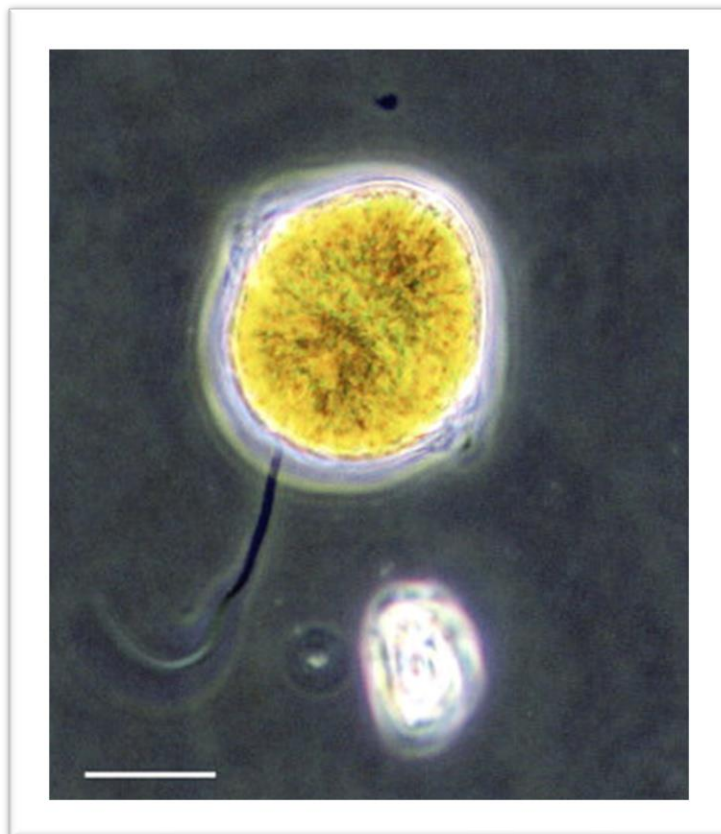


The effect of climate change on the toxic microalga
Alexandrium ostenfeldii (Dinophyceae) in the Dutch
coastal waters



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Abstract

Harmful algal blooms (HABs) are a common phenomenon in most parts of the world and can form a threat to the local economy, environment and human health. As a result of climate change, HABs have become more common as their division rate increases and their niche expands towards the poles. One of the species that can form HABs is *Alexandrium ostenfeldii*, a widespread toxic dinoflagellate that can be found in most temperate waters, including the Netherlands. During the period 2012-2015, large blooms of *A. ostenfeldii* took place in the Ouwerkerkse Kreek, which caused a risk for the mussel farms located in the Oosterschelde. The changing environment due to climate change makes it possible that *A. ostenfeldii* blooms will become more frequent in the Dutch coastal waters. Following the development of the blooms in the Ouwerkerkse Kreek, it was possible to see how the bloom was influenced by temperature, salinity, precipitation and wind speed. Rising temperatures, combined with a more stable water column due to lower wind speeds and less precipitation in summer, create a better environment for the blooms to develop. Therefore, the frequency of large *A. ostenfeldii* blooms may increase due to climate change. However, to get more certainty in how much frequency will increase, more research must be done on the role of wind speed in the germination process in shallow waterbodies.

Introduction

Phytoplankton Blooms (cell density $> 10^6$ cells L⁻¹ (Anderson *et al.*, 2008)) are naturally occurring aquatic events that take place all over the world in both freshwater and marine environments. While the blooms can positively affect their environment by providing a food source for higher trophic levels, they can also have a damaging effect on their environment. These type of blooms are classified as harmful algal blooms (HABs) and are defined as "*all aquatic species (micro-organisms) that are known to produce toxins or to cause harm, directly or indirectly, to aquatic organisms or to terrestrial organisms associated with aquatic habitats or their products*" (Landsberg, 2002). Some of the most common groups of micro-organisms that can form HABs are cyanobacteria, diatoms and dinoflagellates.

The most well-studied types of marine HABs, as a result of the negative effect they have on human health, the economy and the environment (Morabito, Silvestro and Faggio, 2018; Ritzman *et al.*, 2018), are the toxic and high biomass HABs (Tester, 1997; Masó and Garcés, 2006; Armijo *et al.*, 2020). A third, less known type of HAB is the 'mechanical' HAB. These types of HABs produce structures, for example, spines that can irritate the gills of fish and sometimes cause suffocation. (Hallegraeff *et al.*, 2003). However, in some cases, mechanical HABs are classified as a toxin HAB despite not synthesising toxic compounds (Glibert *et al.*, 2005).

Toxic HABs can consist of one or multiple phytoplankton species that produce marine biotoxins (Visciano *et al.*, 2016). Within the group of toxic HABs, a further distinction can be made between toxic species algal species that only cause damage when they reach high bloom densities and species that cause damage at low concentrations ($< 10^6$ cells L⁻¹) (Glibert, 2016). Whether algal species cause harm at high or low concentrations is determined by the toxicity of the chemical compounds the algae produce. Algae that produce these secondary metabolites do this to better compete with other phytoplankton species (allopathy) and to reduce grazing pressure by other organisms (Granéli and Johansson, 2003; Glibert *et al.*, 2005; Granéli, Weberg and Salomon, 2008). Different groups of

micro-organisms often produce different types of toxic, with dinoflagellates being the most diverse with the different types of toxin they synthesise. A short overview of the various toxins and the respective algae that they produce can be found in table 1.

There are different ways the algal toxin can cause harm to human health, the economy and the environment. The first way is to directly ingest microalgal cells by drinking water contaminated or feeding on them (Landsberg, 2002). Other methods of direct exposure are extracellular toxins that some toxic species excrete into the water, contact with toxic chemicals on the surface of the cells and mechanical damage as a result of structures that can cause damage to gills (Kent, Whyte and LaTrace, 1995; Uchida *et al.*, 1995; Hansen, Daugbjerg and Henriksen., 2000). A more indirect pathway is the accumulation of toxin through the food chain, reaching higher concentrations at each trophic level. Shellfish, though the process of filter-feeding, bioaccumulates algal toxin in their tissue, which makes it available for organisms higher up the food chain. (Hégaret, Wikfors and Shumway, 2009). The concentration of toxin in the shellfish reaches higher levels than the surrounding water (bioconcentration). When consumed, it can lead to health issues when consumed by humans and animals (Morabito, Silvestro and Faggio, 2018). When the concentration of algal toxin in commercial seafood species is above the norm deemed safe (by FAO, IOC and WHO), it cannot be sold and result in economic damage (Ritzman *et al.*, 2018; Bechard, 2019).

