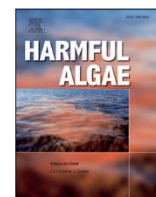




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Review

Harmful algal blooms and their effects in coastal seas of Northern Europe

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ABSTRACT

Harmful algal blooms (HAB) are recurrent phenomena in northern Europe along the coasts of the Baltic Sea, Kattegat-Skagerrak, eastern North Sea, Norwegian Sea and the Barents Sea. These HABs have caused occasional massive losses for the aquaculture industry and have chronically affected socioeconomic interests in several ways. This status review gives an overview of historical HAB events and summarises reports to the Harmful Algae Event Database from 1986 to the end of year 2019 and observations made in long term monitoring programmes of potentially harmful phytoplankton and of phycotoxins in bivalve shellfish. Major HAB taxa causing fish mortalities in the region include blooms of the prymnesiophyte *Chrysochromulina leadbeateri* in northern Norway in 1991 and 2019, resulting in huge economic losses for fish farmers. A bloom of the prymnesiophyte *Prymnesium polylepis* (syn. *Chrysochromulina polylepis*) in the Kattegat-Skagerrak in 1988 was ecosystem disruptive. Blooms of the prymnesiophyte *Phaeocystis* spp. have caused accumulations of foam on beaches in the southwestern North Sea and Wadden Sea coasts and shellfish mortality has been linked to their occurrence. Mortality of shellfish linked to HAB events has been observed in estuarine waters associated with influx of water from the southern North Sea. The first bloom of the dictyochophyte genus *Pseudochattonella* was observed in 1998, and since then such blooms have been observed in high cell densities in spring causing fish mortalities some years. Dinoflagellates, primarily *Dinophysis* spp., intermittently yield concentrations of Diarrhetic Shellfish Toxins (DST) in blue mussels, *Mytilus edulis*, above regulatory limits along the coasts of Norway, Denmark and the Swedish west coast. On average, DST levels in shellfish have decreased along the Swedish and Norwegian Skagerrak coasts since approximately 2006, coinciding with a decrease in the cell abundance of *D. acuta*. Among dinoflagellates, *Alexandrium* species are the major source of Paralytic Shellfish Toxins (PST) in the region. PST concentrations above regulatory levels were rare in the Skagerrak-Kattegat during the three decadal review period, but frequent and often abundant findings of *Alexandrium* resting cysts in surface sediments indicate a high potential risk for blooms. PST levels often above regulatory limits along the west coast of Norway are associated with *A. catenella* (ribotype Group 1) as the main toxin producer. Other *Alexandrium* species, such as *A. ostenfeldii* and *A. minutum*, are capable of producing PST among some populations but are usually not associated with PSP events in the region. The cell abundance of *A. pseudogonyaulax*, a producer of the ichthyotoxin goniodomin (GD),

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has increased in the Skagerrak-Kattegat since 2010, and may constitute an emerging threat. The dinoflagellate *Azadinium* spp. have been unequivocally linked to the presence of azaspiracid toxins (AZT) responsible for Azaspiracid Shellfish Poisoning (AZP) in northern Europe. These toxins were detected in bivalve shellfish at concentrations above regulatory limits for the first time in Norway in blue mussels in 2005 and in Sweden in blue mussels and oysters (*Ostrea edulis* and *Crassostrea gigas*) in 2018. Certain members of the diatom genus *Pseudo-nitzschia* produce the neurotoxin domoic acid and analogs known as Amnesic Shellfish Toxins (AST). Blooms of *Pseudo-nitzschia* were common in the North Sea and the Skagerrak-Kattegat, but levels of AST in bivalve shellfish were rarely above regulatory limits during the review period. Summer cyanobacteria blooms in the Baltic Sea are a concern mainly for tourism by causing massive fouling of bathing water and beaches. Some of the cyanobacteria produce toxins, e.g. *Nodularia spumigena*, producer of nodularin, which may be a human health problem and cause occasional dog mortalities. Coastal and shelf sea regions in northern Europe provide a key supply of seafood, socioeconomic well-being and ecosystem services. Increasing anthropogenic influence and climate change create environmental stressors causing shifts in the biogeography and intensity of HABs. Continued monitoring of HAB and phycotoxins and the operation of historical databases such as HAEDAT provide not only an ongoing status report but also provide a way to interpret causes and mechanisms of HABs.

1. Introduction

1.1. General background

Harmful algal blooms (HABs) are observed globally and have severe effects on fisheries, aquaculture, tourism and recreation (Berdalet et al., 2016; Hallegraeff, 2003). Harmful Algal Blooms can be split into six main categories based upon their deleterious environmental and/or human health effects: 1. those producing phycotoxins that accumulate in suspension-feeders such as bivalve shellfish; 2. those that cause damage to respiratory mechanisms (e.g., fish gills), and/or feeding responses via toxin transfer, and thus result in mortalities of fish and other marine fauna; 3. high biomass blooms that cause nuisance effects and/or result in oxygen depletion; 4. ecosystem disruptive blooms with multiple cascading effects on species interactions; 5. those that produce aerosolized toxins affecting human respiratory health; and 6. localized blooms of harmful benthic or epiphytic microalgae, which differ from planktonic HABs in habitat, mechanisms and extent of harmful effects. Particularly for planktonic versus benthic HABs, the categories overlap to some degree, e.g., certain fish-killing species can produce potent targeted phycotoxins and/or harmful substances linked to mucus production; both planktonic and epiphytic microalgae may produce aerosolized toxins; and some types of phycotoxins (e.g., diarrhetic shellfish toxins, DST) are shared between benthic and planktonic species that are not ecologically or phylogenetically closely related.

This article describes the history of the occurrence and effects of HAB categories 1–4 in the Norwegian Sea, Norwegian part of the Barents Sea, eastern North Sea, Skagerrak, Kattegat and Baltic Sea (Fig. 1). Related marine observations from the coasts of Norway, Sweden, Finland, Poland, Denmark, Germany, the Netherlands and Belgium are included. Phytoplankton have been studied in these seas since the 1800s, when pioneers such as Hans Christian Lyngbye (Lyngbye, 1819), Per Theodor Cleve (Cleve, 1897; Cleve, 1900), Kaarlo Mainio Levander (Levander 1901), Hans Lohmann (Lohmann, 1908, 1911), Carl Hansen Ostenfeld (Ostenfeld, 1908), Haakon Hasberg Gran (Gran, 1902) and Torbjørn Gaarder (Gaarder and Gran, 1927) were active. More detailed investigations of phytoplankton taxonomy, diversity, ecology and bloom dynamics have continued since then, including reference to species now recognized as harmful. In 1962, the first multi-decadal monitoring of phytoplankton within this region was initiated at Helgoland in the south German Bight of the North Sea (Franke et al., 2004; Wiltshire et al., 2010). In the late 1970s and the 1980s more systematic phytoplankton monitoring started in several other locations in northern Europe, primarily as a way to investigate effects of eutrophication. After some dramatic HAB events in the 1980s, phytoplankton monitoring with a focus on harmful species became more commonplace.

1.2. A brief history of harvesting and cultivation of bivalve molluscs in Northern Europe

Oysters (*Ostrea edulis* L.), cockles (*Cerastoderma edule* L.) and other bivalve molluscs have been harvested for human consumption in Scandinavia since the Stone Age (roughly defined as 8,700–2,000 BCE). Archaeologists have found large deposits of shells in prehistoric middens called *køkkenmøddingar* (Andersen, 2000), but it is unknown if phycotoxins affected the prehistoric societies in the area. From the 1700s (and

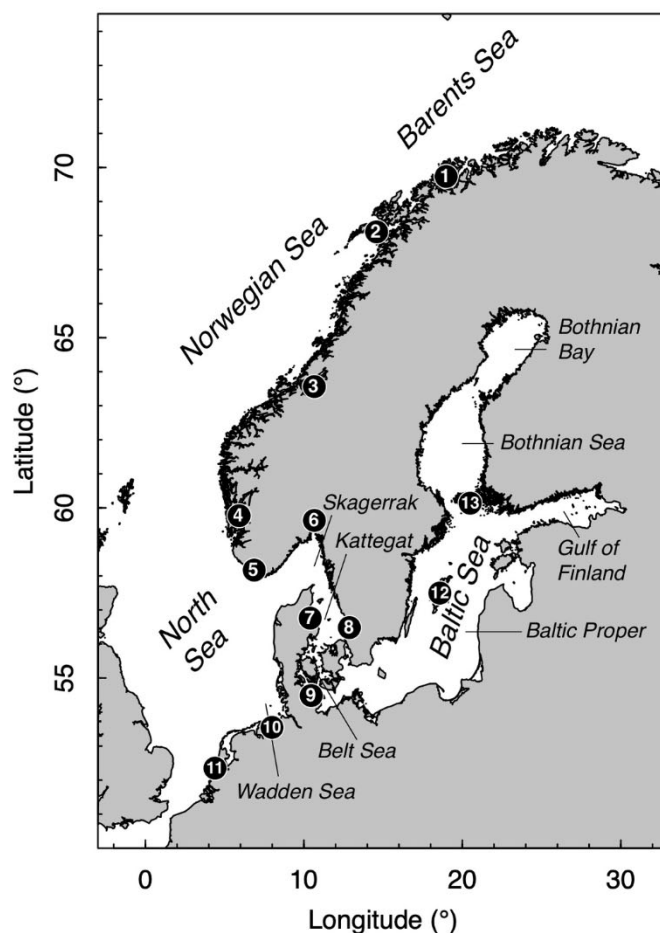


Fig. 1. Map of northeastern Europe with sea areas discussed indicated. Numbers indicate locations discussed in the text: 1. Tromsø, 2. Vestfjorden, 3. Trondheimsfjorden, 4. Sandsfjorden, 5. Flekkefjord, 6. Oslofjorden, 7. Aarhus Bay, Horsens fjord and Mariager fjord, 8. Laholm Bay, 9. Kiel Bight, 10. Wilhelmshaven, 11. Scheveningen, 12. Gotland and 13. Åland.

possibly earlier) until the present, harvesting of various bivalve shellfish with rakes, grabs and dredges has been documented (Bratrein, 1988; Strand and Vølstad, 1997). Similarly, the cultivation of shellfish in our focus region can be traced back as far as 1765, when at least one oyster farm was operating in the Netherlands (Van Beneden and Van Iseghem, 1866). The bivalve molluscs were used as bait for fishing and also for human consumption.

1.3. Historic Shellfish Toxicity problems

There is a report of apparent Paralytic Shellfish Poisoning (PSP) from Wilhelmshaven, Germany, on the coast of the Wadden Sea from 1885 (Virchow, 1885). Other early reports come from Norway; PSP seems to have been common in Trondheimsfjorden and Oslofjorden, with reports of human poisonings consistent with PSP in 1901, 1939, 1959, 1979, and 1981 (Egmond, 1993; Thesen, 1901). In the 1960s, the term “mytilotoxin” derived from the proximal source, the blue mussel (*Mytilus edulis*), was applied in Norway to refer to saxitoxin (STX), the base compound of the paralytic shellfish toxin (PST) group, in bivalve shellfish from Oslofjorden; the causative dinoflagellate species was called *Gonyaulax tamarensis* Lebour at the time (Bøhle, 1965; Oftebro and Bøhle, 1965; Wiborg and Bøhle, 1968), but is likely referable to *Alexandrium catenella* (ribotype Group 1) in current nomenclature (John et al., 2014). In Belgium in 1938, a dinoflagellate identified as *Pyrodinium phoneus* Woloszyńska & Conrad, 1939, but most plausibly referable to *A. ostenfeldii* (Paulsen) Balech & Tangen, was associated with an apparent PSP event in which 4 people died after consuming cultivated mussels (John et al., 2014; Litaker et al., 2018).

Diarrhetic shellfish poisoning (DSP) from consumption of cultured mussels was reported from the Netherlands as early as 1961 (Kat, 1983a). Farming of blue mussels (*M. edulis*) started in Sweden in the 1970s (Haamer, 1975), but it was not until 1983 that the first DSP cases occurred among people consuming mussels in Sweden. In 1984, the presence of Diarrhetic Shellfish Toxin (DST) was confirmed in blue mussels from Sweden (Edebo et al., 1988a; Edebo et al., 1988b; Haamer, 1997) by mouse bioassays and fluorescence-derivatization liquid chromatography (LC-FD). Harvesting of bivalves increased in northern European waters in the early 1980s; at this time, both DST and PST were detected in bivalve shellfish from the region, either by whole animal bioassays or LC-FD chromatographic methods, but high levels of these respective toxin groups were not usually found simultaneously (Kat, 1983b; Langeland et al., 1984; Moestrup and Hansen, 1988; Tangen, 1983). Since then, improved monitoring of phycotoxins in bivalve shellfish, by application of more advanced and standardized LC methods, cell-based and immunodiagnostic techniques, and most importantly the advent of liquid chromatography coupled tandem mass spectrometry (LC-MS/MS) methods for phycotoxins, has provided structural and quantitative confirmation of known and novel toxins in plankton and seafood matrices (Hallegraeff et al., 2004). For example, in northern Europe, the occurrence of amnesic shellfish toxins (AST) produced by the diatom *Pseudo-nitzschia* spp. (Lundholm et al., 2005) and azaspiracid shellfish toxins (AZA) from amphidomatacean dinoflagellates (*Azadinium* spp. and *Amphidoma languida* Tillmann, Salas & Elbrächter) (reports of the ICES-IOC Working Group on Harmful Algal Bloom Dynamics available at www.ices.dk) are now routinely confirmed in monitoring programmes.

