1979; Cloern et al., 2005; Du et al., 2011; Voltolina,

1993)), but Jessup et al. (2009) was the first study to causally link *A. sanguinea*, foam production and seabird mortality. *A. sanguinea* (also known as *Gymnodinium splendens*, Lebour or *Gymnodinium sanguineum*, K. Hirasaka) have also been documented as harmful to abalone larvae and spat (Botes et al., 2003), Pacific oysters (*Ostrea lurida* and *Crassostrea gigas*) and manila littleneck clams (Cardwell et al., 1979; Nightingale, 1936; Woelke, 1961), possibly through surfactant production albeit the exact mechanism has not been documented.

In October–November of 2009, for the first time since 2001 when regular phytoplankton monitoring began in Oregon's (OR) coastal waters, a large bloom of *Akashiwo sanguinea* was detected (Du et al., 2011). High levels of *A. sanguinea* were also observed in Washington (WA) coastal waters in September 2009 (unpublished data, <http://www.pacoos.org/QuarterlyClimaticEcol.html>). As in the Monterey Bay event, this bloom was linked to widespread mortality of seabirds (Phillips et al., 2011). The first reports of seabird deaths were noted in mid-September, with nearly a thousand birds washing up on beaches in WA (Julia Parrish, personal communication). In early October, dead birds began to wash ashore on OR beaches (Sharnelle Fee, Director of the Wildlife Center of the North Coast, personal communication). Over 700 birds noted as 'weak, stressed, and starving' were collected from OR beaches; Red-throated Loons, Western Grebes and Common Murres represented the greatest proportion of the dead (Phillips et al., 2011). Many of these birds were in a primary molt stage during which time they are essentially flightless and have only basic or winter plumage; at this stage they are more susceptible to oiling events (Phillips et al., 2011).

The report of Du et al. (2011) was limited to data collected off the central OR coast along the Newport, OR Hydrographic Line (44.6° N) between August 27th and December 1st, 2009. Given that unpublished reports for WA (at ~47° N) reported a maximum of *Akashiwo sanguinea* cells in September and that the bloom did not peak off Newport, OR until October, Du et al. (2011) hypothesized that this bloom had originated off of WA and propagated southward. Since this early report a research project funded by the National Oceanic and Atmospheric Administration, MOCHA (Monitoring Oregon Coastal Harmful Algae), has compiled a much more extensive dataset of phytoplankton community composition for 2009. This dataset includes two large transect cruises spanning WA-OR coastal waters in August–September of 2009, regular monthly monitoring of nearshore and surfzone locations, and analyses of remote sensing products and data from regional partners in the Olympic Region Harmful Algal Bloom (ORHAB) monitoring program. Here, we evaluate this broad data set to more thoroughly describe the onset, duration and demise of a bloom of *A. sanguinea* spanning the WA and OR coastal margins. Cell count data are combined with upwelling indices, regional climate metrics, and satellite imagery to determine whether the bloom off OR was part of a synchronous coast-wide event, or showed timing and connectivity more consistent with the hypothesis that the bloom began off of WA and was transported south into OR waters. Better understanding of these bloom origins and dynamics should help regional monitoring agencies evaluate the potential threat posed by *A. sanguinea*.

## 2. Materials and methods

### 2.1. Coastal and surfzone sampling

Water samples for quantitative and qualitative analysis of *Akashiwo sanguinea* and the overall diatom and dinoflagellate community were collected in the surf zone and at offshore stations along the OR and WA coasts (spanning 38.25–48.33° N) during 2009. Offshore samples were collected during two

coastwide (WA to OR) cruises in August and September. Additional samples were collected in OR waters at 6 hydrographic lines (encompassing 28 stations, roughly 44.2° N to 45° N at isobaths ranging from 20 to 100 meters deep) by the MOCHA program on a biweekly to monthly basis between May and November of 2009. A higher offshore sampling frequency was conducted on the Newport Hydrographic (NH, 44.65° N) line on a weekly to bi-weekly basis from May to December. Surf zone samples along the WA coast were collected by the ORHAB group and samples along the OR coast were collected by the Oregon Department of Fish and Wildlife (in conjunction with the NOAA-funded MOCHA program). All surf zone samples were collected by surface bucket and gently swirled to provide a well-mixed sample. The water was poured into a 125 ml glass jar pre-loaded with 5 ml of 10% formaldehyde solution buffered with sodium acetate. Ancillary measurements such as temperature and salinity were measured at each sampling location. Profiles of temperature and salinity at offshore stations were performed using a Sea-Bird SBE 19 CTD (conductivity, temperature and depth) while surf zone station measurements were taken using a hand held thermometer and salinity probe.

## 2.2. Light microscopy: 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. Each sampling jar was pre-calibrated at 100 ml and 10 ml and concentrated 10 fold. After 24 h, samples were carefully opened and excess volume was pipetted off until reaching the pre-calibrated 10 ml mark. In the event that the sample had a visually high density of cells the concentrating step was not performed. Samples were then mixed well to equally distribute cells and a subsample was transferred into a Palmer–Maloney slide with a volume of 0.1 ml and set aside for 5 min prior to counting to ensure cell settling. Using a Carl Zeiss compound microscope, at 200× magnification (20× objective, 10× ocular), cell counts proceeded until 500 cells had been counted; otherwise the entire slide was counted. All diatoms and dinoflagellates were identified to the genus level using Tomas (1997) as a reference. Cell counts for WA were performed by ORHAB using the same methods. Community composition was assessed for all OR-WA transect cruises and for all samples collected from regional monitoring of OR hydrographic lines. Collectively, this sampling effort spanned 4/4/2009–12/2/2009 and covered a region of the continental shelf between 38.25° N and 48° N.

