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Effects of an extensive *Prymnesium polylepis* bloom on breeding eiders in the Baltic Sea

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ABSTRACT

The effects of an extensive bloom of the potentially toxic *Prymnesium polylepis* (Haptophyta) on breeding eiders (*Somateria mollissima*) in the Baltic Sea were analysed. Increasing abundances of the alternate stage *P. polylepis* was detected by a marine monitoring programme in the autumn 2007. The bloom peaked between March and May 2008 in the southern, central and northwestern Baltic Proper and abundances of up to 5 × 10^6 cells l^{-1} were recorded. At several sites *P. polylepis* constituted between 30 and 90% of the total phytoplankton biovolume. The flagellate was only recorded in low numbers in the northeastern Baltic Proper and Gulf of Finland. The abundances were low in 2007, 2009 and 2010. In 28 eider colonies situated in the southern and central Baltic Proper, sharp and synchronous declines in the number of nesting eiders were observed from 2007 to 2008. In colonies on Gotland in the central Baltic Proper, a 76% decrease, from 6650 nests to 1620 nests, was followed by increases in 2009 and 2010, although not up to numbers observed in 2007. At Utklippan and Ertholmene in the southern Baltic Proper, the observed decreases of 55%, from 144 to 65 nests, and 36%, from 1660 to 1060 nests, respectively, between 2007 and 2008, were followed by increases in 2009 and 2010 up to the level observed in 2007. By contrast, no general decline of the number of nesting eiders was observed from 2007 to 2008 in 75 colonies in the northeastern Baltic Proper and Gulf of Finland. Hence, the spatial distribution of the *P. polylepis* bloom in 2008 closely matched the observed distribution of extensive non-breeding of female eiders. We suggest that the intensive spring bloom of *P. polylepis*, either through a toxic or non-toxic pathway, affected the main benthic food of eiders, i.e. blue mussels (*Mytilus trossulus* × *Mytilus edulis*), at pre-breeding foraging sites close to the breeding sites, and, subsequently, the body condition of adult female eiders and their breeding propensity.

1. Introduction

Blooms of harmful algae, including blooms of potentially toxic species of the order Prymnesiales (Haptophyta), have been found to affect the grazing activity, growth, condition, survival or reproductive performance of other algae, zooplankton, fish and benthic invertebrates (John et al., 2002; Nielsen et al., 1990; Schmidt and Hansen, 2001; Underdahl et al., 1989). In May 1988, a very intense toxic bloom of *Prymnesium polylepis* (Manton & Parke) Edvardsen, Eikrem & Probert (Prymnesiales, Haptophyta) (previously named *Chrysochromula polylepis* Manton & Parke) was observed along the coasts of Denmark, Sweden and Norway (Dahl et al., 1989; Lindahl and Dahl, 1990; Underdahl et al., 1989). The bloom reached cell concentrations of up to 70 × 10^6 cells l^{-1} and killed benthic and pelagic species of many phyla as well as several hundred tons of fish in more than 120 fish farms in the Kattegatt and Skagerrak regions (Underdahl et al., 1989). Blooms of *P. polylepis* and other Prymnesiales are not always toxic as toxin production is influenced by environmental conditions, cell type and the physiological state of the cells (Edvardsen and Paasche, 1998; Johansson and Granéli, 1999). Several apparently non-toxic blooms of *P. polylepis* and other species of Prymnesiales have occurred in the Kattegatt, Skagerrak and the Baltic Sea since 1988 (Dahl et al., 2005; Lekve et al., 2006; Majaneva et al., 2012). When blooms are not directly lethal, Prymnesiales cells may cause temporary negative effects on grazing zooplankton and filtering benthic fauna. For example, the *P. polylepis* bloom in 1988 was not reported to be lethal for adult blue mussels (*Mytilus edulis*) but the bloom was found to reduce the filtration rate, delay the timing of spawning and to negatively affect fertilization success and early development of the mussels (Granmo et al., 1988; Loo, 1989;

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Loo, pers. comm.). Furthermore, in laboratory experiments high concentrations of *P. polylepis* have been found to negatively affect shell growth of blue mussels (Nielsen and Strømgren, 1991). Filtering adult blue mussels may also accumulate toxins from harmful algae such as *P. polylepis* (Stabell et al., 1993; Underdahl et al., 1989) and thereby become less profitable or harmful for those organisms which feed on blue mussels.

In autumn 2007, routine national monitoring detected increasing numbers of *P. polylepis* in the Baltic Sea (Hajdu et al., 2008; Majaneva et al., 2012). The bloom peaked between March and May 2008 in the southern, central and northwestern parts of the Baltic Sea. At some sites concentrations of up to 5×10^6 cells l^{-1} were recorded (Majaneva et al., 2012). Correlative analyses of the abundances of *P. polylepis*, phytoplankton and zooplankton did not indicate toxic effects of the *P. polylepis* bloom on other plankton species (Hajdu et al., unpubl). Simultaneously, ongoing monitoring and research projects on breeding sea ducks in the Baltic Sea region detected an exceptional and synchronous decline of the number of nesting common eiders (*Somateria mollissima*, hereafter eider) over large geographical areas in spring 2008. Because marine birds previously have been observed to be negatively affected by harmful algal blooms (Armstrong et al., 1978; Shumway et al., 2003), albeit not yet by blooms of Prymnesiales, we decided to further investigate possible direct or indirect effects of the extensive *P. polylepis* bloom on the bivalve-feeding eider.