1.4. Historic information on fish mortalities due to HAB

Blooms of algae causing fish mortalities are known from northern Europe since 1966, when the dinoflagellate *Karenia mikimotoi* (Miyake & Kominami ex Oda) Gert Hansen & Moestrup (formerly known as *Gyrodinium aureolum* Hulbert) caused brown water and fish kills along the south coast of Norway (Braarud and Heimdal, 1970). Since then, prymnesiophytes and dictyochophytes are the predominant algal groups responsible for fish mortalities in the region. In 1988 a bloom of

Prymnesium polylepis (Manton & Parke) Edvardsen, Eikrem & Probert caused fish mortalities and disrupted the ecosystem in the Kattegat-Skagerrak (Dahl et al., 2005; Dahl et al., 1989; Gjosaeter et al., 2000). The bloom negatively affected the whole marine ecosystem, including plankton, benthic invertebrates, fish and macroalgae. Major fish mortalities caused by blooms of *Chrysochromulina leadbeateri* Estep, Davis, Hargreaves & Sieburth occurred in Northern Norway in 1991 and 2019 (Eikrem and Throndsen, 1998; Johnsen et al., 1999; Karlson et al., 2019). The dictyochophyte *Pseudochattonella* spp. has caused fish mortalities in the Kattegat-Skagerrak area since 1998 (Edvardsen et al., 2007). The harmful algal blooms and events have been recorded in monitoring programs and short-term scientific investigations. The aim of this review is to describe the different types of harmful algae and the harmful algal bloom events in a biogeographical and historical context and to describe the linkage between selected HABs and their ecological and societal effects in the chosen geographic area.

2. Methods

This article is partly based on reports of harmful algal bloom events to the IOC-ICES-PICES Harmful Algae Event Database, HAEDAT <http://haedat.iode.org> during the period 1987 to 2019 for northern Europe. In some rare cases, earlier historic events may be included, e.g., a HAEDAT-report on an event in Belgium from 1938. Observations of harmful algae events were entered or supervised by members of the ICES-IOC Working Group on Harmful Algal Bloom Dynamics (WG HABD) representing different countries. Unfortunately, not all countries in northern Europe have participated actively in the WG HABD, and annual national reports for HAEDAT may also be inconsistently entered. For example, for the Baltic Sea region, HAEDAT reports are missing from Russia and there are very few reports entered by Estonia, Latvia and Lithuania. These sporadic reports do not accurately reflect the number of HAB events in these countries and thus such reports were not included in this publication.

The entries in HAEDAT are largely based on the national and regional monitoring programs listed in supplementary material Tables 1 and 2. Methods for phytoplankton analysis are as described by Edler and Elbrächter (2010), Utermöhl (1958), Andersen (2010) and Dahl and Naustvoll (2010). The methods for analysis of phycotoxins in bivalve shellfish follows standards set by the European Union as described in Bresnan et al. (2021).

It should be noted that sampling frequency and intensity differs among and within national and regional monitoring programmes, the methods applied to define events have been inconsistently updated since the inception of HAEDAT. An expanded definition of a HAB event is found in Bresnan et al. (2021). For phycotoxin producing taxa, a HAB event most often refers to a closure of a shellfish harvesting area due to phycotoxin concentrations above regulatory limits set by the European Union. The regulatory limits are described in Bresnan et al. (2021). A fish-killing event most often refers to finfish mortalities in aquaculture facilities due to a specific HAB, but, in some cases, mortalities of wild fish and other collateral damage to marine fauna are also recorded as marine mortality events. HAB events may also refer to high cell abundances or water discoloration, etc., such that a management decision is triggered. A common management decision is a warning to the public by authorities, e.g. because of high biomass of potentially toxic cyanobacteria. A list of toxin-producing taxa observed in the regions addressed in this article is presented in Table 3. The list is based on IOC-UNESCO Taxonomic Reference List of Harmful Microalgae (Moestrup et al., 2020).

3. Fish-killing HAB-taxa and their effects

3.1. General aspects

The prymnesiophyte genera *Prymnesium*, *Chrysochromulina*,

dinoflagellate genera *Akashiwo*, *Karenia*, *Karlodinium* and dictyochophyte genera *Dictyocha* (including *Octonaria*) and *Pseudochattonella* include most of the phytoplankton species that have caused fish mortalities in the region. Fish are killed by one or a combination of the following mechanisms: exposure to algal neurotoxins; gill irritation/damage (either mechanically or via algal production of haemolytic substances); or asphyxiation caused by mucus impeding gill function or oxygen depletion of the surrounding seawater. In northern European waters, fish mortalities have been attributed to each of these mechanisms, although usually based upon circumstantial evidence. Since 2014, several fish kills (*Salmo salar*) in land-based recycling aquaculture systems have been caused by small thecate dinoflagellates, such as *Pfiesteria shumwayae* Glasgow & J.M.Burkholder and *Luciella masanensis* P.L.Mason, Jeong, Litaker, Reece & Steidinger (Moestrup et al., 2014), but it is not clear if these mortalities were due to defined toxins or more non-specific gill membrane-disruptive effects. The costs for fish mortalities due to harmful algae are summarised in Table 4. An increase in fish mortalities due to HABs seems to coincide with an increase in finfish aquaculture but correlations were not testable.

3.2. *Prymnesium* and *Chrysochromulina*

There are >20 species of *Prymnesium* and almost 50 species of *Chrysochromulina* described (Guiry and Guiry, 2020). All are primarily phototrophic flagellates belonging to the order Prymnesiales in the phylum Haptophyta. In general, prymnesiophytes are mixotrophic to some degree and several species are phagotrophic, catching prey using their haptonema. Electron microscopy is often needed to identify *Prymnesium* and *Chrysochromulina* taxa at the species level, based on the morphology of scales. In May–June 1988 a major bloom of *P. polylepis* developed in the Kattegat, the Skagerrak and the eastern North Sea (Dahl et al., 1989; Edvardsen and Paasche, 1998; Kaas et al., 1992; Lekve et al., 2006; Skjoldal and Dundas, 1991). The bloom was ecosystem disruptive and strongly affected plankton communities (Nielsen et al., 1990), as well as benthic flora and fauna, and killed both wild and farmed fish. Long term effects on coastal fish populations and the benthic communities were, however, not observed (Gjosaeter et al., 2000). While the causes of the 1988 bloom are not fully resolved, unusually high N:P ratios of inorganic nutrients and a long period of high irradiance and calm weather may have contributed to the bloom development.

In the second half of May 1991 a bloom of *C. leadbeateri* occurred in Vestfjorden and surrounding areas in northern Norway, causing salmon mortalities at several fish farms. Between early May and early June 2019, *C. leadbeateri* again caused fish mortalities in the same area in Vestfjorden and further north near Tromsø. The direct costs for these fish mortalities due to *Chrysochromulina* are summarised in Table 4. In the 1991 event, the total losses were 742 tons of salmon with an estimated value of 3.5 million USD (Aure and Rey, 1992; Rey, 1991). The economic impacts were far more extensive in 2019; more than 8.2 million farmed salmon died, representing a value of >100 million USD (Karlson et al., 2019).

The flagellate *Prymnesium parvum* N. Carter has caused fish mortalities worldwide (Edvardsen and Paasche, 1998). In Norwegian waters, *P. parvum* has been reported from Oslofjorden (Skagerrak) in the south to Svalbard in the north. However, blooms of *P. parvum* have only been reported from the Sandsfjorden system (in Ryfylke) in western Norway, where the salinity of the surface brackish layer is typically in the range of 4 to 7 during the summer. The first reported bloom in 1989 killed 750 metric tons of caged salmon and trout, with a significant economic loss to the fish farming industry (Johnsen and Lein, 1989; Kaartvedt et al., 1991) (Table 4). Blooms occurred also in subsequent years and as a result the number of fish farms in the area decreased considerably. Following a decrease in the occurrence of *P. parvum* in the early 2000s, in 2005, fish farming was reintroduced to the area. Then the blooms abruptly reappeared; in 2007 a toxic bloom of *P. parvum* killed 135

metric tons of caged fish (Johnsen et al., 2010) (Table 4). Blooms of *Chrysochromulina* and *Prymnesium* caused mortalities of wild fish in in Kyrkjfjärden, a small embayment with restricted water exchange, in the Archipelago of Stockholm, in 1991 and 1992.

3.3. *Pseudochattonella* spp

Pseudochattonella spp., heterokont flagellates belonging to the Dictyochophyceae, have been widely observed on a global scale, including in the Kattegat-Skagerrak, Seto Inland Sea, Japan (Hara, 1994), New Zealand (MacKenzie et al. 2011) and in Chile (Mardones et al., 2019). Fish-killing *Pseudochattonella* blooms in northern Europe have a multi-decadal history, although documentation is incomplete. For example, a fish kill in May 1979 in Loch Striven on the west coast of Scotland was attributed to unidentified “flagellate x” in a report (Tett, 1980); the drawing by M.R. Droop (Fig. 6) is similar to *Pseudochattonella*, but this association cannot be confirmed. The first bloom of *Pseudochattonella* sp. in the Kattegat-Skagerrak-eastern North Sea was registered in 1998 (Aure et al., 2001; Waite and Lindahl, 2006). Just before the end of 1997, a bloom of *Pseudochattonella* sp. was observed in Århus Bay, in the Danish part of the Kattegat (pers. comm., Helene Munk-Sørensen). Mortalities of wild fish (garfish *Belone belone* L., Atlantic mackerel (*Scomber scombrus* L.) and herring (*Clupea harengus* L.), as well as farmed salmon (*Salmo salar* L.) were reported in 1998. Since then, *Pseudochattonella* has formed recurrent extensive blooms in the Kattegat and Skagerrak, causing fish mortalities. Initially, the causative species was referred to as *Chattonella* aff. *verruculosa* of uncertain taxonomic affiliation, then renamed *Verrucophora* (Edvardsen et al., 2007) for a short time, but is currently placed in the genus *Pseudochattonella* (Eikrem, 2009) based upon morphological and molecular considerations. Two species of *Pseudochattonella* have caused fish mortalities in the Kattegat-Skagerrak area: *P. farcimen* (Eikrem, Edvardsen & J.Throndsen) Eikrem and *P. verruculosa* (Y. Hara & M. Chihara) S. Tanabe-Hosoi, D. Honda, S. Fukaya, Y. Inagaki & Y.Sako. Since 1998, *P. farcimen* has been the dominant dictyochophyte bloom-former, with blooms occurring in spring, just after the spring diatom bloom (Andersen et al., 2015; Eckford-Soper and Daugbjerg, 2016; Jakobsen et al., 2012). Blooms during 2001–2019 have caused mortalities of rainbow trout (*Oncorhynchus mykiss* Walbaum) in open water pen-based aquaculture fish farms in Denmark. The approximate total loss of fish in 2006, 2007 and 2019 was 38, 68 and > 400 tonnes, respectively (see also Table 4). In addition to fish kills, observation of blooms of *Pseudochattonella* during early spring has delayed release of fish to the aquaculture sites in the sea in several years during the period 1998–2019 with resulting loss of production to the aquaculture industry.

3.4. *Dictyocha/Octactis/Vicicitus*

Dictyocha spp. are phototrophic flagellates with siliceous skeletons belonging to the class Dictyochophyceae; the genus was recently split into the genera *Octactis* and *Dictyocha* (Chang et al., 2017). In northern Europe, *D. fibula* Ehrenberg and *O. speculum* (Ehrenberg) F.H. Chang, J. M. Grieve & J.E. Sutherland (ex. *Dictyocha speculum* Ehrenberg) are commonly observed in phytoplankton monitoring programs during the autumn. A naked cell stage in the life cycle of *Dictyocha/Octactis* has been connected to fish mortalities (Henriksen et al., 1993; Jochem and Babenerd, 1989; Lømsland et al., 2010; Moestrup and Thomsen, 1990). Another fish-killing member of the order Dictyochales, *Vicicitus globosus* (Y. Hara & Chihara) F.H. Chang (ex. *Chattonella globosa*) (Chang, 2015; Chang et al., 2012) has been observed in the Skagerrak and the south and west coast of Norway (Lømsland et al. 2010). In HAEDAT, one fish kill affecting aquaculture, attributed to the naked form of *O. speculum*, was reported for 2004 in the Belt Sea in the southern Baltic, but no such incidents were recorded for the greater North Sea and adjacent coasts.

3.5. *Karenia mikimotoi*

Karenia mikimotoi, a phototrophic dinoflagellate with unusual chloroplasts of prymnesiophyte origin (Horiguchi, 2006; Tangen and Björnland, 1981; Zapata et al., 2012), is a widely distributed species in temperate waters and is well known as a major fish-killing species (Davidson et al. 2009, Silke et al. 2005). In northern Europe, *K. mikimotoi* was first known as *Gyrodinium aureolum* Hulburt but this was a misidentification. Later, this “European fish-killing taxon” was assigned to *Gymnodinium mikimotoi* Miyake & Kominami ex Oda and/or *Gymnodinium nagasakiense* H.Takayama & M.Adachi. At present, *K. mikimotoi* is accepted as valid. When exposed to high concentrations of cultured cells of *K. mikimotoi*, mortalities of rainbow trout, *Oncorhynchus mykiss*, can rapidly occur (Mitchell and Rodger, 2007; Roberts et al., 1983). A putative toxic mechanism was proposed by Gentien and Arzul (1990), linked to the membrane disruptive potential of unusual fatty acid derivatives produced by *K. mikimotoi*, but this remains controversial. Blooms of *K. mikimotoi* have caused mortalities of fish and benthic invertebrates in northern Europe since 1966, when brown water and fish kills were observed along the south coast of Norway (Braarud and Heimdal, 1970). Blooms were extensive in Norway in the late 1970s and 1980s (Dahl et al., 1982; Dahl and Tangen, 1993; Tangen, 1977) but now appear to be more restricted in geographical extent. Further south, along the Swedish Skagerrak coast, sporadic blooms occurred in the 1980s (Lindahl, 1983; Lindahl, 1986, Karlson, 1989), but are recently uncommon. Major blooms have also been reported from Scottish waters (Davidson et al., 2009), from Ireland (Raine et al., 2001; Silke et al., 2005) and the English Channel (Barnes et al., 2015; Hartman et al., 2014), particularly in periods of stratified water which apparently favours growth of *K. mikimotoi*.