A subset of microscopy samples from the Newport, OR hydrographic line were collected and preserved using the same methods described above but analyzed by removing a 50 ml subsample from the original sample and pouring that volume into a culture flask. This culture flask was then laid on its side and counted using an Leica inverted microscope at 200× (also as in Du et al., 2011). On all available samples a cross comparison of the two methods was performed; total counts were not substantially different between the two methods (data not shown).

## 2.3. Remote sensing

Satellite chlorophyll (CHL) data for 2009 were obtained from the Ocean Biology Processing Group (OBPG; <http://oceancolor.nasa.gov>) as Level-2 (L2) hierarchical data format (HDF) files (processing version R2009.1, created by l2gen version 6.2.5) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS). L2 swath data were extracted from the HDF files and masked according to the following OBPG-defined quality-control flags (<http://oceancolor.gsfc.nasa.gov/VALIDATION/flags.html>): 1,

atmospheric correction failure; 2, pixel is over land; 5, observed radiance very high or saturated; 10, cloud or ice contamination; and 26, navigation failure. L2 CHL data were mapped to an equal-area 1 kilometer (km) standard grid and then temporally-binned over 8 day periods using geometric composite-averaging. Hovmöller maps were compiled by averaging 50 km (50 pixels, the approximate width of the continental shelf) due west of the coast for each day of the year and each pixel of latitude from 42° N to 49° N which spans the extent of the OR and WA coastlines. Full resolution L2 MERIS (MEdium Resolution Imaging Spectrometer) data were obtained from <http://earth.esa.int>, and CHL and maps of the maximum chlorophyll index (MCI) were generated using BEAM software.

Daily Level-3 (L3) 4 km MODIS nighttime sea surface temperature (nSST) standard products (processing version R2012.1) were downloaded from the OBPG for each year that had complete MODIS coverage (2003–2012). 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. The daily climatology was then subtracted from the corresponding daily L3 nSST product in 2009 to yield a daily anomaly product, a descriptor of how much the temperature on a particular day of the year in 2009 deviated above or below the climatological average for that day. Hovmöller maps were then compiled by averaging 48 km (12 pixels) due west of the coast for each day of the year and each pixel of latitude from 42° N to 49° N.

## 2.4. Ancillary data

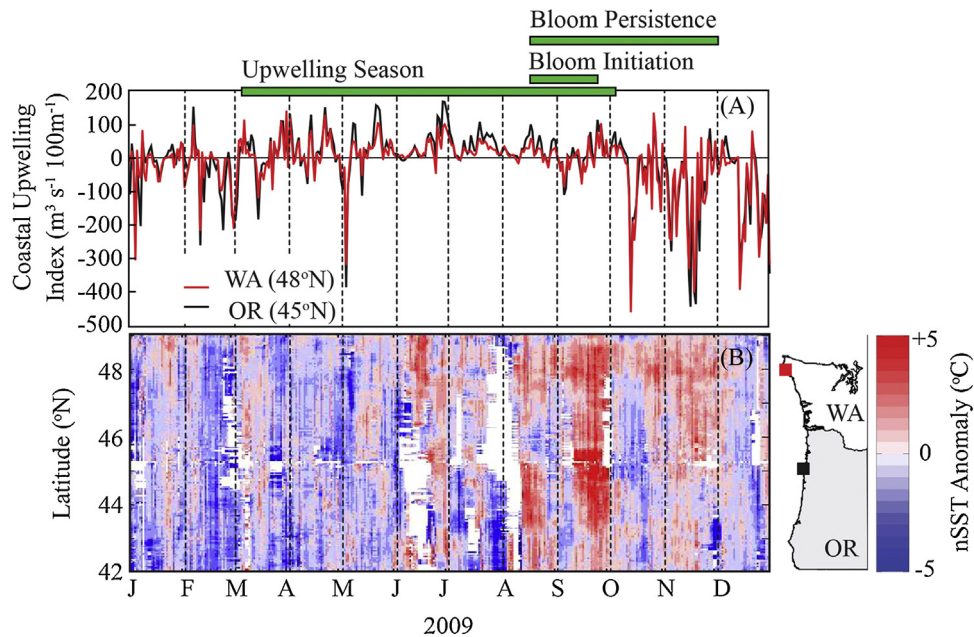
Upwelling index data were downloaded from the University of Washington–Columbia Basin Research site for two locations (45° N, 125° W near Lincoln City, OR, and 48° N, 125° W near La Push, WA; <http://www.cbr.washington.edu/>). This index is a measure of the volume of water that upwells (in m<sup>3</sup>) per second along 100 m swaths of coastline. The dates of the spring and fall transition were obtained from the Pacific Fisheries Environmental Laboratory Columbia Basin Research (PFEL-CBR) index <http://www.cbr.washington.edu/status/trans>. The monthly Oceanic Niño Index (ONI) – a running mean of sea surface temperature anomalies in the Niño 3.4 region (5° N–5° S, 120°–170° W) – was downloaded from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>).