A high biomass HAB is the result of algae that reach such a high cell density that it disturbs environmental processes in the area (Garcés, Masó and Camp, 1999; Masó and Garcés, 2006). Most of the adverse effects the blooms have on the environment take place when they respire. When that happens, the water column under the bloom will be deprived of oxygen because of bacteria that decompose the dying algae. The discolouration of the water and the smell of the decomposing bloom can have a negative effect on tourism and so the local economy (Bechard, 2019).

HABs and climate change

The world's climate is changing due to global warming due to anthropogenic carbon emission (IPCC, 2007; Rosenzweig *et al.*, 2008). Climate change also affects the oceans and the coastal waters worldwide, especially the upper layers of the water column and shallow coastal areas are vulnerable to change (Boyd and Doney, 2002). Some of the more notable changes taking place are the rising ocean temperature, acidification and deoxygenation. But changing weather patterns like change in wind speed and total precipitation can also influence aquatic ecosystems (Mcvicar *et al.*, 2012; Rajczak and Schär, 2017).

In marine environments, algal growth is highly dependent on abiotic environmental factors like temperature, salinity, dissolved CO₂ and, nutrient availability (Anderson *et al.*, 2008; Brandenburg *et al.*, 2017; Jeong *et al.*, 2018; Trainer *et al.*, 2020). For algal blooms to reach those high densities that are needed to form harmful algal blooms, the abiotic environmental conditions have to be right. However, with climate change, these abiotic factors are changing, with some of the changes promoting and others impeding the formation of HABs. The next part of the paper will describe some of the more prominent abiotic environmental factors that are changing due to climate change and how they may influence the formation of HABs.

The first environmental factor is the one that has been the most well studied, the interaction between HABs and the rise in ocean temperature (Moore *et al.*, 2009). The rising water temperature has allowed the range expansion of warm water species into more temperate areas (Gobler, Doherty, Hattenrath-lehmann, *et al.*, 2017; Griffith, Doherty and Gobler, 2019), with at the same time temperate species moving poleward (Hallegraeff, 2010). Rising temperatures have also resulted

in species-specific changes in abundance and period of peak growth (Moore *et al.*, 2009; Hallegraeff, 2010).

The second climate factor that can influence the occurrence of HABs is the amount of dissolved CO₂ in the ocean, which has been increasing with increased atmospheric CO₂. While the exact effect of higher CO₂ levels is not yet understood, it has been hypothesised that especially dinoflagellates will profit from it (Reinfelder, 2011). It has been hypothesised that because the RUBISCO of dinoflagellates has a lower affinity for CO₂ than other phytoplankton species, they will benefit the most.

Although not directly the result of climate change, the third climate factor that will be discussed is related to extreme weather events. Besides the increase in heat waves, an increase in precipitation is also expected for the future. Increased precipitation is connected to eutrophication in the way that increased rainfall will increase the outflow of the rivers into the sea and therefore increase the inflow of nutrient into marine ecosystems (Rajczak and Schär, 2017; Sinha, Michalak and Balaji, 2017). Eutrophic conditions increase and can intensify HABs, and a large part of these high nutrient levels can be attributed to anthropogenic processes like agriculture (Glibert, 2020). However, not all species will benefit from increased nutrient concentrations. For example, some species of the dinoflagellate genus *Alexandrium* have evolved to form blooms under nutrient-poor conditions (Anderson, Glibert and Burkholder, 2002; Anderson *et al.*, 2012).

HABs in the Dutch coastal waters

Toxic HABs have long been present in the Dutch coastal waters, with the first official report of people suffering diarrhetic mussel poisoning in July 1961 (Korringa and Rosman, 1961). Later, it was discovered that this shellfish poisoning was caused by the toxic dinoflagellate *Dinophysis acuminata* (Kat, 1983), which had accumulated in the tissue of the mussel *Mytilus edulis* and, when consumed, resulted in health issues by humans (Hégaret, Wikfors and Shumway, 2009). A more recent HAB event in the Netherlands that got much attention was a large bloom of the toxic dinoflagellate *Alexandrium ostenfeldii* in Ouwerkerkse Kreek in 2012 and the three consecutive years (Burson *et al.*, 2014). *A. ostenfeldii* produces paralytic shellfish poison and is one of the most common bloom-forming toxic algae. The bloom was seen as a possible economic and ecological threat because of the creeks outflow into the Oosterschelde estuary, where a lot of shellfish aquaculture takes place (Kamermans, Blanco and Poelman, 2013). It was also the first time a large *A. ostenfeldii* bloom was ever recorded in the Netherlands. However, low densities of the species were already present in the Dutch coastal waters for the last two decades (Mulderij *et al.*, 2011). It has been suggested that the appearance of this large bloom was the result of the changing environmental conditions due to climate change and that with changes expected in the future, these large blooms will become more common in temperate regions like the Netherlands (Brandenburg *et al.*, 2017). Therefore, the purpose of this literature study is to get an insight into how climate change will possibly affect the presence of the toxic *A. ostenfeldii* in the Dutch coastal waters.

Characteristics of *Alexandrium ostenfeldii*

Alexandrium ostenfeldii is a unicellular species that belongs to the class of the Dinophyceae and was first described as *Goniodoma ostenfeldii* in 1904 in northern Iceland (Paulsen, 1904). The genus *Alexandrium* is known for its high number of toxic species and how widespread they are (Anderson *et al.*, 2012). *A. ostenfeldii* is a thecate dinoflagellate and can be distinguished from other *Alexandrium*

species by a large ventral pore and a large narrow plate 6" (figure 1) (Tomas *et al.*, 2012). *A. ostenfeldii* is like other *Alexandrium* species globally widespread and can be found in most temperate waters on both the northern and southern hemisphere, although it mostly develops blooms in coastal regions (Borkman *et al.*, 2012; Hakanen *et al.*, 2012; Tomas *et al.*, 2012; Burson *et al.*, 2014). Some of the regions *A. ostenfeldii* has been found were; Mexico (Okolodkov and Gárate Lizárraga, 2006), Peru (Kremp *et al.*, 2014), Argentina (Fabro *et al.*, 2017), New Zealand (Rhodes and Smith, 2018), China (Gu, 2011), Japan (Sildever *et al.*, 2019), Baltic Sea (Hällfors, 2004) and the Mediterranean (Gómez, 2003). The genus *Alexandrium* is also characterised by its complex lifecycle (figure 2). One of these characteristics is the formation of resting cysts that rest in the sediment when conditions are unfavourable and germination when the conditions become better (Anderson and Keafer, 1987; Smayda, 2003). Some of the environmental conditions that determine if germination will occur are temperature, upwelling from the sediment and nutrient concentrations (Figueroa and Bravo, 2004; Hakanen *et al.*, 2012; Brandenburg *et al.*, 2017). The conditions for germination can differ between the different species and even between different strains of the same species.