3.6. *Karlodinium veneticum*

Karlodinium is a mixotrophic dinoflagellate genus with several fish killing members. *Karlodinium veneticum* (D.Ballantine) J.Larsen was reported to cause mortalities of wild fish on the Swedish coast of the Baltic Proper in 2012, and on the Finnish coast of the Gulf of Finland in 2015, at a cell density of 14×10^6 cells L⁻¹. This small (<8–12 µm) athecate dinoflagellate is common in coastal aquatic ecosystems, but it frequently overlooked or misidentified. *Karlodinium* species can be identified by molecular techniques, such as for the Gulf of Finland event in 2015. Several toxic compounds (karlotoxins) have been characterized with haemolytic, ichthyotoxic, and cytotoxic properties (Place et al. 2012).

3.7. *Pfiesteria shumwayae* and *Luciella masanensis*

The dinoflagellates *Pfiesteria shumwayae* Glasgow & J.M.Burkholder and *Luciella masanensis* P.L. Mason, Jeong, Litaker, Reece & Steidinger caused mortalities of rainbow trout *Oncorhynchus mykiss* Walbaum in recirculation fish farms in Denmark in 2012 (Moestrup et al., 2014). Whereas fish mortalities due to *P. shumwayae* occurred at a brackish water farm, *L. masanensis* caused fish kills at a land-based farm using pumped seawater. Both dinoflagellate species are small and difficult to identify, with a complex cryptic life history, and therefore under-reported, but likely occur in plankton or bottom waters in temperate areas throughout the world.

4. Phycotoxin producing HAB-taxa and their effects

4.1. *Dinophysis* and *Prorocentrum* species and Diarrhetic Shellfish Toxins

In northern Europe, Diarrhetic Shellfish Toxins (DST) are produced by several *Dinophysis* species (Dahl and Johannessen, 2001) and by the benthic *Prorocentrum lima* (Ehrenberg) F. Stein. Other toxigenic members of the genus *Prorocentrum* (e.g., *P. concavum* and *P. hoffmannianum*) are common in sub-tropical and tropical waters (reviewed in

Durán-Riveroll et al. 2019), but these species are either extremely rare or do not occur in northern European waters. *Prorocentrum lima* is primarily epiphytic, living on sandy or rocky substrates along shores, and attached to macroalgae and seagrass (e.g., *Zostera marina*).

Dinophysis are planktonic, mixotrophic dinoflagellates with a complex and diverse life history, alternative nutritional modes, variable pigmentation and photosynthetic mechanisms, and ecology and behaviour that resists generalization (reviewed by Reguera et al., 1995; Reguera et al., 2012). Three toxigenic *Dinophysis* species, *D. acuta* Ehrenberg, *D. acuminata* Claparède & Lachmann and *D. norvegica* Claparède & Lachmann, are most commonly reported in monitoring programmes in northern Europe.

The cell “toxicity” (or toxin content) of *Dinophysis* cells has been shown to be highly variable and to depend on cell density (Lindahl et al., 2007), and probably on nutritional mode as well. *Dinophysis* cells are capable, although apparently awkward, swimmers (Lassus et al., 1990; Smayda, 2010), and are often observed in dense subsurface layers in stratified waters, such as in subsurface layers in a Swedish fjord (Lindahl et al., 2007). *Dinophysis* species are sometimes infected by parasites, e.g. the dinoflagellate *Amoebophrya* Koeppen (Salomon et al., 2003) and *Parvilucifera* Norén & Moestrup (Lee and Park, 2017), but little is known about effects on cell toxicity. Heterotrophic dinoflagellates from the genus *Fragilidium* Balech ex Loeblich III feed on *Dinophysis* by engulfment (Rodríguez et al., 2014), and hence could act as a DST vector in marine planktonic food webs. The heterotrophic dinoflagellate species *Phalacroma rotundatum* (Claparède & Lachmann) Kofoid & J.R.Michener (syn. *Dinophysis rotundata* Claparède & Lachmann) is likely not a producer of DST at least in North Atlantic waters (Cembella 1989, González-Gil et al. 2011, Pleasance et al. 1990), although it is a possible weak toxin vector via phagotrophy (González-Gil et al. 2011). This species remains on the IOC-UNESCO Taxonomic Reference List of Harmful Microalgae (Moestrup et al., 2020) based upon an early unconfirmed report of species toxicity in Japan (Lee et al. 1989) but *P. rotundatum* is not included in Table 3 as it has not been associated with DST events in northern Europe.

The DST group includes okadaic acid (OA) and >30 naturally occurring dinophysistoxin (DTX) analogues, but not all of them are diarrheagenic toxins or subject to regulation. Okadaic acid (OA), dinophysistoxin-1 (DTX1), and dinophysistoxin-2 (DTX2) are the dominant members of the DST group found in shellfish in northern Europe, but other analogues (e.g., acyl-esters) may also be present in *Dinophysis* and/or produced via biotransformation in shellfish (Blanco, 2018; Durán-Riveroll et al., 2019).

Macrocyclic lactone derivatives, such as pectenotoxins (PTX), previously considered to belong to the “DST group”, may be synthesized by various *Dinophysis* species, but they are not known to be associated with any *Prorocentrum* (Durán-Riveroll et al., 2019). Numerous PTX analogues of uncertain specific toxicity often co-occur with true DSTs, and/or some can be produced by bioconversion in shellfish after ingestion of *Dinophysis* cells. PTXs are non-diarrheagenic, and no oral toxicity in mammals (including humans) has been identified, but they are included as emerging toxins in the “lipophilic toxins” fraction for the DSP mouse assay and LC-MS/MS analysis. PTX is included in the EU regulatory limits at present with a Toxicity Equivalency Factor (TEF) of 1, relative to OA.

Harmful algal events related to DSTs are the most common events reported to HAEDAT for Sweden, Norway, Denmark, Germany, the Netherlands and Belgium (see Table 2). Nevertheless, Diarrhetic Shellfish Poisoning (DSP) incidents are rarely reported for the region; most recorded DSP events are referring to DST levels above the regulatory limit in bivalve shellfish and resulting closures of shellfish harvesting areas. At present the DST regulatory limit in Europe is 160 µg OA equivalents kg⁻¹ of shellfish flesh (EFSA, 2009b), and this appears to provide a margin of security, at least against acute human poisoning (DSP). Most likely, recent ongoing effective monitoring of the dinoflagellate producers of DST and toxin accumulation in shellfish has resulted

in precautionary closures of shellfish harvesting and thus prevented most potential DSP incidents.

The risk of DSP remains the major phycotoxin-related problem in the Netherlands (van der Fels-Klerx et al., 2012), in Norway and in Sweden (Persson et al., 2020). Confirmed DSP events in the Netherlands were reported as early as 1961 (Kat, 1983a), and later in Sweden in 1983 (Haamer, 1997; Krogh et al., 1985). The first confirmed DSP event in Norway occurred in 1984 (Dahl and Yndestad, 1985), although there are undocumented reports as early as 1870 and 1971 (see Table 1, and Tangen and Dahl 1999). DSP is also the main phycotoxin-related concern in Belgium, with events leading to shellfish closures in 2001 and 2008. At Helgoland, in the German Bight, DST was found in the blue mussel *M. edulis* in 2000 (Klöpfer et al., 2003), but was not related to harvestable shellfish or human illness. *Dinophysis tripos* Gouret was first recorded from the long-term Helgoland Roads in the southern North Sea in 2014 (Kraberg et al., 2019). This potentially toxicogenic species has increased in cell abundance in Norway (Johnsen and Lømsland, 2010a) and Sweden (B. Karlson, unpublished) since 2014, but the associated DST risk has not been assessed.

The annual concentrations of DST in bivalve shellfish have shown a decrease along the southern coast of Norway (Naustvoll et al., 2012) and along the Skagerrak coast of Sweden (Persson et al., 2020), in recent years. This coincides with a decrease in cell numbers of *D. acuta* reported from harmful phytoplankton monitoring programmes. In the late 1980s, the highest DST levels in *M. edulis* were observed in autumn (Edebo et al., 1988a; Edebo et al., 1991), but since then the peak in DST levels in this shellfish species has apparently shifted back from autumn towards summer (Naustvoll et al., 2012; Persson et al., 2020). In 2002, an unusual HAB event occurred in the Flekkefjord area in southern Norway. *Cancer pagurus* L., commonly known as the edible (or brown) crab, contained high levels of DST in the viscera, after feeding on mussels containing DST (Castberg et al., 2004; Torgersen et al., 2005). Humans were poisoned after eating these crabs, exhibiting characteristics of the DSP syndrome.

4.2. *Alexandrium* spp. and Paralytic Shellfish Toxins

Alexandrium are globally distributed and occur from polar seas (Okolodkov, 2005) to brackish tropical and subtropical lagoons (Lim et al., 2005) and seem to increase in their global distribution (Penna et al., 2015). Members of the dinoflagellate genus *Alexandrium* (reviewed by Anderson et al. 2012), such as *Alexandrium minutum* Halim, *A. ostenfeldii*, *A. pacificum*, *A. catenella* (Whedon & Kofoid) Balech, *A. australiense* Sh. Murray, and *A. tamiyavanichi* Balech (Murray et al., 2015a; Murray et al., 2015b), are major global producers of the neurotoxins responsible for paralytic shellfish poisoning (PSP), known as “saxitoxins” or PST. The dinoflagellates *Gymnodinium catenatum* H.W. Graham and *Pyrodinium bahamense* L. Plate also cause PSP incidents, but these species are absent from the northern European area reviewed herein. Several toxicogenic *Alexandrium* species capable of producing PSP toxins are common in northern European waters; among them *A. catenella*, *A. ostenfeldii*, and *A. minutum* are the most prominent contributors to PST in shellfish and have a long and well-described historical distributional record in the region. Biogeographical data for this genus and associated PST must be cautiously interpreted because of the frequent and even contradictory taxonomic and nomenclatural revisions of the genus within the last decade and difficulties in cross-referencing events to older species names. For example, the original taxon *Gonyaulax tamarens* Lebour held to be responsible for PSP incidents in northern Europe, and later redescribed as *Alexandrium tamarens* (Lebour) Balech, 1995 (as cited in Table 3), is now considered to be non-toxicogenic. Further redefinitions of *Alexandrium* taxa have been based upon combined morphological and molecular criteria (John et al. 2014) with associated toxin composition (Cembella 2018). Following recent updates to the IOC-UNESCO Taxonomic Reference List of Harmful Microalgae (Moestrup et al., 2020), most PSP events in the

Table 1

Selected major harmful algal bloom events in the eastern North Sea area, the Norwegian Sea, the Barents Sea and the Baltic Sea.

Year/period	Syndrome/type of effect	Taxa	Sea area and description of event
1854	Summer bloom of cyanobacteria	cf. <i>Aphanizomenon</i> and/or <i>Nodularia</i>	Surface accumulation near island of Gotland today attributed to cyanobacteria bloom
1870	DSP	<i>Dinophysis</i> (no confirmed observation)	First recorded human DSP event, Sognefjorden, Norway
1901	PSP	<i>Alexandrium</i> (no confirmed observation)	First documented PSP event in Norway (two deaths), Oslofjorden
1938	PSP	<i>Alexandrium ostenfeldii</i>	First reported PSP event, Belgian coast
1966–1998 and 2020	Fish mortalities	<i>Karenia mikimotoi</i> (at first incorrectly identified as <i>Gyrodinium aureolum</i>)	Skagerrak and the Kattegat (including the event in Limfjorden 2020)
1980 -	DSP	<i>Dinophysis</i> spp.	Skagerrak, Norwegian Sea, Barents Sea
1980s -	PSP	<i>Alexandrium</i> spp.	Skagerrak, Norwegian Sea, Barents Sea, documented PSP events from Skagerrak, Norwegian Sea, Barents Sea
1988	Ecosystem disruptive bloom, including fish mortalities	<i>Prymnesium polylepis</i> (syn. <i>Chrysochromulina polylepis</i>)	Kattegat, Skagerrak, eastern North Sea
1989, 1990, 1991, 1995 and 2007	Fish mortalities	<i>Prymnesium parvum</i>	Ryfylke, Norway
1990	Fish mortalities	<i>Prymnesium parvum</i>	Baltic Sea, Dragsfjård, Finland
1991 and 2019	Fish mortalities	<i>Chrysochromulina leadbeateri</i>	Northern Norway, Lofoten (Vestfjorden) and Tromsø area
1998, 2001, (2004, 2006, 2011), 2017, 2019	Fish mortalities	<i>Pseudochattonella farcimen</i> and <i>P. verruculosa</i>	Skagerrak-Kattegat (in 1998 also eastern North Sea), along Norwegian west coast
2001	Shellfish mortalities	<i>Phaeocystis globosa</i>	North Sea, Eastern Scheldt, Netherlands
1973–1985 1985–2001 2001–2017	Foam on beaches	<i>Phaeocystis</i> spp.	Increasing trend in annual occurrence, but decreasing-stabilised trend in English Channel
2001-	Summer blooms of cyanobacteria	<i>Nodularia spumigena</i> , <i>Aphanizomenon flosaquae</i> , <i>Doliospermum</i> spp.	Baltic Sea, along Polish coast (especially Gulf of Gdańsk)
2005	ASP	<i>Pseudo-nitzschia seriata</i>	Kattegat – first AST event above regulatory level in Scandinavia
2005-	AZA	<i>Azadinium</i> spp.	Sporadic accumulation of

(continued on next page)

Table 1 (continued)

Year/period	Syndrome/type of effect	Taxa	Sea area and description of event
2009	Dog mortality	<i>Nodularia spumigena</i>	AZA in mussels and crabs in mid-Norway (Norwegian Sea)
2012	PSP	<i>Alexandrium ostenfeldii</i>	Baltic Sea, SW coast of Finland
2014	Exceptional blooms of cyanobacteria	<i>Nodularia spumigena</i> , <i>Aphanizomenon flosaquae</i> , <i>Doliospermum</i> spp.	First reported PSP event, Puck Bay (Southern Baltic, Poland)
2015	Fish mortalities	<i>Karlodinium veneticum</i>	Baltic Sea, Finnish sea areas
2018	Exceptional blooms of cyanobacteria	<i>Aphanizomenon flosaquae</i> , <i>Doliospermum</i> spp., <i>Nodularia spumigena</i>	Baltic Sea, Tammisaari, Finland
2018	AZA	<i>Azadinium</i> spp.	Baltic Sea, Finnish and Swedish sea areas
2020	Associated human fatalities	<i>Phaeocystis globosa</i>	AZA levels above regulatory limit – first time from coast of Sweden
			North Sea coast, Netherlands, 5 persons carrying out water sports died.

greater North Sea region linked to the Norwegian Sea and Kattegat-Skagerrak reported in HAEDAT may be referred to *A. catenella* (ribotype Group 1), formerly known as *A. fundyense sensu Balech 1995*.