In this study we combine abundance estimates of the potentially toxic *P. polylepis*, the total abundance of Prymnesiales cells and data on the number of nesting eiders from 2007 to 2010 at selected monitoring and nesting sites in the Baltic Sea. We especially analyse the temporal and spatial relationship between spring cell concentrations of *P. polylepis* and other Prymnesiales and the number of nesting female eiders. We discuss possible alternative causes for the observed dramatic and synchronous decline of nesting eiders in the central and southern part of the Baltic Proper in the spring 2008. We suggest that the intensive spring bloom of *P. polylepis* affected the quality of the main benthic food for eiders, i.e. blue mussels, and, subsequently, the body condition of female eiders and their breeding propensity.

2. Material and methods

2.1. Study species

The Baltic population of eiders winters in the Danish and German waters and breeds mainly along the Swedish, Finnish, Estonian and Danish coasts. Surveys have shown that the population has declined by approximately 50% since the beginning of the 1990s (Ekroos et al., 2012a; Skov et al., 2011). The population decline in recent decades was preceded by a population increase from the 1950s up to the 1980s. The causes for the earlier population increase and the recent rapid decline are not clear. Several non-exclusive hypotheses addressing both bottom-up and top-down effects, such as changes of the availability of high quality food because of eutrophication and climate change, thiamine deficiency, and predation on nesting females by white-tailed eagles (*Haliaeetus albicilla*) have been suggested (Balk et al., 2009; Ekroos et al., 2012a, 2012b; Laursen et al., 2010; Skov et al., 2011; Waldeck and Larsson, 2013).

The Baltic eiders are considered to be capital breeders which for successful breeding are dependent on the nutrient and energy reserves accumulated in winter and early spring at the common wintering sites in the southwestern Baltic Sea, the Danish sounds and the Wadden Sea (Drent and Daan, 1980; Hario and Öst, 2002). Between mid-March and end of April the eiders leave the wintering areas and migrate to the breeding areas in the central and northern Baltic Proper. The eiders usually arrive at the breeding sites 1 to 4 weeks before egg laying starts. Additional accumulation of nutrient and energy reserves at feeding sites in the close vicinity of the nesting sites during the pre-laying period may also affect female condition, breeding propensity, clutch size and incubation efficiency. However, the relative importance of the energy and nutrient intake close to the nesting sites is not fully understood (Christensen, 2000; Hario and Öst, 2002; Parker and Holm, 1990; Rigou and Guillemette, 2010; Sénéchal et al., 2011). Female eiders usually start egg laying from mid-April to mid-May. On average, egg laying starts earlier in the southern than in the northern study sites. During the incubation period, female eiders feed very little or not at all.

In most parts of its distribution eiders prefer to feed on blue mussels. In the wintering areas the eiders consume mussels of up to 60 mm in length (Laursen et al., 2009). In the main Baltic breeding areas in Finland, Sweden and Estonia, blue mussels (*Mytilus trossulus* × *M. edulis*) very rarely grow larger than 35 mm and eiders have been found to mainly feed on blue mussels that are between 5 and 35 mm in length (Öst and Kilpi, 1998). Eiders swallow the mussels whole with the shells and extract energy and nutrients only from the soft body parts. The soft body mass of the mussels vary greatly over the yearly cycle. The gonad development and the increase of the soft body mass of blue mussels in spring are affected by spring phytoplankton densities and plankton species composition but also by the abundance of harmful plankton species (Honkoop and Beukema, 1997; Kautsky, 1982; Loo, 1989; Tracey, 1988). Spring blooms of phytoplankton are known to vary in intensity among regions and years. Therefore, the spatial and temporal variation in breeding performance of eiders and other bivalve-feeding sea ducks may be affected by species interactions at lower trophic levels.

Species of Prymnesiales including *P. polylepis* are found in marine plankton communities worldwide (Edvardsen and Paasche, 1998). The abundances vary greatly among seasons and years. Environmental factors such as low nutrient concentrations and high N:P and N:SiO4 ratios and stratified water masses have been suggested to influence the development of blooms (Lekve et al., 2006). Identification of Prymnesiales species is difficult and requires electron microscopy. Furthermore, *P. polylepis* has two alternating stages in the haplo-diploid life cycle, known as the ‘authentic’ and ‘alternate’ stages (Edvardsen and Vaulot, 1996). In the Baltic Sea the alternate stage is generally larger (>10 μm) than the authentic stage (6–10 μm) (Majaneva et al., 2012). By using electron microscopy and genetic sequencing Majaneva et al. (2012) identified the species that produced the intensive bloom in early spring 2008 in the Baltic Sea as the alternate stage of *P. polylepis* (hereafter referred to as large *P. polylepis*).