Lab experiments have shown that *A. ostenfeldii* showed growth between 11.3–23.7 °C and a salinity of 10-40 psu and reached a maximum division rate under optimal conditions (20 °C and 15-20 psu) of 0.3 divisions d⁻¹ (Jensen and Moestrup, 1997). The size of the cells was between 12x10³ and 20x10³ μm³. The genus *Alexandrium* is the only known genus that produces four different groups of biotoxin; saxitoxins (paralytic shellfish toxin, PST), spirolides (SPX), gymnodimines (GYM) and goniodomins (Anderson *et al.*, 2012). Whereas *A. ostenfeldii* is the only known species within the genus that can produce three types of toxin, the PST's, spirolides and the gymnodimines (Cembella *et al.*, 2001; Martens *et al.*, 2017). Some strains of *A. ostenfeldii* produce the PST characteristic for the *Alexandrium* genus, while other strains produce spirolides instead (Cembella, Lewis and Quilliam, 2000). Spirolides are a group of fast-acting toxins whose toxicity strongly depends on their cycloimine group, which can be highly variable between different strains (Hu *et al.*, 1996). The third type of toxin found within the species *A. ostenfeldii* are the gymnodimines (van Wagoner *et al.*, 2011). Gymnodimines have previously only been associated with species belonging to the genus *Karenia*, but now there also have been some strains of *A. ostenfeldii* that produce the chemical (Miles *et al.*, 2000). Although *A. ostenfeldii* as a species can make different types of toxin, most strains only produce one type of toxin. However, some strains produce multiple types of toxin, including strains found in the Netherlands (Van de Waal *et al.*, 2015). The spirolides and gymnodimines are extracellular; for the PST, it is less clear (Martens *et al.*, 2016). Results from the termination of the 2012 bloom seem to suggest that the toxin is extracellular, but laboratory experiments indicate that they are intracellular (Burson *et al.*, 2014).

History of *Alexandrium* in the Dutch coastal waters

Alexandrium species have been detected in samples collected from the Dutch coastal waters since 1990 (Tripos, 1991). 1990 was also the year that the Dutch government started its monitoring program in which they collected water samples from different locations around the Dutch coastal area to test them for the presence of potentially toxic algal species^a. Throughout the years,

^a The phytoplankton rapport of Rijkswaterstaat did not include a map of all the different sample points nor any coordinates.

Alexandrium species have been present in low concentrations, with the species *A. tamarensis*, *A. minutum* and *A. ostenfeldii* being the most common (Mulderij *et al.*, 2011). From 2000 through 2011, the concentration of Alexandrium remained low for all the different sampling location, with relatively high concentrations being around 200 cell L⁻¹ (Mulderij *et al.*, 2011, 2012).

In Augustus 2012, a dense bloom of *A. ostenfeldii* had formed in the Ouwerkerkse Kreek in the province of Zeeland (figure 3). The bloom had a density of 1-2 million cells L⁻¹, while the predetermined concentration limit that was deemed safe was set at 1000 cells L⁻¹ (Burson *et al.*, 2014). For the next three consecutive years (2013-2015), the bloom formed again in the same location, although the densities and duration of each bloom (figure 4) were different for each year (Brandenburg *et al.*, 2017). In 2014, there were also high densities (10.400 cells L⁻¹) of *A. ostenfeldii* found in Westzaan, a region in the province of Noord-Holland (van Wezel, van den Oever and Wanink, 2015). This region borders the Noordzee Kanaal, which is a channel that connects the Markermeer (starts in Amsterdam) and the North Sea (ends in IJmuiden). In 2015 (5.600 cells L⁻¹) and 2017 (39.000 cells L⁻¹), *A. ostenfeldii* was again found at high densities at the measuring point in Westzaan (van Wezel, van den Oever and Boonstra, 2016; van den Oever *et al.*, 2018). In 2017 and 2018, they also found high densities in IJmuiden, 36.846 cells L⁻¹ and 6766 cells L⁻¹ respectively (van den Oever *et al.*, 2018, 2019). It is interesting to note that although *A. ostenfeldii* has been present at low densities for a long time in the open waters of the North Sea and the Wadden Sea, the high densities of the past few years were all located in brackish areas. However, it was not clear from the reports that the measuring point in IJmuiden was located in the North Sea or in the Noordzee Kanaal. Although it was mentioned that it was previously included in the freshwater monitoring program.

A. ostenfeldii and climate change: case study Ouwerkerkse Kreek

In short, the aspects of the Dutch climate that are changing and have the largest influence on the abiotic environment of marine ecosystems are temperature, precipitation and wind speed (van den Hurk *et al.*, 2007). Overall, it can be summarised that temperatures are expected to increase, precipitation will decrease in summer and increase in winter, and overall wind speeds are decreasing (Mcvicar *et al.*, 2012). All these changes can affect the stratification of the water column, influencing the influx of nutrients from the lower water layers to the upper water layers (Lewandowska *et al.*, 2014). To gain more insight into how different abiotic climate factors can influence *A. ostenfeldii* blooms, the results from three different papers were used. One field study (Brandenburg *et al.*, 2017) and two laboratory experiments (Van de Waal *et al.*, 2015; Martens *et al.*, 2016).

Scientists were able to follow the development of the *A. ostenfeldii* blooms in the Oosterschelde (figure 3) for the years 2013-2015 and compared the blooms' characteristic with factors like temperature, salinity, nutrient concentration and grazing (Brandenburg *et al.*, 2017). While three consecutive years is a relatively short period of time, it may indicate how the Dutch strain of *A. ostenfeldii* will react to climate change. One of the first aspects they looked at was the effect of water temperature on the density of the blooms, for which they found a positive correlation (table 2). At the same time, the North Sea has increased two degrees in temperature in the past 30 years and is expected to warm even further. Based on these facts, the frequency of *A. ostenfeldii* blooms can be expected to increase in the future (Belkin, 2009). However, *A. ostenfeldii* is still a temperate species,

so if the temperature increases above a certain threshold, it could negatively affect blooms' development.