# 3. Results and discussion

## 3.1. Physical forcing

In upwelling systems, the classical paradigm of warm, stratified conditions favoring dinoflagellates over diatoms (Margalef, 1978; Margalef et al., 1979) is somewhat altered as the effects of successive upwelling events, relaxation, and even intermittent downwelling create a complex habitat that can even lead to simultaneous diatom and dinoflagellate blooms at different places along the coast (Smayda and Trainer, 2010). Even so, it appears that dinoflagellate blooms are more common during periods of greater quiescence (Horner et al., 1997; Smayda and Trainer, 2010). In this regard, 2009 was a year when upwelling-favorable winds in the PNW began early and the end of the season had an uncharacteristic period of quiescence followed by renewed upwelling. The PFEL-CBR index indicates that winds off Newport, OR became upwelling favorable on March 8th while the mean transition date for 1967–2012 was March 28th. Upwelling favorable winds persisted through early October. The season was punctuated by several short relaxation events each lasting less than a week and an unusual quiescence/downwelling in September (Fig. 1). The sign and magnitude of coastal upwelling indices were similar at 45° N in





**Fig. 1.** (A) The Pacific Fisheries Environmental Laboratory coastal upwelling index for 45° N, 125° W (black) and 28° N, 125° W (red). Positive values indicate equatorward wind stress and upwelling favorable conditions. Negative values imply downwelling. The bars on the top indicate the duration of the upwelling season (spring–fall transition), the period where *Akashiwo sanguinea* cells were first observed in OR and WA, and the period of bloom persistence, respectively. (B) Anomaly Hovmöller for MODIS nighttime SST (nSST). Throughout the entire region, significantly warm waters ( $\sim +1$ – $5$  °C) were first observed in late August, throughout September and into November. This warm phase corresponds to the period when *A. sanguinea* blooms were recorded in the region.

OR waters and 48° N in WA waters (Fig. 1). *Akashiwo sanguinea* was first detected in the WA surfzone between August 17th and September 30th, whereas they appeared in OR waters once in June and again in July between 46 and 46.5° N, and then more broadly between August 30th and September 22nd (Table 1). When filtered in terms of the date of initial appearance, or date of maximum appearance, latitudinal trends are ambiguous – for example, when a large bloom (e.g.  $10^6$  cells  $L^{-1}$ ) was observed at Quinalt (47.5° N)

noteworthy populations ( $10^4$  cells  $L^{-1}$ ) were already present at Seaside, Oregon (46° N), with sites showing much lower concentrations of cells in between. This finding is more consistent with separate initiation events than propagation of a single bloom from one initiating site.

The period of bloom initiation relative to upwelling indices is indicated in Fig. 1 and came at the end of the upwelling season, with upwelling indices being moderately or weakly upwelling

**Table 1**

Date of observation of the initial and maximum concentrations of *Akashiwo sanguinea* with concurrent sea surface temperature (SST). “Not observed” denotes stations that were sampled yet *Akashiwo sanguinea* cells were never observed. NA indicates regions that were not sampled or where total cell counts are not available (Washington waters). Surfzone sampling sites are denoted by ‘S’ and offshore sampling denoted by ‘O’.

Lat (° N)	Site	Station ID	Date first observed	Initial <i>A. sanguinea</i> (cells $L^{-1}$ )	SST (°C)	% <i>A. sanguinea</i> of total community	Date maximum observed	Max <i>A. sanguinea</i> (cells $L^{-1}$ )	SST (°C)	% <i>A. sanguinea</i> of total community
>47.5	S	Kalaloch	9/10/2009	960,000	17.1	NA	9/10/2009	960,000	17.1	NA
>47.5	S	MocRocks	9/10/2009	282,000	16	NA	10/6/2009	739,000	13.2	NA
>47.5	S	Copalis	9/10/2009	121,000	15.6	NA	10/6/2009	327,000	14.1	NA
>47.5	S	La Push	9/17/2009	554,000	NA	NA	9/29/2009	804,000	NA	NA
>47.5	O	Queets River	8/18/2009	3000	13.9	70%	8/18/2009	3000	13.9	70%
47.0–47.5	S	Quinalt	9/10/2009	1,553,000	16.4	NA	9/10/2009	1,553,000	16.4	NA
47.0–47.5	O	Grays Harbor	8/17/2009	3000	15.9	69%	9/1/2009	14,000	14.5	80%
46.5–47.0	S	Twin Harbors	8/19/2009	16,000	15.2	NA	10/4/2009	1,116,000	13.3	NA
46.0–46.5	S	Long Beach	9/14/2009	315,000	NA	NA	10/26/2009	1,485,000	12.3	NA
46.0–46.5	S	Fort Stevens	8/24/2009	1000	12.8	NA	9/21/2009	108,000	14.1	NA
46.0–46.5	S	Sunset	8/25/2009	1000	14.8	NA	9/21/2009	118,000	14.7	NA
46.0–46.5	O	Columbia River	9/3/2009	98,000	13.8	96%	9/3/2009	98,000	13.8	96%
45.5–46.0	S	Nehalem <sup>a</sup>	9/22/2009	4000	13.7	NA	9/22/2009	4000	13.7	NA
45.5–46.0	S	Seaside	9/8/2009	31,000	15.9	NA	9/17/2009	60,000	17.0	NA
45.5–46.0	S	Barview <sup>a</sup>	9/22/2009	5000	15.5	NA	9/22/2009	5000	15.5	NA
45.5–46.0	S	Cannon	9/8/2009	2000	18.2	76%	11/12/2009	117,000	11.9	99%
45.5–46.0	O	Cape Mearns	8/30/2009	10,000	11.8	73%	8/30/2009	10,000	11.8	73%
45.0–45.5	S	Garibaldi <sup>a</sup>	11/4/2009	224,000	NA	NA	11/4/2009	224,000	NA	NA
44.5–45.0	S	Lincoln	10/19/2009	17,000	10.5	97%	10/28/2009	19,000	11.6	94%
44.5–45.0	O	Newport	6/10/2009	1000	13.5	61%	10/19/2009	347,615	12.6	NA
44.5–45.0	O	Seal Rock	5/19/2009	1000	10.8	60%	5/19/2009	1000	10.8	1%
44.0–45.0	O	Strawberry Hill	9/10/2009	1000	13.2	59%	9/10/2009	1000	13.2	59%
<44.0	O	Heceta Head	Not observed	NA	NA	NA	NA	NA	NA	NA
<44.0	S	Coos Bay	Not observed	NA	NA	NA	NA	NA	NA	NA

