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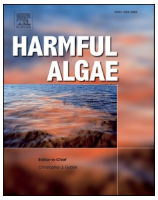

Time series analysis of the toxic dinoflagellate *Alexandrium pseudogonyaulax* across Northern European waters

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ABSTRACT

The harmful dinoflagellate *Alexandrium pseudogonyaulax* has been associated with the mortality of marine organisms, including fish. Recent evidence, although based on limited data, suggests an increasing presence across Northern European waters. To confirm this hypothesis, we analysed comprehensive long-term time series data from monitoring stations in Germany, Sweden, Denmark and Norway to assess whether *A. pseudogonyaulax* has established a sustained presence in the study region and to identify potential environmental drivers of its distribution. The findings show that this species is now a recurrent part of the microalgal community, primarily in the Kattegat, Skagerrak, and southern Baltic Sea. The seasonality of this species was found to be consistent across stations as it primarily occurs from May to October, peaking in July. Logistic regression further revealed increasing trends in occurrence at several sites. No consistent environmental drivers of this expansion were found, although its presence was associated with elevated DIN:PO_4 ratios at some stations, suggesting that other ecological mechanisms, such as top-down processes or species competition, may have facilitated proliferation of *A. pseudogonyaulax*. The species' salinity tolerance, potential dispersal of resting cysts and climate change-induced warming likely promoted its regional spread, especially into the Baltic Sea. The increasing presence and limited understanding of its toxic effects on marine organisms and humans highlight the need for continued monitoring and further research into its ecological impacts.

1. Introduction

Proliferations of toxic algae, termed Harmful Algal Blooms (HABs), severely affect coastal ecosystems and human health worldwide (Anderson et al., 2012; Gobler, 2020). Although the perceived global increase in frequency and abundance of HABs (Anderson et al., 2012, 2002) can be primarily attributed to intensified monitoring, HAB occurrences are increasing in some regions, including European waters (Dai et al., 2023; Hallegraeff et al., 2021). Toxic HABs produce marine toxins, known as phycotoxins, and other structurally uncharacterized bioactive extracellular compounds (BECs, Long et al., 2021). Phycotoxins and/or BECs can accumulate in marine organisms and propagate through marine food webs, ultimately affecting higher trophic level consumers such as marine mammals (Broadwater et al., 2018; Doucette et al., 2006), seabirds (Gibble and Hoover, 2018), and humans (Berdalet et al., 2016). Human intoxication primarily occurs through contaminated seafood, although dermal contact (Moreira-González et al., 2021) and aerosolized toxins (Lim et al., 2023) also pose health risks. Most HAB species are planktonic, yet many also have a benthic cyst life stage capable of enduring longer periods of unfavourable environmental conditions (Granéli and Turner, 2006). The coupling between benthic and pelagic life stages has been suggested to initiate the development of HABs, but also their termination (Brosnahan et al., 2020, 2017).

Eutrophication remains a key driver of HABs (Anderson et al., 2008; Heisler et al., 2008), while climate change likely alters the frequency, distribution and intensity of HABs worldwide (Dai et al., 2023; Gobler,

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2020). These alterations are driven by multiple environmental changes, such as ocean warming (Gobler et al., 2017), acidification (Riebesell et al., 2018), and deoxygenation (Breitburg et al., 2018). Rising sea surface temperatures, in particular, may drive poleward expansions (Gobler et al., 2017; Kléparski et al., 2024) and prolong blooming periods (Hjerne et al., 2019; Viitasalo and Bonsdorff, 2022) as observed in the Baltic Sea (Kahru et al., 2016; Wasmund et al., 2019) and North Sea (Llope et al., 2009). Increasing temperatures may also favour heterotrophs (O'Connor et al., 2009) and stimulate feeding of phagotrophic mixotrophs (Wilken et al., 2013).

Major HAB species in Northern Europe include fish-killing haptophytes (e.g., *Chrysochromulina leadbeateri* or *Prymnesium polylepsis*), dictyochophytes (e.g., *Pseudochattonella*) and several dinoflagellates causing Diarrhetic and Paralytic Shellfish Poisoning (Karlson et al., 2021). Among these, dinoflagellates from the *Alexandrium* genus are prominent (Long et al., 2021), and *Alexandrium pseudogonyaulax* is currently emerging in Northern European waters (Karlson et al., 2021; Kremp et al., 2019). Originally identified in the French Mediterranean Sea (Biecheler, 1952), this dinoflagellate has since been reported globally, primarily in brackish and coastal waters, including the Black Sea (Terenko, 2005), other parts of the Mediterranean Sea (Daly Yahia-Kefi et al., 2001; Montresor, 1995; Zmerli Triki et al., 2015), New Zealand (Rhodes et al., 2020), Japan (Kita et al., 1985), China (Gu et al., 2013), Vietnam (Nguyen-Ngoc et al., 2025), the Gulf of California (Morquecho and Lechuga-Devéze, 2004), the Norwegian Sea, the North Sea and the Baltic Sea (Karlson et al., 2021). This dinoflagellate belongs to the molecularly defined *Gessnerium* clade and for those species the first apical plate is not connected to the apical pore and many, if not all, produce macrocyclic polyketides known as goniodomins (Abdullah et al., 2023). Furthermore, this phagotrophic mixotroph utilizes a unique toxic mucus trap to capture and immobilize prey (Blossom et al., 2017, 2012), that is frequently released, thereby potentially contributing to vertical carbon fluxes similarly to *Prorocentrum* cf. *balticum* (Larsson et al., 2022) or *Phaeocystis antarctica* (Balaguer et al., 2023). Although it remains unclear whether goniodomins or other bioactive extracellular compounds (BECs) play a role in mixotrophy, BECs have been suggested to be the primary driver of toxic effects on microalgae, zooplankton, and fish gill cells (Moeller et al., 2024b). This dinoflagellate can grow in a wide range of light conditions (Möller et al., 2024a; Zmerli Triki et al., 2015) and tolerates a broad range of temperature and salinity (Tulatz et al., 2024).

Despite growing evidence of its expansion (Karlson et al., 2021; Kremp et al., 2019; Tulatz et al., 2024; Zettler et al., 2020), the environmental drivers of *A. pseudogonyaulax* remain poorly understood. In this study, we analyse long-term plankton monitoring data to investigate the introduction of the non-indigenous *A. pseudogonyaulax,* and whether it has established itself in Northern European waters. Furthermore, this study evaluated whether calm and stratified water bodies serve as a refugia for regional dispersal and it assesses potential environmental drivers of the proliferation of *A. pseudogonyaulax*.

