GEOHAB

The Global Ecology and Oceanography of Harmful Algal Blooms Program

MOTIVATION, GOALS, AND LEGACY

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ABSTRACT. In 2001, the first international research program focusing exclusively on harmful marine algae, GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms), was established by the HAB research community, under the sponsorship of the Intergovernmental Oceanographic Commission of UNESCO and the Scientific Committee on Oceanic Research. Its mission was to foster international cooperation to advance understanding of HAB dynamics and to improve our ability to predict them. The main efforts were focused on (1) the physiological, behavioral, and genetic characteristics of harmful microalgal species, and (2) the interactions between physical and other environmental conditions that promote the success of one group of species over another. GEOHAB was designed to study HABs with a view to integrating global data from comparable ecosystems. With an international, multidisciplinary, and comparative approach, GEOHAB advanced our understanding of the mechanisms underlying population dynamics of HABs within an ecological and oceanographic context and from an

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ecosystem perspective at the regional scale. GEOHAB encouraged combined experimental, observational, and modeling tools, using both existing and innovative technologies in a multidisciplinary approach, consistent with the multiple scales and oceanographic complexity of HAB phenomena. GEOHAB established the basis for continued international efforts now and into the future in order to better understand and predict the global complex phenomena of harmful algal blooms.

INTRODUCTION

Photosynthetic algae, which include single-celled organisms (phytoplankton), cyanobacteria (sometimes referred to as blue-green algae), and macroalgae, support healthy aquatic ecosystems by forming the base of the food web, fixing carbon, and producing oxygen. Under certain circumstances, some species can form high-biomass and/or toxic proliferations of cells (known as "blooms") that can cause harm to aquatic ecosystems, including plants and animals, and to humans via direct exposure to waterborne toxins or by consumption of toxic seafood. Ecosystem damage by highbiomass blooms may include, for instance, disruption of food webs, fish killing by gill damage, or the development of lowoxygen "dead zones" after bloom degradation. Some species produce potent natural chemicals (toxins) that can persist in the water or enter the food web, leading to illness or death of aquatic animals and/ or human seafood consumers.

Algal assemblages, visible or not, toxic or not, and irrespective of cell concentration, can have harmful impacts and are often generically referred to as "red tides" (Figure 1). Collectively, all of these organisms and events are referred to as "harmful algal blooms," or HABs. The definition of a HAB is a societal concept rather than a scientific definition, and these organisms and events are considered to be HABs if they negatively impact human health or socioeconomic interests or are detrimental to aquatic systems.

HABs occur in all aquatic systems, including marine, brackish, and freshwater, but they most dramatically affect human activities when they occur in coastal and inland waters. They are present from the Arctic to the Antarctic, even in sparsely settled coastal regions and in offshore areas. They are emerging as serious threats in freshwater systems such as the US Great Lakes, in drinking water reservoirs, and in coastal watersheds that can deliver freshwater HAB cells and toxins to the coastal ocean.

HISTORY OF GEOHAB

Coordinated research on HABs began in earnest in 1974 with the First International Conference on Toxic Dinoflagellate Blooms. This later developed into a series of international conferences on harmful marine phytoplankton, and at the fourth meeting of this group in 1989, it was recommended "that international research efforts be undertaken to evaluate the possibility of global expansion of algal blooms and man's involvement in this phenomenon" (Granéli et al., 1990). This recommendation ultimately led to the request by Member States of the Intergovernmental Oceanographic Commission (IOC) to form an international program on HABs. The the Scientific Committee on Oceanic Research (SCOR)/IOC WG 97 on the Physiological Ecology of Harmful Algal Blooms also played an important role in focusing and starting to develop consensus in the HAB research community. At a 1991 workshop sponsored by the IOC and SCOR, the IOC Harmful Algal Bloom Programme was first initiated, followed shortly thereafter in 1992 by the establishment of the Intergovernmental Panel on Harmful Algal Blooms (IOC/IPHAB), with a goal "to foster the effective management of, and scientific research on, harmful algal blooms in order to understand their causes, predict their occurrences and mitigate their effects." At the fourth IPHAB meeting, IOC and SCOR jointly agreed to develop an international program for the advancement of scientific research on HABs, which led to a workshop and subsequent formation, in 1998, of the Global Ecology and Oceanography of Harmful Algal Blooms Programme (GEOHAB), cosponsored by IOC and SCOR, with wide support from the international community through the Member States of IOC/IPHAB, and with support and guidance, particularly regarding data management, from the Joint Global Ocean Flux Study (JGOFS).

GEOHAB acknowledged from its inception that the HAB problem is global in nature, and that from a scientific perspective, there was incomplete information about the biological, chemical, and physical factors regulating HAB dynamics and impacts (GEOHAB, 2001). Thus, the mission of GEOHAB was established, which was to "foster international co-operative research on HABs in ecosystem types sharing common features, comparing the key species involved and the oceanographic processes that influence their population dynamics." GEOHAB then adopted the goal of "Improv(ing) prediction of HABs by



FIGURE 1. Some algal blooms result in discoloration of the water, known as "red tides," but harmful algal blooms can include highly toxic algae that result in no discoloration, while some dramatic events, such as this bloom caused by the dinoflagellate *Noctiluca* (inset), can be essentially harmless.

determining the ecological and oceanographic mechanisms underlying their population dynamics, integrating biological, chemical, and physical studies supported by enhanced observation and modelling systems."

