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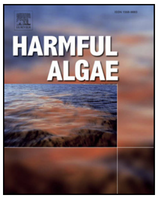

Environmental drivers of unprecedented *Alexandrium catenella* dinoflagellate blooms off eastern Tasmania, 2012–2018

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ABSTRACT

Blooms of the highly toxic dinoflagellate *Alexandrium catenella* (previously referred to as *tamarense* group 1) were first detected off eastern Tasmania in 2012 and have since been responsible for incidences of human paralytic shellfish poisoning and extended closures (up to 25 weeks) of mussel, oyster, scallop, abalone and rock lobster industries (up to 150 mg/kg PST in mussels). Investigation of meteorological and oceanographic influences indicate that the annually recurrent winter-spring blooms (June–Oct) occur within a narrow water temperature window (10–15 °C) under two distinct sets of conditions: (1) following high rainfall and land run-off, under relatively light winds; and (2) following periods of anomalously low air temperatures and associated cooling of shallow coastal waters, again under relatively light winds. The common driver of blooms appears to be the development of stratification in coastal waters, *via* salinity and/or temperature gradients. We propose a framework for evaluating the risk of *Alexandrium* with the aim of developing a forecasting capability, and compare these environmental conditions with historic data to understand the recent advent of these blooms.

1. Introduction

As in many parts of the world, harmful algal blooms (HABs) in the Australian region are having increasing impacts on human society. On the east coast of Tasmania, surveys since 1987 had previously detected low concentrations of *Alexandrium tamarense* (Hallegraeff et al., 1991). However, all cultured strains proved to be non-toxic and belonged to what was initially termed the “Tasmanian ribotype” (now designated group 5 or *Alexandrium australiense*; John et al., 2014). A single small bloom event in 1997 was caused by toxigenic group 4 (now designated *Alexandrium pacificum*), also widespread along the New South Wales and Victorian coasts of Australia (Farrell et al., 2013). Despite this latter event, the Tasmanian east coast continued to be classified as a low biotoxin risk and hence was subject to very limited phytoplankton and biotoxin monitoring.

During October 2012 a shipment of blue mussels from eastern Tasmania was tested by Japanese import authorities and found to be contaminated with unacceptable levels of Paralytic Shellfish Toxins (PST) exceeding 10 mg/kg. This led to a global product recall and loss to the local economy of AUD 23 M. The causative organism proved to be highly potent blooms of *Alexandrium catenella* (previously referred to as *Alexandrium tamarense* group 1 or *Alexandrium fundyense;* Prud’homme van Reine 2017) never previously detected anywhere in Australian nor New Zealand waters.

Following low toxicity during 2013 and 2014 with minimal shellfish farm closures, more severe bloom events occurred during July-Nov 2015, 2016, 2017, with a more restricted range in 2018. Limited water sampling revealed concentrations up to 300,000 *Alexandrium* cells/L, while regular weekly shellfish sampling yielded up to 150 mg/kg PST in mussels; 22 in oysters; 11 in rock lobster viscera; and 1.3 in abalone viscera. Over this period there were four human hospitalisations following consumption of wild shellfish. From both public health and seafood industry perspectives, there is now an urgent need to effectively monitor and forecast *Alexandrium* blooms.

There are major challenges associated with forecasting HABs in complex coastal environments. Internationally, efforts have typically relied on some combination of satellite remote sensing, *in situ* sensors and modelling (Anderson et al., 2012a). High biomass blooms (typically $> 3\,\mathrm{mg\,m^{-3}}$ of chlorophyll-*a*) can sometimes be detected using traditional satellite-based estimates of chlorophyll concentration and algorithms for satellite detection of specific harmful species are under active development (Amin et al., 2009; Shutler et al., 2012). However, low biomass blooms of highly toxic *Alexandrium* cannot usually be detected in this manner. *In situ* sensors, utilising optical properties

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(Campbell et al., 2013) or molecular techniques (Herfort et al., 2016) can provide more reliable species-level data, but the cost of deploying arrays of instruments over large areas are prohibitive.

A complimentary approach to remote and *in situ* sampling is identifying and modelling environmental drivers of HABs (McGillicuddy, 2010; Brown et al., 2013). Experiences across a diverse range of marine and freshwater systems indicate that environmental conditions can have a major influence on the development of HABs (Margalef, 1978; Hallegraeff et al., 1995; Giacobbe et al., 1996; Bormans and Condie, 1998; Smayda and Reynolds, 2001; Weise et al., 2002; Anderson et al., 2012b; Yamamoto et al., 2013). For selected high biomass bloom species, this may be associated with elevated nutrient levels (Heisler et al., 2008), with other ecological factors such as micronutrients (humics), seeding from benthic cyst beds, and migratory swimming speeds also playing a role. However, for many other species, physical oceanographic conditions are the main drivers (Giacobbe et al., 1996; Anderson et al., 2012b; Brown et al., 2013).

The presence of water column stratification indicates low levels of turbulence and vertical mixing, which can allow positively buoyant dinoflagellate species to remain in the photic zone and grow rapidly (Condie and Bormans, 1997; McGillicuddy, 2010). Many factors can influence stratification within coastal waters. Heat exchange with the atmosphere and rainfall can generate temperature and salinity differences that enhance stratification, whereas tides and winds generate turbulence that can erode stratification. Over seasonal timescales (averaging over solar and tidal cycles) this balance is primarily between the input of potential energy by river discharge (driven by rainfall) or cumulative heat exchange (driven by air temperature anomalies) and the input of kinetic energy by wind (that scales with the cubed windspeed) (Simpson and Hunter, 1974; Holloway, 1980; Condie and Webster, 2001).

Here we investigated the influences of meteorological and oceanographic conditions on the development of blooms of *Alexandrium* off eastern Tasmania. Based on 7-years of observations, our analysis suggests that environmental factors, such as water column stratification and coastal circulation, are important drivers that may provide a foundation for forecasting future blooms.

2. Methods

We used a combination of biological observations, *in situ* meteorological and oceanographic observations, remote sensing and hydrodynamic model outputs to explore potential links between the occurrence of *A. catenella* blooms and environmental conditions off eastern Tasmania (Table 1). The unprecedented nature of these blooms has limited the quality and quantity of data available for analysis. Our strategy was therefore to utilise regularly monitored proxies for the presence of blooms (PST levels from aquaculture monitoring) and the presence of stratification (wind, rainfall and air temperatures). Satellite data and hydrodynamic modelling then provided a broader oceanographic context within which to interpret any relationships that could be identified.

2.1. Biological and associated in situ physical observations

The location and timing of blooms were inferred from weekly monitoring of PST levels at more than 20 aquaculture sites along the Tasmanian east coast by the Tasmanian Shellfish Quality Assurance Program (TSQAP) using the AOAC (Association of Official Analytical Chemists) approved LC-FLD (Liquid chromatography fluorescence detector) method (Lawrence et al., 2005). As the measure of most immediate interest to the aquaculture industry, PST is the only indicator of blooms that has been monitored consistently since 2012, with much more limited cell count data recorded at some shellfish farm sites (TSQAP Biotoxin Management Plan 2017). Routine application of qPCR methodology (Ruvindy et al., 2018) has demonstrated that all 2012–2018 Tasmanian bloom samples were consistently dominated by *A. catenella*, but sometimes with sparse ($< 0.1\%$) background levels of the low-toxin *A. australiense* and *A. pacificum* also present.