2. Materials and methods

2.1. Study area

This study analysed the spread of *A. pseudogonyaulax* in the Norwegian Sea, eastern North Sea, Skagerrak, Kattegat and Baltic Sea covering a wide range of hydrographic and meteorological conditions. The Norwegian Sea, with an average depth of 2000 m, is influenced by the warm North Atlantic Current and the cold East Icelandic Current, and features strong thermal stratification, high salinities, and nutrient-rich deeper water layers (ICES, 2024). In the south, the Norwegian Sea transitions into the comparatively shallow and temperate North Sea. Characterized by strong tidal currents and water mixing, the North Sea receives substantial riverine input contributing to its nutrient-rich waters (Wilde et al., 1992). The Skagerrak-Kattegat area, located between Norway, Sweden and Denmark, is a highly dynamic system where circulation changes rapidly in response to changing weather conditions. The area is freshwater influenced due to discharge from large rivers, and it serves as a transitional zone between the Baltic and North Sea. The Skagerrak is much deeper (~700 m) and primarily stratified in contrast to the generally mixed shallow waters of the adjacent North Sea (Van Leeuwen et al., 2015). The Baltic Sea is a brackish, shallow sea with limited water exchange, which can be divided into several sub-basins, each with distinct salinities and nutrient loads. A permanent halocline at deeper depths (60−80 m) separates the water column into normoxic and hypoxic waters (Carstensen et al., 2014), while a seasonal thermocline develops at shallower depths from around April to October (Liblik and Lips, 2019). The drainage basin of the Baltic Sea is inhabited by 85 million people exerting high anthropogenic pressure (Korpinen et al., 2012). The narrow connection to the North Sea, coupled with significant freshwater input, results in a strong surface salinity gradient from about 12 in the southwest (Arkona Basin) to 3 in the northeast (Olofsson et al., 2020).

2.2. Data origin

Marine monitoring data were extracted from the Swedish National Oceanographic Data Centre database provided by the Swedish Meteorological and Hydrological Institute (Swedish Meteorological et al., 2022), the ODIN 2 database provided by the Leibniz Institute for Baltic Sea Research (Leibniz Institute for Baltic Sea Research Warnemünde 2025), the Danish national marine monitoring program for the aquatic and terrestrial environments (NOVANA) provided by Aarhus University. The Swedish dataset is composed of data from the Swedish National Marine Monitoring Program (Swedish Agency for Marine and Water Management and SMHI) as well as from regional monitoring programs, including the County Administration Board of Västra Götaland, the Water Quality Association of the Bohus Coast, the County Administration Board of Halland, the Northwest Skåne Coastal Waters Committee, and the Water Quality Association of Öresund. The Norwegian dataset is composed of data from the national monitoring program "Ecosystem monitoring of coastal waters" (Norwegian Environmental Agency and NIVA) as well as regional monitoring programs in Oslofjorden (The Council for Outer Oslofjorden and the Council for Water and Wastewater Technical Cooperation in Inner Oslofjorden), with data extracted from the database "Vannmiljø" (Norwegian Environment Agency and Trondheim, 2024). Additional phytoplankton cell counts from the national shellfish monitoring program (Norwegian Food Safety Authority) was extracted from the PHYTOMAR database provided by the NIVA.

Plankton samples were analysed following standard quantitative phytoplankton techniques as described under Annex C-6 of the HELCOM-COMBINE manual (HELCOM, 2024). Given that *A.pseudogonyaulax* is a large, distinct dinoflagellate and considering the high scientific interest in the *Alexandrium* genus, we assume that it was correctly identified, if recorded. Nonetheless, species identification with light microscopy is notoriously tricky, and despite its unique morphology, *A. pseudogonyaulax* may have been occasionally classified under broader taxonomic categories such as *Alexandrium* spp. or even as unidentified thecate dinoflagellates. Data on wind conditions were additionally extracted from the Danish Meteorological Institute's (DMI) national monitoring program.

2.3. Data analysis

All statistical analyses and data visualizations were performed using the R 4.1.2 software (R Core Team, 2022). Data transformations were performed using the 'tidyverse' (Wickham et al., 2019). Resampling in the bootstrap analysis was performed using the 'slice_sample' function in the 'tidyverse' and the GAM function of the 'mgcv' package (Wood, 2017). Plots were created using 'ggplot2' (Wickham et al., 2019) with the help of 'extrafont' (Chang, 2023), 'ggthemes' (Arnold, 2021), 'ggtext'

(Wilke and Wiernik, 2022), ‘viridisLite‘ (Garnier, 2015), ‘ggprism‘ (Dawson, 2022), ‘ggpubr‘ (Kassambara, 2023) and ‘patchwork‘ (Pedersen, 2024). Maps were generated with ‘ggOceanMaps‘ (Vihtakari et al., 2024) and ‘ggspatial‘ (Dunnington et al., 2023). Packages were managed with ‘pacman‘ (Rinker and Kurkiewicz, 2018) and package citations were compiled using ‘grateful‘ (Rodrigues-Sanchez and Jackson, 2023).

2.3.1. Data pre-processing

Microalgal data were filtered for *Alexandrium* spp. occurring across Northern European waters, specifically *A. pseudogonyaulax, Alexandrium ostenfeldii, Alexandrium tamarense* and unidentified *Alexandrium* spp. Monitoring stations were included, if sampled annually from 2010 to 2020, allowing for a maximum of three missing years, and if sampled monthly from May throughout September, with at least 10 sampling days each year. Physical and chemical water characteristics were averaged over a water depth of 10 m corresponding to the phytoplankton samples. Station data differing by only one day were also averaged. Stations in proximity, herein defined as stations within 1 km distance, were consolidated through DBSCAN clustering (Hahsler et al., 2019) to pairwise Haversine distances (Hijmans, 2024) and then combined by averaging samples taken on the same date. Applying these filtering criteria to the dataset resulted in a subset of 49 stations, primarily located in the Skagerrak, Kattegat and the south-eastern Baltic Sea (Fig. 1, Fig. S1). A few stations in the Norwegian Sea and the north-eastern Baltic Sea also had sufficient data and were included in the final dataset.

2.3.2. Calculation of the stratification index and definition of nutrient limiting conditions

Seawater density was calculated from temperature and salinity data. The water column was considered stratified (binomial yes/no) if the difference in average density between the upper and lower two metres exceeded a threshold of 1 kg m^{-3}; otherwise, it was considered mixed. Nutrient limiting conditions (binomial yes/no) were assumed if dissolved inorganic nitrogen (DIN) was below 2 μmol L^{-1} and phosphate (PO_4^{3-}) below 0.2 μmol L^{-1}.

2.4. Towards understanding the expansion of A. pseudogonyaulax

2.4.1. Assessing temporal changes in the presence of A. pseudogonyaulax

The objective of this analysis was to evaluate the introduction and whether occurrences of *A. pseudogonyaulax* across Northern European waters have increased over time and to characterize the seasonality of its presence. In addition, it aimed to assess whether observed patterns varied across distinct water body types, including estuarine, coastal and open-water stations.

The occurrence of *A. pseudogonyaulax* was modelled as a binomial variable (present or absent) using generalized linear models (GLM) with a logit link function. Separate models were fitted to assess seasonal (monthly) and interannual (yearly) variations, both at the station level and across water body types. For each station, data were restricted to years after the first appearance of *A. pseudogonyaulax*, in order not to pollute the analysis with too many absence observations before the species had established itself at the respective station. Confidence intervals (CIs, 95 %) for monthly and yearly means were calculated with the ‘confint’ function (R Core Team, 2022). Then, means and CIs were back-transformed to probabilities using the inverse of the logistic transformation. Finally, a logistic regression model was fitted to the yearly probability pattern to assess whether a significant trend or pattern, in the probability of presence of *A. pseudogonyaulax* over the years, exists. Ten stations were selected for logistic regression modelling based on a high number of *A. pseudogonyaulax* presence observations and a broad geographic coverage across Northern European waters.