A core concept of the GEOHAB program has been the comparative approach—indeed, this approach is embedded within both the mission and goal espoused by GEOHAB. Mayr (1982) identified experimental approaches and comparative approaches as "the two great methods of science" (see also Anderson et al., 2005), and the organizers of GEOHAB quickly recognized that a global perspective of HAB phenomena was best addressed with a comparative approach, from the cellular to the ecosystem level. This approach is based on the view that the ecology and oceanography of HABs can best be understood through the study of causative organisms and affected systems in relation to comparable species and systems. The comparative approach directly addresses the fundamental issue that marine systems are generally not amenable to experimental control, and lend themselves to a coordinated, international program where



FIGURE 2. The goals of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program were advanced through the linkages among the program elements.

naturally occurring temporal and spatial variations in existing conditions and phenomena substitute for controlled experimental treatments.

A key requirement for an international, comparative approach to scientific understanding of HABs was the definition of the systems and phenomena to be compared. This was laid out by the GEOHAB Scientific Steering Committee (SSC), chaired by Patrick Gentien, and published as the GEOHAB Science Plan in 2001, the first of many GEOHAB reports. To define the boundary of GEOHAB activities, the Science Plan outlined five program elements to serve as a framework to guide priorities and research (Figure 2): Biodiversity and Biogeography; Nutrients and Eutrophication; Adaptive Strategies; Comparative Ecosystems; and Observation, Modelling, and Prediction. It was envisioned that these elements, when combined, would lead to the scientific basis for improved management and mitigation, and that GEOHAB would interact and coordinate with related programs at the regional, national, and international levels. This Science Plan was both ambitious and forward looking, and served to steer the GEOHAB pro-

gram from publication, in 2001, through transition to the Global HAB program, in 2016.

A major challenge for any international coordinating effort is to implement the high-level vision, mission, and goals of the program. GEOHAB adopted an Implementation Plan in 2003 (GEOHAB, 2003), and issued the following call to scientists:

This plan for implementation of the programme serves as an invitation to the broad scientific community to participate. Scientists working in physical, chemical and/or biological disciplines, or other fields related to harmful algal research, including the development

of relevant instrumentation and models, are encouraged to contribute to this programme. Active participation by the widest international representation of the research community will be essential to ensure the success of GEOHAB.

This invitation served to set the basis for GEOHAB, with the explicit emphasis on open, community participation and consensus-building by international scientists focused on HAB research. One significant difference from other similar international programs, such as Global Ocean Ecosystem Dynamics (GLOBEC; Turner et al., 2013), was that GEOHAB never established an international program office, which led to more emphasis on support and coordination from the IOC and SCOR, and more reliance on the SSC and Core Research Projects (CRPs).

CRPs were developed within GEOHAB as the primary mechanism for coordinating international research, with Targeted Research and Regional/National Projects providing complementary efforts. The CRPs directly addressed Program Element 4 of the Science Plan (comparative research) and comprised oceanographic field studies conducted in, and application of models to, comparable ecosystems, supported by identification of relevant organisms, and measurements of the physical, chemical, and biological processes that control their population dynamics (GEOHAB, 2003). A major objective of core research was the integration achieved by the application of coupled biological/chemical/physical models to HAB dynamics in geographically distinct ecosystems sharing common features.

Four CRPs spanned the lifetime of GEOHAB: "HABs in Upwelling Systems," "HABs in Eutrophic Systems," "HABs in Stratified Systems," and "HABs in Fjords and Coastal Embayments." It was evident midway through the GEOHAB program that a new CRP on "HABs in Benthic Systems" should be established, and in 2010 this CRP was added as a fifth element. Inclusion of benthic HABs (BHABs) arose because, first, BHABs

appear to be increasing in area and impact within the coastal ocean. Second, better attention to the BHAB phenomenon highlighted the disparity in our knowledge of the ecology of the species associated with benthic plankton compared to phytoplanktonic species. A third driver was the opportunity to share the collective experience and expertise accumulated over the years in other systems and organisms on tropical and subtropical benthic HABs.

These five CRPs each had unique scientific questions, participants, and outcomes, but a common feature to all was their development with full and open involvement from the international scientific community, and with an emphasis on the comparative approach as defined in the Science Plan (GEOHAB, 2001; Figure 3). These CRPs are briefly described below with major goals and accomplishments.