2.2. Number of nesting eiders

Breeding eiders were studied at 103 nesting islands within six different regions in the Baltic Sea, i.e. at Ertholmene, Bornholm, Denmark (3 islands), Utklippan, Blekinge, Sweden (3 islands), Gotland, Sweden (21 islands along the eastern coast and 1 island along the western coast), Saaremaa and Hiiumaa, Estonia (37 islands), Kolga, southern Gulf of Finland, Estonia (8 islands) and at Tvärminne, northern Gulf of Finland, Finland (30 islands), between 2007 and 2010 (Fig. 1). The field counts in the different regions were performed as parts of other research or long-term monitoring projects on eiders and costal waterbirds. The characteristics of the nesting islands may range from completely open very small islands to large open or bushy islands of several km^2 in size. Eiders in the Gulf of Finland breed on both open and forested islands in about equal numbers. Several of the studied nesting islands within a region are situated close to each other. High densities of nesting eiders are almost exclusively found on islands that are free from red fox (*Vulpes vulpes*). Most of the study islands on Gotland, at Tvärminne and in Estonia are visited by hunting white-tailed eagles. Additional descriptions of the study areas can be found elsewhere (Ekroos et al., 2012b; Christiansö Fieldstation, 2013; Kullapere, 1983; Larsson, 2004, 2011; Peil and Nilson, 2007).

The number of nesting eiders was obtained from direct total counts of nests or incubating females. Observers usually visited the islands once or twice during the incubation period. Some larger islands were not completely covered. The number of nests was in those cases

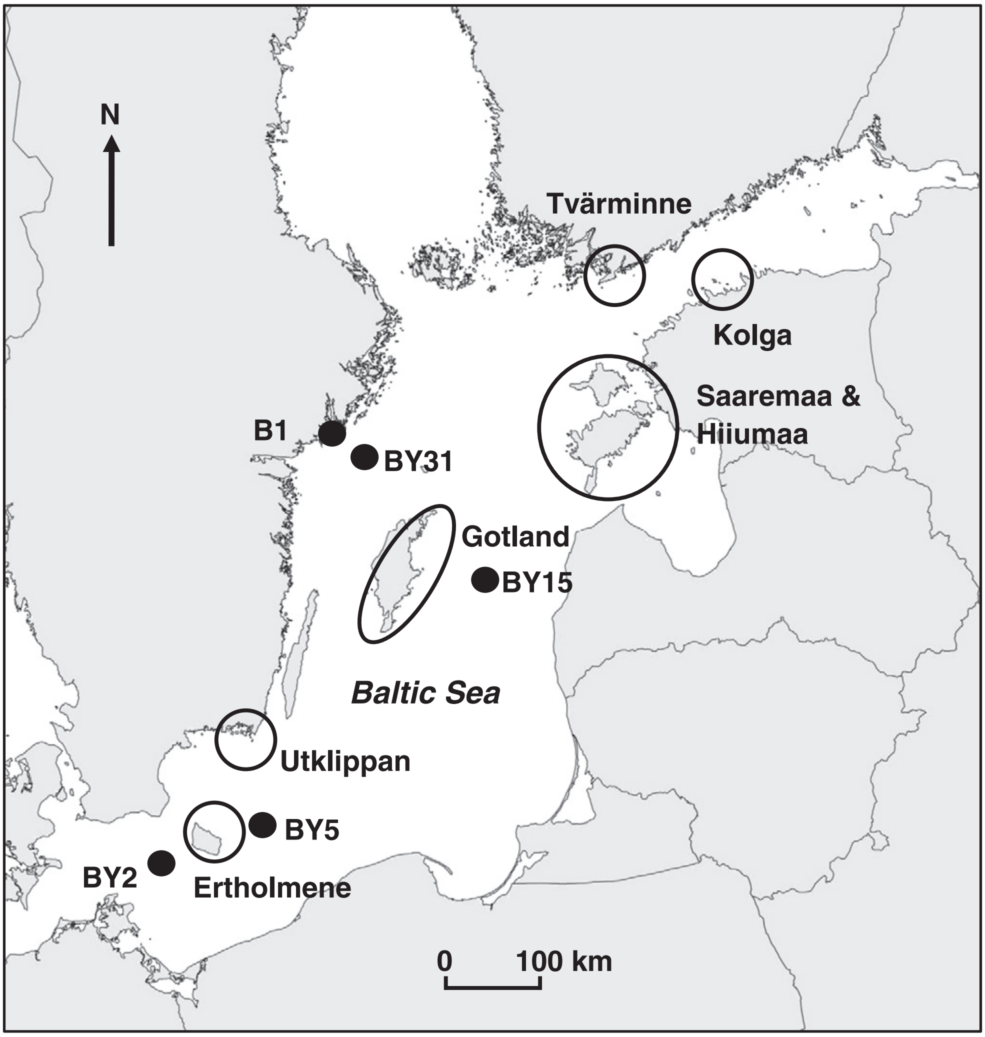

Fig. 1. Map showing the locations of the six regions where nesting eiders were studied (circles), and the monitoring sites BY2, BY5, BY15, BY31, B1, where abundances of Prymnesiales species were measured between 2007 and 2010. In 2008, the abundances of *P. polylepis* were measured at several additional sites.

obtained from extrapolations of nest counts of selected parts of the islands. The counting methods used were constant over years. The number of nests found in a study region is dependent on both population size, i.e. the numbers of adult females in the region, and the frequency of non-breeding (Coulson, 1984, 2010). Mean egg clutch size values were obtained from samples within colonies at Ertholmene, Gotland and Tvärminne.