The relationship between the probability of presence of *A. pseudogonyaulax* and the day of the year (DOY), at a specific station, was modelled by a generalized additive model (GAM) with a smoothing function featuring a cyclic cubic regression spline with penalized complexity to prevent overfitting. GAMs were only processed further if the smoothing function was significant ($p < 0.05$), and only stations with at least 10 observations of *A. pseudogonyaulax* were included ($n = 31$). Knots were manually specified at day 0 and day 365 based on the annual cycle. Key characteristics of the smoothing functions were extracted, including the onset (t_1) and end of the growing season (t_2), defined as the first and last DOY with predicted probabilities exceeding 10 %, as well as the peak of the growing season at which the probability was maximal (p_{max}). Next, all stations were categorized into three distinct water bodies, including estuarine, coastal and open-water stations. Quantification of 95 % CIs and assessment of group differences was then performed through bootstrapping each station’s data (n = 10,000), refitting the GAMs, and recomputing the key characteristics (t_1, t_2 and p_{max}) from the bootstrapped distributions. Effect sizes were calculated as Cohen’s *d* and interpreted as small (< 0.2), medium ($0.2-0.8$), and large (> 0.8).

2.4.2. Analysing which environmental parameters influence the short-term presence of a single species

The objective of this analysis was to identify environmental conditions influencing the short-term presence of *A. pseudogonyaulax*. Seasonal variations in environmental parameters on the day of sampling and up to 5 days lag time at each station (temperature, salinity, ammonium, nitrate, phosphate, wind speed, dissolved inorganic nitrogen and phosphorus (DIN, DIP), total nitrogen (TN), chlorophyll *a* (Chl *a*), silicate, DIN:DIP, DIN:PO_4) were modelled as the sum of a sinusoidal and cosinusoidal function. Lagged versions of environmental parameters were incorporated to assess potential delayed effects on the presence of *A. pseudogonyaulax*. The amplitude was estimated by fitting a nonlinear least squares (NLS) model to the data with initial parameter set at 2. In addition to the seasonal variation, this model describes if the presence or absence of *A. pseudogonyaulax* is associated with an anomaly (deviation from the general seasonal variation) in the environmental parameter indicating a tendency for higher or lower values. All environmental parameters, except for temperature and salinity, were log-transformed prior to this analysis. Quantification of 95 % CIs and assessment of group differences was then performed through bootstrapping each station’s data (n = 10,000), refitting the GLMs, and recomputing deviations from the bootstrapped distributions. For each station, *A. pseudogonyaulax* data were restricted to 2008 onward after which it had established itself across Northern Europe (Fig. S2) and to May throughout October. Parameters with fewer than five absence or presence observations were excluded. This model did not account for potential temporal trends in the specified environmental parameter.

2.4.3. Calculating seasonal means of environmental parameters

Monthly means, between May and October, of each environmental parameter at each station were modelled using a GLM, which estimates the relationship between the specific parameter and the month. Nutrient parameters were modelled with a log link function with a small constant (equal to one-tenth of the smallest positive value in the dataset) added to avoid zero values, stratification and limiting-condition indices using a binomial GLM, while all other models were using a standard gaussian GLM. Nutrient data were filtered to include observations after 2000, when concentrations had levelled following declines in earlier years (Riemann et al., 2016), while *A. pseudogonyaulax* data were restricted to 2008 onward after which it had established itself across Northern Europe (Fig. S2). Finally, monthly means and probabilities of observing *A. pseudogonyaulax* were averaged for each station across years and plotted against each other to assess whether it is more likely to observe *A. pseudogonyaulax* under certain environmental conditions.

2.4.4. Modelling binomial probabilities of presence as a function of temperature and salinity

This approach aimed to assess the optimal temperature and salinity range for the growth of *A. pseudogonyaulax*. The probability of its presence was modelled as a function of either temperature or salinity using a GAM. The model included a smoothing function featuring a cyclic cubic regression spline with penalized complexity to prevent overfitting. The temperature and salinity GAM included three and four manually specified knots, respectively, to constrain the smooth function to an ecologically plausible shape. For each station, data was filtered to include observations from May throughout October and years after 2007 to not pollute the data with too many absent observations. For significant models ($p < 0.05$), probabilities and 95 % CIs were predicted across a temperature range of 10−21.5 °C and a salinity range of 5−32.

3. Results and discussion

3.1. *A. pseudogonyaulax is primarily appearing in the Skagerrak, Kattegat and western Baltic Sea*

Alexandrium pseudogonyaulax was observed 1466 times across all monitoring programs, with most occurrences (~98 %) concentrated in the Skagerrak, Kattegat and the Baltic Sea west of Bornholm Island (Fig. 1, Fig. S1). In contrast, this dinoflagellate was rarely observed along the western Danish coastline (~1 %) and in the Baltic Sea east of Bornholm Island (~1 %) and only a single time along the western Norwegian coastline, from Hidlefjorden in the south up to Tanafjorden in the north (Fig. S1). Notably, *A. pseudogonyaulax* has yet to expand beyond Gotland into the northern Baltic Sea (Fig. 1, Fig. S1). After consolidating nearby stations and applying the filtering criteria, a total of 49 stations (Table S1) remained, which accounted for 1030 (~70 %) of the total *A. pseudogonyaulax* observations. This subset of stations can therefore be considered representative of *A. pseudogonyaulax* populations across Northern Europe.

In this study, the earliest occurrences of *A. pseudogonyaulax* were recorded in August and September 1997 in Aarhus Bay, followed by eight observations in 1999 across the Danish Straits, including Kattegat, Aarhus Bay, Aalborg Bay and the Öresund (Table S1, Fig. S2/S3). Although these represent the first documented occurrences in the long-term monitoring programs, earlier reports from the Norwegian coast suggest that *A. pseudogonyaulax* was present before these observations. For instance, Balech (1995) reported that *A. pseudogonyaulax* cells were "in the mucilaginous state and were abundant" in July and August 1984 in Flekkefjord (Fig. S1) in Southern Norway.

3.2. *A. pseudogonyaulax gradually became the dominant Alexandrium species between 2007 and 2009*

From 1997 to 2006, *A. pseudogonyaulax* was observed 28 times across 10 stations in the Skagerrak and Danish Straits (Fig. S1/S2, Table S1). During the following decade (2007–2016), occurrences increased sharply, totalling 460 observations across 35 stations (Fig. 2/3, Fig. S2). *A. pseudogonyaulax* suddenly appeared in Limfjorden in 2007 (Fig. 2), and by 2009, it had become the only *Alexandrium* species present, displacing the previously dominating *A. ostenfeldii* and *A. tamarense* (Fig. S2/S3; Kremp et al., 2019). A similar shift occurred in the Skagerrak and Danish Straits after 2009/2010 (Fig. 2, Fig. S1–S3). Notably, this shift was preceded by high abundances of *A. pseudogonyaulax* in Limfjorden (St. L1/L2) in 2008/2009, where average cell densities were approximately 4800 cells L^{-1} (data not shown). Similarly, average cell densities of *A. pseudogonyaulax* in Oslofjorden (St. S12, Fig. S1) were high in 2009, reaching approximately 12,500 cells L^{-1} (data not shown). Hence, it may be hypothesized that *A. pseudogonyaulax* populations from estuaries, primarily Limfjorden and Oslofjorden, have seeded populations in the adjacent Kattegat facilitating the establishment of local populations.