HABS IN UPWELLING SYSTEMS

The CRP "HABs in Upwelling Systems" recognized that assessment of the extent to which HAB species respond in a similar way within these systems will allow the oceanographic processes that influence HAB population dynamics and community interactions to be established. Equally important was identification of upwelling systems that have dissimilar HAB species or groupings. The CRP science plan developed at an Open

Science Meeting (OSM) held in 2004 (GEOHAB, 2005), identified eight core questions related to upwelling systems:

- Are there definable adaptive strategies that characterize HAB species in upwelling systems?
- What seeding strategies persist within upwelling regions and are they consistent among regions?
- How do small-scale physical processes affect HAB growth and dispersion in upwelling systems?
- How do nutrient supply, type, and ratios determine HAB population dynamics in upwelling systems?
- What is the role of genetic predisposition versus environmental conditions in toxin production in different upwelling systems within a given genus or species?
- How does coastal morphology and bathymetry affect HAB dynamics in upwelling systems?
- What is the relative importance of cross-shelf and alongshore advection in different upwelling systems for HABs?
- Are climate indicators predictive of HAB events in upwelling systems?

Given the difficulty of launching a truly comparative field program across multiple ecosystems without a concerted national/international effort such as JGOFS (Karl et al., 2001), the Upwelling CRP focused

primarily on comparison of systems using existing data and field efforts. This led to numerous publications, including a special issue of *Progress in Oceanography* (Pitcher and Pillar, 2010) that highlighted progress and still-needed effort related to the eight core objectives of this CRP.

System-based studies have been useful in advancing our knowledge of the ecology and oceanography of HABs, and the comparative approach, as endorsed by GEOHAB, is considered to have added value to regional or national science plans. GEOHAB has provided useful direction to HAB research in upwelling systems over the past decade through formulation of common research objectives and the development of common research approaches that have contributed significantly to improving the availability of comparable data. The strong influence of physical forcing in upwelling systems has allowed a great deal of understanding to be gained from physical models with passive tracers representing HABs. Physical transport models have provided a very useful first step in predicting the movement of blooms through advection. Successful prediction of HABs as a possible outcome of the integration of real-time data into model systems as a component of operational forecasting of the ocean is most likely to be achieved in upwelling systems, thus taking a critical step toward fulfillment of GEOHAB goals.

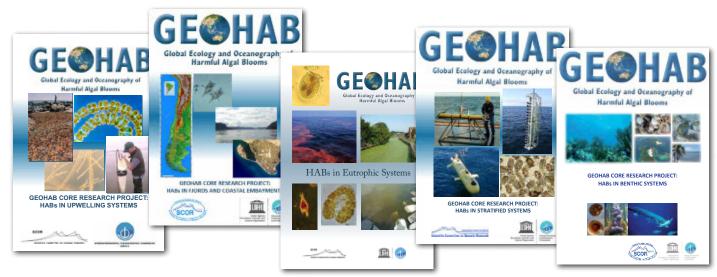


FIGURE 3. Five Core Research Projects provided the backbone for GEOHAB scientific efforts.

HABS IN EUTROPHIC SYSTEMS

The science plan of the CRP "HABs in Eutrophic Systems" (GEOHAB, 2006) was developed at an OSM held in 2005. This meeting identified that an important consequence of eutrophication, or nutrient pollution, is the increased prevalence of HABs primarily through the formation of high-biomass events. These events lead to fish kills, trophic transfer of algal toxins, oxygen depletion, and altered trophic interactions through direct stimulation of HABs by nutrients, but also through more subtle alterations of ecosystem function. This CRP laid out a roadmap for international research, focusing on the following questions:

- Are there clusters or specific types of HAB species that are indicative of global nutrient increases?
- To what extent do residence time and other physical processes impact the relationship between nutrient loading and HAB proliferation?
- How do feedbacks and interactions between nutrients and the planktonic, microbial food webs impact HABs and their detrimental effects?
- Do anthropogenic alterations of the food web, including overfishing and aquaculture activities, synergistically interact with nutrients to favor HABs?
- How do anthropogenic changes in land use, agricultural use of fertilizer, NOx emissions from vehicles, and global changes in land cover affect the delivery of nutrients to coastal waters and the resulting incidence of HABs? How do the stoichiometry and quality of these nutrient sources regulate the biological responses favoring HABs?
- Do climate change and climate variability have impacts on ecosystems that augment the impacts of eutrophication in the formation of HABs?

Members of the CRP focused on establishing collaborative international comparative projects, with eutrophication being a core component of regional and national programs such as CEOHAB in China, the GEOHAB Asia program,

and the US Harmful Algal Research and Response National Environmental Strategy (HARRNESS, 2005). Over the lifetime of GEOHAB, this CRP conducted two OSMs (Baltimore, USA, and Beijing, China), produced two special issues on HABs and eutrophication (in *Harmful Algae* and the *Chinese Journal of Oceanology*; Glibert et al., 2008b, 2011), and published a position paper identifying the negative consequences of urea fertilization for enhanced carbon sequestration and fisheries production (Glibert et al., 2008a).

Historically, the conceptual understanding of the links between nutrients and HABs was based upon the simplistic notion that more nutrients directly lead to higher algal biomass. Results from this GEOHAB CRP led to the recognition that HAB species can be directly and/or indirectly stimulated by nutrient over-enrichment, and that chronic, subtle effects related to nutrient forms, ratios, and loads can be equally or even more important than the obvious, acute effects (Glibert et al., 2011).