Because PST provides no information on the vertical and offshore distribution of *A. catenella* and its relationship to oceanographic conditions, additional plankton, toxin and hydrological data were collected along cross-shore transects at the height of the August 2016 bloom using RV *Southern Cross*. A Seabird SBE 19PlusV2 CTD was used to collect temperature and salinity depth profiles. Plankton counts were obtained from 5 L Niskin bottle samples collected from different depths and after settling of 1 L Lugol preserved samples.

2.2. Meteorological and oceanographic data

Meteorological data from coastal weather stations (Fig. 1a) were accessed through the Bureau of Meteorology (http://www.bom.gov.au/climate/data/). Determinants of seasonal coastal stratification available from weather stations were rainfall, minimum daily air temperature and windspeed. Rainfall provided a proxy for discharge of freshwater from local catchments, contributing to salinity stratification. Minimum daily air temperature provided a proxy for preferential cooling in shallow coastal waters, contributing to thermal stratification. Windspeed provided a proxy for turbulent mixing with potential to erode stratification. Because mixing energy scales with windspeed cubed and windspeed is highly variable over the course of any day, half-hourly wind measurements were used for the analysis.

Flow data from the George River (St Helens), Meredith River (Swansea), Eastern Marshes Rivulet (Little Swanport) and Prosser River (Orford) was accessed through the Tasmania Water Information System (http://wrt.tas.gov.au/wist/), but was used more qualitatively due to data gaps. Remote imaging of sea surface temperature (Fig. 1b) was accessed through the Integrated Marine Observing System (IMOS,

Table 1
Meteorological and oceanographic data used in the analysis of HABs off eastern Tasmania. Locations of monitoring stations are shown in Fig. 1.

Region	Data description	Data source
Tasman Sea	Satellite SST (2012–2018) Altimeter sealevel (2012–2018) Geostrophic current velocity (2012–2018)	http://oceancurrent.imos.org.au
Tasmanian continental shelf	Ocean temperatures from Maria Island monthly sampling (1956–2015)	http://imos.org.au/nrsvesselsampling.html
	Modelled shelf circulation (2012–2015)	(Oliver et al., 2016)
Tasmanian east coast (St Helens, Little Swanport, Swansea, Orford and Maria Island)	Rainfall from coastal weather stations (2008–2018) Air temperature from coastal weather stations (2008–2018) Wind from coastal weather stations (2008–2018) Flow data from the George River, Merdith River, Eastern Marshes Rivulet and Prosser River (2004–2017) Water temperature and salinity profiles from Great Oyster Bay and Mercury Passage (2016–2017)	http://www.bom.gov.au/climate/data/ http://wrt.tas.gov.au/wist/

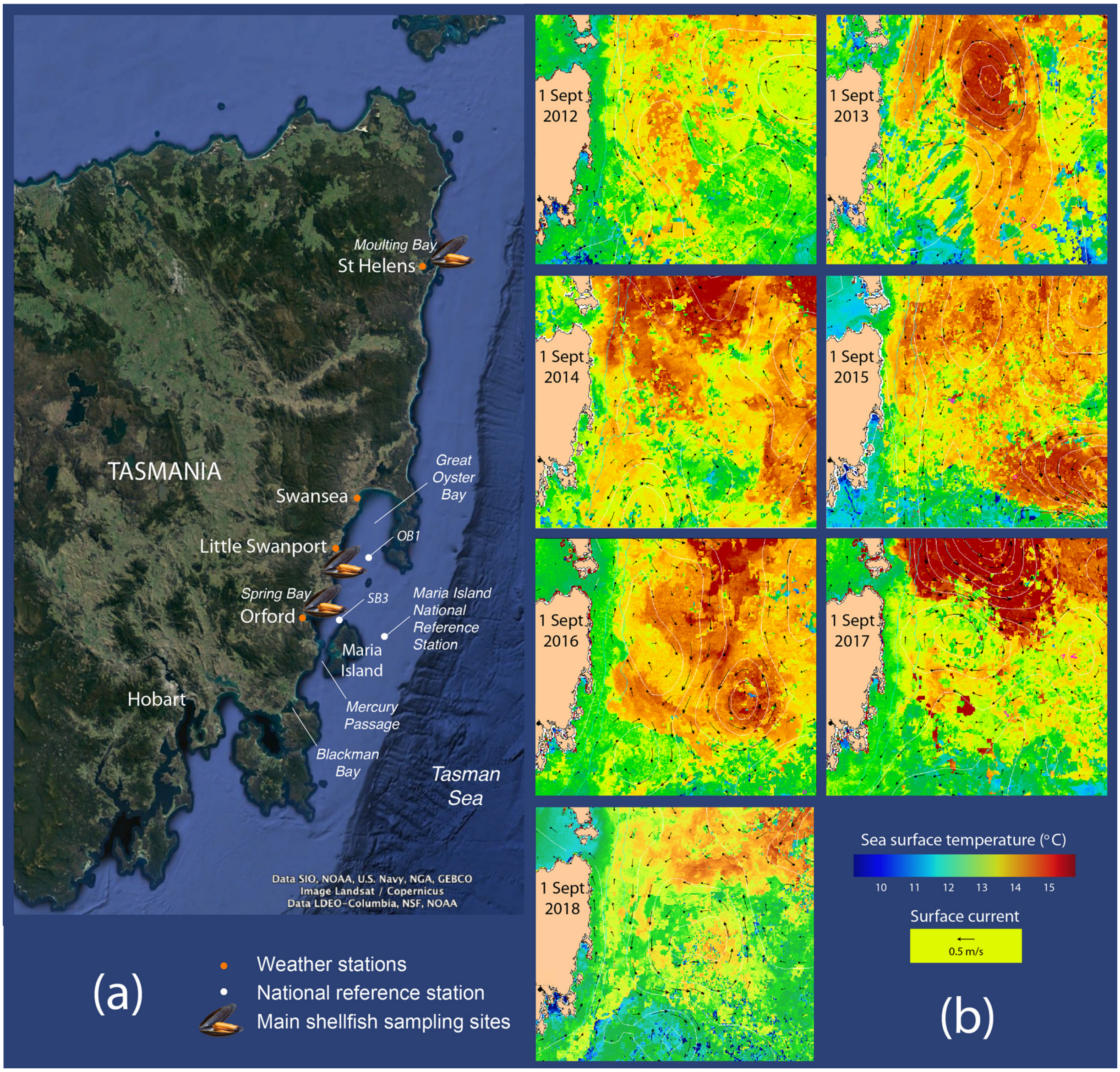

Fig. 1. (a) Map of eastern Tasmania showing observational and sampling sites and other key features. Only the three shellfish sites that were regularly sampled are shown. (b) Satellite sea surface temperature (SST) from NOAA AVHRR sensors for 1 September 2012–2018. Each image also shows 0.1 m interval contours of sea surface height (derived by combining data from satellite altimeters and coastal tide gauges) and surface geostrophic currents estimated from gradients in sea surface height. Further details are available through the IMOS OceanCurrent site (http://oceancurrent.imos.org.au).

http://oceancurrent.imos.org.au/). *In situ* profiles of water temperature and salinity from the IMOS National Reference Station near Maria Island (Fig. 1a) were accessed through the Australian Ocean Data Network (https://portal.aodn.org.au/).

