

Combined physical, chemical and biological factors shape *Alexandrium ostenfeldii* blooms in the Netherlands



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ABSTRACT

Harmful algal blooms (HABs) are globally expanding, compromising water quality worldwide. HAB dynamics are determined by a complex interplay of abiotic and biotic factors, and their emergence has often been linked to eutrophication, and more recently to climate change. The dinoflagellate *Alexandrium ostenfeldii* is one of the most widespread HAB genera and its success is based on key functional traits like allelopathy, mixotrophy, cyst formation and nutrient retrieval migrations. Since 2012, dense *Alexandrium ostenfeldii* blooms (up to 4500 cells mL⁻¹) have recurred annually in a creek located in the southwest of the Netherlands, an area characterized by intense agriculture and aquaculture. We investigated how physical, chemical and biological factors influenced *A. ostenfeldii* bloom dynamics over three consecutive years (2013–2015). Overall, we found a decrease in the magnitude of the bloom over the years that could largely be linked to changing weather conditions during summer. More specifically, low salinities due to excessive rainfall and increased wind speed corresponded to a delayed *A. ostenfeldii* bloom with reduced population densities in 2015. Within each year, highest population densities generally corresponded to high temperatures, low DIN:DIP ratios and low grazer densities. Together, our results demonstrate an important role of nutrient availability, absence of grazing, and particularly of the physical environment on the magnitude and duration of *A. ostenfeldii* blooms. Our results suggest that predicted changes in the physical environment may enhance bloom development in future coastal waters and embayments.

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1. Introduction

Global change is occurring at an unprecedented rate (Stocker et al., 2013), impacting ecosystems worldwide. In addition to climatic changes, anthropogenic activities have accelerated the rate and extent of eutrophication of many aquatic environments as well. These changes greatly affect phytoplankton, standing at the base of aquatic food webs. Over the past few decades, some phytoplankton species have become an increasing nuisance by forming harmful algal blooms (HABs; Anderson et al., 2002; Heisler et al., 2008). The global expansion of HABs has very often been attributed to eutrophication of coastal regions. Changes in nutrient loading, nutrient ratios and nutrient composition have a

tremendous impact on phytoplankton communities living in rivers, estuaries and coastal zones (Anderson et al., 2002; Smith and Schindler, 2009). For instance, enhanced use of urea as a fertilizer and increases in the nitrogen and phosphorus to silicate ratios may promote proliferation of toxic dinoflagellates over diatoms (Glibert et al., 2001; Riegman, 1995). In addition, further changes in climate involving temperature shifts and subsequent weather changes, may lead to an expansion of the ecological niche of many HAB-forming species (Anderson et al., 2012b; Hallegraeff, 2010; Wells et al., 2015).

HABs are known for their adverse effects on ecosystems through their cascading impact on higher trophic levels (Anderson et al., 2002; Hallegraeff, 1993). For instance, HABs can produce toxic compounds that may accumulate in the food chain, leading to the death of fish, seabirds and marine mammals. Moreover, toxins accumulated in seafood may cause shellfish poisoning syndromes in humans (Wang, 2008). Proliferations of HABs can thus have far

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reaching ecological and economic consequences. The dinoflagellate *Alexandrium ostenfeldii* is a globally widespread toxic HAB-forming species (Balech, 1995; Fraga and Sanchez, 1985; Gribble et al., 2005; John et al., 2003; Levasseur et al., 1997; Mackenzie et al., 1996; Okolodkov and Dodge, 1996; Wang et al., 2006). Although it used to occur in low numbers in phytoplankton assemblages, in recent years dense blooms of this species have been reported (Borkman et al., 2012; Burson et al., 2014; Hakanen et al., 2012; Kremp et al., 2009; Tomas et al., 2012). *Alexandrium ostenfeldii* is also known to produce various toxins, including Paralytic Shellfish Poisoning (PSP) toxins and the cyclic imines gymnodimines and spirolides (Anderson et al., 1990; Cembella et al., 2000; Harju et al., 2016; Kremp et al., 2014). In addition to these toxins, *A. ostenfeldii* produces extracellular allelochemicals, which can lyse competing phytoplankton species and small protozoan grazers (Tatters et al., 2012; Tillmann et al., 2007; Tillmann and John, 2002; Van de Waal et al., 2015). Production of toxins and lytic compounds are key traits supporting *Alexandrium* proliferation (John et al., 2015; Wohlrab et al., 2016, 2010), particularly since dinoflagellates are typically poor competitors in terms of growth and nutrient uptake (Litchman et al., 2007; Smayda, 2002). Other important traits include heterotrophic feeding, cyst formation, and nutrient retrieval migrations (Smayda, 1997).

