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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