Paralytic Shellfish Toxins (PST) are produced by marine dinoflagellates belonging to three major genera and among about a dozen genera of freshwater and brackish water cyanobacteria; distribution and mode of action of such guanidinium toxins are reviewed by Durán-Riveroll and Cembella 2017. PSTs are tetrahydropurine neurotoxins, the most potent being the carbamoyl derivatives saxitoxin (STX) and neo-saxitoxin (neoSTX), that block conductance through sodium ion channels of nerve cells causing neuromuscular paralysis (Kao, 1993; Van Dolah, 2000). The accumulation of PSTs in marine species can cause the syndrome PSP in human consumers of seafood (Kao, 1993), and toxin transfer within marine food webs may lead to faunal mortalities and also have severe impacts on ecosystem function (Anderson and Garrison, 1997; Llewellyn, 2006).

In addition to the PSTs (“saxitoxins”), some *Alexandrium* species produce other bioactive compounds (“toxins”) such as the cyclic imines spirolides (SPX) or gymnodimines (GYM), and/or the polyether macrolide goniiodomins (GD). These compounds may play a defensive role in deterring grazers, as has been shown for saxitoxins and copepods (Selander et al., 2006; Wohlrab et al., 2010), or have other unknown ecological functions. None of these compounds are currently subject to regulatory limits within the EU, although they remain on the watch list as emerging or potential toxins.

Reports of high PST concentrations in bivalve molluscs from northern Europe are summarised in Table 5, see also Fig. 2. The first HAEDAT-report of a PSP event in Sweden is from 1987 when mussels (*M. edulis*) along the Swedish Skagerrak coast had PST levels above the regulatory limit (800 µg STXeq kg⁻¹) between late May and early July. Events with PST levels above the regulatory limit were also recorded in 1988 and 1997. In these early cases, the toxin producer was reported as *Gonyaulax excavatum* (Braarud) Balech 1971, but is now considered as *Alexandrium catenella* (Kofoid) Balech in current nomenclature (Litaker et al. 2018). Subsequently, for the Skagerrak area there have been several reports of

elevated levels of PST, e.g. 6.0 × 10³ µg STX eq kg⁻¹ in 2010; the causative dinoflagellate was *A. catenella* (but reported as *A. tamarense*). In 2014, 2015 and 2017 PSP events for the Swedish Skagerrak coast with a maximum PST level of 3.6 × 10 µg STXeq kg⁻¹ were also reported in *M. edulis*.

The first apparent PSP outbreak reported for Norway occurred in 1901 causing two human deaths in Oslo due to consumption of contaminated shellfish (Tangen and Dahl, 1999; Thesen, 1901). The first HAEDAT-report of PST events, i.e. PST concentrations in bivalve molluscs above regulatory limit, in Norway is from 1987. Since then, PST levels well above the regulatory limit have often been recorded in shellfish from the Norwegian Sea, e.g. in 2010 from the northern Norwegian Sea (maximum: 17.7 × 10³ µg STXeq kg⁻¹) and in 2011 from the southern Norwegian Sea (maximum: 12.5 × 10³ µg STXeq kg⁻¹), with highest levels in shellfish from the Norwegian Sea in 2017 (maximum: 5.8 × 10⁴ µg STX eq kg⁻¹). The toxin producer was *A. catenella* (again reported as *A. tamarense*). Events in the Barents Sea were first reported in 1996, with highest PST levels of 3.6 × 10³ µg STXeq kg⁻¹ in 2017.

4.3. *Alexandrium pseudogonyaulax* and associated cyclic imines and macrocyclic polyether toxins

In view of its phylogenetic affinities, nutritional mode and toxigenic potential, *Alexandrium pseudogonyaulax* (Biecheler) Horiguchi ex K.Yuki & Y.Fukuyo in northern Europe is clearly distinct from the *A. catenella/tamarense* and *A. ostenfeldii/peruvianum* species groups. Members of the *A. catenella/tamarense* group are more frequently PST producers, whereas *A. ostenfeldii/peruvianum* may produce PSTs and/or spirolides (SPX), respectively, in this region. Populations of *A. pseudogonyaulax* from the Kattegat-Skagerrak have recently been confirmed to produce the highly toxic macrolide polyether goniiodomin A (GDA) (Krock et al., 2018), known to be cytotoxic and circumstantially associated for decades with fish mortalities. Perhaps all *Alexandrium* species are capable of limited mixotrophy, or at least heterotrophic assimilation of organic nutrients, but *A. pseudogonyaulax* exhibits a unique mucus trap feeding strategy (Blossom et al., 2017). Nevertheless, preliminary evidence suggests that GDA is produced endogenously by *A. pseudogonyaulax* rather than secondarily acquired via capture of toxigenic prey.

In southern Norway *A. pseudogonyaulax* was first observed in 2001, but has become common since 2010. In Oslofjorden it is observed regularly in the summer, sometimes at “bloom” cell densities. Swimmers complain about skin discomfort when cell numbers are high. Since the first observation of a bloom in 2002, spatiotemporal distribution of *A. pseudogonyaulax* in Norway coincides with the pattern of occurrence along the Swedish west coast. Observations along the Swedish Kattegat-Skagerrak coast have shown an increase in cell abundance of *A. pseudogonyaulax* in summer. Analyses of long-term monitoring data from Limfjorden, Denmark confirmed a recent shift to *A. pseudogonyaulax* dominance over *A. ostenfeldii*. These new findings document that *A. pseudogonyaulax* has become a prominent member of the *Alexandrium* species community over the past decade within the region. To date, there are no records of fish mortalities or other HAB events linked to blooms of *A. pseudogonyaulax*, but goniiodomins are not subject to routine analysis in toxin monitoring programs in Europe, in either shellfish or finfish, and the risk therefore cannot be reliably evaluated.

4.4. *Protoceratium reticulatum*, *Gonyaulax spinifera*, *Lingulodinium polyedra* and associated yessotoxins

Three of the four species of gonyaulacoid dinoflagellates (Order: Gonyaulacales) reported to produce ladder-frame disulphated polyether compounds known as yessotoxins (YTX) (Krock et al., 2008) are common in northern European coastal waters: *Lingulodinium polyedra* (Stein) Dodge (syn. *Gonyaulax polyedra*); *Protoceratium reticulatum* (Claparède & Lachmann) Bütschli (syn. *Gonyaulax grindleyi*; and *Gonyaulax spinifera*

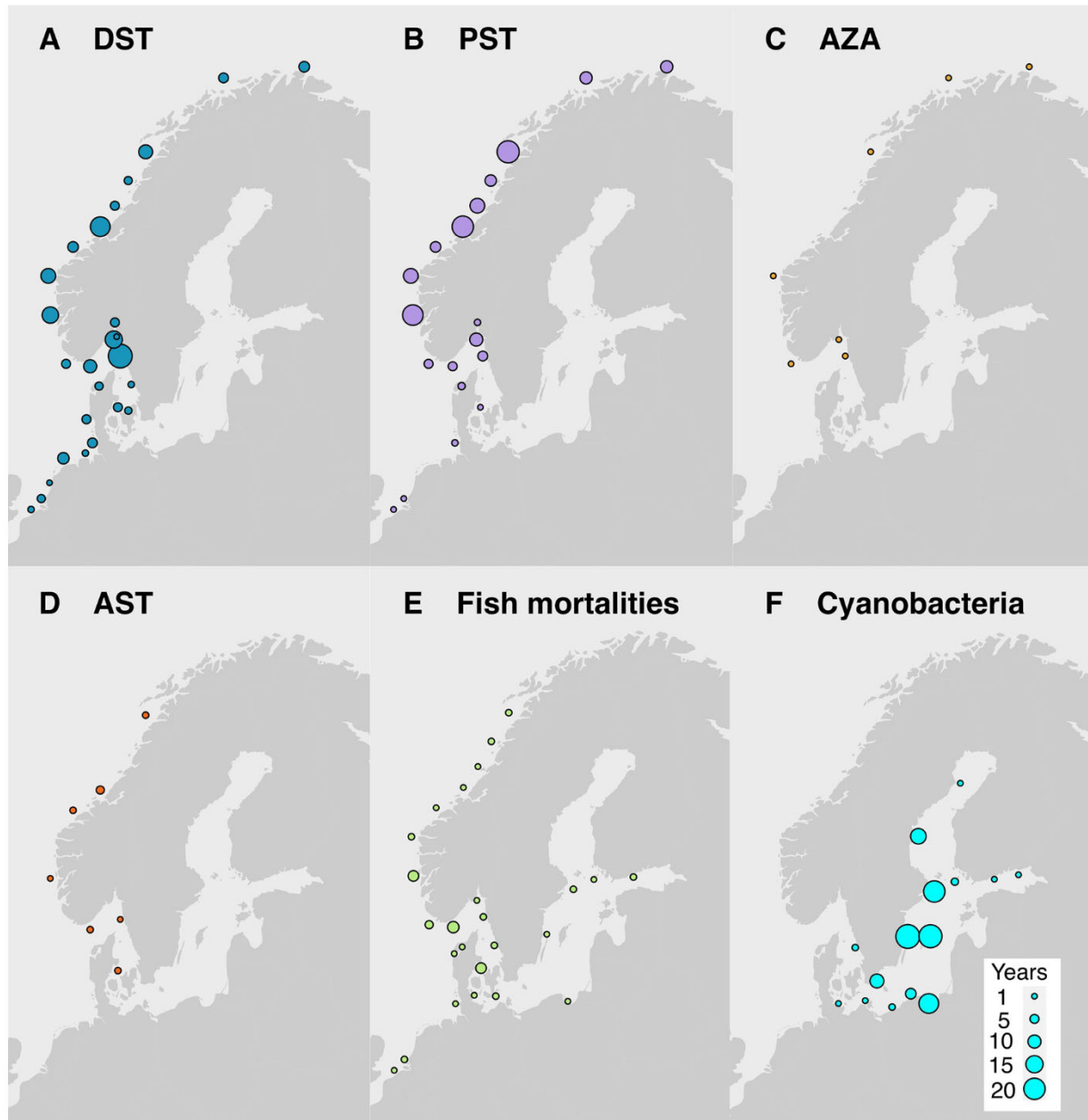


Fig. 2. The distribution of harmful algal events along the northern part of European Atlantic coast as reported to HAEDAT during the period 1987 to 2019. Size of circles represents the number of years of reported events. A. DST events due to *Dinophysis* spp., B. PST events due to *Alexandrium* spp. C. AZA events due to *Azadinium* spp., D. AST events due to *Pseudo-nitzschia* spp. and E. Fish mortalities due to *Karenia mikimotoi*, *Karlodinium veneficum*, *Chrysochromulina leadbeateri*, *Prymnesium parvum*, *P. polylepis* and *Pseudochattonella* spp. F. Cyanobacteria events.

(Claparède & Lachmann) Diesing). Cultured isolates of *L. polyedra* and *P. reticulatum* were first confirmed to be YTX producers in 2004 (Paz et al., 2004), and shortly thereafter Rhodes et al. (2006) confirmed that *G. spinifera* was also capable of YTX production. More recently, *G. taylorii* M.C. Carbonell-Moore was reported to be a producer of YTX in Chilean coastal waters (Alvarez et al., 2016), but this species is not known as a toxic factor in northern European waters.

The toxicology and mode of action of YTX in mammalian targets and cell lines have been described (Paz et al., 2008; Tubaro et al., 2010), although many uncertainties remain. YTX were long classified among the categories of toxins causing DSP. However, as YTXs do not induce diarrhoea, nor inhibit protein phosphatase 2A, unlike true DSP toxins, they were reclassified as toxin group separate from the DSP complex (European-Commission, 2002). YTXs are subject to regulatory limits within Europe; advice about raising the YTX limit based upon new

toxicological evidence was already provided in 2009 (EFSA, 2009c). Until 2013, the European regulatory limit was 1.0 mg YTX kg⁻¹ of shellfish flesh, when it was raised to 3.75 mg YTX kg⁻¹ (European-Commission, 2013). High YTX levels have caused a few closures of shellfish harvesting in northern Europe, e.g. in western Sweden (Persson et al., 2014).

There are no known cases of human poisoning induced by YTX, although YTX-contaminated shellfish, sometimes at high mass equivalent levels well in excess of the European regulatory limit, are reported worldwide. No YTX toxin syndrome has been described or defined, and specific potencies of most YTX analogues are not known. In a study where the combined effects of okadaic acid (OA) and YTX were tested on mice, effects indicative of tumorigenic properties were noted (Franchini et al., 2005), indicating potential synergistic risk of chronic exposure from shellfish consumption. Subacute YTX-immunotoxicity was

reported in experiments with rats (Ferreiro et al., 2017) suggesting that repeated exposure to low amounts of YTX might also pose a threat to human health, especially in immuno-compromised populations.

YTXs were first reported from scallops, *Patinopecten yessoensis*, collected at Mutsu Bay in Japan (Murata et al., 1987), and are frequently detected in shellfish from Japan. On a global scale, YTX have been found in bivalve shellfish in many coastal locations around the world, including New Zealand (MacKenzie et al., 1998), China (Liu et al., 2017) and USA (California) (Armstrong and Kudela, 2006), usually coinciding with blooms of one or more of the causative dinoflagellate species. Within Europe, YTX are commonly detected in shellfish and long known from the northern Adriatic Sea (Ciminiello et al., 1997), Belgium (Orellana et al., 2017), France (Amzil et al., 2008) and Norway (Aasen et al., 2005; Lee et al., 1988; Miles et al., 2002; Samdal et al., 2004).