Depending on the timing, wind can positively or negatively affect the bloom-forming of *A. ostenfeldii*. The resting cysts of the algae need upwelling for successful germination and, in conditions like those found in Ouwerkerkse Kreek, upwelling as a result of strong winds is the most effective (Brandenburg *et al.*, 2017). Strong winds and water turbulation are needed to start a bloom, but overall the Brandenburg *et al.* observed a negative correlation between wind speed and the bloom development during their experiment (table 2). The cause was strong winds that destabilised the water column once the bloom was formed. As *A. ostenfeldii* is very sensitive to turbulent conditions, it resulted in a termination of the bloom (Berdalet *et al.*, 2007). Both the blooms in 2013 and 2014 developed under low wind conditions with a strong decrease in cell density during the bloom in 2014 when wind speed increased. Due to global warming, overall wind speeds have decreased, resulting in a more stable water column and so stronger stratification in the future (Mcvicar *et al.*, 2012).

The next factor that is of interest, with regard to climate change, is precipitation. As mentioned before, *A. ostenfeldii* has the highest growth ratio in laboratory conditions when the salinity is between 15-20 psu. The strain found in the Netherlands was similar in that it has a preference for brackish waters. However, high levels of precipitation in a short amount of time can result in an environment with low salinity levels, which can cause severe mortality in *A. ostenfeldii* (Martens *et al.*, 2016). This is what happened with the bloom in 2015 when heavy rainfall caused the salinity in the Ouwerkerkse Kreek to drop from around 15 to 3.7 psu, resulting in a termination of the algae bloom (Brandenburg *et al.*, 2017). Summers all over Europe have been getting warmer and drier, while precipitation levels in autumn and winter have been increasing (Barriopedro *et al.*, 2011; Rajczak and Schär, 2017; Bastos *et al.*, 2020). Less rainfall during summer will create a more stable saline environment for *A. ostenfeldii* to grow and possibly for blooms to develop.

Some of the things that have not yet been discussed are the roles of nutrient concentration and how toxicity can change within the same strain of *A. ostenfeldii*. Eutrophication resulting from the growing human population and climate change has often been suggested as one of the main reasons for an increase in harmful algal blooms in the past decades (Heisler *et al.*, 2008; Sinha, Michalak and Balaji, 2017; Glibert, 2020). However, *A. ostenfeldii*, just like other species within the genus *Alexandrium*, can form blooms under nutrient-poor conditions, and there are some indications that the species can use both autotroph and heterotroph feeding strategies (Anderson *et al.*, 2012; Brandenburg *et al.*, 2017). That means that when nutrients concentration is low, *A. ostenfeldii* can switch to feeding on other organisms and, using this method, still reach high densities. All these factors make it likely that an increase will not directly influence *A. ostenfeldii* in nutrients. However, it is always a possibility that *A. ostenfeldii* will be indirectly affected, maybe as a result of more competition as other algal species benefit from an increase in nutrient level and proliferate more. However, stronger stratification of the upper water column due to rising temperatures may prevent the upwelling of nutrient, still resulting in nutrient limitation in the upper water layers (Lewandowska *et al.*, 2014).

Another factor that makes it difficult to predict what the social and economic impact of *A. ostenfeldii* blooms will be is their variability in toxicity. The blooms in 2014 and 2015 in the Ouwerkerkse Kreek produced the same level of toxic compounds despite the bloom in 2014 being five times higher in density (figure 4, figure 5) (Brandenburg *et al.*, 2017). Analyses done on samples taken from the 2013 bloom showed high variability in toxic quota and even showed different chemical compounds for the different clones (Van de Waal *et al.*, 2015). The 20 different clones were measured under the same conditions and during the same growth phase, making the variability most likely due to genetic differences. Depending on which genetic variant is dominant during a bloom, the toxicity of an *A.*

ostenfeldii bloom can change considerably. A laboratory experiment done by Martens *et al.* using samples from 2015 bloom showed that *A. ostenfeldii* do produce more toxin when the salinity was very high (35 psu) or very low (5 psu) (Martens *et al.*, 2016).

In conclusion, factors like temperature, salinity, precipitation and wind can influence the development of an *A. ostenfeldii* bloom, and multiple of them are in turn affected by climate change. Rising temperatures will stimulate the growth of the species. Decreased precipitation and wind speed in summer, in combination with the rising temperatures, will stabilise the water column and promote stronger stratification, and as mentioned before, *A. ostenfeldii* will profit from a more stable water column. Altogether, it is, therefore, a logical conclusion that the presence of *A. ostenfeldii* in the Dutch coastal waters will change due to climate change. Based on the information available, I would expect the frequency of large blooms to increase, despite the decrease in strong winds that are needed for the germination process. Wind speeds are expected to slow down; however, the variability in wind speed is also likely to increase. So, it is still possible that the wind is still strong enough to trigger a bloom in some summers. When a bloom is initiated, the environmental conditions will better support a large bloom with the warmer summers with less wind and less precipitation. It can be expected that blooms, once formed, can persist for a longer time and possibly reach higher densities, as seen in the *A. ostenfeldii* bloom of 2014 in the Ouwkerkse Kreek. However, the density of the blooms is not always an indicator of the blooms toxicity, so future blooms will not necessarily be more toxic.

Discussion and Conclusion

What was interesting was that researchers were able to follow the development of the *A. ostenfeldii* bloom for three consecutive years. They managed to combine their findings with abiotic factors like temperature, salinity, nutrient concentration and wind speed (Brandenburg *et al.*, 2017). Samples from two of the three years (2013 and 2015) were used for laboratory experiments (Van de Waal *et al.*, 2015; Martens *et al.*, 2016). However, Van de Waal *et al.* focussed in their research on the different toxins *A. ostenfeldii* could synthesise and did not investigate how it reacts to different abiotic environmental stimuli. Martens *et al.* also focussed on toxin production of the algae, but they were interested in how salinity and temperature can influence the toxicity of the algae. The rapport from Rijkswaterstaat gave a very nice overview of where high concentrations were located, but they did not provide the coordinates of their measuring points nor any environmental data. To better understand how frequent *A. ostenfeldii* blooms will occur in the future, it would be interesting to have more field data and laboratory data from the same bloom.