Ecological changes during the same period support this hypothesis. In 2008 and 2009, zooplankton abundances in Limfjorden were significantly reduced, likely due to extensive grazing by the invasive ctenophore *Mnemiopsis leidyi* (Riisgård et al., 2012a, 2012b), which was also reported from Oslofjorden as early as 2005 (Oliveira, 2007). Although jellyfish-induced trophic cascades are known to favour microalgal proliferation (Dinasquet et al., 2012; Tiselius and Møller, 2017), the connection to the establishment of *A. pseudogonyaulax* remains speculative as it is solely based on the synchrony of reported events since jellyfish abundances were not analysed in this study.

3.3. *Dispersal from the Danish straits may have seeded populations in the Baltic proper*

Given the relatively short average water residence time in the Danish Straits, typically a few months (Gustafsson, 2000), dispersal of

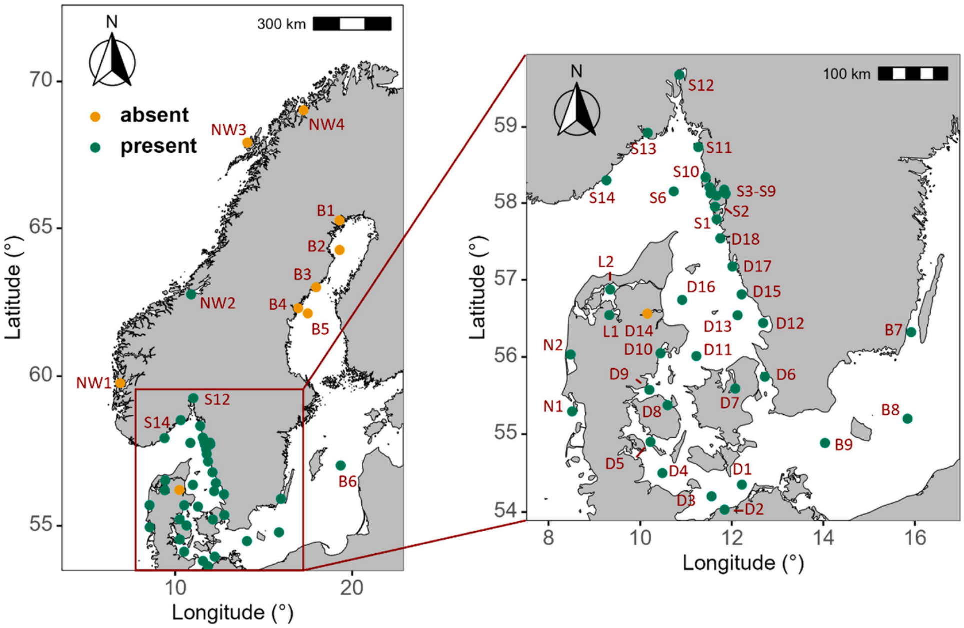

Fig. 1. Monitoring stations included in the data analysis; stations with occurrences of *A. pseudogonyaulax* are depicted in green and those without in orange; *B* = Baltic Sea; *D* = Danish Straits, *S* = Skagerrak, *N* = North Sea, NW = Norwegian Sea.

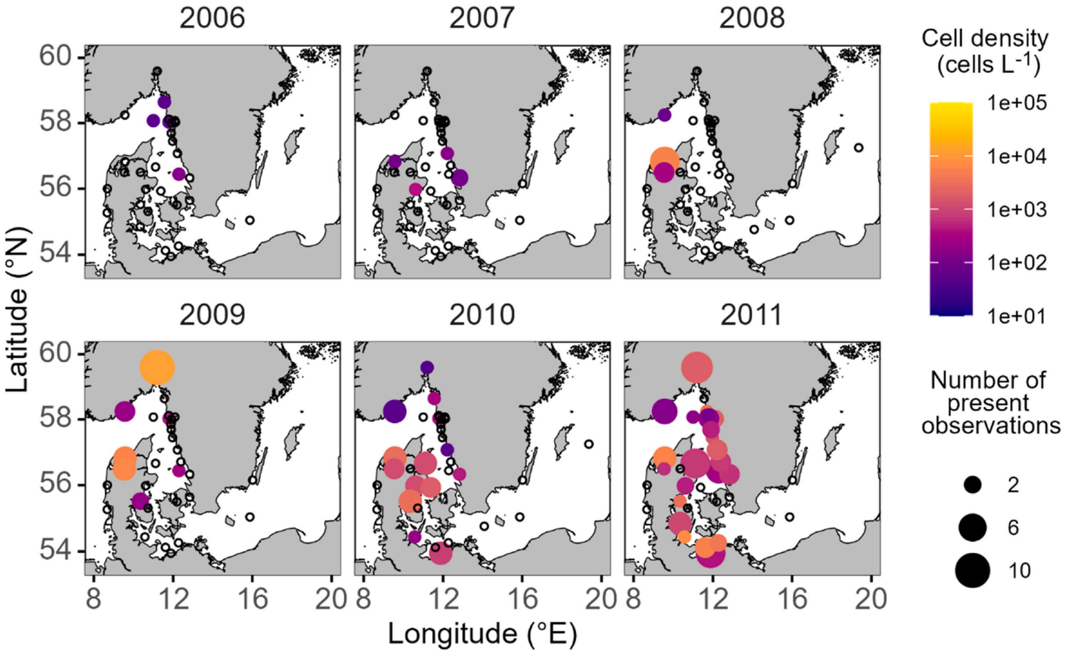

Fig. 2. Occurrences of *A. pseudogonyaulax* across Northern European waters; colour scheme corresponds to the cell densities (cells L^{-1}), the size to the number of present observations during the respective timeframe and black open circles to stations with no occurrences of *A. pseudogonyaulax*.