4.5. Azadinium, Amphidoma and azaspiracids

Members of the marine dinoflagellate family Amphidomataceae including the genera *Azadinium* and *Amphidoma* (Tillmann et al., 2012) have been recognized as producers of a unique group of lipophilic polyether phycotoxins known as azaspiracids (AZAs). The consumption of AZA-contaminated seafood leads to Azaspiracid Shellfish Poisoning (AZP), a serious toxicity syndrome in humans, causing mainly gastrointestinal problems, such as cramps, vomiting, nausea and severe diarrhoea (Abal et al., 2017). It took over a decade to find and describe a small dinoflagellate (<20 µm) *Azadinium spinosum* Elbrächter et Tillmann (Tillmann et al., 2009) isolated from the North Sea coast of Scotland as the first confirmed source organism for AZA. This species was subsequently found in Danish and Irish coastal waters (Salas et al., 2011), and confirmed to be toxigenic. Since then intense research has led to the description of more than a dozen species of *Azadinium* and confirmed the worldwide distribution of this genus (Fabro et al., 2019; Rhodes et al., 2020). The capacity to synthesise AZA is now known for a number of *Azadinium* species, e.g., *A. spinosum*, *A. poporum*, *A. dextroporum* (Krock et al., 2019). Azaspiracids are not only produced by *Azadinium*; the newly described *Amphidoma languida*, a morphologically and phylogenetically close relative of the genus *Azadinium* is also capable of AZA production (Krock et al., 2019).

After the first poisoning incident in the Netherlands in 1995, linked to mussels harvested from the west coast of Ireland, AZA toxins were first isolated and structurally characterized from Irish shellfish (Ito et al., 2000; Satake et al., 1998). Among species of *Azadinium* and *Amphidoma languida* more than 30 AZA analogues have been described (Hess et al., 2014), and several species produce probable AZA analogues that remain to be structurally characterized and are of unknown toxicity.

In HAEDAT for the period 1987–2019, seven reports of events related to AZAs for the coast of Norway, one each for Sweden and the Netherlands, and but none for Denmark, Germany and Belgium, were documented (Table 2). This scarcity of data reports on AZA may be partially due to the fact that AZA analysis by LC-MS/MS was introduced relatively recently to phycotoxin monitoring of bivalve shellfish for

human consumption (e.g. for Sweden in 2009). It might also reflect that high magnitude toxigenic blooms of *Azadinium* (or *Am. languida*) are rather rare events or that the blooms are not persistent long enough to cause significant shellfish toxin levels. The small cell-size and inconspicuous morphological features may also lead to overlooking cryptic *Azadinium* species. Azaspiracids have, for instance, been found in mussels collected in Belgian coastal waters (Orellana et al., 2017), yet none of the putatively associated *Azadinium* species have been observed.

In seafood consumed in northern Europe, AZA toxins pose a major problem mainly for consumption of bivalve shellfish and certain crustaceans, such as crabs, that have accumulated these toxins as food chain vectors. In 2005 AZA was detected in the viscera of the edible (brown) crab, *C. pagurus*, in Norway and in the subsequent year two persons were hospitalised in Norway after eating crabs containing AZA. Accordingly, a regulatory limit of 170 µg AZA kg⁻¹ of crab viscera is applied in Norway.

4.6. Pseudo-nitzschia and Amnesic Shellfish Toxins

Amnesic Shellfish Toxins (AST), i.e. domoic acid (DA) and its isomers (EFSA, 2009a; Jeffery et al., 2004; Zabaglo et al., 2016), are produced by some members of the diatom genera *Pseudo-nitzschia* and *Nitzschia*. At present, more than two dozen species of *Pseudo-nitzschia*, as well as *Nitzschia bizertensis* Smida, Lundholm, Hlaili & Mabrouk and *Nitzschia navis-varingica* Lundholm & Moestrup, are known AST producers (Lundholm, 2020). Domoic acid production in the diatom *Halophora coffeaeformis* (C. Agardh) Levkov has never been confirmed (Bates 2000) and is regarded as doubtful. Apart from DA, related analogues isodomoic acid A, B and C, have also been found in both *Pseudo-nitzschia* and *Nitzschia* species, with different combinations of toxins among strains and species (Hansen et al., 2011; Tan et al., 2016).

Closures of shellfish harvesting due to AST above the regulatory level of 20 mg DA kg⁻¹ mussel meat are rare in northern Europe (Table 2), which is somewhat surprising because *Pseudo-nitzschia* species are ubiquitous and blooms are common in the area. The first documented toxic *Pseudo-nitzschia* bloom in Scandinavia with levels above the regulatory levels happened in 2005, in inner coastal waters of Denmark and the Kattegat (Lundholm et al., 2005). Another toxic bloom was noted after two silos containing nitrogen-containing liquid fertilizer collapsed in Fredericia harbour, Denmark; more than 2,750 tons of fertilizer leaked into inner Danish waters (Olesen et al., 2020).

The toxin content of *Pseudo-nitzschia* cells in the area is similar to levels elsewhere in the world. Toxin levels in the generally highly toxic *P. seriata* is also high in Danish waters (up to 33.6 pg cell⁻¹) (Lundholm et al., 1994), but species such as *P. calliantha* and *P. delicatissima* are non-toxic or only slightly toxic (up to 0.22 pg cell⁻¹) (Lundholm et al., 1997; Lundholm et al., 2003; Lundholm et al., 2006) as elsewhere in the world.

The first overall distribution and diversity of *Pseudo-nitzschia* in the Skagerrak, the North Atlantic, and adjacent waters was reported by Hasle et al. (1996). Based on light and electron microscopy, she

Table 2

The number of harmful algal events in each country reported to the Harmful Algae Event Database (HAEDAT) from 1987 to 2019. Note: The table reflects observed events but also differences in the monitoring efforts and reporting procedures among countries. Reports from freshwater are not included in the table.

Syndrome/effect	Sweden	Norway	Denmark	Germany	Netherlands	Belgium	Finland	Poland
DSP	58	148	17	8	13	2	-	-
PSP	8	207	4	2	1	1	-	1
AZP	1	7	-	-	1	-	-	-
ASP	1	15	2	-	-	-	-	-
Aquaculture fish	1	10	6	-	-	-	-	-
Natural fish	2	3	-	1	1	-	2	-
Mass mortalities of fish or other marine organisms	2	15	4	1	2	1	1	-
Cyanobacteria*	48	-	-	7**	-	-	5	55

* note that the basis for reporting of cyanobacteria events is not consistent between countries

** see text for bloom in Wadden Sea 2012

Table 3

Harmful algae and cyanobacteria of the IOC-UNESCO Taxonomic Reference List of Harmful Microalgae (Moestrup et al. 2020) observed in the Baltic Sea, Kattegat-Skagerrak, Eastern North Sea, Norwegian Sea and Barents Sea. Concerning the Baltic Sea, species that are routinely identified from the HELCOM COMBINE (HELCOM 2017) monitoring samples, and thus are in the HELCOM PEG Biovolume file (version 2020, annually updated Biovolume file is available through <https://helcom.fi/helcom-at-work/projects/peg/>), are included.

Syndrome/effect	Class	Baltic	Other sea area	Species and author
ASP	Bacillariophyceae	X		<i>Halamphora coffeaeformis</i> (C.Agardh) Levkov, 2009
ASP	Bacillariophyceae	X	X	<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup & Hasle, 2003
ASP	Bacillariophyceae		X	<i>Pseudo-nitzschia cuspidata</i> (Hasle) Hasle, 1993
ASP	Bacillariophyceae	X	X	<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden, 1928
ASP	Bacillariophyceae		X	<i>Pseudo-nitzschia fraudulenta</i> (Cleve) Hasle, 1993
ASP	Bacillariophyceae		X	<i>Pseudo-nitzschia multiseriata</i> (Hasle) Hasle, 1995
ASP	Bacillariophyceae	X	X	<i>Pseudo-nitzschia pseudodelicatissima</i> (Hasle) Hasle, 1993
ASP	Bacillariophyceae	X	X	<i>Pseudo-nitzschia pungens</i> (Grunow ex Cleve) G.R.Hasle, 1993
ASP	Bacillariophyceae	X	X	<i>Pseudo-nitzschia seriata</i> (Cleve) H.Peragallo, 1899
Fish killer	Prymnesiophyceae		X	<i>Chrysochromulina leadbeateri</i> Estep, Davis, Hargreaves & Sieburth, 1984
Fish killer	Prymnesiophyceae	X	X	<i>Phaeocystis globosa</i> Scherffel, 1899
Fish killer	Prymnesiophyceae	X	X	<i>Phaeocystis pouchetii</i> (Hariot) Lagerheim, 1896
Fish killer	Prymnesiophyceae		X	<i>Prymnesium parvum</i> N.Carter, 1937
Fish killer	Prymnesiophyceae	X	X	<i>Prymnesium polylepis</i> (Manton & Parke) Edvardsen, Eikrem & Probert, 2011
Fish killer, haemolytic	Dinophyceae	X	X	<i>Amphidinium carterae</i> Hulburt, 1957
Fish killer, haemolytic	Dinophyceae	X	X	<i>Amphidinium operculatum</i> Claparède & Lachmann, 1859
DSP	Dinophyceae	X	X	<i>Dinophysis acuminata</i> Claparède & Lachmann, 1859
DSP	Dinophyceae	X	X	<i>Dinophysis acuta</i> Ehrenberg, 1839
DSP	Dinophyceae		X	<i>Dinophysis caudata</i> Saville-Kent, 1881
DSP	Dinophyceae		X	<i>Dinophysis fortii</i> Pavillard, 1924
DSP	Dinophyceae	X	X	<i>Dinophysis norvegica</i> Claparède & Lachmann, 1859
DSP	Dinophyceae	X	X	<i>Dinophysis tripos</i> Gourret, 1883
PSP	Dinophyceae	X	X	<i>Alexandrium minutum</i> Halim, 1960
PSP	Dinophyceae	X	X	<i>Alexandrium ostenfeldii</i> (Paulsen) Balech & Tangen, 1985
PSP	Dinophyceae	X	X	<i>Alexandrium pseudogonyaulax</i> (Biecheler) Horiguchi ex K.Yuki & Y.Fukuyo, 1992
PSP	Dinophyceae	X	X	<i>Alexandrium tamarense</i> (Lebour) Balech, 1995
YTX	Dinophyceae	X	X	<i>Gonyaulax spinifera</i> (Claparède & Lachmann) Diesing, 1866
YTX	Dinophyceae	X	X	<i>Lingulodinium polyedra</i> (F.Stein) J.D.Dodge, 1989
YTX	Dinophyceae	X	X	<i>Protoceratium reticulatum</i> (Claparède & Lachmann) Bütschli, 1885
Fish killer	Dinophyceae	X	X	<i>Karenia mikimotoi</i> (Miyake & Kominami ex Oda) Gert Hansen & Moestrup, 2000
Fish killer	Dinophyceae	X	X	<i>Karlodinium veneticum</i> (D.Ballantine) J.Larsen, 2000
DSP	Dinophyceae	X	X	<i>Prorocentrum lima</i> (Ehrenberg) F.Stein, 1878
AZA	Dinophyceae	X	X	<i>Azadinium spinosum</i> Elbrächter & Tillmann, 2009
Fish killer	Raphidophyceae	X	X	<i>Fibrocapsa japonica</i> S.Toriumi & H.Takano, 1973
Fish killer	Raphidophyceae	X	X	<i>Heterosigma akashiwo</i> (Y.Hada) Y.Hada ex Y.Hara & M.Chihara, 1987
Fish killer	Dictyochophyceae	X	X	

(continued on next page)

Table 3 (continued)

Syndrome/effect	Class	Baltic	Other sea area	Species and author
Fish killer	Dictyochophyceae	X	X	<i>Pseudochattonella farcimen</i> (Eikrem, Edvardsen & J.Throndsen) Eikrem, 2009
Cyanotoxins	Cyanophyceae	X		<i>Pseudochattonella verruculosa</i> (Y.Hara & M.Chihara) S.Tanabe-Hosoi, D.Honda, S.Fukaya, Y.Inagaki & Y.Sako, 2007
Cyanotoxins	Cyanophyceae	X		<i>Anagnostidinium amphibium</i> (C.Agardh ex Gomont) Strunecský, Bohunická, J.R.Johansen & J.Komárek, 2017
Cyanotoxins	Cyanophyceae			<i>Aphanizomenon flosaquae</i> Ralfs ex Bornet & Flahault, 1886
Cyanotoxins	Cyanophyceae			<i>Coelosphaerium kuetzingianum</i> Nägeli, 1849
Cyanotoxins	Cyanophyceae	X		<i>Dolichospermum flosaquae</i> (Brébisson ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek, 2009
Cyanotoxins	Cyanophyceae	X		<i>Dolichospermum lemmermannii</i> (Richter) P.Wacklin, L.Hoffmann & J.Komárek, 2009
Cyanotoxins	Cyanophyceae	X		<i>Dolichospermum macrosporum</i> (Klebhan) Wacklin, L.Hoffmann & Komárek, 2009
Cyanotoxins	Cyanophyceae	X		<i>Dolichospermum planctonicum</i> (Brunnthal) Wacklin, L.Hoffmann & Komárek, 2009
Cyanotoxins	Cyanophyceae	X		<i>Dolichospermum sigmoideum</i> (Nygaard) Wacklin, L.Hoffmann & Komárek, 2009
Cyanotoxins	Cyanophyceae	X		<i>Dolichospermum spiroides</i> (Klebhan) Wacklin, L.Hoffmann & Komárek, 2009
Cyanotoxins	Cyanophyceae	X		<i>Microcystis aeruginosa</i> (Kützing) Kützing, 1846
Cyanotoxins	Cyanophyceae	X		<i>Microcystis flosaquae</i> (Wittrock) Kirchner, 1898
Cyanotoxins	Cyanophyceae	X		<i>Microcystis ichthyoblabe</i> (G.Kunze) Kützing, 1843
Cyanotoxins	Cyanophyceae	X		<i>Microcystis viridis</i> (A.Braun) Lemmermann, 1903
Cyanotoxins	Cyanophyceae	X	X	<i>Nodularia spumigena</i> Mertens ex Bornet & Flahault, 1888
Cyanotoxins	Cyanophyceae	X		<i>Planktothrix agardhii</i> (Gomont) Anagnostidis & Komárek, 1988

identified *P. pungens*, *P. multiseriata*, *P. seriata*, *P. fraudulenta*, *P. heimii*, *P. delicatissima*, and *P. pseudodelicatissima*. The species *P. pseudodelicatissima* was subsequently divided into several species, and in north European waters, the findings of *P. pseudodelicatissima* are now mainly assigned to *P. calliantha* (Lundholm et al., 2003), but *P. pseudodelicatissima* (Lundholm et al., 2010) and a taxon referred to *P. cf. cuspidata* have also been reported (Hostyeva et al. (2012)). Apart from the above-mentioned taxa, *P. americana* has been seen in both Oslofjord (Hostyeva et al. (2012)) and in the sediment from Mariager Fjord, Denmark (Lundholm et al., 2010); *P. granii* (Hasle, 1964) and *P. obtusa* (Hasle and Lundholm, 2005) have also been found in colder Norwegian waters.

