



ELSEVIER

Contents lists available at ScienceDirect

Deep-Sea Research II

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

Bioturbation, germination and deposition of *Alexandrium fundyense* cysts in the Gulf of Maine

David H. Shull^{a,*}, Anke Kremp^b, Lawrence M. Mayer^c^a Department of Environmental Sciences, Western Washington University, Bellingham, WA 98225, USA^b Finnish Environment Institute (SYKE), Marine Research Centre, P.O. Box 140, 00251 Helsinki, Finland^c Darling Marine Center, University of Maine, Walpole, ME 04573, USA

ARTICLE INFO

Available online 5 October 2013

Keywords:

Bioturbation

Cyst

Germination

Model

Toxic dinoflagellates

Gulf of Maine

Alexandrium fundyense

ABSTRACT

Like many other dinoflagellate species, *Alexandrium fundyense* possesses a benthic resting cyst which enables long-term persistence and annual blooms of this species in the Gulf of Maine. The size and extent of these harmful algal blooms are associated with high cyst concentrations in the top 1 cm of sediment. Despite the importance of this resting stage in the life history of *A. fundyense*, little work has been done on bioturbation of cysts in the deep-water cyst beds of the western Gulf of Maine. Our work intensively examined one site within a major regional “seedbed” from February 2003 until August 2005, a time span that included an extraordinarily large bloom of *A. fundyense* in 2005.

Over the course of 2 years we collected samples for benthic infauna and cyst profiles down to a depth of 30 cm. We also measured sediment porosity, organic carbon, ²¹⁰Pb, and porewater dissolved oxygen. On several dates we measured depth profiles of cyst autofluorescence. Profiles of cysts revealed large subsurface maxima peaking between 10 and 15 cm depth with cyst concentrations declining strongly toward the sediment surface. On one sampling date (August 2004) we observed a cyst concentration peak at the sediment surface. Using these data we constructed a mechanistic model of cyst bioturbation, mortality, germination, and deposition. Modeled bioturbation was calibrated using ²¹⁰Pb and modeled cyst profiles were compared to measured profiles. Model runs with constant and interannually-varying rates of cyst deposition produced similar time-averaged cyst profiles. Results indicate that the deeper portions of cyst profiles are determined primarily by bioturbation, germination and cyst mortality and less so by interannual variation in cyst depositional history. This is due to the relatively low sedimentation rate at the study site compared to the rate of bioturbation, and the fact that the number of cysts deposited each year tends to be a small fraction of the total inventory. Seasonal and interannual variation in cyst deposition strongly influenced concentrations of cysts in the top few millimeters of the sediment, however. When cyst deposition rates are low, bioturbation and germination are sufficient to rapidly deplete cysts in this surface layer, leaving relatively few cysts within the sediment depth range that allows germination. But, bioturbation is not rapid enough to homogenize surface sediments within one year. As a result, cyst deposition results in a concentration peak at the sediment surface that persists to fuel germination the following year. Because of this phenomenon, the model predicted that years with high rates of germination follow years with large levels of cyst deposition. Over longer time scales, bioturbation transports cysts from the sediment surface to depth, which, along with germination, creates a persistent subsurface maximum in cyst concentration. Bioturbation also serves to maintain persistence of *A. fundyense* by transporting older cysts from these deeper layers to the sediment surface where they can germinate. Since high concentrations of cysts near the sediment surface indicate large numbers of cysts deposited during the previous year, if enhanced germination leads to large blooms of *A. fundyense*, these blooms are predicted to occur in years following large cyst deposition events.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Paralytic shellfish poisoning (PSP) in the Gulf of Maine has a long history, dating back perhaps as far as 1889 (Ganong, 1889),

with outbreaks observed sporadically during the 20th century (Bond, 1975; Hurst, 1975). These events are due to blooms of the dinoflagellate *Alexandrium fundyense* (Anderson, 1997; Townsend et al., 2001). Over the past half century, there have been several notable PSP outbreaks. In 1972, an outbreak in the western Gulf of Maine extended as far south as Massachusetts and resulted in expanded monitoring for PSP in the region (Hurst, 1975). PSP in the western Gulf of Maine has been chronic ever since (Townsend

* Corresponding author. Tel.: +1 360 650 3690; fax: +1 360 650 7284.
E-mail address: david.shull@wwu.edu (D.H. Shull).

et al., 2001). The size and toxicity of blooms varied between 1972 and 2005, when an extraordinarily large bloom occurred in the southern and western portions of the Gulf of Maine (Anderson et al., 2005a, 2014). Relatively large and toxic blooms in the western Gulf of Maine have persisted since this time (Anderson et al., 2014a; Kleindinst et al., 2014).

Although many environmental conditions likely concur to produce large PSP events, cyst germination has been implicated as an important determinant of large *Alexandrium* blooms in recent decades and cyst “seed beds” play an important role in PSP persistence (Anderson et al., 2005b; McGillicuddy et al., 2005; He et al., 2008). Cysts of *A. fundyense* remain viable for decades in sediments (Keafer et al., 1992). Other species of *Alexandrium* and other genera of harmful dinoflagellates such as *Pyrodinium*, *Gymnodinium*, *Pfiesteria*, possess species with similar life histories (Matsuoka and Fukuyo, 2000). Thus, it is of both regional and general importance to understand the processes that affect the persistence, fate, and germination of *Alexandrium* cysts in the sediment, as well as their transport and mortality within the sediment column.

