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# Understanding harmful algae in stratified systems: Review of progress and future directions

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ABSTRACT

The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program of the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO, was created in 1999 to foster research on the ecological and oceanographic mechanisms underlying the population dynamics of harmful algal blooms (HABs). The ultimate goal of this research is to develop observational systems and models that will eventually enable the prediction of HABs and thereby minimize their impact on marine ecosystems, human health and economic activities. In August of 2012, a workshop was held under the umbrella of the GEOHAB program at the Monterey Bay Aquarium Research Institute (MBARI). The over arching goal of this workshop was to review the current understanding of the processes governing the structure and dynamics of HABs in stratified systems, and to identify how best to couple physical/chemical and biological measurements at appropriate spatial and temporal scales to quantify the dynamics of HABs in these systems, paying particular attention to thin layers. This contribution provides a review of recent progress in the field of HAB research in stratified systems including thin layers, and identifies the gaps in knowledge that our scientific community should strive to understand in the next decade.



## 1. Introduction

The distribution of phytoplankton in the sea is influenced by a wide range of processes that include ocean circulation, light and nutrient availability, as well as biological interactions. While large scale processes such as climatic forcing may dominate in some situations, the focus of this contribution is on small to mesoscale processes mainly in coastal environments where the water column is often stratified and where this stratification can play a crucial role in phytoplankton dynamics (*e.g.* Berdalet et al., in press; Dekshenieks et al., 2001; Gentien et al., 2005; Ross and Sharples, 2007; Sharples et al., 2001). The adverse effects of high-biomass and/or toxic blooms are particularly pronounced in coastal areas due to their immense economic importance to humans both in terms of aquaculture and tourism. Some areas such as fjords (*e.g.* Norway, Scotland, US Pacific Northwest), coastal lagoons (Mediterranean), and polar regions (Zemmelink et al., 2008) are characterized by freshwater input from land run-off, which may result in very strong vertical density gradients creating unique

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environmental conditions favorable for phytoplankton to persist. In other parts of the world's oceans (*e.g.* Gulf of Maine, Monterey Bay CA, North Sea), populations that are incubated in strongly stratified regions may be advected to neighboring areas where they can lead to elevated levels of primary and secondary production. Interestingly, a large number of HAB species have been observed in subsurface 'thin layers' where coastal waters are most stratified (Dekshenieks et al., 2001; Sullivan et al., 2003, 2005, 2010b; Partensky and Sournia, 1986). Thin layers are vertically thin and horizontally extensive subsurface patches of plankton (reviewed by Sullivan et al. (2010a)), which have been observed to persist from hours to weeks and can contain 50–75% or more or the total biomass in the water column (Cowles and Desiderio, 1993; Holliday et al., 2003; Sullivan et al., 2010a). Thin layers are likely biological 'hotspots' in the water column, important for organism growth rates, reproduction, grazing, and toxin production (Cowles and Desiderio, 1993; Dekshenieks et al., 2001; Hanson and Donaghay, 1998; Lasker, 1978; McManus et al., 2008; Mullin and Brooks, 1976; Rines et al., 2002; Sullivan et al., 2010a; Timmerman et al., 2014).

HABs that develop in stratified systems, including those that form into thin layers, are one of the areas of interest pursued by GEOHAB. The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program was initiated in 1999 with support from the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO. An overall goal of the GEOHAB research program is to allow the development of observational systems and models that facilitate the prediction of HABs, thereby reducing their impact on the marine ecosystem, human health and the local economy (GEOHAB, 2001).

A multidisciplinary, international group of twenty-six scientists including engineers, physicists, biologists and modelers from all over the globe, working on various aspects of phytoplankton dynamics in stratified systems, attended a meeting entitled "Advances and challenges for understanding physical–biological interactions in HABs in Stratified Environments" at the Monterey Bay Aquarium Research Institution (MBARI) from 21–23 August 2012. The aim was to provide a review of recent progress in the field of HAB research in stratified systems, including thin layers, and to identify the gaps in knowledge that our scientific community should strive to understand in the next decade (GEOHAB, 2013). The outcomes of the presentations and discussion sessions during the workshop are presented in this document structured into six main subject areas: (A) physical structure, (B) biological structure: rates and interactions, (C) organism behavior, (D) nutrients, (E) temporal evolution of HABs in stratified systems and thin layers and (F) predictive modeling.