As mentioned before, the summers in the Netherlands are expected to become warmer and drier (Bastos *et al.*, 2020). Combining the rising sea level with drier summers can lead to saltwater intrusions further land inwards, resulting in more places with brackish water and so more possible places that HABs like *A. ostenfeldii* can develop (Werner and Simmons, 2009). At the same time, global warming has caused a shift in climate zones and, therefore, a shift of HABs moving more towards the poles (Gobler, Doherty, Hattenrath-Lehmann, *et al.*, 2017). With the expanding of the niche of multiple toxic species of algae, species like *pseudo-nitzschia*, *Pseudochattonella verruculosa* and *Alexandrium tamarense* (Mulderij *et al.*, 2011; van Wezel and van den Oever, 2017), that are already present in the Dutch coastal waters at low densities, may increase and start to form blooms. Beside species migrating as a result of climate change, new types of toxin are still being discovered.

In 2016 the toxin tetrodotoxin (TTX) was detected above the safety limit in shellfish samples collected in the Zeeuwse Delta (Gerssen *et al.*, 2018; Biessy *et al.*, 2019). This toxin's origin is still unknown, but previously it had mainly been associated with certain fish species (Fernández-Ortega *et al.*, 2010).

In conclusion, *Alexandrium ostenfeldii* is a highly variable species that can switch between different feeding strategies and life stages depending on its environment; this makes it difficult to predict how *A. ostenfeldii* exactly will react to climate change. An experiment that compared the bloom development of consecutive years to the weather gave some insight into how the species could respond to climate change. Warmer summers with less wind and less precipitation will create a more stable environment due to stronger stratification of the water column, which is ideal for *A. ostenfeldii* blooms to develop. Therefore, it is logical that the frequency of large blooms will increase because it will be easier for the algal concentration to reach bloom-level densities once triggered. The only factor that makes it somewhat difficult to predict how frequent blooms will develop is wind speed because of its role in the germination process. The expected increase in nutrient will probably not influence *A. ostenfeldii* as the species seem to prefer lower nutrient concentrations. The toxicity of the blooms will depend on which genetic variant is the most dominant at the moment. Beside their genetic consistency, *A. ostenfeldii* also become more toxic when experiencing high-stress levels for example when they experience very high or low salinities.

Figures and Tables

Table 1: Classification of marine biotoxins and main adverse effects in humans.

Marine biotoxin	Group	Source	Symptomatology
Saxitoxin	PSP	<i>Alexandrium</i> spp. <i>Gymnodinium catenatum</i> <i>Pyrodinium bahamense</i>	<ul style="list-style-type: none"> • Gastrointestinal symptoms • Paralytic phenomena • Recovery or death
Domoic acid	ASP	<i>Pseudo-nitzschia</i> spp. <i>Nitzschia</i> spp.	<ul style="list-style-type: none"> • Gastrointestinal and neurological symptoms • Cardiac or respiratory problems • Recovery or death
Okadaic acid		<i>Prorocentrum lima</i> <i>Dinophysis</i> spp.	<ul style="list-style-type: none"> • Gastrointestinal symptoms • Recovery within 3 days
Pectenotoxin		<i>Dinophysis</i> spp.	<ul style="list-style-type: none"> • Gastrointestinal symptoms
Yessotoxin	DSP	<i>Protoceratium reticulatum</i> <i>Lingulodinium polyedrum</i> <i>Gonyaulax spinifera</i>	<ul style="list-style-type: none"> • Lack of observations in humans
Azaspiracid		<i>Amphidoma languida</i> <i>Azadinium spinosum</i>	<ul style="list-style-type: none"> • Gastrointestinal symptoms
Brevetoxin	NSP	<i>Karenia brevis</i>	<ul style="list-style-type: none"> • Gastrointestinal and neurological symptoms • Respiratory problems • Recovery or death
Ciguatoxin	CFP	<i>Gambierdiscus</i> spp.	<ul style="list-style-type: none"> • Gastrointestinal symptoms • Cardiovascular or neurological problems
Cyclic imine		<i>Alexandrium</i> spp. <i>Karenia</i> spp.	<ul style="list-style-type: none"> • Lack of observations in humans
Palytoxin		<i>Palythoa</i> spp. <i>Ostreopsis</i> spp.	<ul style="list-style-type: none"> • Gastrointestinal symptoms • Muscle and cutaneous problems

Note. Reprinted from " Marine Biotoxins: Occurrence, Toxicity, Regulatory Limits and Reference Methods" by Visciano, P. *et al.*, 2016, *Front. Microbiol.*, 7, 1051, 4.

Table 2: Spearman's rank correlation coefficients (r) describing relationships between *A. ostenfeldii* abundances, temperature and salinity (** P < 0.001, * P < 0.05).

	<i>A. ostenfeldii</i>	Temperature	Salinity
Temperature	0.74**		
Salinity	0.42*	0.40*	
Wind speed	-0.51**	-0.56**	-0.38*
Precipitation	0.16	0.13	-0.41*
DIN	-0.11	-0.57**	-0.54*
DIP	0.64**	0.85**	0.47*

Note. Reprinted from "Combined physical, chemical and biological factors shape *Alexandrium ostenfeldii* blooms in the Netherlands" by Brandenburg, K. M. *et al.*, 2017, *Harmful Algae*, 63, 149.