<sup>a</sup> A single sample was collected at this site/date.

favorable in August and then neutral or downwelling favorable between September 1st and September 20th. Brief pulses of upwelling favorable winds occurred between September 21st and October 8th after which conditions were largely downwelling favorable. The date of the fall transition, marking the initiation of the winter downwelling season when nutrient-depleted warmer water is transported shoreward is estimated by the CBR index to have been October 6th, 2009.

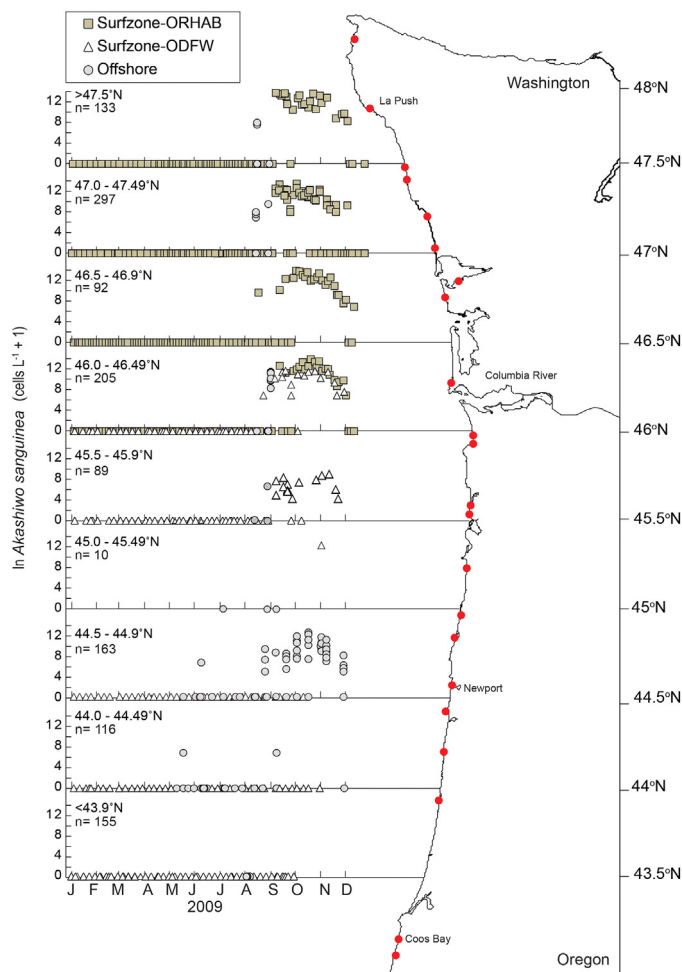
Du et al. (2011) examined the PFEL Cumulative Upwelling Index for 1990–2011 and noted that 2009 was the only year that upwelling ceased for an extended period late in the season (September) and then resumed for several weeks (October). In all previous years, once upwelling weakened in the fall it did not resume again until the following spring. *Akashiwo sanguinea* cells were first observed during this rare quiescent phase at the end of the upwelling season. During this period, surface waters in the PNW were also anomalously warm. Satellite records of sea surface temperature reveal up to a 5 °C positive anomaly in sea surface temperature, with the warmest phase in late September coincident with the period of bloom initiation along the WA and OR coastlines (Fig. 1). These unusually warm conditions may have been related to larger scale ocean forcing as the ONI exceeded the +0.5 °C threshold in July–December (anomalies from +0.61 to +1.78) such that it was classified as a Central Pacific event (McPhaden et al., 2011). The event may have influenced local weather by weakening the North Pacific High thereby leading to a weakening of alongshore winds, the onset of water column stratification and the observed positive sea surface temperature anomalies. These unseasonably high temperatures, weak upwelling/relaxation events and stratification of the water column contributed to the success and prolonged presence of *A. sanguinea* at just the time-period when molting sea-birds were most susceptible.