HABS IN STRATIFIED SYSTEMS

The CRP on "HABs in Stratified Systems" held an OSM in 2005. The resulting CRP science plan (GEOHAB, 2008) focused on understanding the small-scale hydrographic features that are encountered in any environmental system, including the systems the other CRPs focused on (upwelling, fjords, and semienclosed coastal areas, and both eutrophic and non-eutrophic systems). Particular emphasis was placed on thin layers where many harmful phytoplankton organisms can thrive, on rheology dynamics, and on technological and modeling challenges to resolve the biological and physical interactions operating at small physical scales. The overall objective was to determine the factors underlying the development of communities related to HABs in subsurface microlayers and the real-time dispersion of these microlayers as a function of turbulent and advective regimes. Four key questions were identified:

- What are the relative contributions of biological and physical processes to the initial formation of thin layers in stratified systems?
- What are the key processes defining the different strategies that maintain phytoplankton in thin layers?
- What are the biological and chemical outcomes of the physical concentration of plankton into high-density thin layers?
- What causes a high-density population in a thin layer to collapse?

The unique nature of the habitat associated with these events, typically involving subsurface layers, led to a strong emphasis on development of technology and methods for sampling and modeling HAB organisms in stratified systems, culminating in a 2012 workshop in Monterey Bay, California (GEOHAB, 2013; Berdalet et al., 2014) and the publication of a special issue of Deep Sea Research Part II (Raine et al., 2014). A main outcome of the CRP was the recognition that thin layers are important in the initiation and development of HABs, as populations develop inside retentive physical structures that are then transported toward the coast where impacts occur.

HABS IN FJORDS AND COASTAL EMBAYMENTS

Coastal regions represent a small fraction of the world ocean, but are of considerable importance because of the everincreasing human population that lives there, as well as the generally high productivity of these regions. Harmful algal blooms frequently occur in this environment, with negative outcomes on human health, tourism, aquaculture, and commercial fisheries. The CRP "HABs in Fjords and Coastal Embayments" resulted from an OSM held in 2004. The CRP science plan (GEOHAB, 2010) focused on the need to better understand the ecology and oceanography of harmful algal species in these regions, which are characterized by shallow depths and proximity to land. Seven key questions were defined in the science plan:

- Are there definable adaptive strategies that characterize HAB species in confined and semi-confined systems?
- What is the importance of life history transitions and cyst distribution in bloom initiation and maintenance endogenous seed beds versus exogenous introduction?
- How do physical dispersion and aggregation processes within a semiconfined basin affect HAB growth and distribution?
- What is the relative contribution of nutrient flux and supply ratios to HAB dynamics in eutrophic versus noneutrophic coastal embayments?
- What is the importance of spatial scale and retention time in the expression and effects of allelochemicals/toxins in semi-confined systems?
- How do embayment morphology, bathymetry, and hydrodynamic flux affect HAB dynamics?
- Are the effects of anthropogenic activities (e.g., aquaculture) and global climate change on HAB dynamics magnified in enclosed and semi-enclosed embayments?

Following the first OSM, this group held a second one (Victoria, Canada) in 2012 entitled "Progress in Interpreting Life History and Growth Dynamics of Harmful Algal Blooms in Fjords and Coastal Environments." This meeting focused on four themes: (1) life history of HAB species, (2) allelochemical interactions, (3) genetic diversity, and (4) transport and mixing of blooms in small-scale, mesoscale, and semiconfined systems. Progress in this CRP related primarily to the life histories of HAB species, including resistance and sexual reproduction phases, thanks to advances in culturing, microscopy (e.g., nuclei staining and visualization), and molecular tools (e.g., Bravo et al., 2014). Species-specific strategies for cyst germination and encystment coupled to particular water circulation patterns explain in some cases the importance

of cysts to the recurrence of blooms in certain retentive areas (e.g., Onda et al., 2014), but not in others (e.g., Estrada et al., 2010).

A physical/biological numerical model of the population dynamics of *A. fundyense* in the Gulf of Maine has been run routinely each year since 2015. Continued fieldwork provided clear evidence of the interannual variability of cyst beds in the region, and also showed links between cyst distribution patterns and the intensity and extension of blooms

- species from similar habitat types and identification of functional groups
- Identify the important physical and chemical factors that control abundance and distribution over appropriate temporal and spatial scales
- Inform conceptual and numerical models that help to predict BHAB events
- Develop and validate technologies for detailed and extensive monitoring and establish real-time observation platforms

With an international, multidisciplinary, and comparative approach, GEOHAB advanced our understanding of the mechanisms underlying population dynamics of HABs within an ecological and oceanographic context and from an ecosystem perspective at the regional scale.

in the years immediately before and after cyst mapping surveys (McGillicuddy et al., 2011). It is now possible to empirically forecast the geographic extent of a forthcoming bloom based on cyst abundances (Anderson et al., 2014).

