Harmful Algae 10 (2011) 619–628

Contents lists available at ScienceDirect

Harmful Algae

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

Pelagic-benthic transition of the harmful alga, *Heterosigma akashiwo*: Changes in swimming and implications for benthic cell distributions

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ARTICLE INFO

Article history:
Received 29 November 2010
Received in revised form 21 April 2011
Accepted 21 April 2011
Available online 30 April 2011

Keywords:
Benthic distribution
Harmful algal bloom
Heterosigma akashiwo
Life cycle
Motility
Resting cell

ABSTRACT

Many harmful algal blooming (HAB) species transition between a vegetative, motile phase in the water column and a dormant, non-motile resting phase in the sediments. These life history transitions potentially regulate the timing, location and persistence of bloom events. Motility promotes aggregation and influences vertical distributions in the water column. However, the contribution of this behavior to benthic distributions of resting cells is currently unknown. We used video-tracking techniques to test the hypothesis that algal cells use active down-swimming during pelagic-benthic transition to favorably influence benthic distributions. In an experimental water column, we monitored cell swimming trajectories of *Heterosigma akashiwo* for 14 days after cells were signaled to enter the benthic resting stage. Using the statistical characteristics of individual cell trajectories, we developed a video-based motion assay to assign each tracked *Heterosigma* cell to one of three cell states known to occur during pelagic-benthic transition: induced motile, transitional and resting. The primary swimming characteristic influencing benthic distribution, net vertical velocity, was essentially the same for all three cell states. Hence, we found no evidence that active down-swimming influences benthic distributions. Our data suggest that benthic distributions of *Heterosigma* resting cells are similar to distributions of slowly sedimenting passive particles. These observations suggest that *Heterosigma* benthic resting cell distributions can be predicted by modeling the effects of cell sedimentation rates combined with geophysical flow patterns.

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1. Introduction

Many HAB-forming algae exhibit a dual-stage life history, transitioning between a pelagic vegetative stage and a benthic resting stage. These transitions are among the least understood aspects of HAB dynamics. The benthic stage is thought to promote survival during environmental conditions that are unfavorable to growth, to provide refuge from predation, and/or to facilitate long-range transport (Anderson, 1997; Hallegraeff, 1998; Imai and Itakura, 1999; Matrai et al., 2005; Anderson and Rengefors, 2006; Kremp et al., 2009). The rapid transition of pelagic vegetative cells into the benthic resting stage can contribute to HAB termination, while benthic populations can serve as reservoirs that initiate HABs by rapidly reseeding the water column with vegetative cells when favorable conditions return (Anderson, 1984; Akira and Taniguchi, 1996). Hence, transitions into and out of the benthic resting stage may strongly affect the timing, location and magnitude of HABs (Anderson et al., 2005; He et al., 2008).

Transitions between pelagic and benthic habitats often involve significant vertical movements. Vegetative, pelagic cells are typically concentrated in near-surface waters. These cells cannot establish benthic populations until they descend to encounter the benthic substrate, often a depth change of tens of meters. The timing and rate of these depth changes are critical to survival of these cells, because lateral advection in coastal environments can quickly move cells between suitable (usually shallow) benthic habitats and unsuitable (usually deeper) locations. In deep sediments, cells are less likely to experience bottom conditions, principally temperature and light, conducive to germination and subsequent transition to the vegetative stage. However, the mechanisms that control depth during pelagic-benthic transition, and thus ultimately lead to deposition in the sediments, are poorly understood.

HAB-forming algae commonly use active swimming in their pelagic phase to regulate depth and locate favorable growth conditions (Anderson and Stolzenbach, 1985; MacIntyre et al., 1997). Algal swimming often interacts with physical flows to influence cell concentrations and distributions in the water

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doi:10.1016/j.hal.2011.04.014

column (Kessler, 1985; Donaghay and Osborn, 1997; Franks, 1997; Smyada, 2002; Bearon et al., 2006). The prevalence of swimming in HAB-forming algae, together with the apparent importance of resting cell deposition in suitable substrates, suggests that algal cells could use active swimming during the pelagic-benthic transition to favorably influence benthic distributions. If so, motility during formation of benthic resting cells could have important but currently unknown impacts on HAB dynamics.

In this paper, we experimentally test this hypothesis using *Heterosigma akashiwo* as our focal organism. *Heterosigma* is a harmful raphidophyte that forms dense surface blooms associated with kills of wild and pen-reared fish in temperate and subtropical waters worldwide (Smyada, 1998; Rensel et al., 2010). These blooms are often initiated in shallow coastal embayments, but may be advected to deeper waters (Yamochi and Abe, 1984; Imai and Itakura, 1999; Handy et al., 2005; Rensel, 2007; Kempton et al., 2008). *Heterosigma* has an alternating pelagic-benthic life history (Tomas, 1978; Smyada, 1998). Field conditions that signal transition into the benthic resting phase are not well understood. Tomas (1978) reported that cell aggregation seemed to be a preliminary step in the formation of benthic resting cells. These benthic cells had poor survival at higher temperatures ($\geq$15 °C) in the light. Additional laboratory-based studies have also shown that reduced temperature and dark conditions induce formation and extend survival of benthic resting cells (Itakura et al., 1996; Han et al., 2002). Transition out of the benthic stage is controlled largely by temperature, with 10 °C the approximate lower limit for emergence and $\geq$15 °C required for successful proliferation (Taylor and Horner, 1994; Imai and Itakura, 1999; Han et al., 2002; Shikata et al., 2007, 2008). *Heterosigma* exhibits vigorous up-swimming behavior in its vegetative stage, and this swimming behavior has been identified as an important mechanism in bloom formation (Yamochi and Abe, 1984; Hershberger et al., 1997; Bearon et al., 2004, 2006; Handy et al., 2005).

