Deep-Sea Research II ▮ (▮▮▮▮) ▮▮▮–▮▮▮

Contents lists available at SciVerse ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Spatial and temporal variability of *Alexandrium* cyst fluxes in the Gulf of Maine: Relationship to seasonal particle export and resuspension

C.H. Pilskaln [a,*], D.M. Anderson [b], D.J. McGillicuddy [b], B.A. Keafer [b], K. Hayashi [a], K. Norton [b]

[a] School for Marine Science and Technology, University of Massachusetts Dartmouth, New Bedford, MA 02744, USA
[b] Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

ARTICLE INFO

Keywords:
Gulf of Maine
Particulate flux
Sediment traps
Alexandrium
Cysts
Resuspension

ABSTRACT

Quantification of *Alexandrium* cyst fluxes through the Gulf of Maine water column is central to understanding the linkage between the source and fate of annual *Alexandrium* blooms in the offshore waters. These blooms often lead to paralytic shellfish poisoning (PSP) and extensive closures of shellfish beds. We report here on time-series sediment trap deployments completed at four offshore locations in the gulf between 2005 and 2010 as components of two ECOHAB–GOM field programs. Data presented documents the substantial spatial and temporal fluctuations in *Alexandrium fundyense* cyst fluxes in the gulf. Cyst delivery out of the euphotic zone peaked primarily between July and August following annual spring–summer *Alexandrium* blooms and was greatest in the western gulf. At all sites, cyst flux maxima to the subsurface waters were rarely coincident with seasonal peaks in the total mass export of particulate material indicating that cyst delivery was primarily via individually sinking cysts. Where persistent benthic nepheloid layers (BNLs) exist, significant sediment resuspension input of cysts to the near-bottom water column was evidenced by deep cyst fluxes that were up to several orders of magnitude greater than that measured above the BNL. The largest cyst fluxes in the BNL were observed in the eastern gulf, suggesting greater resuspension energy and BNL cyst inventories in this region. Temporal similarities between peak cyst export out of the upper ocean and peak cyst fluxes in the BNL were observed and document the contribution of seasonal, newly formed cysts to the BNL. The data however also suggest that many *Alexandrium* cells comprising the massive, short-lived blooms do not transition into cysts. Time-series flow measurements and a simple 1D model demonstrate that the BNL cyst fluxes reflect the combined effects of tidal energy-maintained resuspension, deposition, and input of cysts from the overlying water column.

1. Introduction

The Gulf of Maine (GOM) is well-known for elevated levels of primary and secondary production, resulting in an abundance of shellfish, finfish and marine mammal biomass (Bigelow, 1926; Shumway et al., 1988; Townsend, 1991; Pershing et al., 2005). This productive shelf sea, and the adjacent Bay of Fundy, is also characterized by the occurrence of seasonal harmful algal blooms (HABs) of the neurotoxin-producing dinoflagellate *Alexandrium fundyense*, hereafter termed *Alexandrium* (Anderson, 1997; Martin et al., 2005). The ecology and oceanography of these HAB species have been relatively well studied through the NOAA/NSF Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) Program (Anderson et al., 2005c). Annual *Alexandrium* blooms in the Gulf of Maine during the spring-early summer months and have been well-documented since the 1990s (Anderson, 1997; Anderson et al., 1994; Townsend et al., 2001; Keafer et al., 2005a,b; McGillicuddy et al., 2005; Townsend et al., 2005). Even though *Alexandrium* typically represents a very small percentage of the total spring–summer bloom phytoplankton assemblage, the ingestion by plankton and shellfish of toxin-containing cells and cysts can result in a substantial negative impact on the health of higher trophic level organisms, including humans (Turner and Borkman, 2005; Turner et al., 2005; Hoagland and Scatasta, 2006; Townsend et al., 2010). Additionally, the settling and accumulation of dormant *Alexandrium* cysts in Gulf sediments provides for a continuous cycle of yearly blooms in the region (Anderson et al., 2005a).

