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Research on the life cycles of harmful algae: A commentary

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ABSTRACT

The knowledge of the life cycles of harmful algae has advanced substantially in the last decade, in part through increased support of major research programs such as the SEED and the ECOHAB – Gulf of Maine projects. As with most research, the new knowledge answers some questions but raises more that require further inquiry, particularly since life-cycle strategies appear to be key to the initiation phase of many harmful algal blooms (HABs) in specific geographic areas. Three major themes can be used to integrate these organisms and their environment in relation to life cycles: benthic–pelagic coupling, endogenous and exogenous feedback loops, and bio-physical concentration mechanisms. With the new knowledge that is being generated, predictive models can be refined and tested. This commentary highlights recent advances in life-cycle research from the perspective of further research needs.

1. Introduction

As studies on life cycles of harmful algae have advanced (see Garcés et al., 2002), a number of high priority topic areas have emerged where new and significant knowledge is accruing. In multi-investigator, focused projects such as the SEED (this volume), these advances are particularly noteworthy, but results need to be viewed in the context of the broader literature. What follows is a brief summary of a few of the topic areas that are advancing rapidly in life-cycle research and that were the focus of efforts in the SEED. Where possible, examples are given from the literature to strengthen the SEED observations. In all cases, considerable work remains in this important area of life-cycle research, and perhaps some of these work can be guided by the perspectives offered here.

2. Benthic–pelagic coupling

Benthic–pelagic coupling is an obvious key component in HAB species – such as dinoflagellates (see Dale, 1983) – that produce pellicle (thin-walled) cysts or resting cysts (thick-walled) that settle to the benthos. Resuspension events may therefore be important to inoculate surface waters (Kirn et al., 2005; Kremp, 2001), though germination directly from the sediment surface also occurs. A meroplanktonic alternation in generations between 1N and 2N stages of phytoplankton, e.g., dinoflagellates, diatoms, and others, is often thought of as an adaptation to survive two different niches seasonally. Triggers for transition between these stages may be gradients in temperature, light, turbulence, sheer, nutrients, cell abundance, endogenous and exogenous infochemicals or nutrients, and even gases.

Benthic–pelagic coupling of life-cycle stages in the development of many HAB species is significant to the point of being predictive. Anderson et al. (2008) mapped the distribution of *Alexandrium fundyense* cysts in Gulf of Maine sediments over large geographic areas and found significant interannual variation in cyst abundance, but more importantly that "…cyst abundance in Gulf of Maine bottom sediments can be a first-order predictor of the magnitude of the resulting regional bloom". They concluded "Our ability to map these stages and utilize those observations to initialize hindcasts and forecasts of bloom incidence is a major advancement in HAB management". Mapping of cysts has been suggested since the 1970s, but Anderson et al. were able to integrate that into a numerical model based on their extensive studies in the Gulf of Maine. How much of an inoculum from benthic seed beds is needed to initiate a bloom is thought to be small, e.g. <10 cysts/cm^2 in shallow systems (Anderson, 1998) or 100–1000 cysts cm^2 in deeper waters with a larger surface mixed layer for growth (Anderson et al., 2005). Estrada et al. (2010) has shown that in shallow systems, once excystment provided an inoculum and those cells started exponential growth, further excystment fluxes had little effect on bloom magnitude.

In addition to classic methods, new mapping technology in the form of PCR assays for dinoflagellate and raphidophyte cysts (Erdner et al., 2010 and Penna et al., 2010), which is comparative or more sensitive than previous light microscopy methods, is encouraging for the application of wider-scale benthos and thin-layer surveys. Also, new research will hopefully produce probes

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for the identification of distinct life-cycle stages, such as gametes, planozygotes, hypnozygotes, and meiocytes. For example, gametes of *Scrippsiella lachrymosa* can be identified by their glycocongugates (Kremp and Anderson, 2004).These tools will be particularly significant when attempting to detect and quantify gametes and zygotes in the natural environment at boundary layers and discontinuities.

3. Sexual phases, encystment, and viability

In many species, the sexual phase is the prerequisite for sexual reproduction; different mating systems (homothallic, heterothallic, and mixed), gamete recognition systems and conditions that favor their proximity in the water column are crucial factors for successful sexual events (Brosnahan et al., 2010). An important feature is that there are environmental and endogenous cues that trigger transition and subsequent growth. At one time it was thought that the benthic stages were all hypnozygotes or hypnospores, but now it is realized that asexual resting or quiescent stages can act as seed populations. Some of these stages can be long-lived in anoxic sediments. The fact that viable dinoflagellate thick-walled resting cysts were isolated from Swedish fjord core strata 100 years old (Ellegaard et al., 2008) suggests that more than the first several centimeters should be studied for cyst distribution since sediments can be reworked. Even cyanophytes and diatoms in soil that are attached to plants pressed on herbarium paper and stored in herbaria are viable, 60–98 years later, if rehydrated and cultured (Lipman, 1941; Becquerel, 1942; Parker et al., 1969) This obviously has to do with reduced metabolism and maintaining DNA integrity and demonstrates species survival adaptations (Binder and Anderson, 1990). Despite this potential, however, it may be that the germination contribution from surface sediments to the bloom inoculum far exceeds that from deeper layers, where bioturbation or other physical disturbances are needed to bring cysts to levels where germination can occur.