Several chemical, physical and biological factors affect the production of DA in *Pseudo-nitzschia* (see reviews by Bates et al., 2018; Lelong et al., 2012; Trainer et al., 2012). Silicate and phosphate depletion, and increasing concentrations of nitrogen, high irradiance and the presence of bacteria tends to enhance DA production. Changes in pH, CO₂, salinity and temperature can affect toxin production, but presently no clear picture has emerged (Bates et al., 2018). Laboratory studies have provided most of this information, but e.g. depletion of silicate and phosphate as triggers for DA content agrees with field studies. The strongest inducers of DA biosynthesis are apparently depletion of silicate and phosphate, and in some circumstances the presence of copepods. Proximity of copepods and their waterborne chemical cues known as copepodamides can enhance DA content in *Pseudo-nitzschia* species and even induce DA production in typically non-toxicogenic species (Harðardóttir et al., 2019a; Harðardóttir et al., 2019b; Selander et al., 2019; Tammi-lehto et al., 2015). Only herbivorous copepods induce such an effect, indicating that DA production is part of a defense mechanism in these diatoms (Lundholm et al., 2018).

Domoic acid is a potent neurotoxin, responsible for causing severe neurological damage and even mortalities in human consumers of DA-contaminated mussels from Atlantic Canada. ASP has also caused

deaths of marine mammals and marine birds via food chain transfer of DA, e.g. along the west coast of North America (De La Riva et al., 2009; McCabe et al., 2016; Scholin et al., 2000; Trainer et al., 2017). Another finding of particular concern is reports of DA being widespread in Alaskan mammals (Lefebvre et al., 2016). Apart from acute poisoning of marine mammals due to DA ingestion, a chronic poisoning syndrome has been reported (Brodie et al., 2006; Goldstein et al., 2008). DA is a stable secondary amino acid that can potentially stay in the food chain for weeks or months (Johannessen, 2000), in the sediments, DA may persist for years (Sekula-Wood et al., 2011). The toxin accumulates in a wide array of marine organisms, including transfer from copepods and krill, marine snails, cephalopods, and polychaetes to seabirds, fish and marine mammals (Bates et al., 2018). Domoic acid has e.g. been found in pelagic fish like anchovies (Lefebvre et al., 2002), indicating that although observations of DA above regulatory levels in bivalve shellfish are uncommon, the consequences of toxic blooms of *Pseudo-nitzschia* can be severe (Lefebvre and Robertson, 2010).

Domoic acid contamination of king scallop (*Pecten maximus*) is frequent in northern European harvest areas for this species (Bogan et al., 2007; Husson et al., 2016; Rowland-Pilgrim et al., 2019). This is mainly due to the fact that *P. maximus* retains DA for an extraordinarily long time (at least several months) particularly in cold deep sediments (Blanco et al., 2002). If harvesting of *P. maximus* would increase e.g. in Sweden, it is likely that DA would pose a significant new monitoring challenge.

Almost nothing is known about DA in marine animals in Scandinavian waters. In northern Europe, DA has been found in harbour seals in Scotland and was shown to affect their immune system (Jensen et al., 2015). Exposure of the seals to DA and PST through contaminated prey are suggested to be an important factor for harbour seal decline in Scotland.

5. *Phaeocystis* and noxious foam in nearshore waters and on beaches

Phaeocystis spp. are small-celled (2–7 µm), bloom-forming prymnesiophytes that are found all over the world (Baumann et al., 1994; Medlin and Zingone, 2007). Rapid cell growth typically follows an early silica-controlled spring bloom of diatom communities, resulting in dense, short-lived, nearly monospecific blooms of *Phaeocystis* colonies (Lancelot et al., 2005; Peperzak et al., 1998; Raabe et al., 1997). *Phaeocystis* can excrete up to 30% of its biomass as mucilage (Peperzak et al., 2000) and the production of exopolymeric particles in response to nutrient limitation has been reported (Mari et al., 2005). Some *Phaeocystis* species possess the unique ability to form floating colonies made from hundreds of cells embedded in a polysaccharide gel matrix that may be induced or enhanced by grazing (Kornmann, 1955) or other physical disruption. When driven by high winds and/or wave activity, *Phaeocystis* blooms can yield thick foul-smelling foams or scums, especially in nearshore zones, thereby fouling adjacent beaches.

Phaeocystis blooms are considered a nuisance due to the potential for various harmful impacts on the ecosystem, including: (1) reduced feeding by suspension-feeders (especially bivalve molluscs, such as mussels) and metazooplankton; (2) allelopathic interactions with diatoms, (3) toxic effects on larvae (e.g. cod), (4) reduction in the trophic efficiency of the food web (Leeuwe et al., 2007; Rousseau et al., 2000; Verity et al., 2007; Weisse et al., 1994). These potential impacts are often not measured and, hence, are not usually included in HAEDAT. *Phaeocystis* blooms are, however, notorious for mucilage problems in the North Sea (Lancelot, 1995). Large quantities of extracellular polysaccharides are released to the water column as the bloom wanes which, depending on currents and the prevailing meteorological conditions, can create thick odorous foams on nearby beaches (Blauw et al., 2010). The impact of these phenomena on beach recreation are not well known.

Two of these species, *P. globosa* and *P. pouchetii*, are common in Belgian, Dutch, German (Wadden Sea) and Danish waters, as well as the Norwegian coast and Barents Sea, but are rarely seen in the Skagerrak-Kattegat (Henriksen, 2009; Schoemann et al., 2005). Dense spring blooms of these colony-forming species are a frequent occurrence in the nutrient-enriched coastal zones of the German Bight and southern North Sea since at least the 1970s (Bätje and Michaelis, 1986; Gypens et al., 2007; Riegman et al., 1992; Veldhuis et al., 1986; Weisse et al., 1986).

Phaeocystis is a major natural component of spring blooms in the Norwegian Sea, where such species bloom together with (or occasionally instead of) diatoms in northern Norway. In Norwegian waters, this genus has not been associated with faunal mortalities, toxicity or any other negative consequences, and is therefore not regarded as a HAB taxon.

Because of the lack of evidence of an actual economic impact, *Phaeocystis* blooms are generally underreported in HAEDAT. To date, in northern Europe only a single case of demonstrable economic effects associated with algal-related beach foam has been entered into HAEDAT (DE-10-002): in July 2010, the beach area of Wilhelmshaven was temporarily closed by local authorities due to heavy fouling by foam associated with *Phaeocystis*. The only other HAEDAT-reported event associated with *Phaeocystis* from our area under review was a large-scale mortality of cultivated mussels that occurred in the Netherlands in 2001 (NL-01-001), apparently caused by hydrodynamic transport of a *Phaeocystis* bloom, followed by sedimentation, anoxia, and finally shellfish mortalities (Peperzak and Poelman, 2008). Most *Phaeocystis* blooms, however, pass without any apparent issue.

In a study carried out in Belgium, fishermen and tourists were asked about their perceptions of *Phaeocystis* blooms. Neither of these groups perceived *Phaeocystis* blooms to be a major nuisance. Economic losses were considered as very limited (Rousseau et al., 2004), but an economic analysis indicated that among tourists, there is a willingness to pay to reduce adverse effects of eutrophication that might be associated with such blooms (Stolte et al., 2004).

Foam is most likely to form at the end of blooms (i.e., when high biomass begins to decline), as colonies disintegrate due to lack of light or sufficient nutrients (nitrogen and phosphate). Protein release is triggered by cell death, often caused by virus infections. *Phaeocystis globosa* produces dimethyl sulfoniopropionate (DMSP), which can be converted extracellularly into dimethyl sulfide (DMS) (Stefels et al., 2007) and released in seawater. DMS is emitted from the sea to the atmosphere under turbulent conditions. This volatile substance smells unpleasant, and may account for some of the foul odor associated with decaying *Phaeocystis* blooms.

In the Dutch monitoring program “Monitoring Waterstaatkundige Toestand des Lands (MWTL)” of the Dutch Water authority *Phaeocystis* has been monitored since 1990. In general, along the Dutch coast, chlorophyll concentrations, an index of phytoplankton biomass, have declined during the period of 1990 to 2016. These monitoring data were analysed for OSPAR (data 1990–2014 and 1990–2016) (OSPAR ICG-Eut 18/3/2(L) to test the hypothesis that *Phaeocystis* is an indicator for eutrophication. This analysis showed that nutrient concentrations have declined over time, but the cell abundance of *Phaeocystis* and annual and spatial variability could not be explained by the ambient nutrient levels nor light conditions.

In May 2020, a fatal incident occurred in Scheveningen, the Netherlands, where five persons carrying out watersports died. The local weather conditions seemed to have induced foam accumulation. The estimates of the maximum thickness of the foam layer vary, from a few meters, based on foam residues (van Wezel, 2020) to 2.5 to 3 m (Philippart et al., 2020). This incident coincided with a bloom of *Phaeocystis globosa* but the direct association with these human mortalities is uncertain.

6. Selected high biomass algal blooms causing harmful events

6.1. *Noctiluca* – water discoloration - red water

Noctiluca scintillans (Macartney) Kofoid & Swezy is a large (up to 2 mm cell diameter) heterotrophic dinoflagellate well known globally to produce dense aggregations of bioluminescent cells. Depending upon the pigmented endosymbiont, *Noctiluca* blooms may be either vivid green or brick red-orange to the naked eye. In northern Europe, especially in the North Sea, *Noctiluca* frequently forms high cell-density surface, exclusively of the red-orange type. Elbrächter and Qi (1998) reported fish mortalities along the German North Sea coast due to oxygen deficiency caused by a dense bloom of *N. scintillans*. Toxin production has never been reported for *N. scintillans* but there is evidence that high release of ammonia by high-biomass blooms may cause localized ecosystem disruptive effects (Baliarsingh et al., 2016).

6.2. *Lepidodinium* spp. – water discoloration - green water

Lepidodinium chlorophorum (M.Elbrächter & E.Schnepf) Gert Hansen and *L. viride* are dinoflagellates with green chloroplasts originating from the Chlorophyceae (Hansen et al., 2007). *Lepidodinium chlorophorum* and *L. viridae* are difficult to discriminate under the light microscope, and hence may have been erroneously reported from northern Europe in some cases. In August 1990 green water coinciding with a bloom of *Lepidodinium viride* M.Watanabe, S.Suda, I.Inouye, T.Sawaguchi & M. Chihara was observed at Helgoland in the Wadden Sea. Cell densities reached 6.5×10^6 cells L⁻¹. In September to November 2018 a bloom of *Lepidodinium* cf. *chlorophorum* caused green water along the east coast of Jutland, Denmark. The western Kattegat (Aarhus Bay and the Horsens fjord) and the Little Belt was affected. Cell densities of *L. cf. chlorophorum* reached 2.4×10^6 million cells L⁻¹ and chlorophyll fluorescence measurements indicated maximum chlorophyll concentrations of 68 µg L⁻¹. Bathing was not recommended at the east coast of Jutland south of Djursland. No direct harmful effects were observed but the degradation of the bloom may have resulted in oxygen deficiency.

6.3. *Tripes Bory* (syn. *Ceratium*) – water discoloration - brown water

Observations of brown water associated with high cell abundances of *Tripes furca* (Ehrenberg) F.Gómez, *T. fusus* (Ehrenberg) F.Gómez, *T. lineatus* (Ehrenberg) F.Gómez and *T. muelleri* Bory have been reported from the Kattegat, Skagerrak and the Norwegian west coast. *Tripes* spp. have not been reported to produce toxins (Moestrup et al., 2020), but may cause harmful effects in high cell densities. Blooms of *Tripes* spp. in Laholm Bay on the Swedish coast of the Kattegat have resulted in low oxygen conditions in near bottom water (Granéli et al., 1989).

6.4. *Coscinodiscus* and mucilage-related harmful events

Coscinodiscus wailesii Gran & Angst is a large (cell diameter up to 500 µm) centric diatom, occasionally associated with harmful but not toxic events in northern Europe. *C. wailesii* can produce mucus that clogs fish nets and other fishing equipment. This species is likely to have been introduced to northern Europe; the species was first observed in the English Channel in 1977 when mucilage attributed to *C. wailesii* hindered trawling (Boalch and Harbour, 1977). *Coscinodiscus wailesii* has subsequently become a significant component of the phytoplankton in the northeast Atlantic (Edwards et al., 2001; Laing and Gollasch, 2002; Rick and Dürselen, 1995). Blooms of diatoms producing mucilage have caused problems in the Adriatic Sea (Alcoverro et al., 2000), off the US east coast (Mahoney and Steinle, 1980) and in Japan (Fukao et al., 2012; Fukao et al., 2009) but reported occurrences from northern Europe are uncommon and poorly documented. Accumulation of mucilage has been observed in western Sweden and Norway; this may be attributable to *C. wailesii*, but has not been confirmed (L.J. Naustvoll unpublished; B. Karlson unpublished). Another diatom, *Coscinodiscus concinnus* W.Smith, caused discoloration of the water and formed a thick (>20 cm) oily layer on the sea surface in the North Sea in the south-western part of Doggerbank in May 1947. The oil adhered to birds feathers and resulted in bird mortalities (Tåning, 1951).