2.3. Abundance and biovolume estimates of P. polylepis and Prymnesiales cells

Measurements of the abundance and biovolume of *P. polylepis* and other Prymnesiales cells as well as of phytoplankton were conducted regularly at several sites in the Baltic Sea by national authorities within the HELCOM monitoring programme (HELCOM, 1988, 2008). Counting methods and biovolume measurements were performed according to the HELCOM standards (HELCOM, 1988, 2008; Olenina et al., 2006). In this paper, we especially analyse abundance and biovolume estimates obtained by Swedish authorities in March, April and May from 2007 to 2010. We also refer to additional previously published abundance measurements collected in 2008 (Hajdu et al., 2008; Majaneva et al., 2012). Sampling intensity differed between sites. Some sites were only sampled once a month whereas others were sampled up to four times per month. In the further analyses we use the monthly maximum abundances.

3. Results

3.1. Number of nesting eiders

In the 28 study colonies situated in the southern and central Baltic Proper, i.e. in the colonies on Ertholmene, Utklippan and along the coast of Gotland, a dramatic decline of the number of nesting eiders was observed from 2007 to 2008 (Fig. 2). In the 22 study colonies on Gotland, the 76% decrease (from approx. 6650 nests to approx. 1620 nests) was followed by increases in 2009 and 2010, although not up to numbers observed in 2007. Despite the study colonies on Gotland were situated along a 200 km coastline the changes in nest numbers was highly synchronous. All but one of the 22 study colonies declined from 2007 to 2008 and all but two increased from 2008 to 2009 (Fig. 2). At Utklippan and Ertholmene the observed decreases of 55%, (from 144 to 65 nests), and 36% (from 1660 to 1060 nests), respectively, between 2007 and 2008, were followed by increases in 2009 and 2010 up to the level observed in 2007. By contrast, no general decline of the number of nesting eiders was observed from 2007 to 2008 in the 75 study colonies situated in the northeastern Baltic Proper, i.e. in the colonies on islands along the coasts of Saaremaa and Hiiumaa in western Estonia and at Kolga and Tvärminne in the Gulf of Finland (Fig. 2). Actually, the total number of eider nests increased slightly from 2007 to 2008 in the study colonies along the coast of Saaremaa and Hiiumaa and at Tvärminne.

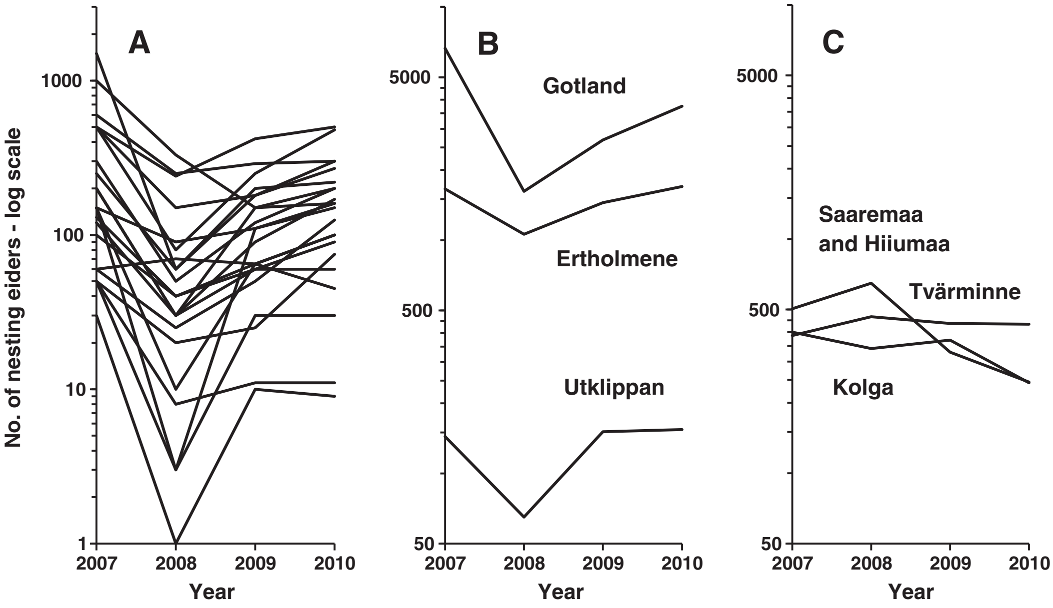

Fig. 2. (A) Number of nesting female eiders from 2007 to 2010 at 22 study colonies along the coast of Gotland (Sweden). Note the synchronous sharp decline of the number of nests in 21 of the 22 colonies from 2007 to 2008 and the subsequent synchronous increase in 2009. (B) Total number of nesting female eiders at all study colonies on Gotland, Ertholmene (Bornholm, Denmark) and Utklippan (Blekinge, Sweden) and (C) at Saaremaa and Hiiumaa (Estonia), Tvärminne (northern Gulf of Finland, Finland), and Kolga (southern Gulf of Finland, Estonia). Note the low number of nesting eiders in 2008 at sites presented in B. High abundances of *Prymnesium polylepis* was observed in spring 2008 at sites included in A and B. *P. polylepis* were absent or occurred in low numbers in spring 2008 at sites included in C.

The mean egg clutch size in colonies on Gotland was lower in 2008 (mean $= 3.12$, $N = 125$, $SE = 0.10$ than in 2009 (mean $= 3.53$, $N = 1028$, $SE = 0.04$) and 2010 (mean $= 3.67$, $M = 859$, $SE = 0.04$) ($F_{(2;2009)} = 10.4$, $p < 0.0001$, ANOVA). Clutch size data was not collected on Gotland in 2007. The mean clutch sizes at Ertholmene and at Tvärminne were not lower in 2008 than in other years.