Models of bioturbation have been used to better understand these processes (e.g., Keafer et al., 1992; Cox et al., 2008). Keafer et al. (1992) developed a model of *Alexandrium* cyst bioturbation based on cyst profiles from the western Gulf of Maine and Massachusetts salt ponds and inferred that the shape of these profiles were due to mixing, germination at the sediment surface, and mortality at depth. The model of Cox et al. (2008) linked historical variation in PSP concentration in shellfish and profiles of *Alexandrium catenella* cysts in sediment profiles from several locations in Puget Sound in Washington State. The authors inferred from this comparison that blooms of *A. catenella* were initiated in certain embayments, perhaps by cyst germination, and that vegetative cells in the water column were then advected to other sites. The profiles of *A. catenella* examined by Cox et al. (2008) preserved information on the history of cyst deposition in addition to information on bioturbation, germination and mortality. Given the potential utility of bioturbation models for inferring cyst dynamics from cyst profiles, we developed a mechanistic model of cyst bioturbation, mortality, deposition and germination. We used this model to better understand profiles of *A. fundyense* cysts collected from the largest cyst deposition area in the western Gulf of Maine over a period of time that included the massive 2005 bloom. This intensive sampling and modeling of a cyst deposition center enabled better understanding of processes leading to initiation and persistence of *A. fundyense* blooms in this region.

2. Methods

2.1. Bioturbation model

We used a one-dimensional transition-matrix model (Shull, 2001) to simulate biological mixing, sedimentation, and cyst germination, deposition and mortality. We applied this model to simulate both ²¹⁰Pb, a naturally-occurring radionuclide tracer of bioturbation and sedimentation, and cysts (Fig. 1). Rates of movement among states are determined by transition probabilities (Fig. 2). The transition probabilities in Figs. 1 and 2, f_{ij} , show only a subset of all possible cyst trajectories and the method for prescribing the full complement of transitions is described below. Nevertheless, the trajectories shown represent some important deposit feeding mechanisms including conveyor-belt feeding (f_{51}), subductive feeding (f_{14}), and interior feeding (f_{32}). The elements s_i , along the main diagonal of the transition matrix (Fig. 2), represent the probability of not transitioning in a given model time step.

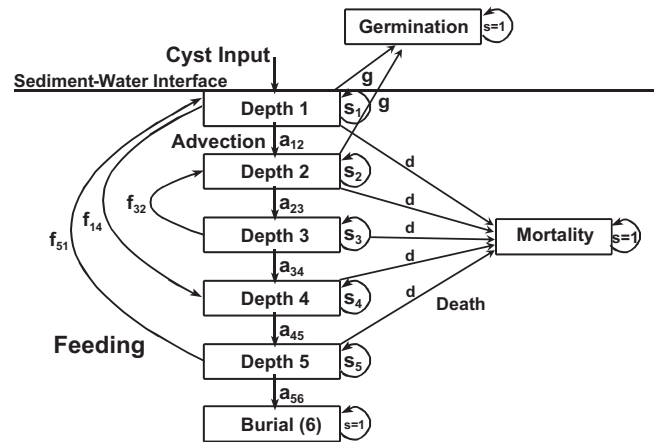


Fig. 1. Diagrammatic representation of the transition-matrix model of bioturbation and cyst dynamics. The boxes represent stratigraphic layers in the sediment of thickness Δz , and states such as burial below the mixed layer, cyst death, and germination. Arrows represent hypothetical cyst transitions and transport trajectories. Non-dimensional variables f , a , s , d , and g determine the probability or, equivalently, the fraction of cysts transitioning among model states. Note that for the sake of clarity only some of the many possible trajectories are shown in the diagram.

State at time t	State at time t+1							
	1	2	3	4	5	Burial	Death	Germination
s	$a_{12}(1-d)$	0	$f_{14}(1-d)$	0	0	0	d	$g(1-d)$
0	s	$a_{23}(1-d)$	0	0	0	0	d	$g(1-d)$
0	$f_{32}(1-d)$	s	$a_{34}(1-d)$	0	0	0	d	0
0	0	0	s	$a_{45}(1-d)$	0	0	d	0
$f_{51}(1-d)$	0	0	0	s	$a_{56}(1-d)$	0	d	0
0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	1	0
0	0	0	0	0	0	0	0	1

Fig. 2. Elements of the transition matrix determine rates of cyst movement among model states. The elements along the main diagonal represent the fraction of cysts not moving during each model time step. The fraction of cysts remaining in the burial, mortality, and germination states equals 1 because these processes permanently remove cysts from the system.

Our model requires the following assumptions. We assumed that cysts were mixed at the same rate as other particles at the site. This assumption is not unreasonable given that *A. fundyense* cysts fall within the particle size range selected by species of cirratulid, capitellid and maldanid polychaetes (approximately 5–50 μm , Self and Jumars, 1988; Shull and Yasuda, 2001), the primary particle reworkers at the study site. Cyst density is less than that of sediment grains, however (Anderson et al., 1982). Particle mixing is assumed to be due to deposit feeding. This assumption has proven to be reasonable when tested in the field (Shull, 2001; Shull and Yasuda, 2001), although we recognize that other mixing processes such as bottom trawling might influence tracer profiles at our site. Transitions among model states are assumed to be constant in time. This means that seasonal variation in rates of deposit feeding, for example, and longer term changes in benthic community structure are ignored. Although it is impossible to know how rates and mechanisms of bioturbation varied in the past, the assumption that benthic community structure has remained constant is consistent with the relatively constant pattern of benthic community structure we observed at the study site (see Section 3.1). But, our dataset covers just a few years. Given these assumptions, the transition matrix, P , can be analyzed using Markov chain theory, which provides simple analytical solutions to the model (Kemeny and Snell, 1976; Shull, 2001).

Transport probabilities in the matrix P are directly related to the feeding and burrowing activities of deposit-feeding benthos. Details on the calculation of these parameters have been described

Download English Version:

<https://daneshyari.com/en/article/6384217>

Download Persian Version:

<https://daneshyari.com/article/6384217>

[Daneshyari.com](https://daneshyari.com)