HABS IN BENTHIC SYSTEMS

The newest CRP, "HABs in Benthic Systems," developed out of the recognition that BHABs are becoming increasingly significant globally, and that international coordination would benefit this research community. Following from an OSM in 2010 (GEOHAB, 2012), this CRP developed an approach to facilitate this coordination:

- Determine the primary physiological, genetic, environmental, or behavioral processes that regulate cellular growth and toxicity
- Define common characteristics, including the groupings of harmful

Discoveries over the last five to seven years have brought new researchers into the field, with a considerable increase in related publications. The establishment of an international program that can coordinate information and data sharing of different science communities, many of which are geographically separated, was the objective of the BHAB CRP, and this activity continues under the GlobalHAB program.

Although GEOHAB made progress on many of the research questions listed above, many still remain to be fully explored through future research, as the BHAB group is one of the most difficult types of HABs to mitigate, and the demand for improved approaches and methods is widespread, given that benthic HABs are associated with both high-value tourism (e.g., coral reef systems) and high-impact consequences (such as ciguatera fish poisoning).

GEOHAB TARGETED, REGIONAL, AND NATIONAL RESEARCH

The GEOHAB SSC was well aware that the CRPs focused on specific objectives within the larger Science Plan, and that coordination with related and complementary programs was critical to the successful development of a coordinated international program. Targeted research included numerous projects that requested endorsement by GEOHAB or were aligned with the goals of the CRPs. Regional and national research activities were identified as relevant to the GEOHAB Science Plan, but were coordinated by regional or national organizations independent of the GEOHAB SSC. These projects and programs ranged from narrowly focused efforts, such as a program entitled "Dynamics of Alexandrium fundyense distributions in the Gulf of Maine: An observational and modeling study of nearshore and offshore shellfish toxicity, vertical toxin flux, and bloom dynamics in a complex shelf sea," (GOMTOX) to large, national programs including Ecology and Oceanography of

Harmful Algal Blooms in the Philippines (PhilHABs) and Chinese Ecology and Oceanography of Harmful Algal Blooms (CEOHAB). The mission and goals of GEOHAB were also articulated and implemented at a regional level through development of the EU-US Scientific Initiative on Harmful Algal Blooms (European Commission, 2013), which developed a coordinated research effort between the US and the EU EUROHAB programs. A total of eight regional/national programs were endorsed by GEOHAB (Figure 4).

Another significant accomplishment facilitated by GEOHAB was the establishment of a regional plan for HAB research in Asia. This plan developed out of two regional meetings (Tokyo, Japan, in 2007 and Nha Trang, Vietnam, in 2008). These meetings were held in coordination with IOC/WESTPAC and the IOC HABViet program, culminating in the GEOHAB "Harmful Algal Blooms in Asia: A Regional Comparative Programme" (GEOHAB, 2010; Furuya et al., 2010). The report developed an overview of Asian

HAB problems, and provided a framework for guiding priorities for research based on the five GEOHAB program elements. The need to develop a comparative, international program on HABs in Asia was particularly compelling for several reasons. Asia is characterized by (1) the highest production of aquaculture fish and shellfish globally, and thus the greatest impacts from HABs on these resources; (2) a diversity of harmful syndromes and causative organisms occur in Asia; (3) an apparent trend of increasing HABs throughout the region has been observed; and (4) an increasing trend toward regional eutrophication has been linked to HABs. The ecological and economic impacts of HABs in Asia are thus profound and apparently increasing. GEOHAB Asia provided, and still provides, a template for regional coordination on HAB research, leading to further partnerships under both GEOHAB and now GlobalHAB, as well as through ongoing efforts by IOC/WESTPAC and other regional organizations.

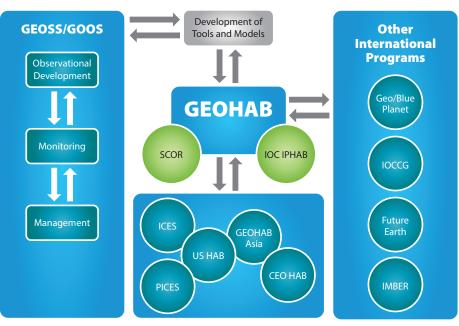


FIGURE 4. GEOHAB cooperated and coordinated with relevant national, regional, and international programs. GEOSS/GOOS = Global Earth Observation System of Systems/Global Ocean Observing System. SCOR = Scientific Committee on Oceanic Research. IOC IPHAB = Intergovernmental Oceanographic Commission Intergovernmental Panel on Harmful Algal Blooms. ICES = International Council for the Exploration of the Sea. PICES = North Pacific Marine Science Organization. IOCCG = International Ocean-Colour Coordinating Group. IMBER = Integrated Marine Biogeochemistry and Ecosystem Research.