Alexandrium encystment and excystment dynamics have been detailed by Anderson et al. (2005a). It is believed that germination from the dormant cyst stage to the vegetative cell stage initiates the planktonic blooms, which are facilitated by favorable nutrient concentrations (specifically high inorganic nitrogen levels) and increasing temperature and light conditions

* Corresponding author.
E-mail address: cpilskaln@umassd.edu (C.H. Pilskaln).

0967-0645/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.dsr2.2012.11.001

(Anderson, 1980, 1998; Etheridge and Roesler, 2005; Love et al., 2005; Matrai et al., 2005; Townsend et al., 2005). In turn, the water column transformation of asexual vegetative cells to sexually-reproducing gametes is believed to be induced by decreasing nutrient, temperature and light levels in the late summer and early fall (Dale, 1983; Anderson and Keafer, 1985; Anderson, 1998; Anderson et al., 2005a; Kirn et al., 2005). Sexual fusion of gametes results in the formation of a planozygote cell, which transforms within approximately a week into a hypnozygote cyst that remains dormant for a minimal period of 2–6 months (Anderson, 1988). Sedimentary accumulation of the dormant cysts in the Gulf of Maine (and the Bay of Fundy) has been shown to be widespread along the coast as well as offshore (Lewis et al., 1979; Anderson et al., 2005a, this issue).

Since 2004, ECOHAB studies (ECOHAB-GOM and GOMTOX) have produced large-scale surveys of *Alexandrium* distributions and maps of benthic cyst abundance (Townsend et al., 2001, 2005; Anderson et al., 2005a,b,c; Keafer et al., 2005a,b; Anderson et al., this issue). The water column and sediment distributions of *Alexandrium* cells and cysts suggest that a very large cyst seed-bed in the Bay of Fundy (BOF) is a source of recurrent spring-summer blooms that feed the Maine Coastal Current (MCC) (Townsend et al., 2001; Anderson et al., 2005a; McGillicuddy et al., 2005; Pettigrew et al., 2005). Another cyst bed offshore of Casco and Penobscot Bays is hypothesized to be an additional source of *Alexandrium* blooms occurring in the western GOM and Massachusetts Bay region via the western segment of the MCC, transporting *Alexandrium* to the west and south (McGillicuddy et al., 2003, 2005; Anderson et al., 2005a,b; Pettigrew et al., 2005; Townsend et al., 2005).

The purpose of the current communication is to report on the measured time-series fluxes of *Alexandrium* cysts through the water column at several locations in the offshore regions of the western and eastern Gulf of Maine. The data sets were collected in ECOHAB field programs spanning five years (2005–2010). Our objectives in making the time-series measurements were to provide a temporal connection between the near-surface *Alexandrium* blooms and the delivery of sinking cysts to sub-euphotic depths and the underlying sediments, and to examine the relationship of cyst fluxes to the seasonal mass flux of particulate material. Understanding the timing and magnitude of *Alexandrium* cyst fluxes and the temporal and spatial dynamics of their movement (i.e., sinking, resuspension, etc.) are presently not included in Gulf of Maine *Alexandrium* bloom forecast models (He et al., 2008; Li et al., 2009). However, water column cyst fluxes provide the link between bloom senescence and the formation of underlying sedimentary seed-beds which provide the inoculum for the annual blooms and as such represent a significant factor that should be included in the forecast models.