On Gotland, large numbers of female eiders which did not bred or failed at an early stage in spring 2008 were observed foraging in the vicinity of the breeding sites later in June. Hence, no exceptional mass mortality or large scale movements of female eiders away from the area were observed. Information on the behaviour or body condition of male eiders in 2008 is lacking.

3.2. Abundance and distribution of P. polylepis and Prymnesiales cells

The abundance of large *P. polylepis* cells at the monitoring sites BY2, BY5, BY15, BY31 and B1 were high, often above 1×10^6 cells l^{-1} between March and May in 2008 (Fig. 3a). At site BY15 in the central Baltic Proper the abundance was up to 2.9×10^6 cells l^{-1} in March 2008. In May, abundances between 2.9×10^6 and 3.5×10^6 cells l^{-1} were recorded at BY31 and B1 in the northwestern Baltic Proper. It has previously been reported that *P. polylepis* cells started to slowly increase at sites B1 and BY31 already in late October 2007 although cell concentrations above 1×10^6 cells l^{-1} was not reached until March 2008 (Majaneva et al., 2012). The abundance of large *P. polylepis* was low or close to zero in 2007, 2009 and 2010 (Fig. 3a).

The total abundance of all Prymnesiales cells, i.e. the total abundance of large (>10 μm) and small (6–10 μm) *P. polylepis* cells as well as of cells of other Prymnesiales species were high in 2008 and low in other years (Fig. 3b). In April 2008, total abundances of about 2.0×10^6 cells l^{-1} were recorded at all five sites and the majority of these cells were large (>10 μm). Later in May, total abundances had increased to between 5×10^6 and 8×10^6 cells l^{-1}. The majority of the cells observed in May 2008 were either large (>10 μm) or between 6 and 10 μm. Only a minor part of the cells was smaller than 6 μm (Majaneva et al, 2012). It is likely that a large part of the cells in the size range of 6 to 10 μm was small *P. polylepis* cells. In May 2007, total abundances of up to 2×10^6 cells l^{-1} were found at sites BY2 and BY15 (Fig. 3b). However, more than 90% of these cells were smaller than 6 μm, and, hence, were cells of other Prymnesiales species than *P. polylepis*. In May 2009, total abundances between 2×10^6 and 4×10^6 cells l^{-1} were found at sites BY5 and BY2. Only 3% of the total abundances were large *P. polylepis* cells.

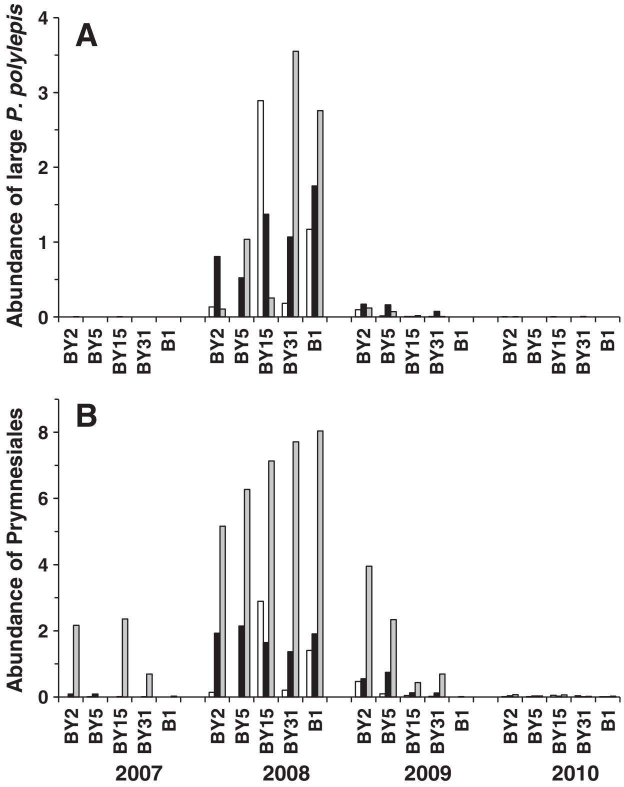

Fig. 3. (A) Maximum abundances of large *P. polylepis* cells (expressed as 10^6 cells l^{-1}), in March (white bars), April (black bars) and May (grey bars) between 2007 and 2010 at five plankton monitoring sites in the Baltic Sea. High abundances were only found in 2008. (B) Total maximum abundances of all Prymnesiales cells. High abundances were mainly found in 2008.

About 71% and 38% of the cells, at sites BY5 and BY2, respectively, were between 6 and 10 μm. To what extent the 6–10 μm cells were small *P. polylepis* cells or cells of other Prymnesiales species is unknown. In 2010, the total abundance of all Prymnesiales cells was very low at all sites (Fig. 3b).

In spring 2008, the abundance of Prymnesiales cells was measured at a large number of additional sites in the Baltic Sea by national authorities in the region. These additional abundance measurements have been published previously by Hajdu et al. (2008) and Majaneva et al. (2012). In contrast to the high abundances observed at sites BY2, BY5, BY15, BY31 and B1 and at other sites in the southern, central and northwestern Baltic Proper, large *P. polylepis* was not observed or only observed in low numbers in the northeastern Baltic Proper, Gulf of Riga and Gulf of Finland (Fig. 4) (Hajdu et al., 2008 map).