2.3. Analysis

High-frequency variability in the meteorological data (associated with moving weather systems) was removed by monthly averaging. However, this still left significant temporal-lags relative to trends in PST. For example, rainfall over the local catchment, followed by freshwater discharge into coastal waters, development of a bloom, and finally ingestion by shellfish, could potentially take months. Indeed, monthly-averaged data were found to be broadly consistent with lags of 1–3 months (not shown). However, confounding factors such as the pre-existing state of local catchments or coastal waters influenced the timing and strength of responses. Quantitative analyses therefore focused on cumulative seasonal responses (June to October when water temperatures are generally in the range 10–15 °C that is favorable to *Alexandrium* growth).

Local meteorological data can be combined into a single parameter refered to here as the *meteorological risk factor* (*MRF*):

$$MRF = \frac{\begin{array}{l}\mathit{max}\,(\mathit{average\ daily\ rainfall},\ \mathit{average\ daily\ minimum\ air}\\ \mathit{temperature\ anomaly} \times \mathit{weighting})\end{array}}{\mathit{average\ cubed\ windspeed}} \tag{1}$$

This functional form reflects the underlying energetics for the development of stratification with the numerator variables tending to enhance stratification and the denominator variable tending to erode stratification. It is also consistent with previously derived predictors of stratification from a diverse range of water bodies (Simpson and Hunter, 1974; Holloway, 1980; Condie and Webster, 2001). If stratification supports the development of toxic blooms off eastern Tasmania as hypothesised, then the *MRF* should correlate with high PST in shellfish.

The *weighting* in Eq. (1) allows contributions to stratification from

Table 2
Correlation between PST and the meteorological risk factor (MRF, Eq. (1)). Weightings (that allow rainfall and air temperature effects to be combined) assumed that average rainfall is in millimetres per day and average minimum air temperature anomaly is in degrees Celsius.

Location	Number of years (N)	Correlation coefficient (r)	p-value (2-tailed)	Weighting
St Helens	6	0.755	< 0.1	0.66
Swansea	4	0.993	< 0.01	0.66
Little Swanport	6	0.793	< 0.1	0.76
Orford	6	0.933	< 0.01	0.99

rainfall and air temperature to be combined (assuming a linear relationship). Physically, their relative contributions will depend on a range of complex hydrological and hydrodynamic interactions across local catchments and coastal waters. However, for the purposes of empirical prediction, our objective is to maximise the correlation between *MFR* and annual PST in each region. Pearson's correlation coefficients (*r*) had only a single maximum in each region and this was found by iteratively varying the weighting value and using the bisection method to converge on the optimal solution (Burden and Faires, 1985). P-values were then calculated for each region using this optimal weighting (Table 2).

Using the optimal weighting value for a region, the *MRF* was first calculated for each month within the bloom season (June to October) and then averaged over the season. Starting with monthly averages reduced the effect of short-term fluctuations unlikely to have a sustained influence on stratification, but still allowed for switching between rainfall and surface cooling within a season (in Eq. (1)). Averaging over the season then removed the confounding effects of lagged responses.

2.4. Hydrodynamic modelling

Outputs from a calibrated hydrodynamic model of Eastern Tasmanian coastal waters (ETAS) were used to explore coastal stratification and circulation patterns over the period 2012–2015 (Oliver et al., 2016). The ETAS model was implemented on an orthogonal curvilinear horizontal grid covering the continental shelf and slope off eastern Tasmania, with the seaward boundary approximately following the 2500 m isobath. The horizontal resolution was less than 1 km in the estuaries, expanding to more than 3 km near the southern and eastern extremities, with an average of 1.9 km. The vertical resolution expanded from 1 m near the surface to 230 m in the deepest part of the domain. The ETAS model included realistic forcing by river discharges (Derwent and Huon), surface atmospheric conditions (wind, air temperature, precipitation and solar radiation), tides and offshore ocean conditions (currents, water temperature and salinity) (Oliver et al., 2016).

3. Results

3.1. Dinoflagellate blooms and shellfish toxins

The first unexpected 2012 bloom event was only detected in its terminal stages, and hence there is no information available on its development. Following low PST during 2013 and 2014 with minimal shellfish farm closures implemented, more severe bloom events occurred during July-November 2015, 2016, 2017 and 2018 (Fig. 2). In 2015 highest PST occurred to the south in Spring Bay, but in 2016 highest PST occurred further north in Little Swanport and Great Oyster Bay. In 2017 blooms started in the north of Great Oyster Bay in June,

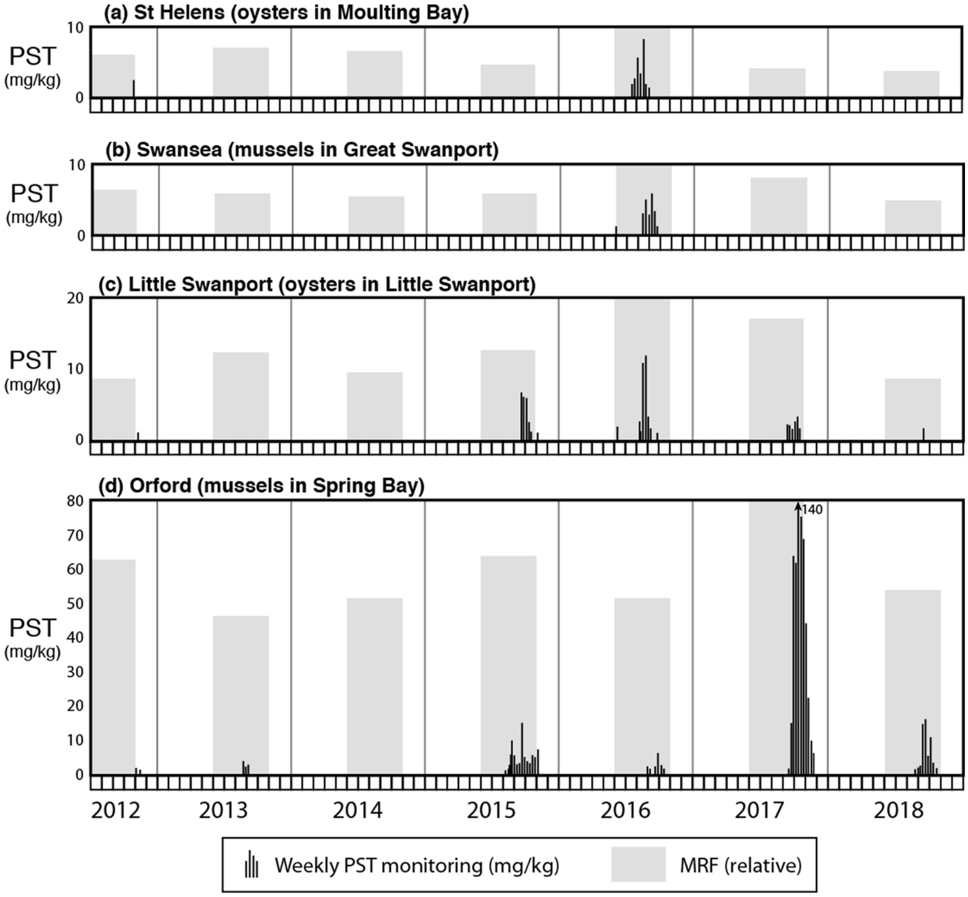

Fig. 2. Shellfish toxicity (values greater than 1.0 mg STX eq. kg^{-1}) during 2012–2018 in (a) oysters from Moulting Bay (St Helens); (b) mussels from Great Swanport (Swansea); (c) oysters from Little Swanport; and (d) mussels from Spring Bay (Orford). The width of the grey zones indicate the seasonal water temperature window for growth of *A. catenella* (10–15 °C), and their heights are proportional to the meteorological risk factor (MRF, Eq. (1)).