Although these traits are effective for supporting growth, the abiotic environment also plays a crucial role in HAB initiation and subsequent development. Dinoflagellates reside as resting cysts in the sediment and, besides using endogenous clocks observed in some species (Anderson and Keafer, 1987), require various environmental stimuli in order to germinate (Anderson et al., 2005). Specifically, temperature, oxygen concentration and light play a role in cyst germination (Anderson et al., 1987; Dale, 1983). Therefore, cyst resuspension induced by wind mixing may facilitate bloom initiation. Once emerged from the cystbank, however, dinoflagellates are very sensitive to turbulence (Berdalet et al., 2007; Berdalet and Estrada, 2005; Wyatt and Horwood, 1973), and their blooms are often associated with calm weather and water column stability (Berman and Shteinman, 1998; Margalef et al., 1979 Wyatt and Horwood, 1973). Other physical controls, such as temperature and salinity, as well as chemical controls, such as nutrient availability are also important in

determining the development of HABs. Thus, a combination of environmental conditions will set the window of opportunity for HABs to develop (Anderson et al., 2012a).

Massive annual recurring *A. ostenfeldii* blooms only recently emerged in a Dutch brackish water creek (Burson et al., 2014), and were first observed in 2012. The inflow of water is derived from the agricultural hinterlands, subsequently supplying the creek ample nutrients. The outflow is regulated by a pumping station, which discharges into the Eastern Scheldt, an estuary with the main shellfish farming areas of the Netherlands (Van Der Heijden, 2007). Discharge of creek water with high *A. ostenfeldii* population densities thus forms a potential threat to the public health. Little, however, is known about the drivers underlying the proliferation of *A. ostenfeldii* in this creek. Therefore, we investigated how various physical, chemical and biological factors affected the timing and magnitude of *A. ostenfeldii* blooms in these brackish waters. To this end, we closely followed an *A. ostenfeldii* population for three consecutive years, together with temperature, wind speed, rainfall, salinity, nutrients, and zooplankton.

2. Material & methods

The brackish water creek Ouwerkerkse kreek (51°62'N, 3°99'E) is located in the Rhine-Meuse-Scheldt delta of the Netherlands (Fig. 1A; Burson et al., 2014; Van de Waal et al., 2015). It has a mean depth of 5 m with a maximum depth of 8 m, covering roughly 0.12 km².

Field data was collected for three consecutive years, starting in April 2013. At three locations in the creek (Fig. 1B), samples were taken for *Alexandrium ostenfeldii* population densities, toxin concentrations (2014–2015), and bacterial abundances (2015) once every week or every two weeks from spring until autumn. In the same period, additional monthly samples were taken at two locations for phytoplankton and zooplankton determination. Moreover, monthly samples were taken each year for salinity, inorganic nutrient concentrations and chlorophyll-a concentrations (Fig. 1B). Hourly meteorological data, i.e. temperature, wind speed and precipitation, was derived from the weather station in Vlissingen, approximately 20 km from our study site (with very similar meteorological conditions) and a moving average was calculated.

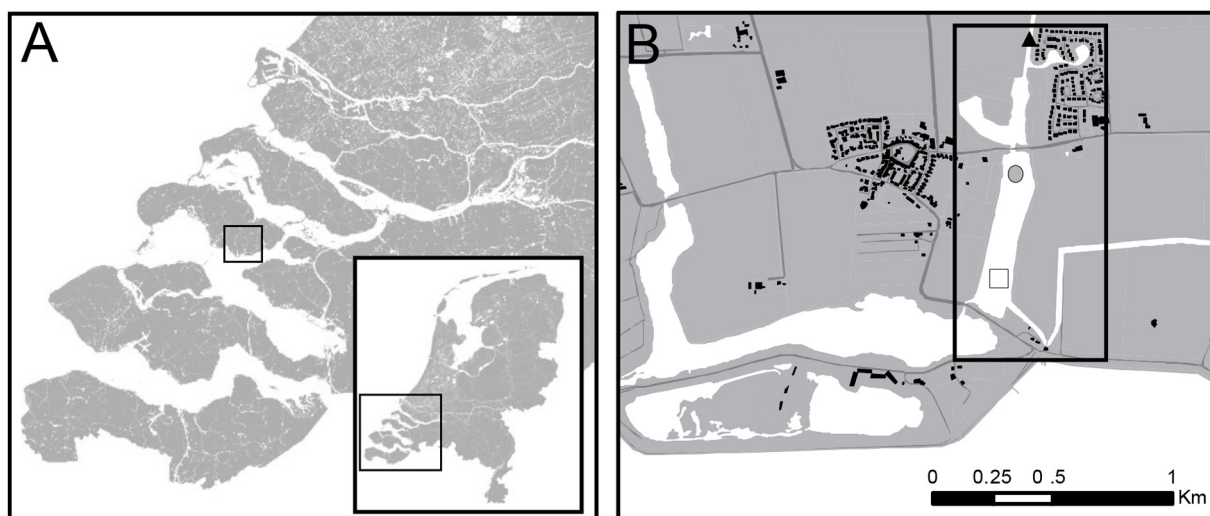


Fig. 1. Location of A) the Ouwerkerkse kreek in the Netherlands, and B) sampling points in the Ouwerkerkse kreek, where the triangle (northern part) and square (southern part) represent the sample locations for all measurements and the circle (middle part) the extra sample location for *A. ostenfeldii* abundances and toxins.

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