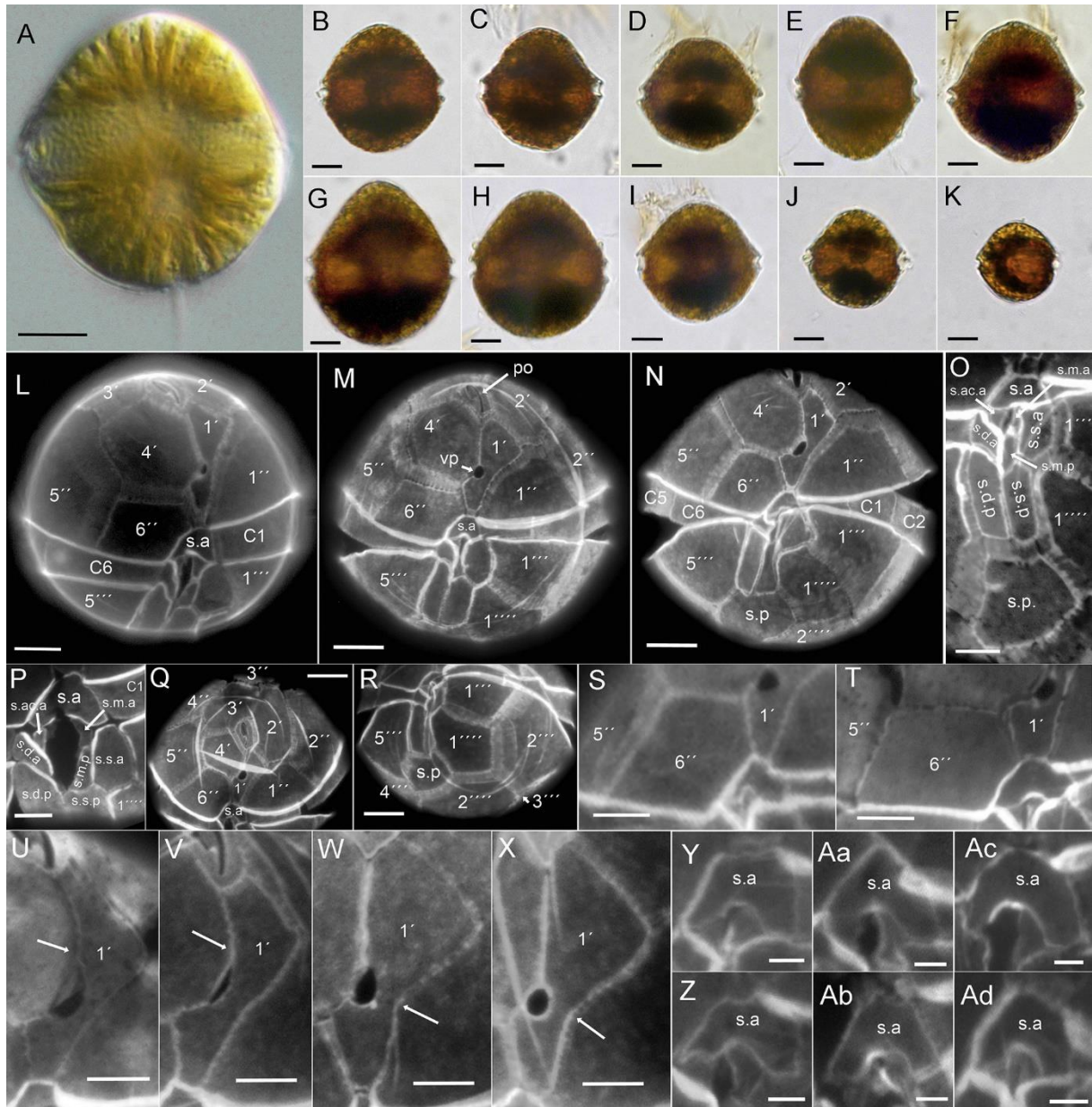


Figure 1: *Alexandrium ostenfeldii* morphology. (A–K) Bright field images of a living cell (A), and Lugol-stained cells (B–K) to show variability in cell shape (A–F) and cell size (G–K). (L–Ad) Epifluorescence images of calcofluor stained cells showing the plate pattern (L–R), and details of the 6'' place (S and T), the 1' plate and ventral pore (U–X), and the s.a plate (Y–Ad). Plate labels according to the Kofoidian system. Sulcal plates abbreviations: s.p. = posterior sulcal plate. s.s.p. = left posterior sulcal plate. s.d.p. = right posterior sulcal plate. s.m.p. = median posterior sulcal plate. s.d.a. = right anterior sulcal plate. s.s.a. = left anterior sulcal plate. s.ac.a. = anterior accessory sulcal plate. s.m.a. = median anterior sulcal plate. s.a. = anterior sulcal plate.

Note. Reprinted from “Characterization of multiple isolates from an *Alexandrium ostenfeldii* bloom in The Netherlands” by D.B. Van de Waal et al. *et al.*, 2012, *Harmful Algae*, 49, 98.