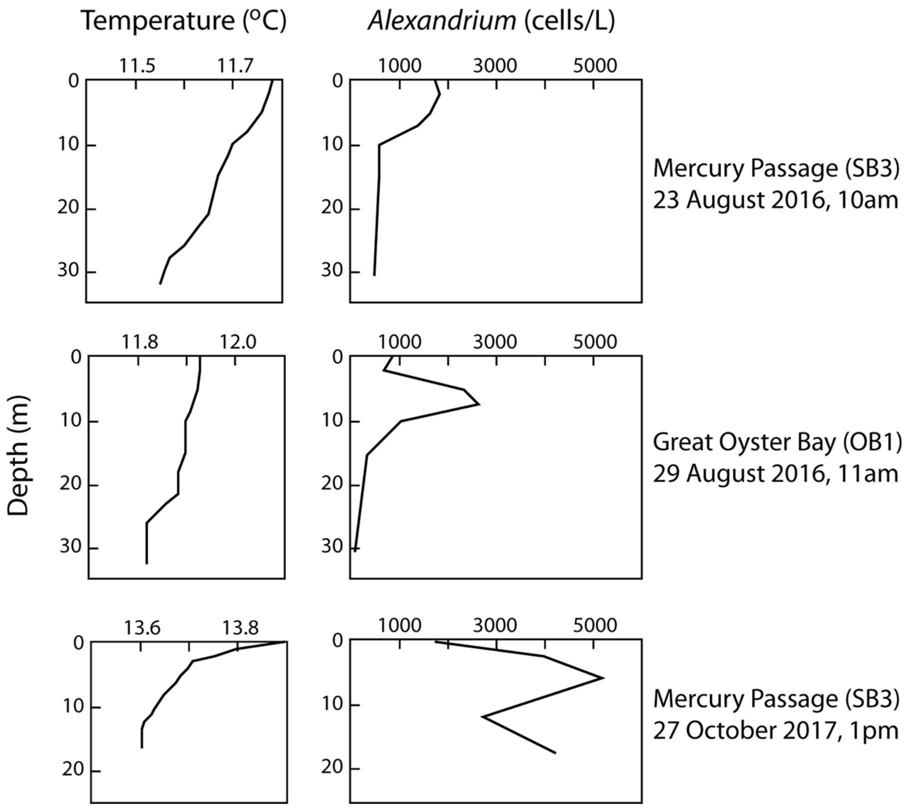

Fig. 3. Vertical profiles of water temperature (°C) and Alexandrium cell concentration (cells/L) from stations in Mercury Passage and Great Oyster Bay in 2016, and Mercury Passage in 2017 (locations SB3 and OB1 in Fig. 1). The salinity was uniform over the full depth of each of the profiles.

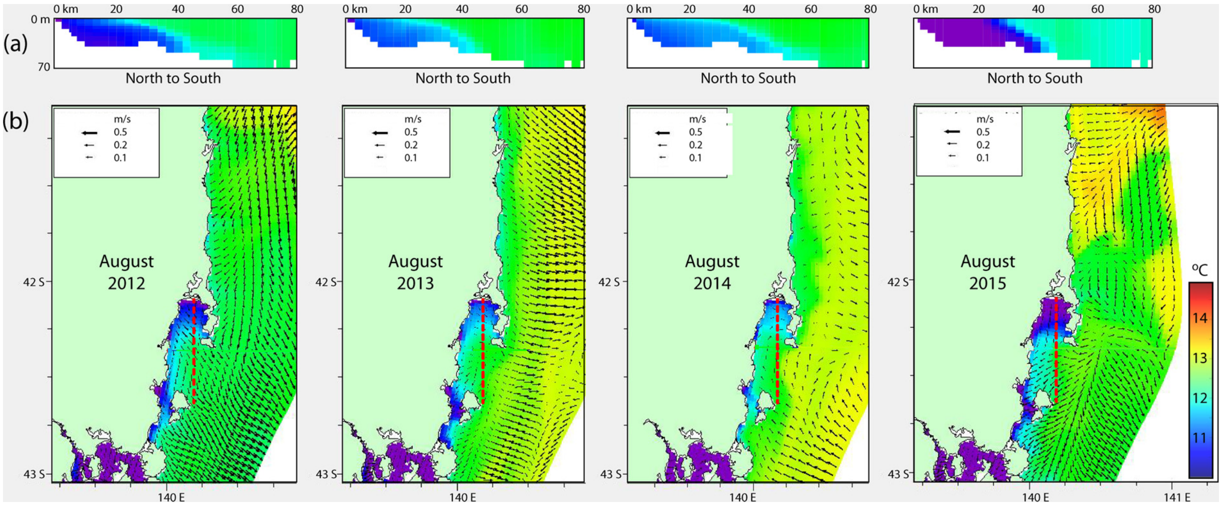

Fig. 4. Results from the coastal circulation model (Oliver et al., 2016) for mid-August 2012–2015. (a) North-south vertical water temperature sections from northern Great Oyster Bay to east of Maria Island. (b) Surface water temperature and surface current velocity vectors. The position of the vertical temperature section is shown by the red dashed line (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

peaked in late August and then moved south as far as Blackman Bay. In 2018 blooms were mostly restricted to the south in Spring Bay.

During some bloom years shellfish toxicity stretched over 200 km of coastline from St Helens in the north down to Blackman Bay in the south. However, in all bloom years, the continental shelf (35–50 m depth) between Great Oyster Bay and Mercury Passage consistently exhibited bloom events. Detailed surveys in August 2016 revealed *Alexandrium* populations thriving in inner shelf waters and just inside the sand bar of the main shellfish growing estuaries of Little Swanport, Great Oyster Bay and Moulting Bay. Highest cell counts typically occurred within the upper 15 m of the water column (Fig. 3). However, *Alexandrium* were virtually absent from the shallow (1–2 m) turbid waters of those estuaries, and also were absent from deeper (100 m) offshore waters (such as the Maria Island National Reference Station) dominated instead by spring bloom diatoms. *Alexandrium* cyst surveys during August 2016 along the entire east coast of Tasmania found consistently low abundances of cysts (0.1–3 cysts per gram of sediment wet weight), but no dense cyst beds (Hallegraeff et al., 2017).