2. Methods

High-resolution, time-series sediment traps (model Mark 7, McLane Research Labs, Inc.; Honjo and Doherty, 1988; Honjo et al., 2000; Pilskaln et al., 1996, 2004) were deployed on subsurface moorings at two depths, at four sites between 2005 and 2010 as field components of two NOAA ECOHAB programs: Cyst Dynamics I (2004–2007) and GOMTOX (2006–2011). The former project's mooring work was focused in the eastern Gulf and the latter (GOMTOX) was focused in the western Gulf. The mooring locations were north-central Jordan Basin (JB, 12 months: 2005–2006), offshore Penobscot Bay (PB, 18 months: 2005–2006), northern Stellwagen Bank (SB, 12 months: 2007–2008) and northern Wilkinson Basin (WB, 26 months: 2008–2010) (Fig. 1; Table 1). The traps had a baffled surface collection area of 0.5 m^2 and collected time-series samples in thirteen 250 ml volume cups per deployment. Prior to deployment, trap cups were pre-poisoned with an 8% density-adjusted formalin solution in filtered seawater buffered to a pH of 8.0–8.1. Recovery and redeployment of the trap moorings occurred approximately every 5–9 months with individual cup collection periods varying from ~10–21 days. The traps were programmed to insure that per deployment period, the cups on the upper and lower traps rotated and collected sinking particulate material on the same time interval.

Particulate sample handling and processing followed the standard procedures detailed in Pilskaln and Paduan (1992) and Pilskaln et al. (2004). Immediately following trap recoveries, sample cup supernatant pH values were recorded, additional buffered formalin solution was added and all samples were refrigerated stored at 4 °C. Total cup samples were gently washed with filtered seawater through 1 mm and 500 μm Nylon mesh sieves to remove crustacean and molluscan swimmers (e.g., copepods, euphausids, amphipods and pteropods), and the remaining particulate sample material was quantitatively split into quarters using a four-section wet splitter (McLane Research labs, Inc.). Two wet splits were filtered, dried and weighed for mass flux determination and dried ground subsamples were analyzed for particulate organic carbon composition (POC) using standard coulometric carbon analysis techniques (Pilskaln et al., 1996, 2004).

One 1/4 wet split was set aside and processed for *Alexandrium* cyst counting. If the volume of particulate material in the split was minimal, the full volume of the split was processed. If the particulate volume was high, then a known volume of the split was removed for further processing. The subsamples were initially sieved through a 20 μm Nylon mesh sieve with filtered seawater to concentrate the cysts and to remove the formalin solution. The >20 μm particulate fraction containing the cysts was retained on the sieve and further processed using standard cyst concentrating protocols (Anderson et al., 2003; Anderson et al., 2005a). Briefly, the samples were resuspended off the 20 μm sieve into 45 ml of filtered seawater and sonified for 60 s. The disaggregated sample was sieved to remove fine material of <20 μm, and the >20 μm fraction with cysts was resuspended into 14 ml of filtered seawater. For primuline staining of the cysts, the sample was centrifuged, the seawater was removed by aspiration, and the resulting pellet of centrifuged cysts was resuspended into cold methanol and stored for at least 24 h. The sample was centrifuged again, the methanol removed, and the pellet resuspended in 10 ml of distilled water. After centrifugation, 2 ml of primuline stock (2 mg ml^{-1}) was added directly to the pellet and incubated at 4 °C for 1 hour. The stained sample was centrifuged, excess primuline removed, and the pellet resuspended in a final known volume of distilled water (usually 5–10 ml). One ml of the processed sample was loaded into a Sedgewick-Rafter chamber and the green fluorescently-stained cysts were counted at 10x with a Zeiss epi-fluorescent microscope (excitation=450–490 nm BP; emission=510 nm LP). The number of cysts per trap was calculated from the known volumes of each step during the processing and the fraction of the whole sample represented by the split. Only intact, pigmented cysts were counted; empty cysts were not quantified.

A lack of sub-surface, time-series current velocity measurements for our trap sites coupled with the potential impact of lateral flow on the total particulate and cyst fluxes necessitated the collection of current measurements at the trap depths. Our specific objective in making coincident flow speed and direction measurements at the trap depths was to determine if sustained flows of ≥ 20 cm s^{-1} were present which could lead to an under-sampling bias of small settling particles, including cysts

Please cite this article as: Pilskaln, C.H., et al., Spatial and temporal variability of *Alexandrium* cyst fluxes in the Gulf of Maine: Relationship to seasonal particle export and resuspension. Deep-Sea Res. II (2013), http://dx.doi.org/10.1016/j.dsr2.2012.11.001