### 3.2. *Akashiwo sanguinea* bloom dynamics and community composition

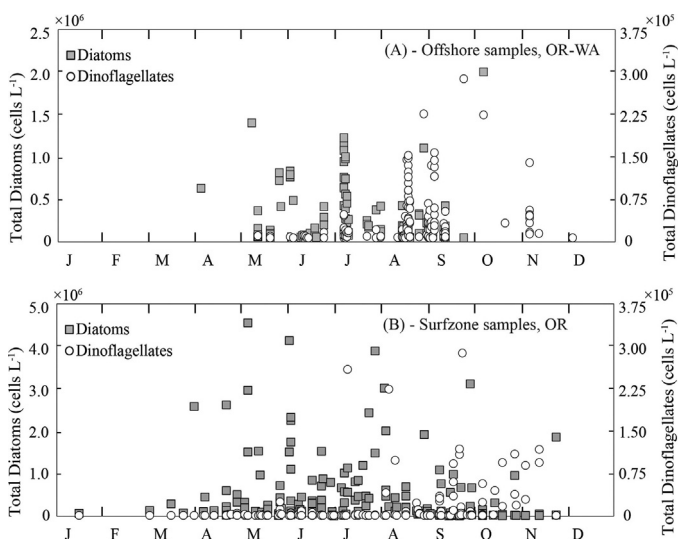
Community composition data are available for (1) OR-WA transect cruises, (2) regional cruises in OR, and (3) OR surf zone samples collected in the spring–winter of 2009. These data reveal that diatoms dominated the early upwelling phase (May–June) with a transition to dinoflagellates in August–September (Fig. 2). *Akashiwo sanguinea* was first recorded in offshore samples in May

and June on the NH (44.45° N) and Seal Rock (44.45° N) lines followed by no presence until the bloom was detected in late August–September in OR and WA coastal waters (Table 1 and Fig. 4). Bloom initiation appears to have been synchronous, with cells detected within days-weeks at all sampling sites in waters north of ~44° N (Fig. 4). Interestingly, the bloom did not extend south of 44.2° N: only 2 samples of the 271 collected contained *A. sanguinea*; no cells were observed in any surf zone data for this southern region. This may have been a consequence of local circulation as the surface flow separates from the coast at ~44° N at the southern end of Heceta Bank. Offshore branching of the poleward undercurrent occurs at this location as well (Barth et al., 2000).

This was not a mono-culture bloom of *Akashiwo sanguinea*; other dinoflagellates were also abundant during this period. Phytoplankton community counts in offshore OR-WA samples revealed *Alexandrium catenella*, *Prorocentrum gracile*, *Dinophysis caudata* and *Dinophysis acuminata* and several *Ceratium* spp. at concentrations equivalent to or greater than *A. sanguinea* (spanning concentrations of  $10^3$  to  $1.5 \times 10^6$  cells L<sup>-1</sup>). The diatoms *Chaetoceros* spp. and *Thalassiosira* spp. were also observed at similar concentrations ( $\leq 10^6$  cells L<sup>-1</sup>) between August and November 2009. *A. sanguinea* cells accounted for 59–99% of total phytoplankton counts when *A. sanguinea* was detectable (Table 1).



**Fig. 3.** Time series of *Akashiwo sanguinea* cell counts within 1/2 degree latitudinal bands spanning Oregon-Washington coastal waters. Data were collected in the surfzone (triangles for Oregon, squares for Washington) and during offshore cruises on the continental shelf within 50 km of the Oregon coast (circles). With a few outliers, bloom onset is coast wide in late August and persists into the December 2009. Some symbols overlap. Zero values indicate that water samples were counted and *A. sanguinea* was not detected.



**Fig. 2.** Total cells L<sup>-1</sup> of diatoms and dinoflagellates for 2009 (A) offshore OR-WA coastal samples and (B) OR surfzone samples.

By location, *A. sanguinea* accounted for  $35 \pm 34\%$  and  $39 \pm 35\%$  of total cell counts in OR-WA offshore and OR surf zone samples, respectively (Table 1). The percent *A. sanguinea* to the dinoflagellate community was  $47 \pm 35\%$  and in OR-WA offshore and  $91 \pm 24\%$  in OR surfzone samples. *A. sanguinea* was a major contributor to phytoplankton cell numbers in the full study region.