3.2. Offshore oceanographic environment

While there is no evidence that *A. catenella* blooms originate

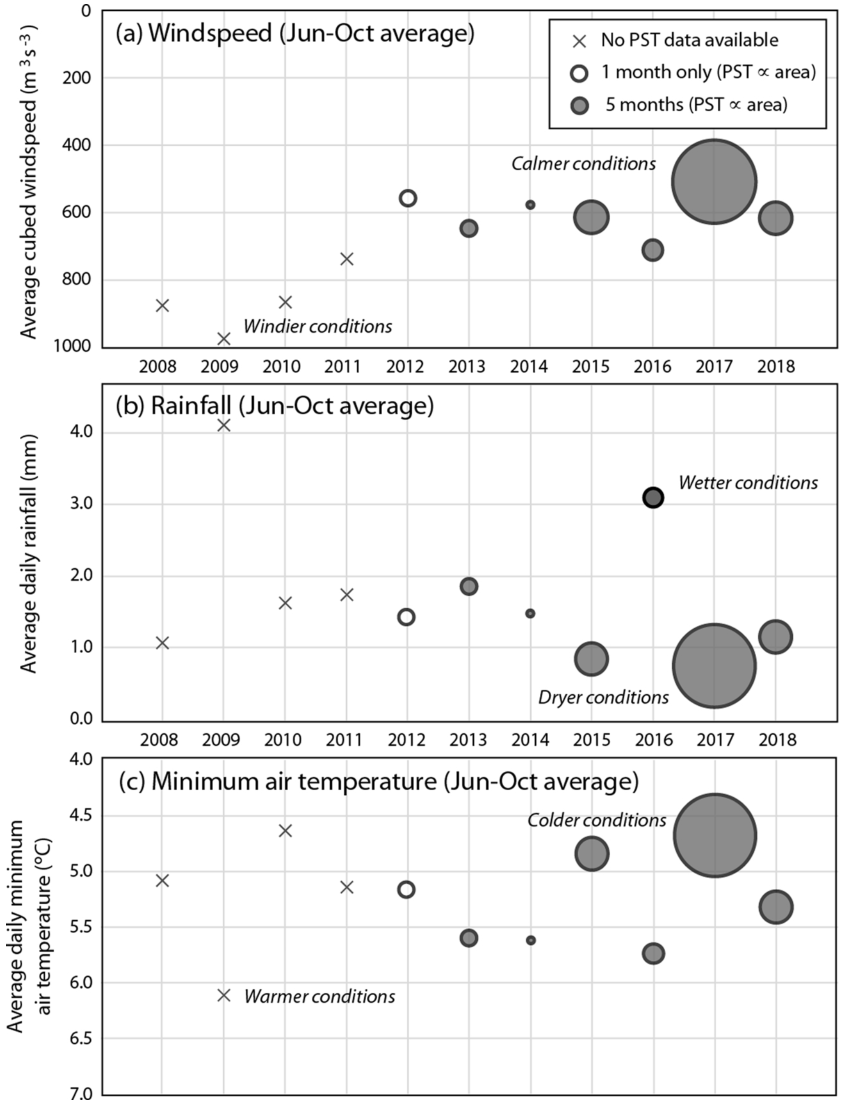

Fig. 5. Meteorological conditions near Orford, averaged over the bloom season (June to October) for 2008-2018. (a) Average cubed windspeed at Maria Island based on 30-minute data; (b) average daily rainfall; and (c) average daily minimum air temperature (Australian Bureau of Meteorology: http://www.bom.gov.au/climate/data/). In each case, conditions tending to be more favourable to blooms are upward on the vertical axis and bubble area is proportional to measured PST (2012–2018).

offshore, the offshore environment may play a role in moderating coastal water conditions. The East Australia Current (EAC) flows generally southward, although off eastern Tasmania the current direction is strongly dependent on the location of individual ocean eddies (Fig. 1b). In 2014, when no blooms were reported, flows in early spring were relatively weak and variable. However, during 2012, 2013, 2016 and 2018, flow on the adjacent continental shelf was predominantly northward in spring, with relatively uniform sea surface temperature (SST). In 2017 flows were again mostly northward, but waters in Great Oyster Bay and Mercury Passsage were anomalously cold. Similar cold anomalies were also present in 2015, although in this case flows tended to be southward with warm EAC water intruding over the shelf in the northern half of the state (Fig. 1b).

Data from the IMOS Maria Island National Reference Station (not shown) indicates that thermal stratification usually developed on the continental shelf over late spring (November). However, since 2009 the strengthening EAC has been accompanied by earlier development of stratified conditions. The strongest and most persistent springtime stratification over the available 61-year record (1956–2016) occurred in 1963, 2009, 2012, 2015 and 2016.

3.3. Coastal circulation and stratification

Results from the ETAS coastal circulation model confirm the presence of anomalously cold water ($< 10\,^{\circ}$C) inside Great Oyster Bay during August 2015 (Fig. 4). As this cold water sank and flowed out of the mouth of the bay beneath warmer shelf water, it created a large region of enhanced thermal stratification around Swansea and Little Swanport (Fig. 4a). Similarly, cooling in the shallows of Mercury Passage, west of Maria Island, enhanced the stratification around Orford. These conditions were followed by detection of high levels of shellfish toxicity at both Little Swanport and Orford (Fig. 2). While circulation model outputs were not available for 2017, satellite data again suggests the presence of anomalously cold water in the northern end of Great Oyster Bay (Fig. 1b).

At the time that blooms were developing near Orford in 2015, surface ocean currents were largely directed onshore (Fig. 4b). This pattern is indicative of coastal downwelling, which in this system could be driven by winds from the south, southeast or east (historically around 30% of spring winds) and may support retention and accumulation of dinoflagellates within the coastal zone.

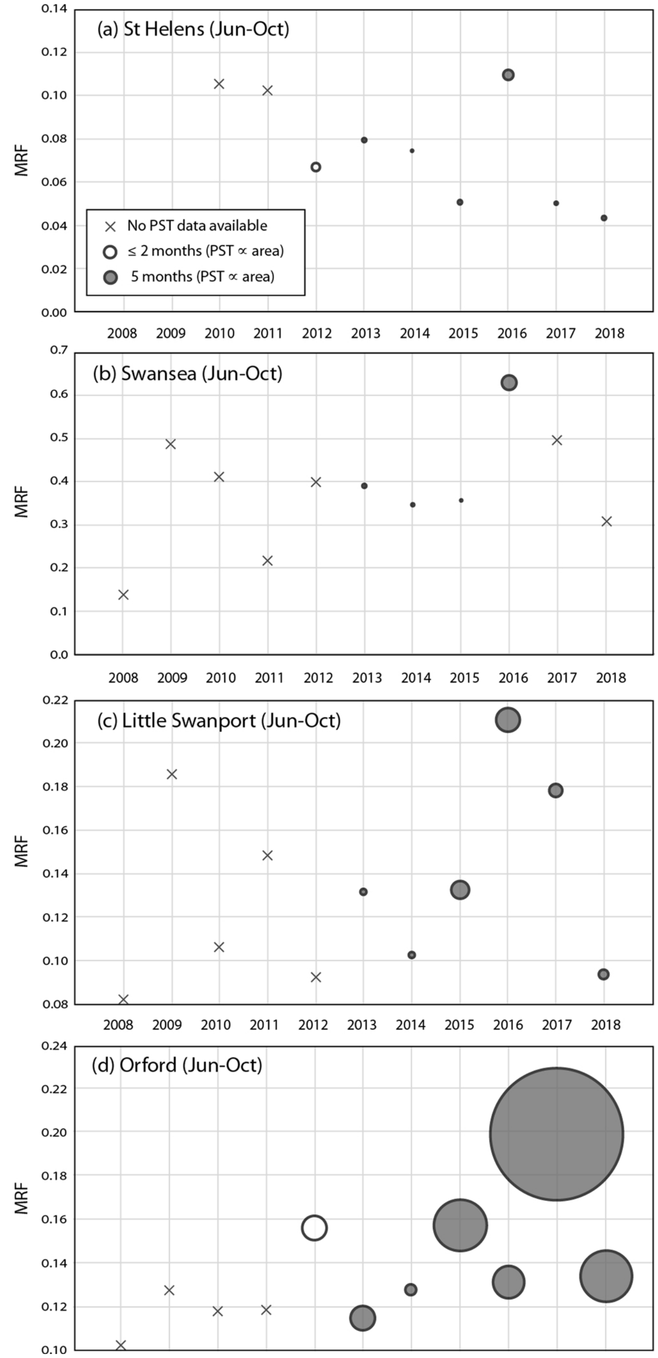

Fig. 6. Meteorological risk factor (MRF, Eq. (1)) calculated monthly for the bloom season (June to October) and then annually averaged for 2008-2018. (a) St Helens; (b) Swansea; (c) Little Swanport; and (d) Orford. Note that mean minimum monthly air temperatures were not available at Little Swanport, where the average of Swansea and Orford was used instead. Bubble area is proportional to measured PST (2012–2018).