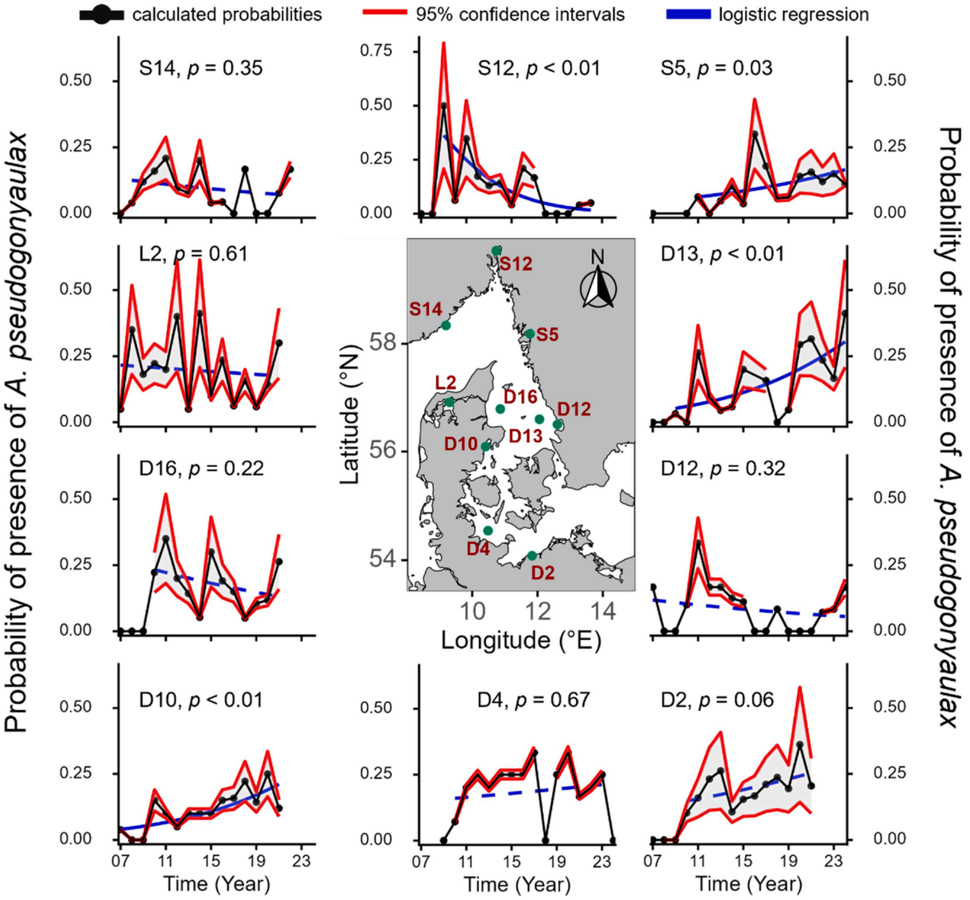

Fig. 3. Probability of presence of *A. pseudogonyaulax* across Northern European waters; black points and lines correspond to yearly calculated probabilities; red lines and grey ribbons correspond to calculated 95 % confidence intervals and the blue line and p-value to a logistic regression model fitted to the yearly probability pattern; note the different y-axis scale for station S12.

A. pseudogonyaulax from neighbouring estuaries into Kiel Bight (St. D4, Fig. S1) within one growing season is plausible. In the Baltic proper, *A. pseudogonyaulax* was first observed in the Bornholm Basin in 2014 (St. B8), in the Arkona Basin in 2018 (St. B9) and near Gotland (St. B6) in 2020 (Fig. S1). This could be explained by the fewer and less frequently sampled stations in the basins, as well as the potential impact of monitoring stations being located offshore, as opposed to the numerous coastal stations in the Danish Straits (Fig. S1).

Due to the long residence time of the central Baltic Sea and denser inflows from the Danish Straits replenishing bottom waters (Gustafsson, 2000; Wulff and Stigebrandt, 1989), it is unlikely that the presence of *A. pseudogonyaulax* in the Baltic Proper was caused by the dispersal of living cells from the Danish Straits. However, the dispersal of quiescent or dormant resting cysts cannot be excluded. Notably, *Alexandrium* cysts can remain viable for multiple years (Fischer and Brosnahan, 2022; Keafer et al., 1992; Mizushima and Matsuoka, 2004) or even decades (Feifel et al., 2015). Although cysts of *Alexandrium* are resilient towards environmental stressors, including hypoxia, germination requires oxygen (Anderson, 1998; Blanco et al., 2009). Hence, it may be speculated that perennial hypoxia in the Bornholm and Gotland Basin (Kuliński et al., 2022) prevents germination of *A. pseudogonyaulax* cysts and that the rare observations of this species, at these stations, are caused by the dispersal of cells that germinated in coastal waters, such as at station B7 near Öland (Fig. 1, S1).

3.4. High *A. pseudogonyaulax* density near Arendal in 2018 may be linked to cyst dispersal via spring flood

The highest recorded cell density of *A. pseudogonyaulax*, based on a single sample, was 2.51×10^5 cells L^{-1} in July 2018, in the Skagerrak near Arendal (St. S14, Fig. 1), at a salinity of 27.6 (Table S1). This salinity was 2.9 units lower than the mean July salinity of the preceding five years (30.5). Preceding this event was an unusually strong spring flood in Southern Norway during May 2018 followed by a period of drought (Frigstad et al., 2020). This flooding event provided significant riverine inputs, which resulted in reduced salinity and increased nutrient conditions.

Seawater around Arendal is primarily a mix of North Sea water flowing into the Skagerrak and outflowing surface waters from the Kattegat (Aure, 1998). It may thus be hypothesized that this unusually high abundance of *A. pseudogonyaulax* was caused by dispersal from Oslofjorden, initiated by the spring flood. However, no preceding *Alexandrium* blooms were observed at any adjacent stations (i.e., S10–S13). This again suggests that resting cysts, likely quiescent as they require no dormancy period (Anderson, 1998), were dispersed to Arendal (St. S14), highlighting the importance of assessing cyst abundances of HAB species that regularly bloom in coastal waters. Cell densities of *A. pseudogonyaulax* above 10^4 cells L^{-1} were recorded 22 times, primarily in polyhaline estuaries like Limfjorden and Oslofjorden (∼82 %), with only four observations (∼10 %) in meso-polyhaline open waters of Kiel Bight (St. D4) and Mecklenburg Bight (St. D3, Table S1). However, ANOVA results indicated no significant difference in cell densities between estuaries, coastal, and open-water stations ($F_{2,968}$= 0.17, p= 0.85).

3.5. Cell densities likely lower than the threshold required for ichthyotoxic effects

At 43 stations, cell densities of *A. pseudogonyaulax* never exceeded 10^4 cells L^{-1}, while at nine stations they were always below 10^3 cells L^{-1} (Table S1). That said, *A. pseudogonyaulax* is a large dinoflagellate (∼25–40 μm, Möller et al., 2024a), and hence cell densities may be misleading. For instance, in the Arkona Basin in late July 2019, *A. pseudogonyaulax* constituted over half of the total biomass in a single sample, despite a cell density of only 3.3×10^4 cells L^{-1} (Fig. S1, Zettler et al., 2020). Just eight days later, cell densities dropped sharply to 9.4×10^2 cells L^{-1} at the same station, highlighting a pronounced spatiotemporal variability of this species.

Cell densities are likely below the threshold required to cause ichthyotoxic effects, as estimated by fish gill cell bioassays (Möller et al., 2024b). However, these bioassays are generally less sensitive than whole fish bioassays (Tanneberger et al., 2013), and microalgae have been reported to form dense patches characterized by higher cell densities than their surroundings (Breier et al., 2018; Durham et al., 2013). Nevertheless, *A. pseudogonyaulax* also adversely affects microalgae, as well as micro- and meso-zooplankton (Möller et al., 2024b). Such impacts on lower trophic levels could trigger cascading effects through the food web such as reducing food availability to higher marine organisms.

