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Global and local factors driving the phenology of *Alexandrium minutum* (Halim) blooms and its toxicity

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ABSTRACT

The dinoflagellate *Alexandrium minutum* is a toxic bloom-forming species distributed worldwide. The mechanisms driving and promoting the species blooms and their toxicity are studied and presented here. Most previously published work focuses on local and/or short-term scales. In this study, a broad temporal and spatial approach is addressed using time series covering several sites over several years and combining environmental variables and *A. minutum* abundances from the French English Channel – Atlantic coasts. Data were explored by means of phenology and threshold analysis.

The *A. minutum* bloom characteristics are defined. Only one bloom per year is measured and it may reach more than a million of cells L^{-1}. Bloom period extends from April to October and the bloom length ranges from two weeks to six months. In the ecosystems studied, water temperature and river flow, as regional and local factors respectively, are the main environmental drivers influencing the magnitude, growth rate and length of the blooms. Bloom toxicity is linked to the bloom maximum abundance and river flow. This work provides new knowledge for further managing tools for *A. minutum* blooms in the ecosystems studied.

1. Introduction

Harmful Algal Blooms (HABs) are phytoplankton proliferations responsible for negative ecological, public health and economical repercussions in aquatic ecosystems all over the world (Hallegraeff, 2003). Among them are toxic microalgae, which produce toxins (Hallegraeff, 2003). One of the major significant toxic species in coastal and estuarine ecosystems is the globally distributed *Alexandrium minutum* (Anderson et al., 2012). The main threat of this species is its ability to produce Paralytic Shellfish Poisoning (PSP) toxins, contaminating shellfish resources and causing illness and even death in human consumers (Anderson et al., 2012).

Many studies have been carried out to understand *A. minutum* dynamics and the conditions promoting its toxicity. Laboratory experiments generally focused on a few factors affecting growth, toxin production or determining life-cycle transitions (Chang and McClean, 1997; Figueroa et al., 2007, 2011; Grzebyk et al., 2003; Laabir et al., 2011, 2013; Lim et al., 2006), but these factors usually do not cover the range of environmental conditions. In many field studies dealing with the dynamics and toxicity of this species, only local and/or short-term scales were considered and the findings were therefore constrained by the boundaries of the temporal window and the ecosystem studied (Abdenadher et al., 2012; Bravo et al., 2010; Calbet et al., 2003; Pitcher et al., 2007; Vila et al., 2005; among others).

Monitoring programmes give the opportunity to conduct studies on long time-space scales as they provide continuity through time and broad spatial coverage, as well as information on the onset, termination, intensity and toxicity of outbreaks (Wells et al., 2015). The French programme for phytoplankton and phycotoxin monitoring (REPHY), managed by Ifremer, has been recording occurrences of toxic and non-toxic species and also environmental variables (*inter alia* salinity, temperature, turbidity) since 1984. Several studies highlighted the valuable information gathered, including phytoplankton community shifts (Hernández-Fariñas et al., 2014) or species niche characterization (Hernández-Fariñas et al., 2015; Husson et al., 2016).

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The first *A. minutum* bloom detected in the French English Channel – Atlantic coasts was in the Bay of Vilaine in 1987 (Lassus and Bardouil, 1988) and since then regularly proliferated causing PSP shellfish closure. Therefore, more than 25 years of data on *A. minutum* in this area allow an approach on a scale never studied before.

Phytoplankton blooms present recurrent cycles and show variations in the timing and amplitude from year to year and zone, resulting from the integrated interplay of physical and biological processes (Ferreira et al., 2014). Therefore, large temporal and spatial studies of these events can provide great insight into the mechanisms driving them. Phenology is a valuable tool to detect these changes. Many examples exist with terrestrial and limnological species (Parmesan and Yohe, 2003; Walther et al., 2002), and recently, studies in marine science have linked species cardinal dates to climate change (Edwards and Richardson, 2004; Greve et al., 2005; Ji et al., 2010; among others). In the present study, the methodology developed by Rolinski et al. (2007) was chosen to study the *A. minutum* blooms, as it is adapted to the data set features. Several phenological parameters were determined and related to environmental variables, including PSP toxicity.

This approach aims to identify the global factors modulating the bloom shape. Since the effect of some variables may be masked by the local characteristics of each region studied, a threshold analysis was performed to complement phenology and to bring out the local characteristics of the regions included in the study. It is similar to a niche analysis in which the effect of the environmental variables constraining or triggering *A. minutum* blooms is studied using the abundance data. This analysis was carried out at local and global scale to better understand the variable effect on the species dynamics. This information was then used to determine the environmental condition modulating each bloom.

The objectives of this study were to (i) characterise the blooms of *A. minutum* through the phenology analysis and relate their variability to environmental conditions, and to (ii) study the effect of the environmental conditions triggering or limiting this species abundance and its blooms.