Little is known about how *Heterosigma's* swimming behaviors influence benthic distributions following HAB termination. In one of the few published studies of *Heterosigma* benthic resting cell formation, Han et al. (2002) used microscopy to show that vegetative cells transitioning into benthic resting cells express a distinct "transitional" stage of reduced motility. These transitional cells are characterized by reduced swimming velocity and directionality (rotating in circles or spinning in place) as flagellar movement is lost. Because it was not the ultimate goal of that study to characterize cell swimming behaviors, Han et al.'s observations did not establish how cell movements progress from the up-swimming vegetative stage to the non-motile benthic stage, or the consequences of those movements for benthic distributions. Bearon et al. (2004) suggested that the oscillatory movement of helical swimming algae like *Heterosigma* could provide useful diagnostic information about the type and state of cells. The existence of a distinct transitional phase identifiable by movement characteristics also suggests that movement-based assays have the potential to identify cell state during pelagic-benthic transition on a cell-by-cell level.

To obtain quantitative information about individual *Heterosigma* cell movements during pelagic-benthic transition, we used a video-based tracking technique to monitor cell swimming in an experimental water column. Similar motion analysis techniques have been used to assess movement behaviors, physiological state and health of algal cells (e.g., Iken et al., 2001; Bearon et al., 2004, 2006; Mayali et al., 2008). We developed statistical methods to classify each tracked cell into one of three physiological states based on fine scale horizontal movements, and then quantified net vertical movements associated with each state. We then used state-specific vertical movement data to test the hypothesis that *Heterosigma* cells actively influence their benthic distribution by shifting from up-swimming to down-swimming prior to forming benthic resting cells. The specific goals of this study were: (1) to develop a video-based motion assay to identify cell state using swimming characteristics during pelagic-benthic transition, and to verify that assay with traditional microscope techniques; (2) to determine whether *Heterosigma* exhibits distinct state-specific vertical movement behaviors during transition; and (3) to assess the potential consequences of transitional behaviors for benthic distributions of *Heterosigma* resting cells.

2. Materials and procedure

2.1. Cell maintenance and resting cell induction

A *H. akashiwo* strain CCMP452 culture was maintained in 1 L reduced salinity (22‰) artificial seawater O-3 medium (McIntosh & Cattolico, 1978) and grown to stationary phase ($>2 \times 10^5$ cells mL^{-1}) at 20 °C, on a 12 h dark:12 h light (50 μmol/m^2/s; LI-COR Inc. LI-250A, NE, USA) photoperiod under continuous rotary agitation (60 rpm). This culture was used to inoculate eighteen 250 mL experimental flasks, each containing 125 mL medium, to 2.5×10^4 cells mL^{-1}. These sub-cultures were maintained at 15 °C on a 12 h dark: 12 h light (50 μmol/m^2/s) photoperiod for five days prior to the start of the experiment. Concentrations of cell cultures were determined with a ZBI Coulter Counter (Coulter Electronics, Inc. Hialeah, FL, USA) equipped with a 100 μm aperture. On the starting day of the experiment (Day 0), cell concentrations were approximately 6–8 $\times 10^4$ cells mL^{-1} in each flask. To induce *Heterosigma* cells to enter their benthic resting stage on Day 0, the experimental flasks were placed in the dark at 10 °C (Han et al., 2002). Because even short exposures to very low light levels ($<$0.1 μmol/m^2/s) inhibit resting cell formation (Han et al., 2002; Cattolico, unpublished) each experimental flask was wrapped in foil prior to being stored in the darkened environmental chamber. Preliminary experiments conducted to test the viability of resting cells formed under our induction conditions showed up to 95% survival when these resting cells were activated to return to the vegetative stage after 16 days by restoring light to ~50 μmol/m^2/s and temperature to 20 °C (data not shown).

2.2. Experimental tank for cell observations

Cell movements were observed in a 190 mm × 140 mm × 60 mm experimental tank constructed with six equally spaced replicate partitions (Fig. 1). Each partition was filled from the bottom using a peristaltic pump. This method enabled the formation of a two-layer stratified water column that suppressed fluid convection (Bearon et al., 2006). A halocline was established between a 100 mL bottom layer that had a weakly stratified linear salinity gradient ranging from 30 psu at the base to 26 psu at the top and a 50 mL top layer of modified O-3 medium at 22 psu (Fig. 1). The salinity gradient was established with O3 medium (30 psu) diluted with fresh (de-ionized) water to generate the specified salinity structure. Each observation day, 0.5 mL of cell culture was taken from two of the 250 mL experimental flasks (one flask for partitions 1, 3 and 5; the other for partitions 2, 4 and 6). These cells were added slowly to the top layer of each partition of the tank, so that each top layer contained approximately 7–8 $\times 10^2$ cells mL^{-1}. Prior to experiments, we used fluorescein added to the top, lower salinity layer to verify that cell addition did not disturb the stratified water column. All cell transfers were performed inside a dark environmental chamber under red light (620–750 nm), to which *Heterosigma* cells do not respond (Lakeman and Cattolico, unpublished; personal observation). The experimental tank was then covered with a light-tight box made

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