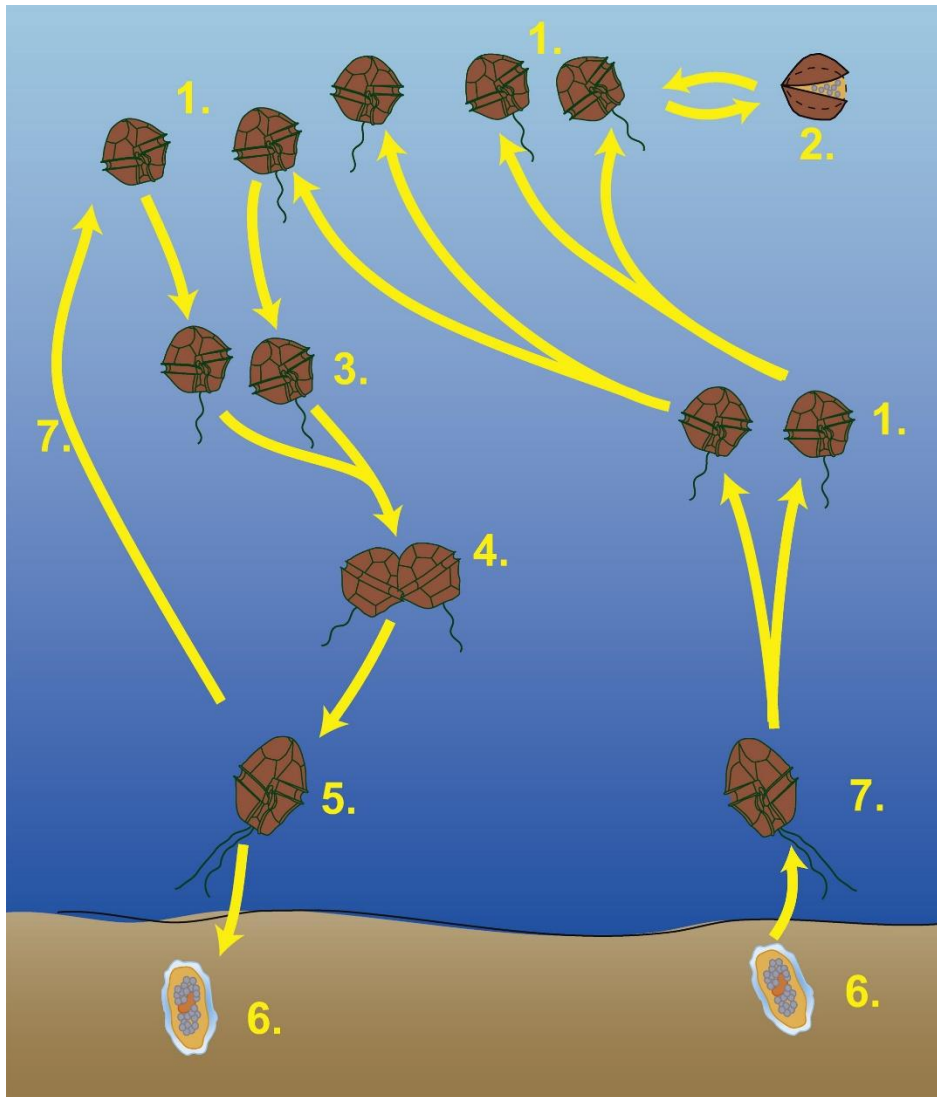


Figure 2: Schematic representation of the life cycle of heterothallic *Alexandrium* species. Species have a haplontic life cycle, i.e. the motile vegetative cells (1) are haploid. Under specific conditions, usually related to stress, some vegetative cells can transform into a non-motile pellicle cyst (2) that can rapidly switch back to the motile stage when conditions improve. The sexual phase starts with the formation of gametes (3), which conjugate (4) and form a diploid planozygote (5). Depending on environmental conditions, the planozygote can transform into a resting cyst (hypnozygote (6) or, for some species, can undergo meiosis and produce a vegetative cell (1). Cysts can spend variable periods of time in the sediments and, upon germination, release a motile cell termed a planomeiocyte (7) which divides to produce vegetative cells (1).

Note. Reprinted from “The globally distributed genus *Alexandrium* : Multifaceted roles in marine ecosystems and impacts on human health” by Anderson, D. M. *et al.*, 2012, *Harmful Algae*, 14, 19.

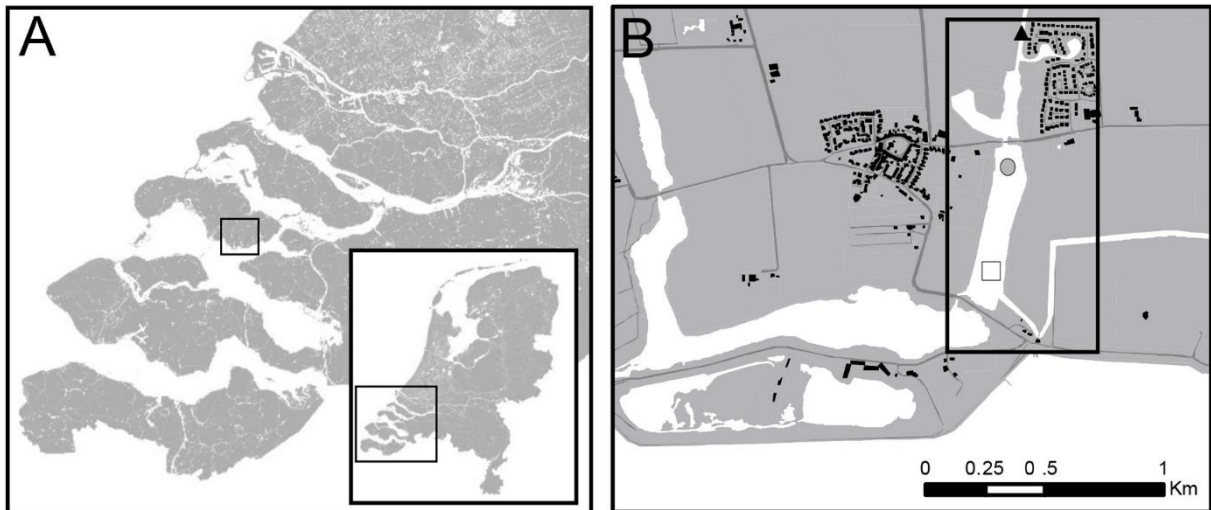


Figure 3: Location of A) the Ouwerkerkse kreek in the Netherlands, and B) sampling points in the Ouwerkerkse kreek, where the triangle (northern part) and square (southern part) represent the sample locations for all measurements and the circle (middle part) the extra sample location for *A. ostenfeldii* abundances and toxins

Note. Reprinted from “Combined physical, chemical and biological factors shape *Alexandrium ostenfeldii* blooms in the Netherlands” by Brandenburg, K. M. *et al.*, 2017, *Harmful Algae*, 63, 147.