3.3. Proportion Prymnesiales of the total phytoplankton biovolume

Possible effects of Prymnesiales cells on plankton filtering organisms may be related not only to the total abundance, or the abundance of specific species, but also to the proportion of the total phytoplankton biovolume that consists of Prymnesiales cells. The proportion of large *P. polylepis* cells of the total phytoplankton biovolume was high in 2008 at sites BY2, BY5, BY15, BY31 and B1 (Fig. 5a). In March 2008, at site BY15, large *P. polylepis* cells constituted almost 90% of the total phytoplankton biovolume. Later in April 2008, large *P. polylepis* cells constituted between 27 and 53% of the total biovolume at all sites. The proportion of large *P. polylepis* cells of the total phytoplankton biovolume was low in 2009 and close to zero in 2007 and 2010.

The proportion of all Prymnesiales cells of the total phytoplankton volume was high in 2008, generally low in 2007 and 2009, and close to zero in 2010 (Fig. 4B). In April and May 2008, the Prymnesiales cells, most of which were larger than 6 μm, constituted between 30 and 80% of the total phytoplankton biovolume. In 2007 and 2009 some high values was observed in May at the southern monitoring sites (Fig. 5b). No other harmful algal species have been observed in high abundances in spring during the study period.

4. Discussion

Counts of nesting eiders in 103 study colonies around the Baltic Sea between 2007 and 2010 showed that colonies situated in the central and southern Baltic Proper declined very sharply in size from 2007 to 2008. The declines were followed by increases in the same colonies in 2009 and 2010, although not always up to the level observed in 2007. By contrast, in the study colonies situated in the northeastern Baltic Sea and in the Gulf of Finland no general decline of the number of nesting eiders were observed between 2007 and 2008.

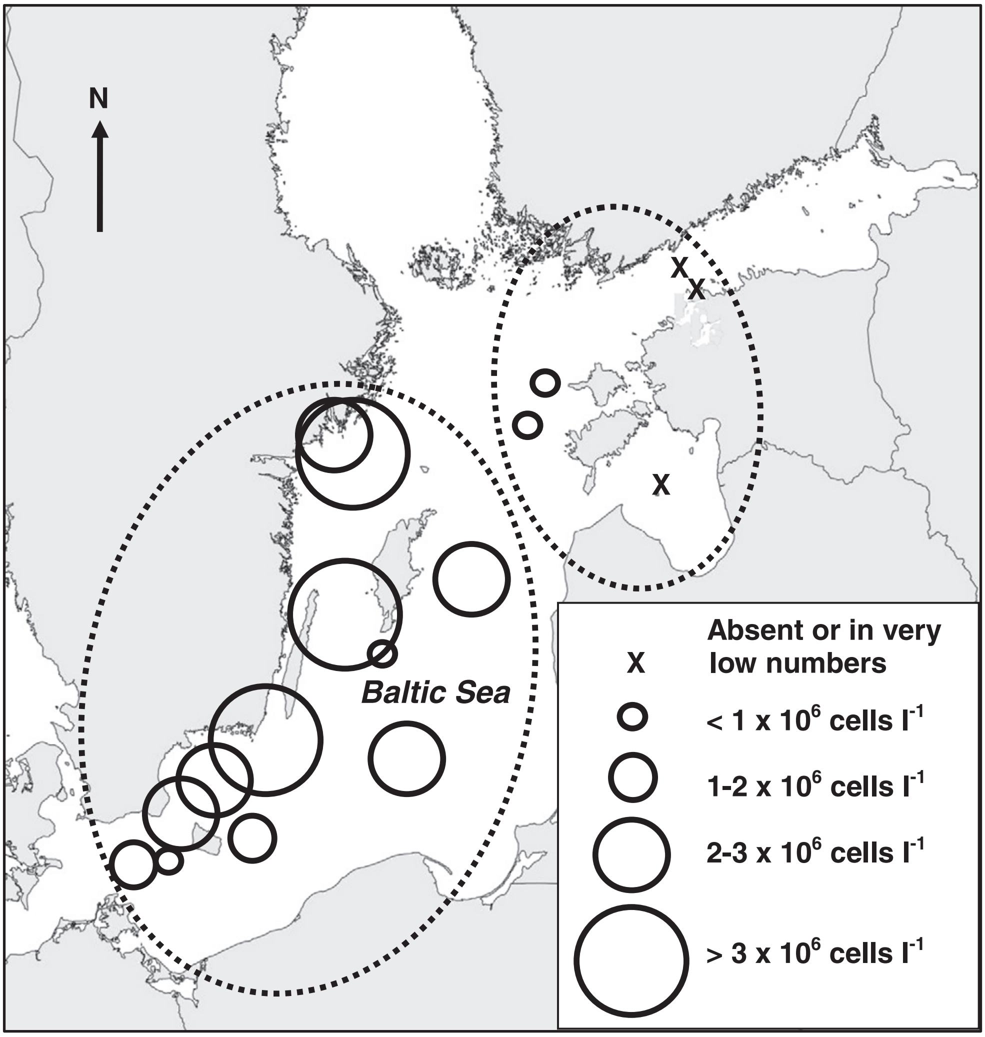

Fig. 4. Maximum abundances of large *P. polylepis* cells in March to May 2008. High abundances were generally found in the central and southwestern Baltic Proper and low abundances in the northeastern Baltic Proper. The map is based on data from the monitoring sites BY2, BY5, BY15, BY31, B1 and on data from additional sites presented in Hajdu et al. (2008) and Majaneva et al. (2012).