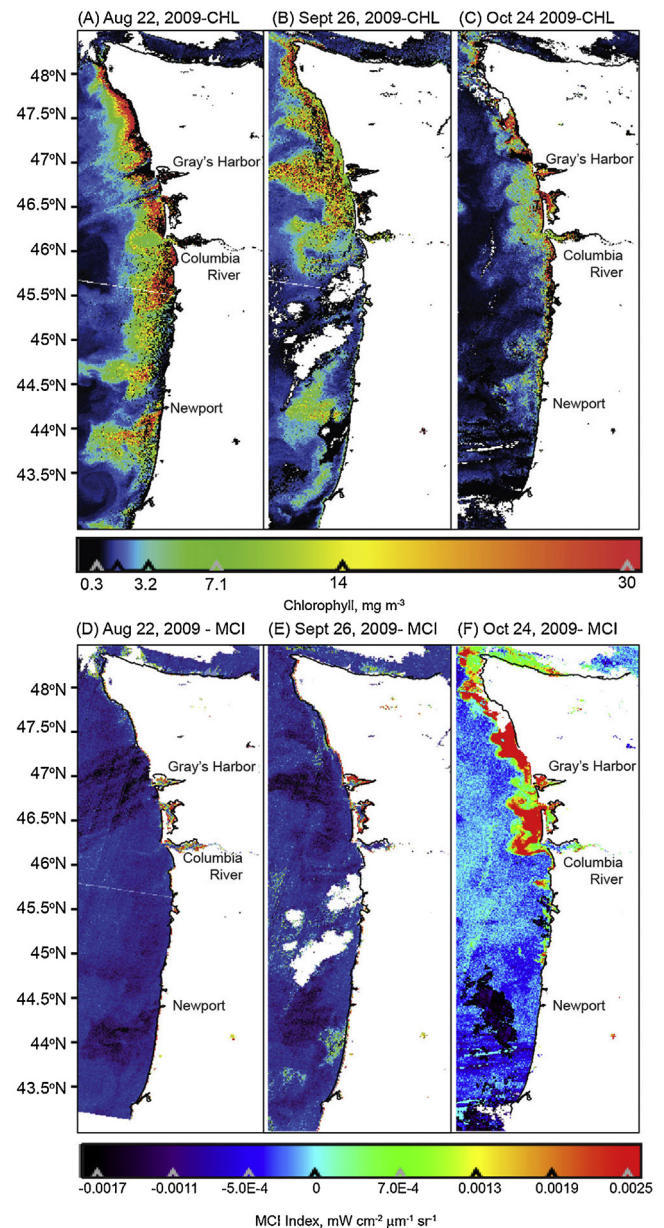
While bloom origin was latitudinally synchronous, the bloom peaked earlier and at higher levels to the north. In WA, maximum cell counts were observed between 8/18/2009 and 10/26/2009 as compared to 8/30/2009–11/14/2009 in OR waters (Table 1). Surf zone samples collected in WA were 7% higher than surf zone samples collected along the OR coast. This peak is partially explained by temperature; northern stations were warmer ( $SST = 1.07 \times LAT - 35$ ,  $r^2 = 0.35$ ,  $t$ -test  $p$  value = 0.03) and there is a positive correlation between the measured sea surface temperature and the initial concentration of *A. sanguinea* cells ( $r^2 = 0.17$ ,  $t$ -test  $p$  value = 0.03, data in Table 1). The highest recorded *A. sanguinea* cell counts ( $1.6 \times 10^6$  cells  $L^{-1}$ ) were collected on September 10th in Quinault, WA (Table 1) consistent with one of the highest SST values ( $16.4^\circ C$ ). This bloom persisted through November in coastal waters north of  $44^\circ N$  (Fig. 3).

*Akashiwo sanguinea* has been observed in OR waters in prior and subsequent years to 2009 but not at such high levels (2009 maximum of 134,000 cells  $L^{-1}$  offshore and  $>1,000,000$  cells  $L^{-1}$  in the surfzone, Table 1). MOCHA sampling of the OR surf zone recorded maximum cell concentrations for *A. sanguinea* of 4000 cells  $L^{-1}$  in 2007, 7000 cells  $L^{-1}$  in 2008, 13,000 cells  $L^{-1}$  in 2010 and 1000 cells  $L^{-1}$  in 2011. This organism has also been detected offshore in subsequent years via MOCHA sampling along OR hydrographic lines: *A. sanguinea* concentrations reached 17,000 cells  $L^{-1}$  in 2010 (NH line, 5 km offshore, September) and 7000 cells  $L^{-1}$  in 2011 (Strawberry Hill line, 15 km offshore, April).

### 3.3. Remote sensing

We further investigated the spatial and temporal extent of this algal bloom by exploring a series of remote sensing products. Regional distributions of chlorophyll-*a* are a proxy for total phytoplankton biomass and the MERIS MCI index can be used to indicate the presence of intense surface chlorophyll blooms (Gower et al., 2005). Notably, standard CHL algorithms tend to underestimate CHL at high in situ concentrations; alternately, the MCI index is only becomes positive at very high biomass ( $\geq 15$  mg  $m^{-3}$ ) as scattering and absorption in dense blooms lead to a peak in water leaving radiance near 709 nm (the center of the MCI line height) (Gower et al., 2008). We selected three relatively clear sky days over the period when *A. sanguinea* were observed in coastal waters for which MERIS passes encompassed the Pacific Northwest: August 22nd, September 26th and October 24th. Regional maps of the MCI index and MERIS derived CHL are shown in Fig. 4. There is no defined threshold value for a bloom: however winter-fall mean composite chlorophyll values are  $<10$  mg  $m^{-3}$  for this region; for our purposes values greater than  $10$  mg  $m^{-3}$  were considered to reflect bloom conditions. By this metric, extensive blooms were apparent in August–October with the most concentrated features along the WA coast, coincident with the mouth of the Columbia River as well as offshore of Newport, OR. Circulation is sluggish and retention of water high over the broad Heceta Bank (Hickey and Banas, 2008) at and south of Newport ( $44.0$ – $44.6^\circ N$ ); this may explain why cells had a maxima in abundance off Newport but not on the very narrow shelf between the Columbia River and Newport.