3.4. Meteorological conditions and PST

Rainfall, air temperatures and windspeeds off eastern Tasmania were highly variable and appear to have had a strong influence on coastal blooms. For example, in Spring Bay high PST years generally corresponded to lower winds and either higher rainfall or lower minimum air temperatures (Fig. 5). Indeed, the highest PST levels observed off eastern Tasmania corresponded to the lowest monthly-mean winds (Fig. 5a) and near-lowest monthly-mean minimum air temperature observed since 2008 (Fig. 5c). August mean minimum air temperatures dropped to record levels in 2015 and there was associated cooling of coastal waters evident in satellite data (Fig. 1b). In 2017, July mean minimum air temperatures were the lowest since 1982 and coincided with an anomalously early bloom.

High monthly rainfall (> 50 mm) and associated high monthly averaged flow in the George River at St Helens (> 10 m^3s^{-1}), Meredith River at Swansea (> 3 m^3s^{-1}), Prosser River at Orford (> 5 m^3s^{-1}) and Eastern Marshes Rivulet at Little Swanport (> 4 m^3s^{-1}) was usually followed by high PST (> 1.0 mg STX eq. kg^{-1}). This occurred in 2012 around St Helens (Moulting Bay), in 2013 around Orford (Spring Bay), and in 2016 along most of the east coast (Fig. 2).

Over the period that PST has been monitored (2012–2018) there has been a significant correlation with the MRF, albeit based on a relatively small number of years (Fig. 2, Table 2). In some locations relatively high MRF values have also occurred prior to 2012, such as around Little Swanport in 2011 (Fig. 6c) and around St Helens in 2010 and 2011 (Fig. 6a). Whereas around Orford, MRF remained low from 2008 to 2011 (Fig. 6d) reflecting stronger than average windspeeds (Fig. 5a).

The relative weighting of average minimum air temperature to average rainfall increased from north to south (Table 2). This is consistent with observed southward meteorological trends towards lower rainfall and lower minimum air temperatures, and implies that cooling of shallow coastal waters played a relatively larger role in generating stratification in the south.

4. Discussion

4.1. Environmental drivers

Understanding the environmental drivers of HABs is essential for the development of biophysical models and forecasting capabilities (Fauchot et al., 2008; He et al., 2008; McGillicuddy, 2010; Anderson et al., 2013). Preliminary culture experiments indicate that local *Alexandrium* strains can reach growth rates as high as 0.5–0.8 divisions/day, with a preference for low phosphorus and stimulation by humics (R. Quinlan, unpublished). The observations and model results described here further show that bloom events off eastern Tasmania tend to be favoured by high rainfall, low minimum air temperatures, and low windspeeds, all of which have the potential to enhance coastal stratification.

High PST levels observed in 2013 and 2016 both followed episodes of high local rainfall. The associated freshwater river plume enhanced coastal stratification, thereby suppressing vertical mixing of nutrients and plankton (Fig. 7a). Coastal stratification was also enhanced during the 2015 and 2017 bloom periods, albeit through a different mechanism involving the subsurface outflow of anomalous cold water from Great Oyster Bay and Mercury Passage (Fig. 7b). Blooms in other years (2012 and 2018) may have been driven by a combination of these mechanisms, along with relatively low wind conditions (Fig. 5). Throughout this period, seed populations are assumed to have developed from dispersed benthic cysts (Hallegraeff et al., 2017). It appears that similar environmental conditions also occurred less frequently prior to 2012, suggesting either that occasional blooms went undetected, or that *Alexandrium* populations have only established at problematic levels since more favourable conditions became the norm.

While a range of environmental processes can potentially interact with *A. catenella* ecology, stratification (within the photic zone) appears to be the strong underlying driver for bloom formation. This finding is consistent with the few available *in situ* profiles of *A. catenella* (Fig. 3), as well as observations made in other coastal systems (Giacobbe et al., 1996; Anderson et al., 2012b; Yamamoto et al., 2013). It suggests that the stability associated with a stratified water column can provide dinoflagellate species with a significant competitive advantage over diatom species (Condie and Bormans, 1997). In stably stratified systems diatoms tend to sink out of the photic zone, whereas vertically migrating dinoflagellates can accumulate in the photic zone. Additionally,