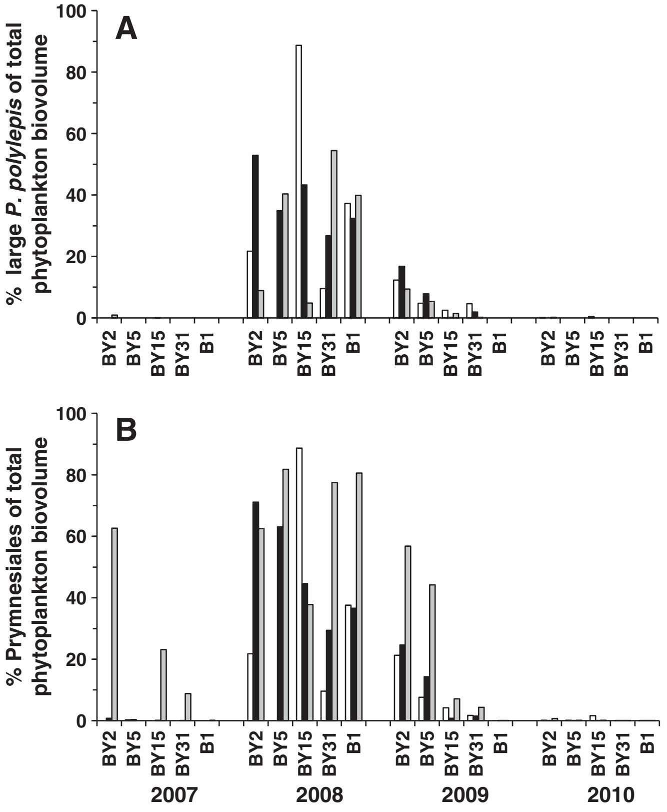

Fig. 5. (A) The proportion of large *P. polylepis* cells of the total phytoplankton biovolume between 2007 and 2010 in March (white bars), April (black bars) and May (grey bars). In April 2008, large *P. polylepis* cells constituted between 27 and 53% of the total biovolume at all five sites. In March 2008, at site BY15, large *P. polylepis* cells constituted almost 90% of the total phytoplankton biovolume. (B) The proportion of all Prymnesiales cells of the total phytoplankton biovolume between 2007 and 2010.

Earlier studies have shown that the total Baltic eider population has undergone a steady decrease by about 50% from the beginning of the 1990s to 2007 (Ekroos et al., 2012a; Skov et al., 2011). Declines in eider populations in other parts of Europe and North America have also been recorded in recent decades (Coulson, 2010). The observed decline in the Baltic Sea region has been suggested to be caused by several interacting contributing causes such as increased predation by white tailed eagle at eider breeding sites, changes in the availability of high quality benthic food because of changes in the nutrient levels in sea water and climate change, and to thiamine deficiency. However, earlier studies in the Baltic Sea region have not to our knowledge recorded such a sharp and synchronous decline of the number of nesting eiders over large geographical areas between two consecutive years as we here report. The subsequent recovery in 2009 and 2010 from the dip in 2008 was faster than what can be expected from recruitment of new young birds only. It is therefore most likely that the factor that caused the sharp decline in nest numbers in 2008 mainly affected the frequency of non-breeding, i.e. the frequency of nest initiation and the frequency of nest abandonment in the early incubation period, and not to a very large extent the mortality rates of adult female eiders. Varying frequencies of non-breeding have previously been recorded in long-term studies of marked eider populations in for example the North Sea and have been assumed to be coupled to the availability of food during the preceding winter and spring (Coulson, 1984, 2010).

In the early spring 2008, the plankton monitoring programme detected very high abundances of the alternate form of the potentially toxic haptophyte *P. polylepis* in the southern, central and northwestern Baltic Proper. Only low abundances and absences were recorded in the northeastern Baltic Proper, Gulf of Finland and Gulf of Riga. In 2007, 2009 and 2010 only low concentrations of *P. polylepis* cells were recorded in the Baltic Sea. Hence, the temporal and the spatial distribution of the *P. polylepis* bloom in the Baltic Sea closely matched the observed distribution of extensive non-breeding in Baltic eider colonies. However, because a correlative match alone does not imply causation we discuss other possible alternative causes for the exceptional decline of nesting eiders in 2008 in parts of the Baltic Sea.

It is well known that individual colonies, or groups of eider colonies within a region, can be greatly affected or eradicated, for example, by fox predation or by outbreaks of avian cholera or other diseases during the nesting stage (Christensen et al., 1997; Pedersen et al., 2003). However, none of the 28 study island in the southern and central Baltic Sea showed any signs of fox predation during the four year study period. We neither found indications of any outbreak of avian cholera or other acute diseases.

