Harmful Algae 59 (2016) 100–111

Contents lists available at ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

Ecological niche partitioning of the invasive dinoflagellate *Prorocentrum minimum* and its native congeners in the Baltic Sea

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ARTICLE INFO

Article history:
Received 25 May 2016
Received in revised form 15 September 2016
Accepted 15 September 2016

Keywords:
Algal blooms
Baltic Sea
Biological invasions
Dinoflagellates
Ecological niche
Prorocentrum minimum

ABSTRACT

This study analyses three decades of the peculiar bloom-formation history of the potentially toxic invasive planktonic dinoflagellates *Prorocentrum minimum* (Pavillard) Schiller in the SW Baltic Sea. We tested a research hypothesis that the unexpectedly long delay (nearly two decades) in population development of *P. minimum* prior to its first bloom was caused by competition with one or several closely related native dinoflagellate species due to ecological niche partitioning which hampered the spread and bloom-forming potential of the invader. We applied the ecological niche concept to a large, long-term phytoplankton database and analysed the invasion history and population dynamics of *P. minimum* in the SW Baltic Sea coastal waters using the data on phytoplankton composition, abundance and biomass. The ecological niche dimensions of *P. minimum* and its congener *P. balticum* were identified as the optimum environmental conditions for the species during the bloom events based on water temperature, salinity, pH, concentration of nutrients (PO_4^{3-}; total phosphorus, TP; total nitrogen, TN; SiO_4^{4-}), TN/TP-ratio and habitat type. The data on spatial distribution and ecological niche dimensions of *P. minimum* have contributed to the development of the "protistan species maximum concept". High microplankton diversity at critical salinities in the Baltic Sea may be considered as a possible reason for the significant niche overlap and strong competitive interactions among congeners leading to prolonged delay in population growth of *P. minimum* preceding its first bloom in the highly variable brackishwater environment.

1. Introduction

A bloom-forming, potentially toxic, mixotrophic planktonic dinoflagellate *Prorocentrum minimum* (Pavillard) Schiller, 1933, also known as *Prorocentrum cordatum*[1] (Ostenfeld) Dodge, 1975, is one of the most remarkable nonindigenous species in the Baltic Sea. According to published records, the alien *P. minimum* colonised the Baltic Sea more than three decades ago (Kimor et al., 1985; Olenina et al., 2010). This invasion process was effective. After its massive bloom in the Skagerrak area in 1979, *P. minimum* was first recorded in the Baltic waters in 1981 (Edler et al., 1982), and by 1999 this eurytopic marine species has already expanded its range to almost the entire brackishwater Baltic Sea (except for the Gulf of Bothnia) reaching as far to the NE as the oligohaline Gulf of Finland (Hajdu et al., 2000, 2005; Witek and Pliński, 2000; Pertola, 2006).

P. minimum is one of the five dinoflagellate species from the genus *Prorocentrum* that currently inhabit the Baltic Sea ecosystem; the other four are *P. balticum* (Lohmann) Loeblich, 1970, *P. micans* Ehrenberg, 1833, *P. compressum* (Bailey) Abé ex Dodge, 1975, and *P. triestinum* Schiller, 1918, among more than 2000 other phytoplankton species (Hällfors, 2004; Telesh et al., 2011a). Nevertheless, the dinoflagellate *P. minimum* is the only one phytoplankton species in the Baltic Sea which can be considered truly invasive (Olenina et al., 2010), because the dynamics and importance of only this unicellular alien meets the major established requirements of the "invader" (as given in: IUCN, 1999; Occhipinti-Ambrogi and Galil, 2004; Ojaveer et al., 2010). Firstly, the population of *P. minimum* is growing exponentially, rapidly expanding its range and, secondly, this potentially toxic

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[1] Although the Latin name *Prorocentrum cordatum* (Ostenfeld) Dodge, 1975 should be preferably used for the indication of this dinoflagellate species according to the priority rule, in the present paper we use the name *Prorocentrum minimum* to better relate our data to the results of the previous findings.

http://dx.doi.org/10.1016/j.hal.2016.09.006
1568-9883/

species is widely known to be able to cause environmental damage, economic loss or harm to human health being implicated in the elevated fish mortalities and human poisoning during blooms (Heil et al., 2005; Olenina et al., 2010; Glibert et al., 2012; Al-Hashmi et al., 2015).

The invaders usually conquer new environments and extend their range fast due to lack of competitors, predators and parasites, which allows them to quickly achieve high population densities (Carlton, 1996, 2002). One such example of a very rapid colonisation process among aquatic metazoans is the invasion of the Lake Ontario (the Great Laurentian Lakes, USA) by the planktonic predatory water flea *Cercopagis pengoi* (Ostroumov, 1891): this species reached its maximum population density already within the first invasion year (Makarewicz et al., 2001; Laxson et al., 2003). This scenario must be particularly true for the unicellular eukaryotes as well as the prokaryotes due to their exceptionally rapid reproduction and very short generation times (Hülsmann and Galil, 2002).