3.6. Logistic regression modelling revealed no uniform trend in occurrences of *A. pseudogonyaulax*

The probability of presence of *A. pseudogonyaulax* across selected Northern European stations has not uniformly increased over the past two decades (Fig. 3), highlighting spatial variability in introduction dynamics. Logistic regression modelling suggests a gradual increase at four out of ten stations (St. S5, K5, K8 and B11), located in the Kattegat and Baltic Sea. At these stations, the probability of presence of *A. pseudogonyaulax* currently ranges between 15 and 40 %, hence this species can be considered a regular component of the plankton community. No significant trend was found for five stations ($p > 0.05$), including Limfjorden (St. L2), Arendal (St. S14), Aalborg Bight (St. D16), Laholmsbukten (St. D12) and Kiel Bight (St. D4, Fig. 3). For these, except St. D12, the probability appears constant over time suggesting a stable ecological niche through displacement of other species. In contrast, occurrences in Oslofjorden (St. S12) increased rapidly around 2009 and 2011 followed by sharp declines thereafter ($p < 0.01$), resembling a recurrent boom-and-bust dynamics. A similar pattern is apparent for St. D12 with a peak around 2011 and decline thereafter, yet the regression did not indicate a significant trend. These findings are especially notable for Oslofjorden and Limfjorden, which had previously exhibited the most frequent high-density ($> 10^4$ cells L^{-1}) occurrences of *A. pseudogonyaulax*.

3.7. Seasonality of *A. pseudogonyaulax* starts earlier in estuaries than coastal and open water stations

The seasonality of *A. pseudogonyaulax* in Northern European waters followed a consistent pattern across all surveyed stations with the highest probabilities of presence occurring between May and October, peaking in July (Fig. 4, Fig. S3) in accordance with results obtained by Carstensen and Jakobsen (2023), albeit only for Limfjorden. Based on the assumption that calm and stratified estuaries serve as a refugium, the onset of the growing season of *A. pseudogonyaulax* was expected to begin earlier in estuaries. Supporting this, it was found that the growing season in estuarine stations starts approximately 37 days earlier than at open water stations (95 % CI: [−69, −3], $d = -0.86$) and 20 days earlier than at coastal stations (95 % CI: [−52, 12], $d = -0.39$). Although the difference between estuarine and coastal stations was not significant at the 95 % CI (i.e., CI includes zero), the effect size suggests a moderate difference. Additionally, 88 % of bootstrap samples feature an earlier onset of the growing season in estuarine systems, suggesting that the effect may still hold ecological relevance. In contrast, the timing of peak and end of the growing season were consistent across all water bodies (Fig. 4, Fig. S4). Altogether, these results demonstrate that *A. pseudogonyaulax* populations follow a synchronized seasonal development across northern European water bodies and hint towards estuaries seeding adjacent coastal and open waters with vegetative cells or cysts at the onset of the season.

3.8. No single environmental driver explains the expansion of *A. pseudogonyaulax*

The preceding sections collectively demonstrate that

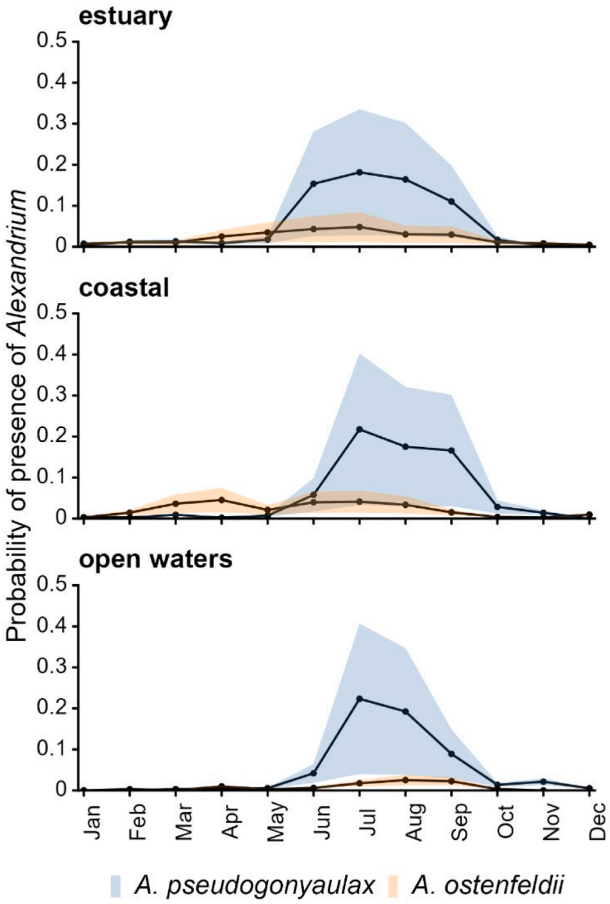

Fig. 4. Seasonality of *A. pseudogonyaulax* and *A. ostenfeldii* in estuarine, coastal and open water stations; black points and line correspond to calculated probabilities and the coloured ribbon to the 95 % confidence interval, respectively.

A. pseudogonyaulax has transitioned from sporadic occurrence to recurrent seasonal presence across Northern European waters prompting evaluation of the environmental mechanisms underlying this establishment. This study therefore examined the relationship between environmental factors and the probability of presence of *A. pseudogonyaulax* during the summer months (Fig. 5), as well as the potential influence of these factors on the short-term presence of *A. pseudogonyaulax* (Fig. 6). The temperature and salinity ranges at which *A. pseudogonyaulax* has been observed are presented in Table S1. No clear relationship was found between the likelihood of nutrient-limiting conditions or stratification and the probability of presence of *A. pseudogonyaulax* (Fig. 5). Additionally, no clear relationship between any environmental parameters, including nutrient concentrations, chlorophyll *a*, temperature, and salinity, and the probability of *A. pseudogonyaulax* presence was evident (Fig. 5). Similarly, no consistent environmental drivers, including the 1–5 day lagged versions of these parameters, were associated with the short-term presence of *A. pseudogonyaulax* as bootstrap CIs mostly overlap zero (Fig. 6).

Nevertheless, higher NO$_3$ and elevated DIN:PO$_4$ were associated with the presence of *A.pseudogonyaulax* at a subset of stations, primarily in the Skagerrak (Fig. 6). Although N:P is conventionally expressed as DIN:DIP, a strong linear correlation between PO$_4$ and DIP ($R^2 = 0.86$) suggests that DIN:PO$_4$ provides a reasonable proxy. Elevated N:P ratios, which may indicate potential phosphorus limitation, are generally considered favourable for low biomass forming dinoflagellates (Anderson et al., 2002; Glibert, 2016; Li et al., 2009). These observations provide preliminary evidence for nutrient stoichiometry playing a role in the bloom dynamics of *A. pseudogonyaulax*.