6.5. *Emiliania huxleyi* – high densities cause fish fleeing from fjords

Emiliania huxleyi (Lohmann) W.W.Hay & H.P.Mohler is a prymnesiophyte with calcareous scales. This species is an important primary producer in the oceans and plays a central part in the global carbonate cycle (Thierstein and Young, 2013). Blooms of *E. huxleyi* are frequently observed in the Barents Sea, the Norwegian Sea and the North Sea, and adjacent waters including the Kattegat and the Skagerrak. This species is not typically considered to be harmful, but fish has been observed to flee Norwegian fjords when *E. huxleyi* blooms occur. This is likely due to the fact that visual predators have difficulties finding prey during the reduced water transparency conditions during blooms.

6.6. *Peridinium cf. quadridentatum* or *cf. Blixaea quinquecornis*

Peridinium quadridentatum (F.Stein) Gert Hansen (syn. *Peridinium quinquecorne* Abé) is a phototrophic dinoflagellate with chloroplasts of diatom origin (Horiguchi and Pienaar, 1991; Horiguchi and Takano, 2006). *Peridinium quadridentatum* was associated with a fish kill in the Red Sea (Alkawri et al., 2016). In June 2007 a swimmer bathing at the public beach at Askimbadet outside Gothenburg, Sweden noticed feelings of paralysis, and sensation of numbness, stinging needles and burning on her skin. Symptoms remained the next day. Other swimmers were also affected, but less so. Phytoplankton sampling revealed a dinoflagellate identified as *Peridinium quinquecorne* by light microscopy, at a cell abundance of 2.4×10^6 cells L⁻¹. Scanning electron microscopy of samples from the same geographical area collected in 2018 revealed the presence of *Blixaea quinquecornis* (Abé) Gottschling (M. Hoppenrath, pers. comm.). *Peridinium quadridentatum* and *B. quinquecornis* have a similar appearance under the light microscope and there may have been a misidentification in 2007.

6.7. *Nodularia spumigena* and other filamentous cyanobacteria

Blooms of cyanobacteria are common in the brackish water Baltic Sea (Kahru and Elmgren, 2014; Olofsson et al., 2020). The history of cyanobacteria blooms in the Baltic was reviewed by Finni et al. (2001). Surface accumulations of putative cyanobacteria were observed in 1854 at the island of Gotland in the Baltic Proper, but no harmful effects were reported (Lindström, 1855). Molecular analysis of sediment has shown *N. spumigena* to have been present in the Baltic for thousands of years (Ceglowska et al., 2018).

Harmful algal events associated with cyanobacterial blooms are reported within the brackish waters of the Baltic but few events have been recorded from the coastal waters of the Atlantic. Events in the Baltic Sea were reported almost every year for the period 1987–2019. The distribution of events is shown in Fig. 2. The majority of events are reported from Sweden where multiple methods are applied to define events. Reports also come from the coast of Finland and Poland, as well as the Baltic coast of Germany, but different criteria are used to define cyanobacterial events (see Section 2). Recent data from Russia, Estonia, Latvia and Lithuania are lacking, but it is unlikely that this reflects the current status of cyanobacterial bloom. A number of cyanobacterial species are recorded in the Baltic, with the majority of the visible surface blooms formed by three filamentous, nitrogen-fixing taxa: *Nodularia spumigena* Mertens ex Bornet & Flahault, *Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault and *Dolichospermum* spp. *N. spumigena*, producer of the cyanotoxin nodularin (NOD), is common in the whole Baltic Proper, in the Gulf of Finland and nowadays also in the Bothnian Sea. Surface accumulations of filamentous cyanobacteria were also observed in the Kattegat in 1997, 2006, 2018 and in 2020. Beach fouling occurred along the coast of Halland, Sweden. The filaments were most likely transported to this area from the Baltic Sea through the Öresund strait. The transport of *N. spumigena* in summer 2018 was described by Carlsson and Rita (2019). In 2012 an unusual and massive bloom of *N. spumigena* was observed in the western Wadden Sea along the coast of Ostfriesland (Lower Saxony), Germany. This bloom caused heavy localized beach fouling but was not analysed for toxins and was not associated with other harmful algal events.

While NOD has been recorded in biota from the Baltic (fish, shellfish) there has yet to be a management action or record of human illness associated with cyanotoxins in seafood. NOD-related poisoning of dogs after drinking contaminated water have been reported (Algermissen et al. 2011, Simola et al. 2012). Accumulation of a high cyanobacterial biomass in bathing waters has resulted in beach closures due to human health concerns, as recommended in the Bathing Water Directive (2006/7/EC). These beach closures impact the tourism industry in these local areas and are the main human impact of cyanobacterial blooms in the Baltic Sea. The potentially microcystin (MC) -producing *Dolichospermum* spp. occur throughout the Baltic Sea, but are more common in the lower-salinity (north and east) basins. Microcystins, mainly produced by freshwater cyanobacteria, have also been recorded in brackish waters and estuaries where the presence of the toxin producers, *Dolichospermum*, *Microcystis* and *Planktothrix* have been recorded (Karlsson et al., 2005, Halinen et al., 2007, Chernova et al., 2019). The highest concentrations of dissolved MCs to date (up to 49 µg L⁻¹) were reported from the Russian easternmost part of the Gulf of Finland (Chernova et al., 2019) but are not recorded in the HAEDAT database. The most common bloom-forming cyanobacterium in the Baltic Sea, *Aphanizomenon flosaquae*, is not considered a toxin producer. It is harmful in the sense that it causes strong accumulations of biomass affecting leisure activities and tourism. Cyanobacteria blooms also produces noxious odours, particular upon decay of high biomass accumulations.

The occurrence of the acute neurotoxic alkaloid, anatoxin-a (AN-a) is limited to coastal waters in the Baltic. So far, species of *Dolichospermum* and *Oscillatoria* as well as *Aphanizomenon flosaquae* (most likely of freshwater origin) have been indicated as potential AN-a producers in the Baltic Sea (Rantala-Ylinen et al. 2011; Chernova et al. 2019). To date

no harmful events have been associated with this toxin. BMAA (β -methylamino-L-alanine), a widely occurring cyanobacterial neurotoxin, has also been found in cyanobacterial samples from the Baltic Sea and from many other water bodies, including Florida Bay and the Mediterranean Sea (Lance et al. 2018). However, due to analytical challenges, the real health risk associated with human exposure to the toxin is difficult to assess.

7. Societal impacts of HABs

The societal impacts of HABs are highly context-specific and relate to the HAB species and impact areas in question and the ways affected regions and stakeholders understand, anticipate, communicate and respond to HAB risks. Impacts may include both direct and indirect economic (market) impacts, as well as intangible, or non-economic impacts (Adams and Larkin, 2013). As in other regions, the socio-economic impacts of HABs in the North, Norwegian, Barents and Baltic Seas can be broken down into those associated with loss or hindrance of seafood production, human health consequences, costs of monitoring and deleterious effects on tourism and recreation in coastal zones. These interactions can be multifaceted and synergistic, with effects as follows on: i) Shellfish – negative human health impacts (illness or deaths resulting from consumption of toxin contaminated shellfish), as well as economic impacts from precautionary closure of shellfish farms and recalls of shellfish products; ii) Farmed and wild fish, through direct fish mortalities and sub-lethal impacts on farmed fish production, health and welfare costs and losses to affected producers, harvesters and communities; and iii) Exploitation and use of beaches and nearshore zones, including harvesting activities, tourism, recreation, and food gathering practices, through closures of beaches and shellfish harvesting areas.

The HAB species/genera of major concern for the greater North Sea region and Norwegian Sea with respect to these defined socioeconomic impacts on shellfish production and consumption, are mainly species of *Alexandrium*, *Dinophysis*, *Azadinium*, and *Pseudo-nitzschia*. In these cases, human health implications are linked to consumption of toxic shellfish (both farmed and wild harvested), and economic impacts result from shellfish farm or harvesting area closures and recalls of toxic shellfish. With respect to the socioeconomic effects related to fish production and harvesting, the major culprits are phytoflagellates belonging to the prymnesiophytes, and to a lesser extent the dinoflagellates and dictyochophytes. *P. polylepis* has caused large-scale ecosystem disruptions and mortalities of wild and farmed fish in the Kattegat-Skagerrak region; *Pseudochattonella* has been responsible for periodic mortalities of farmed fish in southern Norway and in Denmark, and likely affected farmed fish health via sub-lethal impacts; *C. leadbeateri* has been associated with infrequent mass mortality events of farmed fish in northern Norway. In the North Sea and adjacent waters, socioeconomic impairment of enjoyment and exploitation of shoreline and beach areas, have been primarily linked to *Phaeocystis*. This prymnesiophyte is capable of producing large amounts of mucilaginous foam which accumulates on German and Dutch beaches along the Wadden Sea coast, causing major short-term impacts on tourism and recreational activities.

All of these HABs have the highest socioeconomic impacts and effects on coastal communities, because coastal areas are where fish and shellfish aquaculture, wild harvesting of seafood species and tourism and recreation activities are dominant. The affected and concerned stakeholders in these regions include the general public, relevant authorities engaged in public health, fisheries, aquaculture, food safety, water quality management, coastal and marine (hazard) planning and management, environmental monitoring, as well as commercial aquaculture and fisheries industry representatives, researchers, knowledge brokers and public interest organizations.

7.1. Effects on fish farms and fisheries

Harmful Algal blooms (HABs) negatively impact finfish most directly via fish mortalities that can have major socio-economic consequences for affected aquaculture producers and regions, but they can also cause sub-lethal effects such as decreased growth rates, and increased susceptibility to diseases and parasites in farmed fish, which remain under-reported (Davidson et al., 2020). Wider societal impacts linked to loss of jobs and incomes in land-based processing and related service industries may also occur. HABs causing large fish kills may also contribute to supply volatility that affects retail and final consumer prices, though the evidence of this in the Norwegian/North Sea region is scarce. When assessing the impacts of HABs on fish farming, the costs to be considered include expenses for HAB mitigation measures, such as communication and coordination of emergency measures during a HAB event, increased logistical and clean-up up associated with handling large quantities of dead fish, emergency or contingency measures, such as moving fish to new locations and undertaking precautionary slaughtering of fish, as well as the costs of monitoring, research and development underpinning preventative measures (Anderson et al., 2000; Chávez et al., 2019). Experiences from the *C. leadbeateri* bloom in northern Norway 2019 indicate that it is also important to consider risk transfer measures such as insurance held by independent aquaculture companies, and “compensatory” measures that governments and authorities may introduce in the wake of major HAB events aimed at reducing the total economic impacts, in order to better understand the “net” societal impacts of fish-killing bloom events. The economic impacts of HABs for finfish aquaculture can moreover change greatly over time due to structural changes that shift the exposure of particular regions, companies or types of production to HAB events. For example, in southern Norway, a large part of the finfish aquaculture industry closed down after the major 1988 *Prymnesium polylepis* bloom that killed both wild and farmed fish as well as affecting wider ecosystems in the Kattegat-Skagerrak. Fish cages and other equipment were moved to the west coast of Norway in the wake of the event. In May 2019, an extensive bloom of *C. leadbeateri* occurred in parts of Nordland and Troms counties, northern Norway (Karlsen et al., 2019). The event resulted in the loss of 14 500 tonnes of Atlantic Salmon in Nordland and Troms Counties (Table 4), representing approximately 6.5% of the total biomass in the region, and 2% of the biomass at national level (Marthinussen et al., 2020). This resulted in a reduction of nearly a quarter of the combined slaughtering potential of the affected companies at the time of the event. The direct and indirect gross economic effects of the 2019 bloom have been estimated at between 2.3 and 2.8 billion NOK (Marthinussen et al., 2020). These costs include, in addition to the value of lost fish, substantial clean-up costs and lost future profits for affected companies, as well as estimated knock-on effects for the land-based processing and service supply industries and lost tax revenues level (Marthinussen et al., 2020).

7.2. Effects on mussel farmers and collectors

Reported effects of HABs on mussel farmers in Norway, Denmark and Sweden relate mainly to the economic and reputational costs associated with periodic shellfish closures due to the presence of *Dinophysis* spp. and *Alexandrium* spp., and more rarely caused by *Pseudo-nitzschia* and *Azadinium* species. Wider societal impacts linked to loss of jobs and incomes in land-based processing and related service industries may also occur (Pérez Agúndez et al., 2013) though the size of the shellfish industry in these countries is very small compared to other shellfish producing regions in Europe, hence the total impacts of HABs are difficult to assess. Interviews with stakeholders in Norway and Sweden conducted within the European CoCliME project indicate that for individual shellfish producers and harvesters, the economic impacts of HAB events depend on the time of year, the amount and type of product affected, and the extent to which producers and harvesters have effective risk

Table 4
Estimated amount and cost of fish kill damage for selected blooms of fish killing taxa.