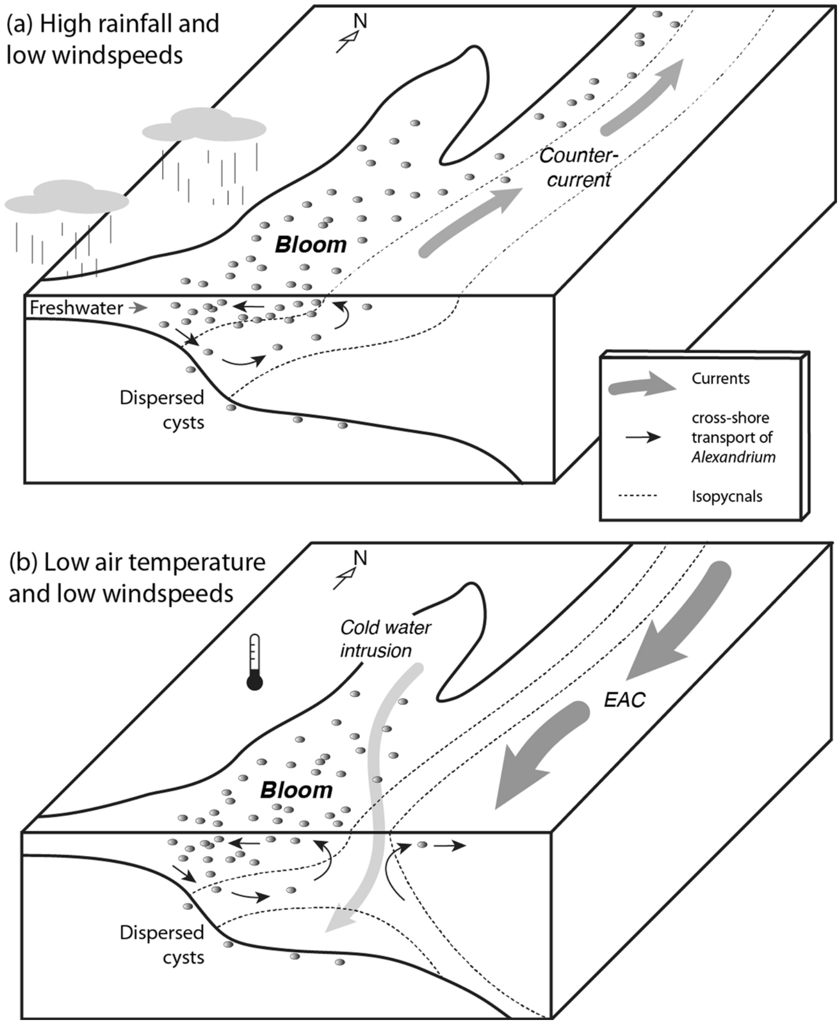

Fig. 7. Hypotheses for the environmental drivers of HABs off eastern Tasmania. (a) High rainfall, potentially accompanied by light southerly or onshore winds, generates a freshwater plume and enhanced coastal stratification supportive of dinoflagellate blooms. (b) Low air temperatures, potentially accompanied by light southerly or onshore winds, generate anomalously cold water in shallow areas such as Great Oyster Bay, which then flows beneath warmer offshore waters to enhance stratification and support dinoflagellate blooms. These conditions are often accompanied by intrusion of the East Australia Current (EAC) along the edge of the continental shelf. Both hypotheses assume that seed populations develop from dispersed benthic cysts (Hallegraeff et al., 2017).

the absence of vertical mixing can lead to rapid depletion of nitrogen and silicate in the photic zone, which can be limiting for diatoms but not for dinoflagellates.

Results from the coastal circulation model also revealed that blooms were sometimes associated with coastal downwelling (Fig. 4), which is likely to lead to further nutrient depletion. The cross-shelf flow patterns associated with downwelling conditions are also advantageous to positively buoyant dinoflagellates and limiting to diatoms (He et al., 2008). Specifically, diatoms tend to follow downwelling flow offshore and descend below the euphotic zone, whereas dinoflagellates rising toward the surface tend to be carried onshore where they accumulate (Condie and Sherwood, 2006).

4.2. Implications for forecasting HABs off eastern Tasmania

An ability to forecast *A. catenella* blooms off eastern Tasmania would allow shellfish aquaculture, commercial and recreational fisheries, and their regulators to plan closures and minimise risks to human health. While we have so far only studied 7 years of blooms, the emerging patterns are broadly consistent with theoretical expectations (Condie and Bormans, 1997; Condie and Sherwood, 2006) and empirical research conducted in other regions where *A. catenella* has been problematic over a number of decades, such as the Gulf of Maine (Anderson et al., 2012b; Yamamoto et al., 2013). Early identification of the biophysical relationships that might underpin a forecasting system can help guide ongoing research by shifting the focus towards risk assessment and mitigation (Anderson et al., 2013).

The MRF (Eq. (1)) has been shown to be correlated with PST and potentially provides a basis for developing a HAB risk forecasting system for the region. This relationship uses existing (low cost) meteorological information (rainfall, air temperature and windspeed) to provide early warning (1–3 months) that bloom condition may be developing. It could be further supplemented with river flow and satellite SST information to trigger *in situ* sampling of stratification and/or *Alexandrium* (Fig. 3). It should be feasible to implement a limited forecasting system quite rapidly, with a view to expanding its capability into the future. Given the short history of *A. catenella* bloom observations off eastern Tasmania, implementation of any forecasting system will require ongoing assessment, refinement and validation. In the long-term, the use of a dynamical atmosphere-ocean seasonal forecasting system (*e.g.* POAMA, ACCESS-S) would be highly valuable for the accurate prediction of environmental conditions favorable to HABs.

4.3. Implications of longer term environmental change

The ocean environment off eastern Tasmania is well documented as a climate change hotspot, characterized by a stronger EAC and rapidly increasing ocean temperatures (2.3 °C increase since the 1940s) as well as changing marine communities (Suthers et al., 2011). These novel *Alexandrium* blooms are not a simple response to increasing water temperatures, since they occur during the cold winter-spring months when water temperatures are within the range 10–15 °C. Preliminary genetic evidence (John et al., 2018) suggests that the Tasmanian *Alexandrium catenella* population exhibits a unique microsatellite signature and therefore may not represent a ballast water introduction or range expansion (Sydney coastal waters exclusively host *A. pacificum*). Preliminary sediment DNA results (Shaw et al., 2019) suggest that *A. catenella* existed in Tasmanian waters as early as 1987, remaining undetected for 25 years. *Alexandrium* cyst surveys during August 2016 along the entire east coast of Tasmania found consistently low abundances of cysts (0.1–3 cysts per gram of sediment wet weight) (Hallegraeff et al., 2017). This also suggests that these blooms are recent events. Paleogenomic research is in progress using ancient DNA methods on dated sediment depth cores (11,000 years old) from the area to document historic shifts in *Alexandrium* genotypes 1, 4 and 5. Our working hypothesis is that this may have been a previously cryptic genotype, newly stimulated by climate-driven increases in the frequency and persistence of coastal stratification during winter and early spring.

A trend towards lower minimum air temperatures with higher regional water temperatures may be contributing towards enhanced thermal stratification. Data from the Maria Island National Reference Station on the mid-shelf (Fig. 1a) indicates that spring-time thermal stratification over the upper 80 m has strengthened substantially over the last decade (springtime months with stratification exceeding 0.01 °C m-1 has increased from an average of 16% for the period 1956 to 2008 to 48% since 2009; http://imos.org.au/nrsvesselsampling.html). The recent downward trend in winter and spring windspeeds in this region (Fig. 5) may also be contributing to the persistence of this stratification.

In the future, continued strengthening of the EAC and increasing water temperatures may actually reduce the length of the *Alexandrium* growth season (10–15 °C). Such conditions will likely favor earlier winter blooms whenever there is significant winter rainfall (*e.g.* 2016) or whenever these warmer waters spread over colder inner shelf waters so as to enhance the thermal stratification across the shelf (as occurred in 2017). The strengthening EAC has also been associated with decreasing silica concentrations, which would further favour dinoflagellates and select against competing diatom blooms (Thompson et al., 2009).

Alexandrium blooms off eastern Tasmania may also be influenced by climate driven changes in seasonal rainfall. Downscaled climate projections from the IPCC Fourth Assessment Report predict relatively little change in east coast winter rainfall (Grose et al., 2013). However, rainfall projections for this region are highly uncertain due to the dependence on episodic high-intensity cutoff lows in the atmosphere, that tend to be poorly resolved by most climate models (Grose et al., 2012). We can therefore expect that rainfall will continue to be a significant driver in some years.

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References

Amin, R., Zhou, J., Gilerson, A., Gross, B., Moshary, F., Ahmed, S., 2009. Novel optical techniques for detecting and classifying toxic dinoflagellate Karenia brevis blooms using satellite imagery. Opt. Express 17, 9126–9144.

Anderson, D.M., Cembella, A.D., Hallegraeff, G.M., 2012a. Progress in understanding harmful algal blooms: paradigm shifts and new technologies for research, monitoring, and management. Ann. Rev. Mar. Sci. 4 (4), 143–176.

Anderson, D.M., Keafer, B.A., McGillicuddy, D.J., Solow, A.R., Kleindinst, J.L., 2013. Improving the accuracy and utility of harmful algal bloom forecasting systems. Biol. Geol. Perspect. Dinoflagell. 141–147.