Meanwhile, the uncommonly long (for the unicellular organisms) period of time – nearly a decade – passed between *P. minimum* first appeared in the Baltic waters until it has become an established species in this semi-closed brackishwater sea, with the population ability to reach pronounced abundances exceeding 100 cells mL^{-1}, such as e.g. in September 1989 (Olenina et al., 2010). Moreover, the first real bloom of *P. minimum* with densities >3000 cells mL^{-1}, according to the definition of a "bloom" proposed for the Chesapeake Bay (EPA, 2003; Tango et al., 2005), in the Baltic Sea was registered only in the late 1990s, i.e. nearly two decades after the invasion (see Table 5 in Olenina et al., 2010). To our knowledge, the possible reasons of this long though successful invasion history preceding the first bloom have neither been named nor discussed in literature.

This research aims at unveiling the possible mechanisms behind the specific invasion history, spatial distribution and the bloom-forming potential of the planktonic dinoflagellates *P. minimum* in the Baltic Sea. To reach this goal, we applied the ecological niche concept (Hutchinson, 1957; Leibold, 1995; Chesson, 2000; Chesson and Kuang, 2008; Litchman et al., 2012) to a large, long-term phytoplankton database from the SW Baltic Sea and analysed the possible reasons for the successful invasion of the Baltic Sea by *P. minimum* which was characterised by the peculiar delay in the species' ability to form blooms. We analysed in detail the timeline of *P. minimum*' colonisation of the SW Baltic Sea coastal waters using a long-term data on phytoplankton composition, abundance and biomass. The ecological niche dimensions of *P. minimum* and its congeners were identified as the optimum environmental conditions for the species based on water temperature, salinity, pH, concentration of nutrients (PO_4^{3-}; total phosphorus, TP; total nitrogen, TN; SiO_4^{4-}), TN/TP-ratio and habitat types during the bloom events. The frequency of those optimum environmental conditions which were most likely backing up the massive development of *P. minimum* in the SW Baltic Sea was determined, and the most probable competitors of *P. minimum* were identified.

We proposed and tested a research hypothesis which argues that the lag-phase in the *P. minimum* population development prior to the formation of the first bloom in the Baltic Sea was caused by the biotic restrictions: namely, by competition with one or several species which were occupying at least part of the same ecological niche thus hampering the spread and massive development of the invader. This phenomenon is supposed to be backed up by high overall protistan diversity in the brackish SW Baltic coastal waters.

2. Material and methods

2.1. The database

For the analysis of the occurrence of the dinoflagellate species from the genus *Prorocentrum* in general and the description of the ecological niche dimensions of *P. minimum* in particular, the long-term phytoplankton database described by Sagert et al. (2008a) was used. The database consists of 7934 datasets containing the information on the biotic and abiotic parameters and phytoplankton samples taken at 64 stations along the German Baltic Sea coast (Fig. 1) and covering the sampling period of 33 years: from 1972 till 2005. This collection of data was not entirely uniform as it was compiled from different sources, such as monitoring programmes, short- and mid-term experiments and projects performed by several institutions, with the respective differences in methodology of sampling, phytoplankton identification, counts and biomass determination techniques, and different priorities for the measurement of various abiotic parameters (Sagert et al., 2008a). Therefore, the critical sorting of the available data was performed prior to the analyses.

For most of the phytoplankton samples, the simultaneously collected abiotic parameters were available; however, in some cases such important parameters as, e.g., nutrient concentrations, were missing. Those sets of data were excluded from the statistical

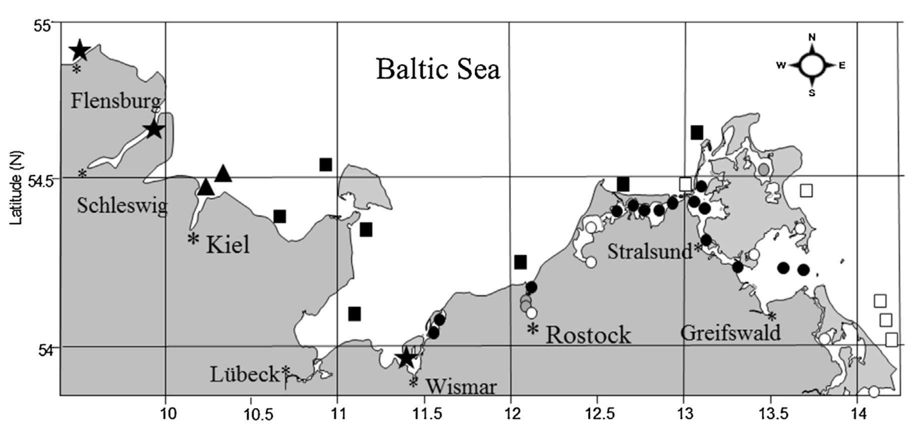

Fig. 1. Phytoplankton sampling sites along the German Baltic Sea coast. The principal sampling sites are shown. Due to changes in the monitoring programme in different years, the position of some sites was shifted by a few miles; in such cases only the most recent positions are shown. Symbols indicate habitat types; CW – coastal waters. Open circles: β-oligohaline inner CW (salinity 0.5–3; B1a); grey circles: α-oligohaline inner CW (salinity 3–5; B1b); black circles: β-mesohaline inner CW (salinity 5–10; B2a); stars: α-mesohaline inner CW (salinity 10–18; B2b); open squares: β-mesohaline outer CW (salinity 5–10; B3a); black squares: α-mesohaline outer CW (salinity 10–18; B3b); black triangles: seasonally stratified outer CW (salinity 10–30; B4).