CROSSCUTTING AND FRAMEWORK ACTIVITIES

In addition to the research efforts supported by GEOHAB, the Implementation Plan also called for Framework activities focusing on data management, protocols, and quality control; capacity building; modeling; and coordination with other international programs. An early and highly successful example of GEOHAB activity within this category was the "Workshop on Real-Time Coastal Observing Systems for Ecosystem Dynamics and Harmful Algal Blooms," or HABWatch, held in 2003 at the Observatoire Océanologique and Citadelle of Villefranche-sur-Mer, France (e.g., Figure 5). The idea for the workshop initially emerged from the Working Group on Harmful Algal Blooms Dynamics of ICES (International Council for the Exploration of the Sea), and was supported by GEOHAB and the Coastal Ocean Observing Panel (COOP) of the Global Ocean Observing System (GOOS), and initiated with major support from the European Commission. This workshop, attended by an international audience, provided participants with both the theory relevant to understanding the basic principles of real-time observation and modelling tools and tutorials to allow the use of these tools. The lectures and tutorials are still available at http://HABWatch.obs-vlfr.fr, and the workshop culminated in the publication of a manual within the UNESCO Oceanographic Methodology Series, Real-Time Coastal Observing Systems for Marine Ecosystem Dynamics and Harmful Algal Blooms: Theory, Instrumentation, and Modeling (Babin et al., 2008).

Following on from HABWatch, GEOHAB ran another very successful workshop and training activity in 2009 in Galway, Ireland, focused on modeling: "GEOHAB Modeling: Linking Observations to Predictions" (GEOHAB, 2011). Similar to HABWatch, it emphasized training young investigators, facilitating international coordination, developing strategies for using observations and models to address GEOHAB CRP science questions, and furthering the goals of the GEOHAB Science Plan. The workshop focused specifically on the science questions articulated by the Eutrophic, Stratified, and Upwelling Systems CRPs, with a significant outcome being the publication of a special issue of the Journal of Marine Systems (McGillicuddy, 2011).

One of the most recent crosscutting activities supported by GEOHAB, continuing under the GlobalHAB program,

has been the development of a series of workshops on the relationship between HABs and climate change (Wells et al., 2015). The general topic of climate change was acknowledged in the GEOHAB science and implementation plans but was not a primary focus of the various CRPs in large part because it was felt that there was insufficient information about the link(s) and causative relationships between HABs and climate change while the CRPs were active. The first workshop was jointly sponsored by GEOHAB, ICES, and the North Pacific Marine Sciences Organization (PICES), under the auspices of the "Workshop on Harmful Algae Blooms in a Changing World" (ICES, 2013). Outcomes from this workshop included assessment of the current state of knowledge (Wells et al., 2015), description of two types of "sentinel" sites for observing change based on long-term observations, and planning for a larger OSM.

The follow-on OSM took place in Gothenburg, Sweden, in 2015, again cosponsored by GEOHAB, ICES, and PICES. Workshop participants developed several urgent recommendations on research priorities related to HABs and climate change. These include focusing more intensive research on key organisms; continuing to develop ecological and forecast models; strengthening linkages among global, national, and regional observation programs to establish the recommend HAB sentinel sites; and development of a "best practices" manual for assessment of climate change linkages

to HAB events and organisms.

Moving forward, GlobalHAB is also expected to interact with the IOC-UNESCO working group GO₂NE (Global Ocean Oxygen Network), recently formed in response to a need for a global analysis of ocean deoxygenation and its impacts. This international network of ocean oxygen scientists will benefit investigation of ocean deoxygenation in response to climate change and eutrophication. Formal collaboration between GlobalHAB and GO₂NE will serve investigation of the likely global increase in episodic oxygen depletion associated with increasing HABs in the coastal environment.

GEOHAB LEGACIES

There are many potential ways to gauge the successes and impacts of international research programs; one of the most tangible is to document the outcomes of these activities within the scientific literature. In addition to the GEOHAB report series, multiple special issues were produced during the lifetime of the GEOHAB program. GEOHAB also directly coordinated research activities, cosponsored other activities, and provided endorsement for targeted, national, and regional programs aligned with program objectives. There was no requirement for acknowledgment of GEOHAB in publications, but many authors identified GEOHAB as a contributor to these research efforts. The SSC tracked the GEOHAB documents, acknowledgments in other peer-reviewed manuscripts, and publications from key endorsed projects



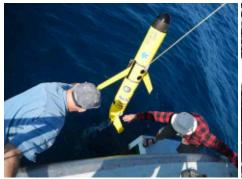




FIGURE 5. GEOHAB workshops, including HABWatch and Stratified Systems, focused on the use of advanced technology to detect HABs, such as (left) the Environmental Sample Processor, (middle) buoyancy gliders, and (right) the wave-powered WireWalker.

and special journal issues sponsored by GEOHAB. At the end of 2016, there were 330 publications in 75 journals, while the GEOHAB science and implementation plans were cited 220 times. Expanding this to include all publications that reference GEOHAB in the title or text, there were more than 1,000 publications as of 2016 (Figure 6).