Anderson, D.M., Alpermann, T.J., Cembella, A.D., Collos, Y., Masseret, E., Montresor, M., 2012b. The globally distributed genus Alexandrium: multifaceted roles in marine ecosystems and impacts on human health. Harmful Algae 14, 10–35.

Bormans, M., Condie, S.A., 1998. Modelling the distribution of Anabaena and Melosira in a stratified river weir pool. Hydrobiologia 364, 3–13.

Brown, C.W., Hood, R.R., Long, W., Jacobs, J., Ramers, D.L., Wazniak, C., Wiggert, J.D., Wood, R., Xu, J., 2013. Ecological forecasting in Chesapeake Bay: using a mechanistic-empirical modeling approach. J. Mar. Syst. 125, 113–125.

Burden, R.L., Faires, J.D., 1985. Numerical Analysis, 3rd ed. PWS Publishers ISBN 0-87150-857-5.

Campbell, L., Henrichs, D.W., Olson, R.J., Sosik, H.M., 2013. Continuous automated imaging-in-flow cytometry for detection and early warning of Karenia brevis blooms in the Gulf of Mexico. Environ. Sci. Pollut. Res. – Int. 20, 6896–6902.

Condie, S.A., Bormans, M., 1997. The influence of density stratification on particle settling, dispersion and population growth. J. Theor. Biol. 187, 65–75.

Condie, S.A., Webster, I.T., 2001. Estimating stratification in shallow water bodies from mean meteorological conditions. J. Hydraulic Eng.-Asce 127, 286–292.

Condie, S.A., Sherwood, C.R., 2006. Sediment distribution and transport across the continental shelf and slope under idealized wind forcing. Prog. Oceanogr. 70, 255–270.

Fauchot, J., Saucier, F.J., Levasseur, M., Roy, S., Zakardjian, B., 2008. Wind-driven river plume dynamics and toxic Alexandrium tamarense blooms in the St. Lawrence estuary (Canada): a modeling study. Harmful Algae 7, 214–227.

Giacobbe, M.G., Oliva, F.D., Maimone, G., 1996. Environmental factors and seasonal occurrence of the dinoflagellate Alexandrium minutum, a PSP potential producer, in a Mediterranean lagoon. Estuar. Coast. Shelf Sci. 42, 539–549.

Grose, M.R., Pook, M.J., McIntosh, P.C., Risbey, J.S., Bindoff, N.L., 2012. The simulation of cutoff lows in a regional climate model: reliability and future trends. Clim. Dyn. 39, 445–459.

Grose, M.R., Corney, S.P., Katzfey, J.J., Bennett, J.C., Holz, G.K., White, C.J., Bindoff, N.L., 2013. A regional response in mean westerly circulation and rainfall to projected climate warming over Tasmania, Australia. Clim. Dyn. 40, 2035–2048.

Hallegraeff, G., Bolch, C., Condie, S., Dorantes-Aranda, J.J., Murray, S., Quinlan, R., Ruvindy, R., Turnbull, A., Ugalde, S., Wilson, K., 2017. Unprecedented Alexandrium blooms in a previously low biotoxin risk area of Tasmania, Australia. Proenca, L.a.O., Hallegraeff, G.M. (Eds.), The 17th International Conference on Harmful Algae.

Hallegraeff, G.M., Mccausland, M.A., Brown, R.K., 1995. Early warning of toxic dinoflagellate blooms of gymnodinium-catenatum in southern tasmanian waters. J. Plankton Res. 17, 1163–1176.

He, R.Y., McGillicuddy, D.J., Keafer, B.A., Anderson, D.M., 2008. Historic 2005 toxic bloom of Alexandrium fundyense in the western Gulf of Maine: 2. Coupled biophysical numerical modeling. J. Geophys. Res.-Oceans 113.

Heisler, J., Glibert, P.M., Burkholder, J.M., Anderson, D.M., Cochlan, W., Dennison, W.C., Dortch, Q., Gobler, C.J., Heil, C.A., Humphries, E., Lewitus, A., Magnien, R., Marshall, H.G., Sellner, K., Stockwell, D.A., Stoecker, D.K., Suddleson, M., 2008. Eutrophication and harmful algal blooms: a scientific consensus. Harmful Algae 8, 3–13.

Herfort, L., Seaton, C., Wilkin, M., Roman, B., Preston, C.M., Marin, R., Seitz, K., Smith, M.W., Haynes, V., Scholin, C.A., Baptista, A.M., Simon, H.M., 2016. Use of continuous, real-time observations and model simulations to achieve autonomous, adaptive sampling of microbial processes with a robotic sampler. Limnol. Oceanogr.-Methods 14, 50–67.

Holloway, P.E., 1980. A criterion for thermal stratification in a wind-mixed system. J. Phys. Oceanogr. 10, 861–869.

Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta 1, 493–509.

McGillicuddy, D.J., 2010. Models of harmful algal blooms conceptual, empirical, and numerical approaches preface. J. Mar. Syst. 83, 105–107.

Oliver, E.C.J., Herzfeld, M., Holbrook, N.J., 2016. Modelling the shelf circulation off eastern Tasmania. Cont. Shelf Res. 130, 14–33.

Ruvindy, R., Bolch, C.J., MacKenzie, L., Smith, K.F., Murray, S.A., 2018. qPCR assays for the detection and quantification of multiple paralytic shellfish toxin-producing species of Alexandrium. Front. Microbiol. 9.

Shutler, J.D., Davidson, K., Miller, P.I., Swan, S.C., Grant, M.G., Bresnan, E., 2012. An adaptive approach to detect high-biomass algal blooms from EO chlorophyll-a data in support of harmful algal bloom monitoring. Remote. Sens. Lett. 3, 101–110.

Simpson, J.H., Hunter, J.R., 1974. Fronts in Irish Sea. Nature 250, 404–406.

Smayda, T.J., Reynolds, C.S., 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. J. Plankton Res. 23, 447–461.

Suthers, I.M., Everett, J.D., Roughan, M., Young, J.W., Oke, P.R., Condie, S.A., Hartog, J.R., Hobday, A.J., Thompson, P.A., Ridgway, K., Baird, M.E., Hassler, C.S., Brassington, G.B., Byrne, M., Holbrook, N.J., Malcolm, H.A., 2011. The strengthening East Australian Current, its eddies and biological effects - an introduction and overview. Deep-Sea Res. Part Ii-Top. Stud. Oceanogr. 58, 538–546.

Thompson, P.A., Baird, M.E., Ingleton, T., Doblin, M.A., 2009. Long-term changes in temperate Australian coastal waters: implications for phytoplankton. Mar. Ecol. Prog. Ser. 394, 1–19.

Weise, A.M., Levasseur, M., Saucier, F.J., Senneville, S., Bonneau, E., Roy, S., SauvT, G., Michaud, S., Fauchot, J., 2002. The link between precipitation, river runoff, and blooms of the toxic dinoflagellate Alexandrium tamarense in the St. Lawrence. Can. J. Fish. Aquat. Sci. 59, 464–473.

Yamamoto, K., Tsujimura, H., Nakajima, M., Harrison, P.J., 2013. Flushing rate and salinity may control the blooms of the toxic dinoflagellate Alexandrium tamarense in a river/estuary in Osaka Bay, Japan. J. Oceanogr. 69, 727–736.