To further investigate the influence of environmental conditions, the probability of presence of *A. pseudogonyaulax* was modelled as a function of salinity and temperature using GAMs (Fig. 7). These models revealed a unimodal relationship with the top quartile of presence probabilities observed at water temperatures between 18 and 21 °C and salinities between 20 and 27. Thus, *A. pseudogonyaulax* prefers moderately warm and meso- and polyhaline conditions consistent with its relatively frequent occurrence in estuarine and coastal waters. This also aligns with Balech's description of *A. pseudogonyaulax* as "a coastal and brackish water species" (Balech, 1995). Moreover, the findings suggest that *A. pseudogonyaulax* has a high salinity tolerance, supported by observations of *A. pseudogonyaulax* in the Baltic proper at salinities below 10, albeit scarce. Tulatz et al. (2024) demonstrated a high salinity tolerance of three strains of *A. pseudogonyaulax* isolated from Limfjorden showing only slightly diminished growth at salinities of 10 compared to higher salinities. High tolerance to low salinities is further supported by

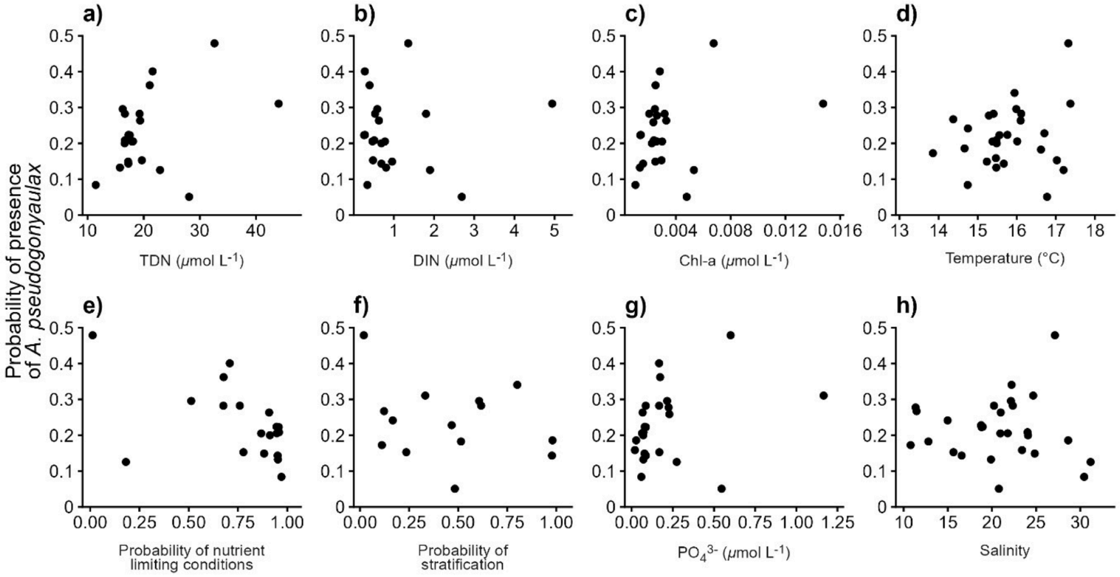

Fig. 5. Seasonal means (May throughout October) of environmental conditions vs. the seasonal probability of presence of *A. pseudogonyaulax*; nutrient limiting conditions correspond to DIN < 2 and PO$_4$ < 0.2 μmol L^{-1}; each point corresponds to one station.

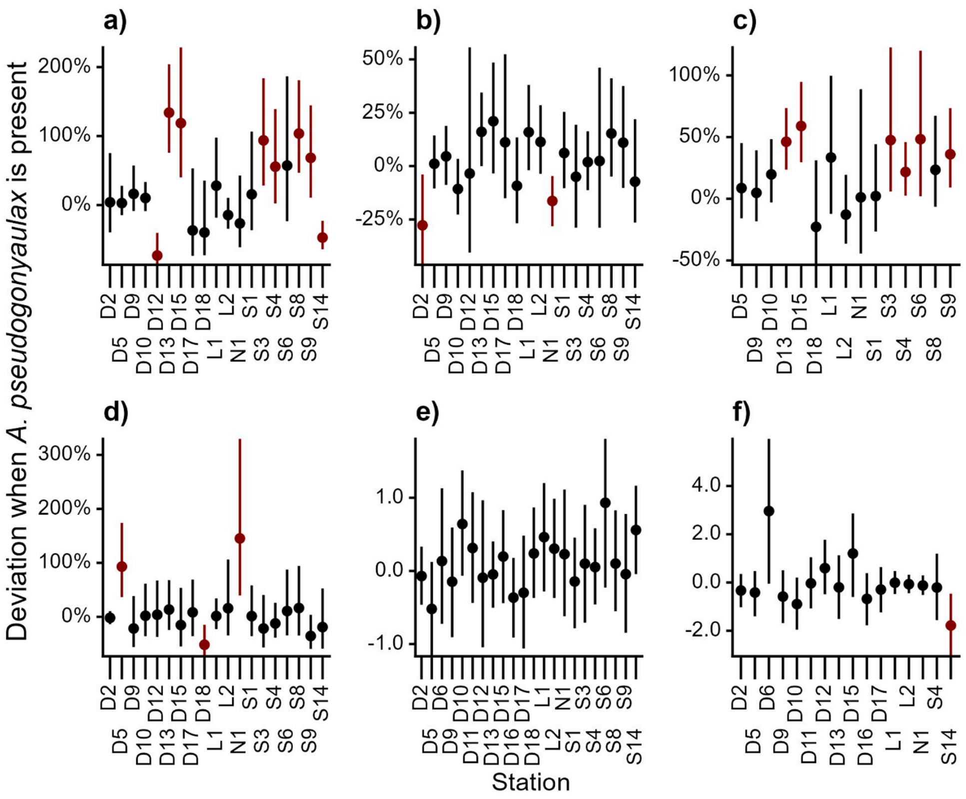

Fig. 6. Seasonal deviations in environmental parameters, including **a)** NO_3 (%), **b)** PO_4 (%) **c)** DIN:PO_4 (%), **d)** silicate (%), **e)** temperature (°C) and **f)** salinity, associated with occurrences of *A. pseudogonyaulax*; error bars correspond to the 95 % confidence intervals based on bootstrap resampling.

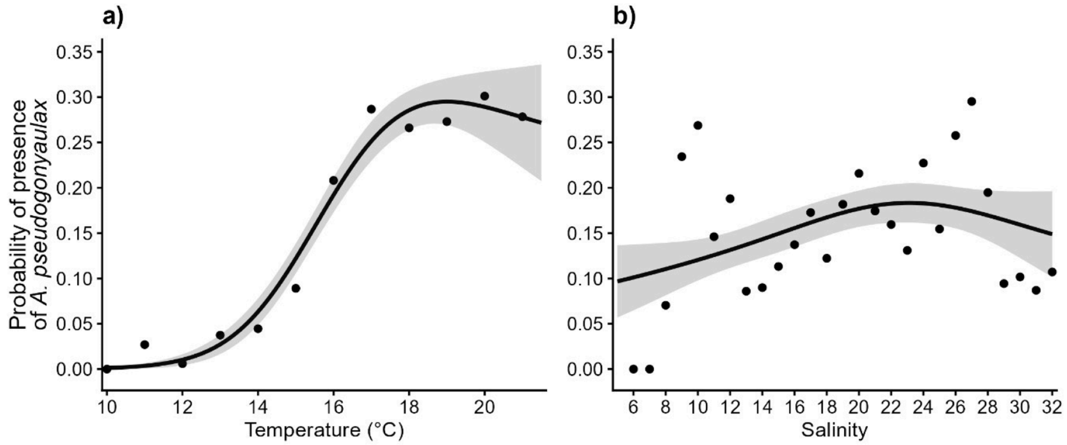

Fig. 7. Probability of presence of *A. pseudogonyaulax* as a function of **a)** temperature and **b)** salinity; points represent averaged observed probabilities across stations when *A. pseudogonyaulax* had been established (i.e., after 2007 and between May and October), while solid lines and grey ribbon correspond to the predicted probabilities and 95 % confidence intervals.

findings from a 2022 research cruise, where goniodomins, a proxy for the presence of *A. pseudogonyaulax* in Northern Europe, were detected east of Bornholm at a salinity of 7.5 (Fig. S1, Tulatz et al., 2024). This proxy is reliable because no other goniodomin-producing *Alexandrium* species are known to occur in Northern European waters. Considering that surface salinities in the Gotland Basin and the Bothnia Sea range from 5 to 10 (Fig. S1, Lehmann et al., 2022), *A. pseudogonyaulax* likely has the physiological capacity to expand further north into the Baltic Sea, potentially competing with the currently dominating *A. ostenfeldii* in shallow coastal waters of Poland, Sweden, and Finland (Hakanen et al., 2012; Kremp et al., 2009).