GEOHAB also had a positive influence on other international programs. Beginning with HABWatch, GEOHAB has partnered with GOOS; the increased visibility of HABs provided by GEOHAB and other efforts has led to the inclusion of phytoplankton generally, and HAB organisms specifically, as proposed Biological Core Variables within the US Integrated Ocean Observing System (National Ocean Council, 2016), while the GOOS Biology and Ecosystems Panel has identified phytoplankton species, and HABs as a specific subset, as an Essential Ocean Variable. OSMs such as the "HABs in a Changing World" symposium, cohosted by GEOHAB, ICES, and PICES, continue to define research priorities for the next decade by these programs, while the regional planning and implementation activities established both nationally and regionally contribute to the mission and goals identified by the GEOHAB program. As importantly, GEOHAB has continued to raise awareness of the general scientific consensus that public health, recreational and tourism, fishery, aquaculture, and ecosystem impacts from HABs have all increased over the past few decades and need to be addressed with a coordinated, international effort. GEOHAB recently published Harmful Algal Blooms: A Scientific Summary for Policy Makers (Kudela et al., 2015) and has contributed to the "Oceans and Society: Blue Planet" initiative coordinated by the Group on Earth Observations (Bernard et al., 2014). These efforts, while more intangible than a list of publications, continue to inform and guide research activities on harmful algal blooms well beyond the formal end of the GEOHAB program.

The GEOHAB legacy also continues beyond 2016 through ongoing activities initiated by GEOHAB and now maintained by GEOHAB partners. For example, the ICES, PICES, and GEOHAB efforts on HABs and climate change are expected to produce a "best practices" manual in the near future. Another partnership was established between GEOHAB and the International Ocean

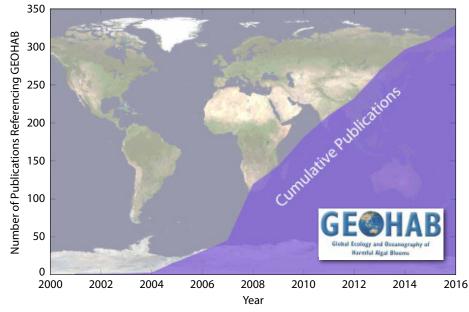


FIGURE 6. GEOHAB is directly acknowledged in or central to 330 publications in 75 journals. Expanding this to include all publications that reference GEOHAB, there were more than 1,000 publications as of 2016.

Colour Coordinating Group (IOCCG), with the anticipated production of a monograph on satellite remote sensing of HABs in 2017. Finally, while GEOHAB has ended, a result of the final OSM, held in Paris in 2013, was that the international scientific community requested that a program like GEOHAB continue into the future. As one participant summarized, "we all came to Paris because we recognize a fundamental problem (HABs), and cannot solve this problem in our individual laboratories. This requires an international approach." From this recognition came the formal adoption of the GlobalHAB program, adopted by IOC (through IPHAB) and SCOR, and endorsed by the International Atomic Energy Agency. The GlobalHAB Science and Implementation plan builds on the GEOHAB Science Plan, and incorporates suggestions from members of the international HAB community who participated in the GEOHAB OSM in Paris. It is also enriched by many other contributions during the first year of the program and by subsequent inputs at the International Conference on Harmful Algae in Florianópolis, Brazil (October 2016), where the first draft of the plan was presented. GlobalHAB builds on the scientific framework provided by GEOHAB and also expands into new disciplines and addresses emerging issues. GlobalHAB will address the scientific and societal challenges of HABs through the application of advanced technologies, training, and capacity building, with a multidisciplinary approach. It will also build linkages with broader science domains (climate, toxicology, economy, medicine, public health), emphasize social science communications, and address management priorities.

We are proud of what the GEOHAB program accomplished, and we look forward to future research programs such as GlobalHAB that both benefit from and build upon this legacy of informed science and international coordination to continue improving the prediction of HABs by determining the ecological and

oceanographic mechanisms underlying their population dynamics, integrating biological, chemical, and physical studies supported by enhanced observation and modeling systems, and also incorporating new challenges and a wider scope in order to translate this knowledge into sound policy- and decision-making based on sound science.

The following papers in this special issue of *Oceanography* will provide more detail on the specific accomplishments in each area of GEOHAB.