## 2. Theme (A): physical structure

### 2.1. Vertical physical structure and phytoplankton distribution

The existence of physical oceanographic microstructure in the form of small-scale velocity, temperature and salinity variations has been appreciated for several decades (*e.g.* Osborn and Cox, 1972; Osborn, 1974). More recently, technological advances in *in situ* biological and chemical instrumentation have allowed progress in the understanding of HAB dynamics and thin layer formation within the context of small-scale physical variability (Gentien et al., 2005). Understanding physical oceanographic structure and processes is critical for the comprehension of phytoplankton abundance, their dynamics and potential to cause harm. The physical modulation of any tracer in the ocean results from the combination of advective and diffusive (mixing) components. In stratified marine systems, strong vertical stratification acts as a barrier against the vertical propagation of turbulence from adjacent high mixing layers (wind mixed surface and/or tidally mixed bottom layers). In addition, it provides a sanctuary from the high mixing in those adjacent layers allowing for biological processes to create vertically heterogeneous phytoplankton distributions (Sharples et al., 2001; Stacey et al., 2007; Yamazaki et al., 2010). For example, thin layer formation can be the result of a combination of vertically inhomogeneous mixing and directed swimming (Doubell et al., 2014; Ross and Sharples, 2007; Steinbuck et al., 2009). Recent work has suggested that the ability to swim, even at speeds that are small compared to the turbulent velocity scales in adjacent high turbulence layers, provides a competitive advantage to phytoplankton in stratified systems (Lips et al., 2011; Ross and Sharples, 2008; see also Theme (C). In addition, Durham et al. (2009) suggested that disruption of phytoplankton vertical migration by hydrodynamic shear could also be a mechanism of thin layer formation, the so-called "gyrotactic trapping".

*In situ* data, which can concurrently quantify physical and biological parameters with high resolution, are necessary to identify the sources of the spatial and temporal variability of phytoplankton layers, HAB formation, and thin layer dynamics. As one example, recent experiments with an autonomous profiling vehicle equipped with instrumentation for turbulence characterization documented the importance of internal wave phenomena to the vertical structure of the subsurface plankton maximum and the ultimate fate of a phytoplankton bloom (Fig. 1). An intense proliferation of *Tetraselmis spp*. offshore of Scripps Institution of Oceanography (La Jolla, CA) in July 2012 coincided with a pilot deployment of a wave-powered profiling vehicle (instrumented with a Rockland Scientific MicroRider turbulence profiler, Seabird CTD, Turner designs fluorometer, and Nortek current meter). The eight-day pilot deployment in 28 m of water occurred during the termination of the surface signature of the bloom and, ultimately, the disappearance of high chlorophyll concentrations from the water column. This region is subject to a strong internal wave climate, particularly in the semidiurnal tidal band. A snapshot of a portion of the tidal cycle (Fig. 1) demonstrates the influence of the internal tide on the vertical distribution of chlorophyll in the water column during the pilot deployment. As surface water moved onshore, and bottom waters offshore, the pycnocline and associated chlorophyll maximum are pushed downwards (Fig. 1C). High rates of turbulent kinetic energy dissipation ($\varepsilon$, Fig. 1A) and mixing (represented by the vertical eddy diffusivity $K_z$, Fig. 1B) in the bottom boundary layer acted to erode the base of the chlorophyll layer such that the vertical distribution of chlorophyll was very asymmetric, with a sharper gradient above the maximum than below (Fig. 1A–C, see also Steinbuck et al., 2009). The vertical divergence of the chlorophyll flux indicated that the chlorophyll maximum was decreasing rapidly, and that the net chlorophyll flux was into the bottom boundary layer and presumably to the benthos (Fig. 1D). Although *Tetraselmis spp*. are motile phytoplankton capable of strong swimming behavior (see Theme (C), Organism Behavior), it seems possible that bloom termination may have been related in part to a decrease in physiological health and subsequent degraded swimming ability. Concurrently, strong turbulence at the base of the chlorophyll maximum contributed to the dilution of the layer, and ultimately the dispersal of the bloom. Future *in situ* and modeling studies of the competing effects of physical dynamics (advection, turbulence, and mixing) and biological dynamics (growth, swimming, sinking, and aggregation) are needed.

A second example illustrates new possibilities to track the fine-scale temporal variability of phytoplankton biomass in shallow coastal waters. The instrument, a new Tow-Yo free-fall YODA Profiler (Yoing Ocean Data Acquisition Profiler, Masunaga and Yamazaki, 2014) is a portable instrument with a 0.04 m and 50 to 200 m, vertical and horizontal resolution respectively, that sinks