Distribution into the Sea of Bothnia and the Bothnian Bay currently appears constrained by temperature, as mean sea surface temperatures in July and August (~14–16 °C) are below the species' optimal range (Fig. 7). Notably, the largest projected summer SST increases in the Baltic Sea are expected in its northern basins, including the Sea of Bothnia and Bothnian Bay (Meier et al., 2022). Under RCP4.5 and RCP8.5, summer SSTs in this region are projected to rise by 2–4 °C, potentially creating favourable conditions for the northward expansion of *A. pseudogonyaulax*.

Although some environmental patterns linked to the presence of *A. pseudogonyaulax* were identified, the absence of consistent drivers across stations suggests that establishment in Northern European waters cannot be attributed to a single controlling factor. Mechanisms commonly promoting dinoflagellate proliferation, such as enhanced stratification (Erga et al., 2015; Zheng et al., 2023) or nutrient limiting conditions favouring mixotrophic taxa (Flynn et al., 2019; Jeong et al., 2010) appear unlikely to represent dominant drivers at the regional scale.

One potentially plausible mechanism supported by the present results is nutrient stoichiometry, as elevated nitrate concentrations and DIN:PO_4 ratios (Fig. 7) were associated with the presence of *A. pseudogonyaulax* at a subset of stations. However, the spatial restriction of this relationship indicates that nutrient stoichiometry alone cannot explain the species' broader regional establishment. Several additional ecological mechanisms remain unresolved due to data limitations, including top-down regulation mediated by grazing or trophic cascades (e.g., involving gelatinous zooplankton) and benthic-pelagic coupling via resting cyst dynamics. Resolving these mechanisms would require coordinated observations of grazing pressure and cyst abundances, which are currently not part of routine Northern European monitoring programmes. Moreover, although the temporal emergence of *A. pseudogonyaulax* in Limfjorden coincided with reduced abundances of other *Alexandrium*, suggesting potential interspecific competition, the limited temporal overlap among species impedes robust assessment of competitive dynamics.

3.9. Northern European establishment of A. pseudogonyaulax in a global context

Available field observations from outside Northern Europe indicate that *A. pseudogonyaulax* is globally widespread and predominantly associated with confined coastal lagoons and brackish systems. In most regions, this species has been reported as an infrequent or newly recorded taxon, often detected through cyst surveys or short-term observations, with limited evidence for long-term population establishment or recurrent blooms. High average cyst densities (639 cysts g^{-1} of dry sediment) have been reported in the Bizerte lagoon in Tunisia (Triki et al., 2014); yet, these were associated with only low to moderate cell densities (< 1000 cells L^{-1}) in the water column. Comparative vegetative cell densities have been reported from the Gulf of Venice (< 2000 cells L^{-1}; Giacobbe et al., 1998) and Odessa Bay ($\sim$1500 cells L^{-1}; Terenko, 2005). The highest documented cell density of *A. pseudogonyaulax* to date (4.73×10^5 cells L^{-1}) was reported from coastal waters of the Iberian Peninsula between 2002 and 2003 (López-Flores et al., 2006).

The occurrence of this species has been linked to elevated nitrate concentrations in the Iberian Peninsula (López-Flores et al., 2006) and the Gulf of California (Morquecho and Lechuga-Devéze, 2004) consistent with patterns identified in the present study. To date, blooming field populations of *A. pseudogonyaulax* have not been directly associated with mortality of marine biota. Nevertheless, mass occurrences of the closely related goniodomin-producing *A. monilatum* have been linked to fish kills and mortality of marine gastropods in the York river in Virginia, USA (Harding et al., 2009).

Across regions, reported occurrences are generally confined to late summer broadly consistent with the seasonal pattern observed in this study. However, available studies do not document multi-decadal persistence or spatial expansion at the scale observed in Northern European waters. In contrast, the records analysed here reveal recurrent seasonal presence across open, coastal, and estuarine environments over more than two decades. The consistency, spatial extent, and temporal persistence of these observations suggest a shift from sporadic occurrence toward regional establishment, a pattern that has not been documented elsewhere to date. This distinction highlights Northern Europe as one of the few regions where *A. pseudogonyaulax* can be assessed at population scale, underscoring the importance of long-term species-level monitoring for evaluating ecological risk and potential future expansion under changing environmental conditions.

4. Conclusions

Goniodomin producing *Alexandrium* species, such as *A. pseudogonyaulax*, have received less scientific attention than the more common PSP-producing members. However, recent findings indicate toxic effects towards a wide range of marine organisms, including fish. Consequently, the primary objective of this study was to analyse the invasion and subsequent expansion of *A. pseudogonyaulax* across Northern Europe and understand the mechanisms behind this expansion. The findings demonstrate that *A. pseudogonyaulax* has become a regular component of the plankton community, primarily in the Kattegat, Skagerrak and the southern part of the Baltic Sea, with local increases in occurrences indicated by logistic regression modelling. Expansion into the Baltic Sea appears to be facilitated by high salinity tolerance and potential dispersal via estuarine seeding and the transport of resting cysts. However, further studies are needed to confirm these hypotheses. Additionally, future comparative studies integrating regional, such as the one presented here, and global datasets on the abundance and ecological impacts of *A. pseudogonyaulax* would greatly enhance our understanding of its responses under varying and changing climatic conditions. While cell densities generally remain below thresholds for ichthyotoxic effects, the toxicity of goniodomins and other toxic BECs on broader food web dynamics remains poorly resolved. Therefore, continuous monitoring and further research into the toxicological properties and food web interactions of *A. pseudogonyaulax* are essential for effective ecosystem management and risk assessment.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the first author used Le Chat / Mistral AI in order to improve readability, language and grammar of the manuscript. After using this tool/service, the first author reviewed and edited the content as needed and takes full responsibility for the content of the published article.

CRediT authorship contribution statement

Kristof Moeller: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Hans H. Jakobsen:** Writing – review & editing, Supervision, Resources, Methodology, Data curation, Conceptualization. **Anette Engesmo:** Writing – review & editing, Resources, Data curation. **Bengt Karlson:** Writing – review & editing, Resources, Data curation. **Jacob Carstensen:** Writing – review & editing, Supervision, Resources, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Kristof Moeller reports financial support was provided by Deutsche Bundesstiftung Umwelt. Kristof Moeller reports financial support was provided by Helmholtz Association of German Research Centres. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2026.103060.

Data availability

Swedish and German monitoring data is publicly available. Norwegian monitoring data is publicly available, except for the national shellfish monitoring which is not accessible to the public. The authors do not have permission to share Danish data.

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