Gamete pairing and planozygote formation in dinoflagellates have been observed at the termination of blooms (Persson et al., 2008; Anderson and Wall, 1978) or during active growth in nature with smaller cells becoming gametes that go through a mating pattern of dancing, pairing, and then fusing (Fukuyo, 2002). This dance like many other behavioral patterns might have something to do with cell-to-cell communication and identification of reproductive compatibility. It was only recently documented that sequential progression in sexual development in HAB species can be reversed and gametes and zygotes can revert to vegetative cell division (Figueroa and Bravo, 2005b; Figueroa et al., 2006b). Interestingly, some gametes and planozygotes (Uchida et al. 1996; Figueroa and Bravo, 2005a, Figueroa et al., 2006a) of *Gymnodinium nolleri, Gymnodinium catenatum*, and *Alexandrium taylori* can revert to an asexual phase and undergo binary fission rather than fusion or production of a hypnozygote, but in culture this depends on whether or not the gametes or planozygotes are in nutrient-replete media (asexual division) or nutrient-deplete media (sexual progression). This too involves a feedback mechanism tied to external nutrients and their concentration. Uchida (2001) also noted that in culture, zygotes of *Gyrodinium instriatum* and *Scrippsiella trochoidea* became cysts only if they were with vegetative cells at a certain density. If zygotes were cultured alone, i.e. without vegetative cells, they divided asexually, and it was thought that the frequency of cell-to-cell encounters triggered division (few encounters) or encystment (many encounters). Most of the research on life-cycle stage requirements, tolerances, and windows of transition has been in the laboratory under controlled conditions and not in the field. Field studies will be the challenge, particularly with the 3D physical forcing in coastal areas.

In many protist lineages, besides long-term cysts produced following sexual reproduction; there are asexual stages such as pellicle cysts (Bravo et al., 2010b) that can be quiescent for a limited period of time. However, dinoflagellate life-cycle schemes are even more complex, because *Gymnodinium* sp. and *Biecheleria baltica* in culture produced "resting" cysts that had DNA content similar to 1N motile cells and had a dormancy of six months (Parrow and Kremp, 2008). Both sexual and asexual resting stages represent a significant benthic–pelagic coupling mechanism as stages that can re-inoculate the water column (e.g. Bravo et al., 2010a).

4. Physics, chemistry, and behavior during mating

A successful mating requires recognition systems – visual, chemical, or perhaps tactical. These all require organisms to be in reasonable proximity. With phytoplankton living in an aquatic world, it may be assumed that high cell abundance and blooms provide the environment for close proximity of cells. However, blooms are often patchy in cell abundance and therefore it has been proposed that physical factors such as discontinuity layers and boundary conditions bring cells, and particularly gametes, together (Smith and Persson, 2004; Gentien et al., 2005; Persson et al., 2008). Vertical migration studies on two HAB dinoflagellates – *G. catenatum* and *Alexandrium tamarense* – showed that the populations in N-deficient media aggregated at a pycnocline and stopped migrating (Doblin et al., 2006; Rasmussen and Richardson, 1989). The same is true for gametes under culture conditions. Smith and Persson (2004) suggested that sexual cyst formation can be facilitated by increasing the potential for gamete encounters, e.g. using restricted water volume like a boundary layer. On the other hand, small-scale turbulence has an opposite effect, interrupting the thin-walled cyst production and gamete pairing.

Over the last two decades, there have been studies that looked upon the physical accumulation of plankton at pycnoclines or fronts (Franks, 1992; Smayda, 2002). New technology has allowed the detection of subsurface coastal phytoplankton in "thin layers" that are several centimeters to meters thick, extend horizontally over kilometers, and last several days (Dekshenieks et al., 2001; Cheriton et al., 2009). Moreover, these phytoplankton layers are a frequent recurring feature (Dekshenicks et al., 2001).

The onset of HABs or phytoplankton blooms could easily be missed in thin layers when using standard sampling methods and gear, and such thin layers could act as a seed bank or reservoir for HABs, the example being *Pseudo-nitzschia* in Monterey Bay (McManus et al., 2008). Durham et al. (2009) showed that dense thin layers of phytoplankton in the upper 50 m of the ocean can be bio-physical accumulations of cells that swam up or floated up to a level of instability caused by shear.

Thin layers are perhaps the most provocative of the current HAB frontiers in the context of life cycles. True, discontinuites and boundary layers were known previously to concentrate and move plankton, but the size, frequency, duration, and recurrence of thin layers were not realized until new technology was able to successfully sample and characterize them. The fact that motile and non-motile harmful algal bloom species can concentrate in these layers deserves further attention and study, particularly in dynamic coastal systems with recurring blooms. The role that these features play in facilitating cell–cell communication and pairing is likely to be significant.