Several observations indicated that female eiders in the southern and central Baltic Sea were in poor body condition in spring 2008. For example, very lean female eiders were observed abandoning the study nesting islands on Gotland during the incubation period. We also found that birds that did lay eggs in colonies on Gotland in 2008, on average, laid significantly smaller clutches. Dead eiders were also found on the study islands although not in exceptional numbers. The poor body condition seemed to be restricted to eiders as the number of nests of barnacle geese (*Branta leucopsis*), a similar sized herbivorous waterfowl that nests along the coast of Gotland intermingled with eiders, did not change in any significant way from 2007 to 2008 on the study islands. Furthermore, several reports from the public concerning seemingly sick or dead female eiders at sites along the Swedish east coast from the Stockholm archipelago in the north to Blekinge in the south were sent to the Swedish National Veterinary Institute in spring 2008 (SVA, 2008). Dissections performed at the Swedish National Veterinary Institute of eiders from the Stockholm archipelago also indicated that eiders were in poor body condition at the beginning of the incubation period (SVA, 2008). Low body condition index of female eiders were also observed in 2008 at Bornholm (Christiansö Fieldstation, 2008). By contrast, at Tvärminne in the northeastern Baltic Sea, where female body condition during incubation has been measured between 1997 and 2009 (Jaatinen et al., 2011), no particular deviation was observed in 2008 (Kilpi, unpubl).

The water temperature in the southern and central Baltic Sea during the winter 2007/08 was unusually high at monitoring sites BY2, BY5 and BY15 (SMHI, 2013). For example, the water temperature at 10 m depth in March at BY15 was 4.1 °C. The water temperature in March during other winters between 1993/94 and 2011/12 ranged between 0.6 and 3.3 °C (mean 2.3 °C). Furthermore, the maximum ice coverage, i.e. an index of winter severity, was the lowest recorded since the measurements started in 1957 (SMHI, 2013; Waldeck and Larsson, 2013). It has been found previously in both the Baltic and the Wadden Sea that the mass loss of the soft body parts of blue mussels and other bivalves during winters are higher in mild than in cold winters (Beukema et al., 2009; Honkoop and Beukema, 1997; Waldeck and Larsson, 2013). It is therefore likely that the average quality of the food for wintering eiders, expressed as the ratio between soft body mass and shell mass of mussels, were lower in the winter 2007/08 than in the other winters during the study period. Hence, the mild winter probably impaired the possibility for wintering eiders to build up nutrient and energy stores for the subsequent breeding season and could therefore be one important contributing cause for the decline of nesting eiders in spring 2008. However, because eiders from the Baltic breeding population winter in the same geographical area in the southwestern Baltic Sea and the Wadden Sea (Lehikoinen et al., 2008; Noer, 1991), the mild winter phenomenon alone cannot explain the spatial pattern observed, i.e. why nest numbers only declined sharply in the southern and central Baltic Proper but not in the northeastern Baltic Proper and in the Gulf of Finland.

The factor responsible for the synchronous declines in eider nest numbers in 2008 in parts of the Baltic Sea must at least have been in effect during the time window spanning from the eider's departure from the wintering sites in March and April to the start of egg-laying at the end of April or beginning of May. The factor must also have been in effect not only at specific local sites but over large areas in the southern and central Baltic Sea but not in the northeastern Baltic Proper. To our knowledge, the most likely proximate factor fitting these criteria is the exceptional bloom of the potentially toxic *P. polylepis* in spring 2008.

The *P.polylepis* bloom in 1988 in the Kattegatt and Skagerack was very toxic for several different phyla and a chemical analysis showed that the involved toxin had hemolytic properties (Stabell et al., 1993). Unfortunately, the *P. polylepis* bloom in the Baltic Sea in 2008 was not chemically tested for toxins. Hajdu et al., (unpubl) could not find any toxic effects of the *P. polylepis* bloom on other plankton species. However, the result of their study does not exclude the possibility that female eiders were affected by the *P polylepis* bloom through a toxic pathway because mussels may accumulate toxic substances making the mussels themselves toxic or detrimental for mussel feeding organisms. Thus, although a link between the *P. polylepis* bloom and breeding eiders via a toxin is possible, direct evidence is lacking.

We hypothesise that Prymnesiales cells and especially the cells of *P. polylepis*, even if not always toxin producers, are food items of low quality for filtering blue mussels. Support for this hypothesis comes from studies of blue mussels during the *P. polylepis* bloom in 1988 in the Kattegatt and Skagerack region. For example, Loo (1989; pers comm) found that blue mussels reduced their filtering activity and postponed spawning until cell concentrations of *P. polylepis* declined. Other occasions when algal blooms, either for toxic reasons or reasons related to cell features, have led to reduced filtration rate or reduced soft body mass in blue mussels have also been described earlier (Gainey and Shumway, 1988; Pieters et al., 1980; Tracey, 1988). Between March and May 2008, Prymnesiales cells including cells of *P. polylepis* constituted at some Baltic monitoring sites of up to 80% or more of the total phytoplankton biovolume. We therefore suggest that the *P. polylepis* bloom in early spring 2008 reduced or delayed the soft body mass increase and gonad build-up of blue mussels, and thereby reduced the availability of high quality food for eiders at foraging sites close to their nesting sites during the pre-laying period. Intensive blooms of *P. polylepis* have not been recorded before in the Baltic Sea. Such blooms therefore cannot explain the steady decline of the Baltic eider population since the mid 1990s. However, the spatial and temporal match between the *P. polylepis* bloom and the extensive non-breeding of eiders observed in this study does suggest that breeding eiders can be significantly affected by species interactions at low trophic levels as well as by the quality of the food obtained close to the breeding sites during the pre-laying period.

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