Positive MCI indices show intense surface blooms in the large coastal bays of WA and the mouth of the Columbia River in August and September with a smaller feature just south of Newport, OR in September. In the October 24th scene, a very large surface bloom

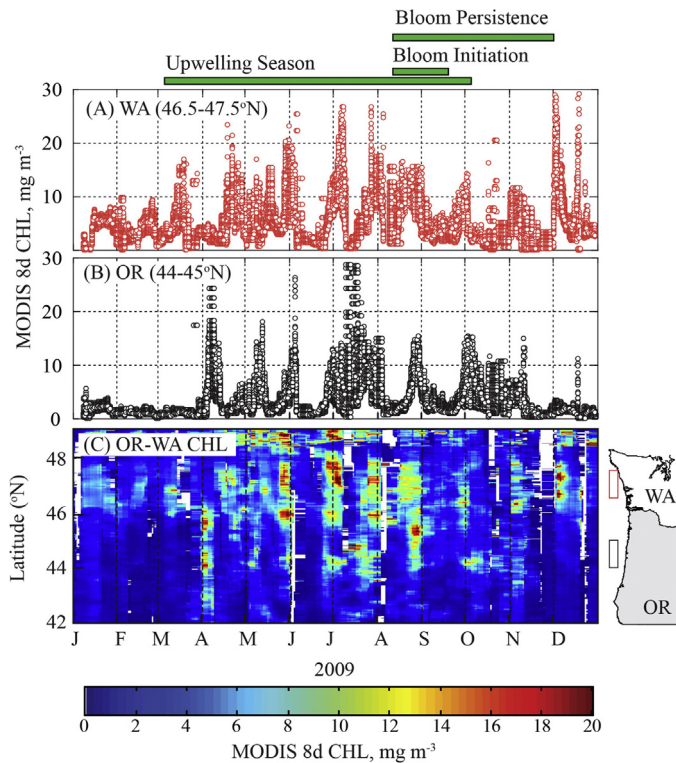


**Fig. 4.** MERIS chlorophyll (A–C) and the MCI index (D–F) for surface blooms for three relatively clear-sky dates spanning the *A. sanguinea* bloom period: August 22, 2009 (A and D), September 26th, 2009 (B and E) and October 24th, 2009 (C and F).

was observed off WA and nearshore in OR waters north of Newport. These blooms cannot be linked to any one phytoplankton taxa, but they do suggest elevated phytoplankton biomass spanning the full Pacific Northwest coastal margin, with hot-spots of activity near the coastal bays of WA, the Columbia River and offshore of Newport. For the limited clear-sky MERIS data available, intense surface blooms were most apparent in late October in the north (Fig. 4). This is consistent with the range of maximum observed *A. sanguinea* concentrations north of the Columbia (9/1/2009–10/26/2009).

Since MERIS coverage of the PNW is not of high temporal resolution, we have also examined MODIS CHL records (Fig. 5). Upwelling favorable winds are typically followed by increases in satellite chlorophyll (Frolov et al., 2013; McKibben et al., 2012). As noted in Fig. 1, the *Akashiwo sanguinea* bloom developed at the end of an upwelling event in late August. The late August event clearly resulted in a coherent bloom spanning  $44$ – $48^\circ N$  with bloom





**Fig. 5.** Time-series of MODIS CHL for (A) hotspot regions WA between 46.5 and 47.5 °C and (B) band in OR between 44 and 45 °C. (C) Hovmöller of 8-d mean MODIS CHL for the Oregon-Washington coastal region in 2009. CHL values were averaged over the continental shelf for each 1-km pixel (see Section 2). Increased CHL values roughly correspond to upwelling events. These increases are apparent over the full OR-WA coastal region.

decline in September just as surface waters were warming and winds relaxed (Fig. 1). Cohesive latitudinal blooms are again seen in late September and late October as upwelling was renewed briefly. These data support the hypothesis that bloom initiation was synchronous between 44 and 48° N.

## 4. Conclusions

### 4.1. Summary of bloom characteristics and forcing

*Akashiwo sanguinea* blooms appear to have initiated synchronously in OR-WA coastal waters in early September of 2009 yet peaked earlier and reached higher abundances north of the Columbia River. Bloom decline began in November of 2009. The timing of this bloom coincided with the primary molt in populations of overwintering seabirds such as Red-throated Loons, Western Grebes and Common Murres (Phillips et al., 2011). This unfortunate synchrony resulted in thousands of documented seabird deaths as a result of hypothermia and the resulting physiological stress. While *A. sanguinea* has been detected in the Pacific Northwest in other years, this was the first event to result in widespread bird mortalities and only the third ever documented case on the west coast (Monterey Bay being first, see Jessup et al., 2009).

In early September, when these blooms were first detected, winds had just shifted from upwelling favorable and a strong surface bloom evident between 44 and 48° N in the MODIS ocean color data had just subsided (Fig. 5). Over the *Akashiwo sanguinea* bloom phase (September–November) satellite chlorophyll (MODIS, Fig. 5 and MERIS, Fig. 4) indicated reduced bulk phytoplankton standing stocks as compared to the late August upwelling event and relatively strong positive sea surface

temperature anomalies (Fig. 1, up to 5 °C). On October 24th intense surface blooms, as indicated by a positive MERIS MCI index, were detected north of the Columbia River. This result is consistent with the northward intensification of the bloom that was evident in offshore and surf zone cell count data and positively correlated to sea surface temperatures. Just like the *A. sanguinea* blooms observed in Monterey Bay and San Francisco Bay (Cloern et al., 2005; Jessup et al., 2009), the OR-WA blooms documented here were associated with climate anomalies that led to periods of unusually calm and warm regional conditions. In the PNW, 2009 was characterized by anomalously warm surface waters likely related to a warm phase of the El Niño Southern Oscillation (ENSO) and a weakening of the North Pacific High. Moreover, 2009 was unusual in the sense that a quiescent downwelling period in September was followed by a rare renewal of upwelling in October–November; this was the first observation of this pattern in analyses spanning 1990–2011 (Du et al., 2011). The warm surface waters in August–September appear to have allowed for the bloom onset whereas the upwelling in October led to foam generation that endangered molting seabirds.