2. Material and methods

2.1. Primary data set

Data were collected from different sources. The main source was the REPHY monitoring programme, implemented and managed by IFREMER. It includes stations scattered all over the French coastline. Other sources include data from research projects carried out at Ifremer and at the Station Biologique Roscoff (CNRS) from the same area.

Stations and sampling frequencies changed over time as a response to different requirements of the monitoring programme. Three sampling strategies were implemented: *Flortot*, carried out in few stations with monthly frequency, where all the phytoplankton species >20 μm are enumerated; *Florind*, to control exceptional phytoplankton blooms (abundances > 10^5 cells L^{-1}) or the presence of toxic species with sanitary purposes; and *Florpar*, to monitor toxic species with fortnightly sampling, increasing to weekly sampling when abundances are higher than the species alert threshold (10^4 cells L^{-1} for *A. minutum*). In addition, data from other research projects carried out by IFREMER or Station Biologique Roscoff (CNRS) were acquired. For quantitative phytoplankton analysis, lugol-preserved samples were counted with an inverted microscope (Utermöhl, 1958). Only surface samples (0–1m) were retained.

Many environmental parameters were added to *A. minutum* counts. Water temperature (°C) and salinity (PSU) were obtained *in situ* at the same sampling point with a portable probe, although not for all samples. Water samples (100 mL) were also taken occasionally for inorganic nutrient analysis with Niskin bottles (5 L). They were stored at −20 °C until the analysis within the following month from the sampling. An autoanalyzer (Technicon III) was used following standard protocols (Hydes et al., 2010). Only $NO_3^- + NO_2^-$ and PO_4^{3-} was used in this study. Data from the other inorganic nutrients (NO_3^-, NO_2^-, NH_4^+ and SiO_4^{2-}) were discarded because they were scarce.

Daily river flow data were obtained from the data centre for French coastal operational oceanography (CDOCO). One river was assigned to each station based on the situation and its plume influence. Tidal influence in the ecosystem was integrated with two measures, the tidal coefficient and the tidal range. Daily tidal range was calculated from vertical difference between the high tides and the succeeding low tides of each day. Tides were acquired from the WXTide32 software (Flater). Tidal coefficient is a relative measure of the daily tidal range. This parameter enables easy identification of the neap–spring cycle, and varies between 20 (neap tide minimum) and 120 (spring tide maximum). Daily values are all the same for the French English Channel – Atlantic coast. It is calculated by the SHOM (Service Hydrographique et Oce'anographique de la Marine). When two tidal cycles coincided in one day, their mean was used as the tidal value of that day.

Meteorological variables used in this study were daily wind velocity (m s^{-1}) and direction (°) and daily atmospheric pressure (hPa). They were acquired from two numerical models operated by MétéoFrance: Aladin and Arôme (Seity et al., 2011). The Aladin model has a space and time resolution of 15 km and 6 h, respectively, and was used from 3rd July 1997 to 11th October 2011. The Arôme model has a space and time resolution of 2.5 km and 1 h, respectively, and was used from 12th October 2011 to 18th November 2014. The coherence between both models was tested with a correlation analysis. It was applied for a half-year period, in which both models were active (between October 2011 and March 2012). Models showed high coherence for wind and atmospheric pressure (uwind: R = 0.88; vwind: R = 0.85; atmospheric pressure: R = 0.99; n = 21 360).

Daily Sea Surface Irradiance (SSI) was derived from METEOSAT visible imagery and daily Sea Surface Temperature (SST) was derived from the Advanced Very High Resolution Radiometer (AVHRR, Le Borgne et al., 2006a,b). The situation of the stations inside bays or estuaries made the direct assignation of data from SSI and SST pixels difficult due to the lack of satellite data near the coast. In order to resolve this issue, the nearest pixel with sufficient data was assigned. SST data obtained were highly correlated with *in situ* water temperature (R = 0.93, n = 857, $p < 0.001$; Guallar et al., 2015).

Time-Series (TS) of daily variables with gaps were completed with interpolated values with a maximum of 5 days as a maximum of consecutive missing values to fill. Interpolation in longer gaps could underestimate variability in the data when trends are not linear (Cole et al., 2012).

2.2. Phenology analysis

For the phenology analysis, *A. minutum* TS were split by years and stations. They were log-transformed ($y' = \log_{10}(y+1)$) to compensate for the large weight of the extreme values in the analysis. To avoid incomplete or low quality TS, only those with more than eight samples and at least one of them with a value higher than 10^4 cells L^{-1} (*A. minutum* alert threshold value according to REPHY) were selected. Subsequently, nine-phenology variables were extracted (Fig. 1).

The Maximum Abundance (MA) and the Day of the Maximum Abundance (DMA) were directly obtained from the TS. To obtain