Contents lists available at ScienceDirect

Harmful Algae

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

The influence of bloom intensity on the encystment rate and persistence of *Alexandrium minutum* in Cork Harbor, Ireland

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ARTICLE INFO

Received 29 July 2013

Accepted 16 October 2013

Received in revised form 16 October 2013

Article history

Keywords:

Alexandrium

Cyst stocks

Ireland

Bloom dynamics

Encystment rate

ABSTRACT

Toxic Alexandrium minutum blooms recur annually in Cork Harbor, Ireland where they initiate in an inlet known as the North Channel. The dynamics of these blooms have been studied since 2003, and a high degree of inter-annual variability in the cell densities has been observed. Two intense blooms, with maximum cell densities >500,000 cells L⁻¹, were observed in the summers of 2004 and 2011. Annual cyst surveys during winter found that cyst densities decreased after the 2004 bloom, and by 2010 an average of ca. 40 cysts g dry wt sediment⁻¹ was recorded. The intensity of blooms was found to be independent of the cyst density measured the previous winter. The cyst input to the sediment during both intense and low density blooms was measured directly through the deployment of sediment traps in the North Channel. The data allowed an estimate of the proportion of the A. minutum vegetative cells that underwent successful encystment, which averaged at 2.5% across a range of cell densities spanning three orders of magnitude. Maturation times of fresh cysts were determined at 5, 10 and 15 °C. The maturation time at 15 °C was found to be approximately 5 months, a value which increased by two months for a 5° decrease in temperature. A cyst dynamics model was constructed based on the field data to simulate the temporal variation of A. minutum cysts in the oxic layer of sediment. It revealed that a degree of resuspension is required to prevent cyst stocks from becoming exhausted in the thin oxic layer at the surface of the sediment. The model also demonstrated that the cysts supplied by periodic intense blooms, which occur with a frequency of every 7-8 years, are not in themselves enough to allow the population to persist over long time scales (decades). The cyst input from interim blooms of lower density is however enough to ensure the annual inoculation of the water column with A. minutum cells. © 2013 Elsevier B.V. All rights reserved.

1. Introduction

Paralytic Shellfish Poisoning (PSP) is a potentially lethal syndrome in humans caused by the ingestion of potent neurotoxins collectively known as saxitoxins which are vectored through shellfish. These toxins concentrate in shellfish as a consequence of filter-feeding on toxin-producing microorganisms, and have had a substantial impact on cultured and wild shellfish production, often leading to harvest closures. The toxins are produced in the marine dinoflagellates *Pyrodinium bahamense, Gymnodinium catenatum* and species from the genus *Alexandrium*, notably the *A. tamarense* species complex (Cembella, 1998) comprising *A. tamarense*, *A. fundyense* and *A. catenella* (Balech 1985). In Europe, however, *A. minutum* has a history of causing toxic blooms along the Atlantic coasts of France (Chambouvet

et al., 2008), Spain (Franco et al., 1994), UK (Blanco et al., 2009) and Ireland (Touzet et al., 2008) as well as along the Mediterranean coast (Vila et al., 2005).

A characteristic of Alexandrium blooms is that they often recur annually in the same location (e.g. Garcés et al., 2004; Giacobbe et al., 2007). This is due to a sessile resting cyst stage, or hypnozygote, in its life cycle, which can remain dormant in marine sediments for several years, even in anoxic conditions (Anderson et al., 2005; Lewis, 1998). A seasonal germination pattern has been observed in Alexandrium cysts with maximum excystment rates occurring in spring (Anderson, 1998; Matrai et al., 2005; Ní Rathaille and Raine, 2011; Anglès et al., 2012). This germination initiates a bloom the following late spring/summer (Anderson, 1997), enhancing sexual recombination and promoting the persistence of an Alexandrium population (Bravo et al., 2006). It is the retentive nature of a sheltered channel, bay or estuary that fosters chronic infestation with this toxic organism by creating a habitat suitable for seed stocks to be replenished, which then provide the inoculum for blooms annually. In contrast to open coastal waters, the benthic and pelagic life stages of Alexandrium





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spp. become closely linked within shallow retentive regions (Anderson et al., 2012).

A variability in the between year bloom intensity of Alexandrium has been recorded in several locations. For example, Anderson et al. (1994) note that in some years blooms and toxic events in the Gulf of Maine are more intense than others. Given that the year to year survival strategy of a population revolves around the replenishment and persistence of the dormant cvst stage, cvst beds must play a central role in maintaining stocks through periods when cyst recruitment is low, or even nonexistent. Wyatt and Jenkinson (1997) review the survival strategies of Alexandrium and argue that since gamete formation apparently occurs at relatively low cell densities $(10^2 - 10^3 L^{-1})$; specialized traits such as motility or the use of allelopathic signaling must have evolved in order for gametes to find each other. They argue that otherwise the characteristic time-scale for the fusion of gametes would be of the order of months, even with cell densities of $10^5 - 10^6 L^{-1}$.

Once fusion of the gametes and formation of the hypnozygote has occurred, it is now recognized that a maturation period is required before the cysts become fully mature and ready for germination. Maturation times of the order of months have been reported for *Alexandrium minutum* and *Alexandrium tamarense* cysts (Ní Rathaille and Raine, 2011), and generally increase with decreased temperatures (Anderson, 1980; Band-Schmidt et al., 2003; Ní Rathaille and Raine, 2011). Cysts of *A. tamarense* from the St. Lawrence Estuary in Canada have been reported to take a year to mature at a temperature of 4 °C (Castell Pérez et al., 1998). In two separate studies, a substantial difference was found between the maturation times of *A. tamarense* from Cork Harbor and Perch Pond, Cape Cod (Ní Rathaille and Raine, 2011; Anderson, 1980). Such variability in the maturation of cyst species is potentially due to different geographic isolates having different dormancy requirements based on their ecological needs (Hallegraeff et al., 1998). Nevertheless, the excystment, growth, gametogenesis, encystment and maturation cycle is highly successful as a survival strategy in dinoflagellates such as *Alexandrium*.

Here we present nearly a decade of sampling data from Cork Harbor, Ireland. The data set illustrates the variability in the magnitude of summer blooms of *Alexandrium minutum*. The role of intense blooms in maintaining the population over time scales of years was investigated, and the relationship between the maturation time of freshly formed *A. minutum* cysts and water temperature was also determined.

2. Methods

2.1. Study area

Water and sediment sampling was carried out in Cork Harbor, Ireland (Fig. 1A) between the years 2003–2012. The prominent bathymetric feature in Cork Harbor is the hydrodynamically



Fig. 1. The study area. (A) Bathymetric map of Cork Harbor, Ireland, highlighting the North Channel located in the northeastern half of the Harbor. The boxed areas are the geographic boundaries of the regions outside of the North Channel used to group cyst densities in Table 1. (B) Map of the North Channel showing the five water sampling stations occupied on each field survey. The locations where the sediment traps were deployed and the position of the temperature sensor mooring are also indicated.

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