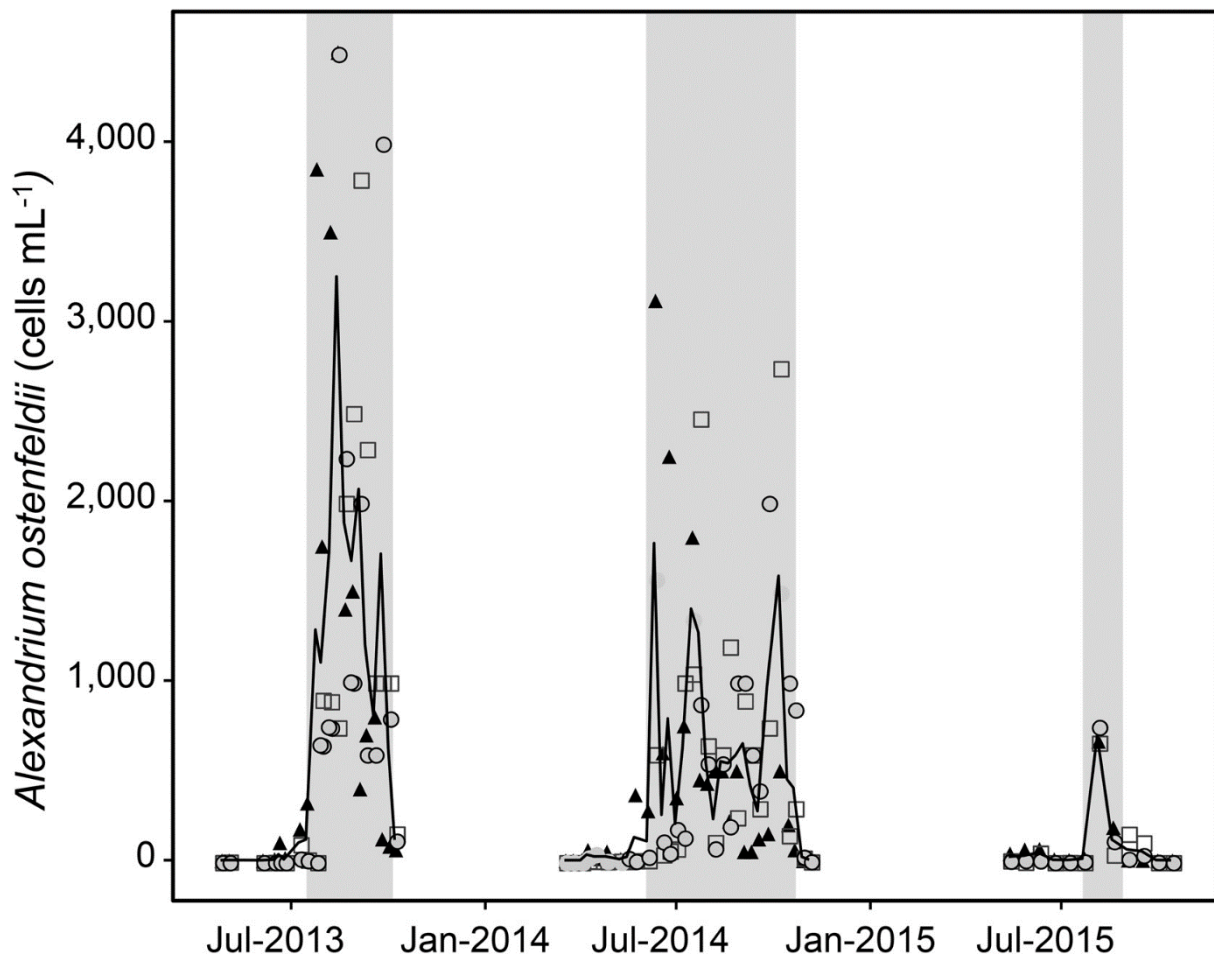


Figure 4: Seasonal dynamics of *A. ostenfeldii* population densities, where symbols (triangle the northern part, square the southern part and circle the middle part of the creek) represent the population densities at the three sample locations and the black line indicates the average.

Note. Reprinted from “Combined physical, chemical and biological factors shape *Alexandrium ostenfeldii* blooms in the Netherlands” by Brandenburg, K. M. *et al.*, 2017, *Harmful Algae*, 63, 148.

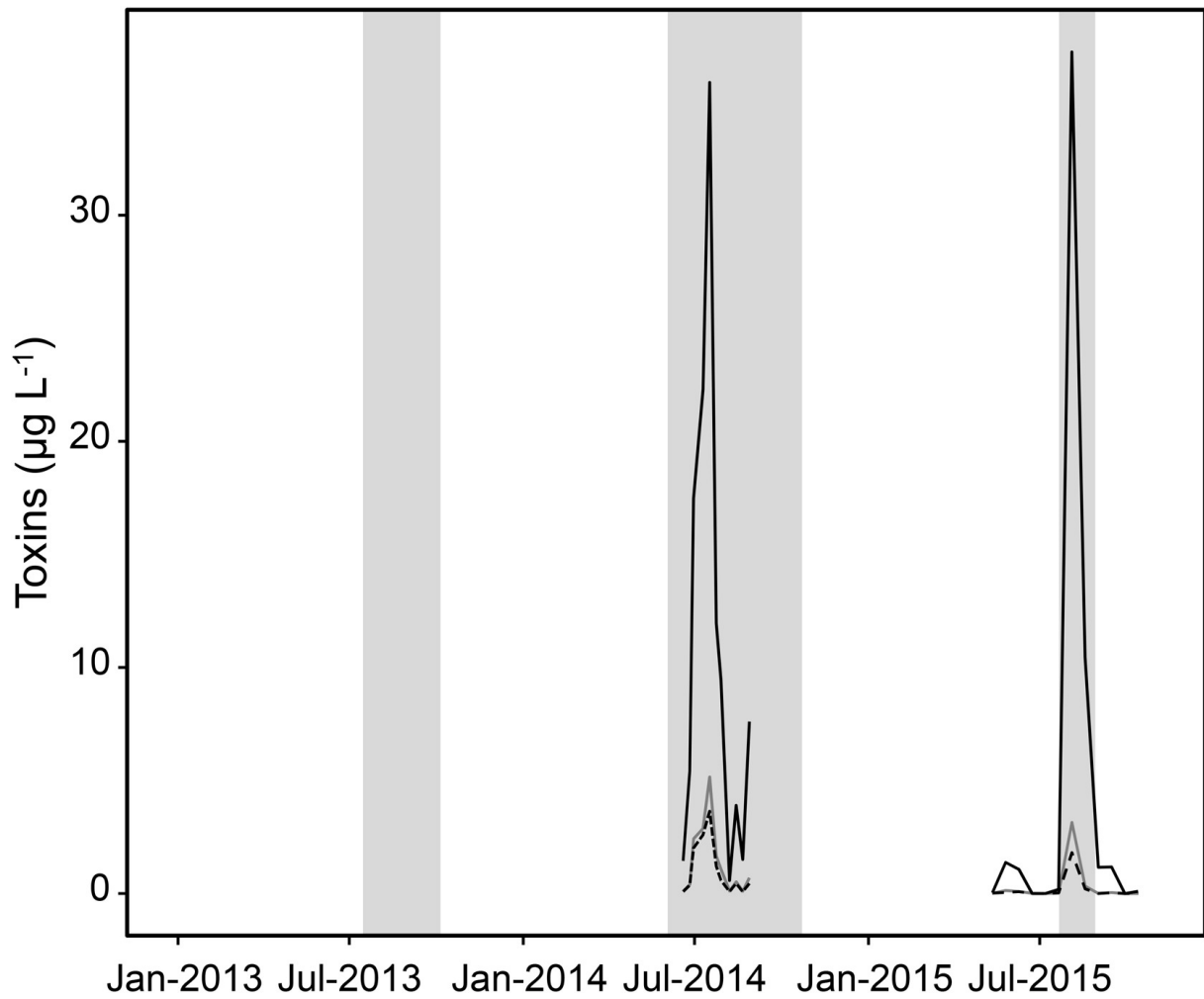


Figure 5: Seasonal dynamics in PSP toxins (black line), spiroclides (grey line) and gymnodimines (grey dotted line) during the *A. ostenfeldii* blooms of 2014 and 2015. The light grey areas in the background of each graph indicate the occurrence of an *A. ostenfeldii* bloom event.

Note. Reprinted from “Combined physical, chemical and biological factors shape *Alexandrium ostenfeldii* blooms in the Netherlands” by Brandenburg, K. M. *et al.*, 2017, *Harmful Algae*, 63, 150.

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