	<i>Prymnesium polylepis</i>	<i>Prymnesium parvum</i>	<i>Chrysochromulina leadbeateri</i>	<i>Pseudochattonella</i> spp.	Reference
Sweden 1988	100 tonnes USD 1 million				Skjoldal and Dundas 1991
Norway 1988	800 tonnes USD 9 million				Skjoldal and Dundas 1991
Norway 1989		750 tonnes USD ~9 million			Johnsen and Lein, 1989; Kaartvedt et al., 1991
Norway 1991			742 tonnes USD ~3.5 million		Aure and Rey, 1992; Rey, 1991
Norway 1995		50 tonnes USD 0.3 million			
Norway 1998				350 tonnes USD 1.4 million	Aure et al. 2000, 2001
Norway 2001				1100 tonnes USD 3.5 million	Naustvoll et al. 2002
Denmark 2006				38 tonnes USD 0.5 million	This publication
Denmark 2007				70 tonnes USD 0.8 million	This publication
Norway 2007		135 tonnes USD no estimate			Johnsen et al., 2010
Denmark 2017				25 tonnes USD 0.3 million	This publication
Norway 2019			14 500 tonnes > USD 100 million		Karlson et al., 2019
Denmark 2019				> 400 tonnes USD 1.4 million	This publication

Table 5
Maximum PST levels in mussel meat of *M. edulis* in selected years. The EU regulatory limit is 800 STXeq kg⁻¹ of mussel meat.

	µg STXeq kg ⁻¹
Sweden 1987	
Skagerrak coast	800
Norway 1987	First closures of harvesting
Southern and western coasts	
Denmark 1987	400-200
Limfjorden	
Norway 2010	17700
Norwegian Sea coast	
Norway 2011	12500
Norwegian Sea coast	
Denmark 2016	200-720
Norway 2017	58000
Norwegian Sea coast	
Norway 2017	3600
Barent Sea coast	
Sweden 2017	3600
Skagerrak coast	

mitigation measures in place to deal with HABs. The main strategy that consulted shellfish producers employ to deal with HABs and other environmental risks involves diversifying the location of production sites (maintaining harvesting and production licences in different areas), and in some cases, the types of species produced or marketed. Overstocking is also employed, for example keeping twice as many mussels as needed, in case they are killed by a disease, adverse environmental conditions, or predators. Maintaining stock of different age classes across locations is also employed in some cases to prevent disruptions in harvesting.

7.3. Effects on tourism and recreational activities

Blooms of *Phaeocystis* create foam on beaches in the North Sea. Nowadays the public in Belgium and the Netherlands seems to perceive this as a normal situation. If this is the case, recreational activities and tourism are likely not strongly affected. However, the loss of human life in connection with foam on the beach at Scheveningen in 2020 (Table 1)

may have changed the perception. Turbid waters due to phytoplankton blooms (e.g. of cyanobacteria, *Lepidodinium*, etc.) is likely to deter swimmers from going into the water. Recurrent blooms would affect tourism. In the Baltic Sea region, warnings of cyanobacteria blooms from the Marine Information Centres in Sweden and authorities in Finland and Poland attract attention from the public and the media. In Poland, closures of beaches due to high abundance of cyanobacteria and the detection of cyanotoxins are common some years. This is likely to affect tourism but the authors are not aware of any quantitative investigations of effects. The authors know of no attempts to investigate the economic consequences in a quantitative way. Swimmers may be directly affected by the dinoflagellates *A. pseudogonyaulax* and *P. quadridentatum* by skin irritations as described above. These events have been rare and are likely to have no or very small effects on tourism. Harvesting (digging) of clams along the North Sea coast is common, whereas it is rare or unknown for Norway, Sweden and the Baltic Sea coast. Economic effects of HABs on primarily recreational clam digging activities is not known.

8. Discussion

Harmful algal bloom events along the coasts of northern Europe are frequent today but they also have a long history. Clearly, the socio-economic costs are substantial and have increased throughout the past three decades reviewed with access to HAEDAT. The massive blooms causing fish mortalities have high direct short-term costs that are fairly easy to quantify (Table 4). Longer term effects, e.g. the costs for reduced customer interest in fish is more difficult to quantify. The total costs for making sure that fish mortalities are minimized, i.e. enhanced monitoring, early warning systems for HABs and costs for mitigating effects are difficult to quantify. This also applies to HABs affecting harvesting of bivalve shellfish, e.g., primarily mussels, scallops and oysters in northern Europe, and the related costs. We have not attempted to summarise costs for sampling and analyses of bivalve shellfish, sampling and analyses of harmful algae, managing data and visualising and presenting results to stakeholders. Rough empirical estimates do indicate that such costs are would be lower than those incurred for human health care due to ingestion of toxins, loss of income by the aquaculture and fisheries industries and the whole value chain of companies and stakeholders

involved. Costs associated with cyanobacterial blooms are also substantial, but less targeted to the seafood industry and human health aspects. Tourism is primarily affected by these blooms but the ecosystem and ecosystem services are also impacted in a way that is more difficult to quantify.

8.1. Trends

The long-term monitoring data of harmful algae and of phycotoxins in bivalve shellfish in marine and brackish waters in northern Europe show incremental but measurable changes. These include an increase in the abundance of some nitrogen-fixing cyanobacteria in the Baltic Sea as observed in water samples analysed by microscopy (Olofsson et al. 2020) and also from satellite observations of near surface accumulations of filamentous cyanobacteria (Kahru and Elmgren 2014). The dataset on harmful algal events in HAEDAT is at present not suitable to detect trends of changes in the frequency or extent of cyanobacterial blooms, because it is not a true time-series record of the magnitude and frequency of blooms. More consistent reporting is needed.

An observed increase in the number of mortalities of farmed fish due to HABs coincides with an increase in the number of fish farms along the coasts. This does not mean that the fish farms cause the blooms of fish killing HAB organisms but rather that the blooms of HAB species are observed in connection with the fish mortalities. Blooms of *C. leadbeaterii* have had the largest direct impact on the aquaculture industry in northern Europe. The blooms in northern Norway in 1991 and 2019 resulted in substantial losses for the fish farmers (Table 4). These harmful blooms were observed with long time intervals with no harmful blooms in between, and thus no trends are evident. One has to keep in mind that the monitoring effort has not been consistent. Monitoring of fish-killing HAB species was absent for a long time in northern Norway. The blooms of *Pseudochattonella* in the Kattegat and the Skagerrak show a different pattern compared to the blooms of *C. leadbeaterii*. These blooms are recurrent events right after the diatom spring bloom causing mortalities of farmed fish, mainly in the Danish part of the Kattegat. At present there are no, or very few, fish farms along the Swedish coast of the Kattegat and the Skagerrak. If such farms were established, they would likely be affected by *Pseudochattonella* blooms. The same applies to the Norwegian Skagerrak coast. Here most fish farms were moved or shut down after the bloom of *Prymnesium polylepis* in 1988.

The most common reports to HAEDAT in northern Europe are closures of bivalve shellfish harvesting areas due to concentrations of phycotoxins in bivalve shellfish above regulatory levels. Diarrhetic Shellfish Toxins (DST) produced by *Dinophysis* species are most common in the Skagerrak area. Here a decrease in the cell abundance of *D. acuta*, especially in autumn, co-occurs with a decrease in total DST levels in blue mussels (*M. edulis*). This also applies to southern Norway. The DST problem did not go away; instead, DST levels in summertime due to *D. acuminata* has increased. Blooms of *Alexandrium* and resulting high levels of PSTs in bivalve shellfish are rare events in the Skagerrak and the Kattegat but remain common along the west coast of Norway. There are also observations of *Alexandrium* in the Baltic Sea, e.g. at Åland (Kremp et al. 2009), in the Stockholm archipelago and at the coast of Poland, but these have not affected aquaculture. No trend related to PST is obvious from the HAEDAT reports, the phycotoxin data sets or from the phytoplankton monitoring data. *Azadinium*, *Amphidoma* and AZA are recent observations in northern Europe and no trends are yet observed. *Azadinium* is difficult to identify with the light microscope or even using calcofluor staining and fluorescence microscopy (Andersen, 2010). Thus, the present data may include misidentifications of *Azadinium* as *Heterocapsa* and other small thecate dinoflagellates. Introducing methods such as metabarcoding (Hu et al. 2016, Gran-Stadniczenko, 2019, Stern et al. 2018) and qPCR (Hatfield et al. 2019, Ruvindey et al. 2018, Wietkamp et al. 2020) in monitoring programs would be useful in this context. This also applies to *Pseudo-nitzschia* taxa which are difficult

to identify to the species level using light microscopy. There are very few HAEDAT reports of events due to *Pseudo-nitzschia* in northern Europe and no trends were observed. A toxic *Pseudo-nitzschia* bloom may have severe effects if shellfish with high AST levels reach consumers. The potential problem is large because *Pseudo-nitzschia* blooms are frequent and toxigenicity of blooms is often uncertain for northern Europe.

8.2. Drivers

Changes of environmental conditions in the sea due to climate change are affecting the biogeography and seasonal distribution of phytoplankton. The increase in the abundance of *Alexandrium pseudogonyaulax* and *Dinophysis tripos* in the Kattegat and the Skagerrak are likely examples of this. Longer time series are needed to verify the recent observations. The nitrogen fixing (diazotrophic) filamentous cyanobacteria in the Baltic Sea have a competitive advantage compared to other phytoplankton when concentrations of dissolved inorganic nitrogen is low and there is phosphate available. This has resulted in an increase in cyanobacterial blooms in the Baltic Sea. It also means that nitrogen originating from N₂ gas in the air is introduced into the Baltic Sea system, a form of natural eutrophication that is an effect of nutrients introduced anthropogenically. Nitrogen fixation is more metabolically costly at higher salinities and although the diazotrophic cyanobacteria from the Baltic Sea may grow in the Kattegat and the Skagerrak their competitive advantage is lost.

Most of the phycotoxin-producing phytoplankton only constitute a small part of the phytoplankton biomass. Many of the species are mixotrophic. This implies that dissolved inorganic nutrient concentrations may not directly limit the growth of these species. However, there may be indirect effects. For example, *Dinophysis* feeds on the ciliate *Mesodinium rubrum*, which in turn steals its chloroplasts from the cryptophyte *Tealeulax amphioxeia*. If *T. amphioxeia* is favoured by high nutrient concentrations *Dinophysis* may be favoured indirectly. *Pseudochattonella* blooms were not observed in the Skagerrak and the Kattegat before 1998. The blooms are now common in this area and *Pseudochattonella* is also observed in the Southern Baltic Proper, but not in bloom abundances. It is possible that *Pseudochattonella* was introduced to the area, e.g. by ballast water.

8.3. Future scenarios

Climate change, introduction of non-indigenous taxa and eutrophication/urbanisation are likely to change the distribution and frequency of HAB events in northern Europe. An increased water temperature (Høyer and Karagali 2016) will result in changed biogeography of HAB taxa and also in different seasonal distribution. HAB taxa today found only in southern Europe may become established in northern Europe. Candidates include *Ostreopsis ovata* Y.Fukuyo, a benthic species observed in the Mediterranean, but now also in the Bay of Biscay, producing aerosolised toxins at the coasts during windy conditions. Another potentially invasive candidate is *Karenia papilionacea* A.J.Haywood & K.A.Steindinger, a fish-killer today found in the Bay of Biscay, but could likely thrive further north. Due to transport of phytoplankton and their resting stages in ballast water there are many more candidates worldwide. Stratification of the water column may change due to changes in temperature, salinity and wind speed.

A projected increase in strength of stratification in large parts of the North Sea and the Baltic Sea between the periods 1970–1999 and 2070–2099 (Gröger et al. 2019) may favour some HAB taxa, e.g. *Dinophysis* spp., that thrive at the pycnocline and form thin layers. Climate change driven ocean temperature rises could intensify the distribution and frequency of *Alexandrium* blooms by an earlier and enhanced cyst formation and higher cyst deposition with temperature-regulated life cycle transformations (Warns et al., 2013). Freshening of surface waters could affect *Alexandrium* blooms and toxic outbreaks by modifying the patterns of water column stratification. High

cell abundances of both *A. ostenfeldii* and *A. pseudogonyaulax* along the coast of Denmark at brackish salinities and high water temperature suggests that the composition of *Alexandrium* species may be changing in response to climatic conditions in the area. Furthermore, cyst and toxin records of the species in Kiel Bight suggest a potential spreading into the brackish Baltic Sea, where *Alexandrium* might expand and form blooms under future ocean warming scenarios (Kremp et al., 2019). Dinoflagellates typically benefit from stratified and low nutrient conditions since these lead to the exclusion of non-motile competitors and allow motile dinoflagellates to actively aggregate. *Alexandrium* blooms are commonly associated with stratified water (Brandenburg et al., 2017; Fauchot et al., 2005; Murray et al., 2015a).

Urbanisation and increased agricultural intensity are global trends that often leads to eutrophication. Nutrient input to coastal waters affects phytoplankton in general and favour some HAB taxa. Changed nutrient ratios may have direct effects. An increase in phosphate will favour nitrogen fixing cyanobacteria in brackish waters. In the eutrophicated Baltic Sea nutrient input has been reduced since the 1980's but the concentrations of inorganic nutrients have not changed much (Saraiva et al. 2019). Climate change is likely to have an effect on rainfall and on nutrient input to the Baltic Sea. Model studies, using combinations of climate change and a reduction of nutrient input (the Baltic Sea Action Plan), show that the reduction of nutrient input will have a larger effect on future conditions than the climate (Saraiva et al. 2019). A decrease in silicate input to coastal waters (Burson et al. 2016) may favour non-siliceous plankton, e.g. *Phaeocystis*, and the relative abundance of diatoms may decrease. Changed nutrient ratios also affect toxin production as discussed above in the *Pseudo-nitzschia* section. Urbanisation and climate change also result in the construction of harbours and other facilities such as dikes and sea gates along the coasts. Inside these artificial enclosures water conditions are often calm and here several HAB species are likely to thrive.

For millennia coastal and shelf sea regions in northern Europe have provided a key supply of seafood, socioeconomic well-being and ecosystem services, such as natural recreational facilities. Increasing anthropogenic influence and climate change create environmental stressors, causing shifts in the biogeography and intensity of HABs. In turn, this threatens the future well-being of coastal populations and ecosystem stability. Continuing historical databases such as HAEDAT provide not only an ongoing status report but also provide a template for interpretation of causes and mechanisms of HABs. Review of the data sources on HAB events, as provided herein, can also assist in developing monitoring.

Declaration of Competing Interest

The authors 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

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