### 4.2. Speculation on bloom sources

*Akashiwo sanguinea* have been observed in this region annually since 2007, but never at such high concentrations as in 2009. The annual reoccurrence of this organism suggests a seed stock or perhaps allochthonous origin. At the cell level, dinoflagellates can be seeded as vegetative cells, resting cells, temporary cysts, or resting cysts (Smayda and Trainer, 2010). Smayda and Trainer (2010) described *A. sanguinea* as a holoplanktonic species that utilizes reduction in size and possible swimming motility to maintain seed populations in turbulent regimes like upwelling fronts (c.f. Smayda, 2002 for discussion of adaptation to turbulence regimes). However, it is not entirely clear that *A. sanguinea* is truly holoplanktonic; seed banks of cysts may offer another source of cells for bloom initiation. Benthic resting stages or temporary cyst forms have only been documented as the seed for recurrent red tides for a few species of the order Gymnodiniales (e.g. Matsuoka, 1985) and the literature for *A. sanguinea* is conflicting. Robinson and Brown (1983) describe the presence of possible sexual stages of *A. sanguinea* (referred to as *Gymnodinium sanguineum*) but they could not detect hypnozygotes, nor could they obtain viable *A. sanguinea* cells when incubating cysts isolated from sediments following a bloom. In comparison, Voltolina (1993) deployed ~12 m<sup>3</sup> reinforced bags in Esquimalt lagoon in the Juan de Fuca Strait. The presence of *A. sanguinea* was not initially detected in these bags, but was observed months later in the surrounding lagoon. Voltolina (1993) also demonstrated that incubation of sediment samples collected from this lagoon led to growth of vegetative cells of *A. sanguinea*. Taken together, these findings were seen as a strong indication that *A. sanguinea* produce resting stages that can overwinter in sediment.

Further evidence for existence of a cyst stage for *Akashiwo sanguinea* comes from the Gulf of Mexico region. Robichaux et al. (1998) collected a sample from a bloom off the Texas coast (USA) in which *A. sanguinea* (referred to as *Gymnodinium sanguineum*) was the dominant phytoplankter ( $5.4 \times 10^6$  cells L<sup>-1</sup>); these samples were incubated in the laboratory in the light. After a month there were no vegetative cells in the live sample but cyst-like structures, characterized by a typical dinoflagellate nucleus and a red accumulation body similar to that of other naked dinoflagellates, were present at concentrations of  $6.5 \times 10^5$  cysts L<sup>-1</sup>. Steidinger et al. (1998) described a similar cyst-like structure in samples collected from an *A. sanguinea* bloom along the Louisiana-Texas coast. Finally, *A. sanguinea* are one of several dinoflagellates known to form what Silva and Faust (1995) term “small cells” under



unfavorable conditions, typically as nutrients are exhausted. These small cells have a smaller nucleus, reduced cytoplasmic components and a thin wall and may behave as vegetative cells or as gametes. Silva and Faust (1995) note that when small cells of some dinoflagellates (it is not clear if *A. sanguinea* are included) act as gametes, sexual reproduction of the fusing gametes produce a zygote that increases in size and rounds up before forming a cyst. So while it is not definitive, we cannot rule out the conclusion that cysts of *A. sanguinea* in sediments could provide the seed population for recurring blooms.

Alternately, as suggested by Robinson and Brown (1983), seed populations for these recurring blooms may be transported from an external population. *Akashiwo sanguinea* is commonly observed in the subsurface chlorophyll maximum layer off California (Cullen and Horrigan, 1981; Jessup et al., 2009) and it could be the case that vegetative cells of this organism (perhaps as small cell propagules as per Silva and Faust, 1995) become entrained in the north-flowing California undercurrent. In 2009 in our study region, *A. sanguinea* cells were observed just after a major upwelling event (late August, see Fig. 1) that generated enhanced chlorophyll over a latitudinal band spanning 44–48° N. Upwelling taps into deeper water masses and may transport viable vegetative cells or cyst populations to the surface euphotic zone. Of course, *A. sanguinea* are motile and can vertically migrate; and so upwelling is not a requirement for a deeper population to emerge in surface waters. The presence of either sediment or pelagic seed banks needs to be explored further in order to identify the source of this nuisance species.

Regardless of the origin of this bloom, the oceanic and ecological conditions that favored *Akashiwo sanguinea* growth in 2009 as well as the timing with the primary molt for several species of seabirds led to widespread bird mortality. The anomalously warm and stratified conditions observed in fall of 2009 appear to have strongly favored dinoflagellate growth. Without a better understanding of the life cycle of this organism, specifically the potential for a cyst stage, it is difficult to predict whether *A. sanguinea* are likely to pose a persistent threat in the Pacific Northwest coastal region. Moreover, lacking an understanding of why the bloom occurred only in 2009 but not in any other year between 2007 and 2011 makes it impossible to predict when next a bloom might occur. Without a predictive capacity for this organism, we would suggest that the only means to mitigate the impacts of another instance of widespread foam-induced seabird mortality is a combination of routine algal monitoring and close communication between monitoring agencies and local wildlife rehabilitation centers.

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