REFERENCES

- Anderson, D.M., G.C. Pitcher, and M. Estrada. 2005. The comparative "systems" approach to HAB research. *Oceanography* 18(2):148–157, https://doi.org/10.5670/oceanog.2005.50.
- Anderson, D.M., B.A. Keafer, J.L. Kleindinst, D.J. McGillicuddy, J.L. Martin, K. Norton, C.H. Pilskaln, J.L. Smith, C.R. Sherwood, and B. Butman. 2014. *Alexandrium fundyense* cysts in the Gulf of Maine: Long-term time series of abundance and distribution, and linkages to past and future blooms. *Deep Sea Research Part II* 103:6–26, https://doi.org/10.1016/j.dsr.2.2013.10.002.
- Babin, M., C.S. Roesler, and J.J. Cullen, eds. 2008. Real-Time Coastal Observing Systems for Marine Ecosystem Dynamics and Harmful Algal Blooms: Theory, Instrumentation and Modelling. Oceanographic Methodology series, UNESCO, Paris, 830 pp.
- Berdalet, E., M.A. McManus, O.N. Ross, H. Burchard, F.P. Chavez, J.S. Jaffe, I.R. Jenkinson, R. Kudela, I. Lips, U. Lips, and A. Lucas. 2014. Understanding harmful algae in stratified systems: Review of progress and future directions. *Deep Sea Research Part II* 101:4–20, https://doi.org/10.1016/j.dsr2.2013.09.042.
- Bernard, S., R. Kudela, and L. Velo-Suárez. 2014.
 Developing global capabilities for the observation and prediction of harmful algal blooms. Pp. 46–52 in Oceans and Society: Blue Planet. S. Djavidnia, V. Cheung, M. Ott, and S. Seeyave, eds, Cambridge Scholars Publishing.
- Bravo, I., R.I. Figueroa, and S. Fraga. 2014. Cellular and nuclear morphological variability within a single species of the toxigenic dinoflagellate genus *Gambierdiscus*: Relationship to life-cycle processes. *Harmful Algae* 40:1–8, https://doi.org/10.1016/j.hal.2014.09.009.
- Estrada, M., J. Solé, S., Anglès, and E. Garcés. 2010. The role of resting cysts in *Alexandrium minutum* population dynamics. *Deep-Sea Research Part II* 57:308–321, https://doi.org/10.1016/j.dsr2.2009.09.007.
- European Commission. 2013. The EU-US Scientific Initiative on Harmful Algal Blooms: A Report from a Workshop Jointly Funded by the European Commission Environment and Sustainable Development Programme and the US National Science Foundation. EUR 20578, https://cordis.europa.eu/pub/sustdev/docs/environment/ki-na-20578-en-c_eu-us_algal_blooms.pdf.
- Furuya, K., P.M. Glibert, M. Zhou, and R. Raine. 2010. GEOHAB Asia. Global Ecology and Oceanography of Harmful Algal Blooms in Asia: A Regional Comparative Programme. IOC and SCOR, Baltimore and Paris, 68 pp.
- GEOHAB. 2001. Global Ecology and Oceanography of Harmful Algal Blooms: Science Plan. P. Glibert and G. Pitcher, eds, SCOR and IOC, Baltimore and Paris, 86 pp.

- GEOHAB. 2003. Global Ecology and Oceanography of Harmful Algal Blooms: Implementation Plan.
 P. Gentien, G. Pitcher, A. Cembella, and P. Glibert, eds, SCOR and IOC, Baltimore and Paris, 36 pp.
- GEOHAB. 2005. Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Upwelling Systems. G. Pitcher, T. Moita, V. Trainer, R. Kudela, F. Figuieras, and T. Probyn, eds, IOC and SCOR, Paris and Baltimore, 88 pp.
- GEOHAB. 2006. Global Ecology and Oceanography of Harmful Algal Blooms: Eutrophication and HABs. SCOR and IOC, Paris and Baltimore, 74 pp.
- GEOHAB. 2008. Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Stratified Systems. SCOR and IOC, Paris, France, and Newark, Delaware, USA, 59 pp.
- GEOHAB. 2010. Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Fjords and Coastal Embayments. A. Cembella, L. Guzmán, S. Roy, J. Diogène, eds, IOC and SCOR, Paris, France, and Newark, Delaware, 57 pp.
- GEOHAB. 2011. GEOHAB Modelling: A Workshop Report. D.J. McGillicuddy Jr., P.M. Glibert, E. Berdalet, C. Edwards, P. Franks, and O. Ross, eds, IOC and SCOR, Paris and Newark, Delaware, 85 pp.
- GEOHAB. 2012. Global Ecology and Oceanography of Harmful Algal Blooms, Core Research Project: Harmful Algal Blooms in Benthic Systems. E. Berdalet, P. Tester, and A. Zingone, eds, IOC and SCOR, Paris and Newark, 64 pp.
- GEOHAB. 2013. Global Ecology and Oceanography of Harmful Algal Blooms, GEOHAB Core Research Project: HABs in Stratified Systems. Workshop on "Advances and Challenges for Understanding Physical-Biological Interactions in HABs in Stratified Environments." M.A. McManus, E. Berdalet, J. Ryan, H. Yamazaki, J.S. Jaffe, O.N. Ross, H. Burchard, and F.P. Chavez, eds, IOC and SCOR, Paris and Newark, Delaware, USA, 88 pp.
- Glibert, P.M., R. Azanza, M. Burford, K. Furuya, E. Abal, A. Al-Azri, F. Al-Yamani, P. Andersen, D.M. Anderson, J. Beardall, and others. 2008. Ocean urea fertilization for carbon credits poses high ecological risks. *Marine Pollution Bulletin* 56(6):1,049–1,056, https://doi.org/10.1016/ j.marpolbul.2008.03.010.
- Glibert, P.M., J.M. Burkholder, E. Granéli, and D.M. Anderson. 2008. Advances and insights in the complex relationships between eutrophication and HABs: Preface to the special issue. *Harmful Algae* 8:1–2, https://doi.org/10.1016/j.hal.2008.08.020.
- Glibert, P.M., M. Zhou, M. Zhu, and M.A. Burford. 2011. Preface to the special issue on eutrophication and HABs: The GEOHAB approach. *Chinese Journal of Oceanology and Limnology* 29(4):719–723, https://doi.org/10.1007/s00343-011-0501-0.
- Granéli, E., B. Sundström, L. Edler, and D. Anderson, eds. 1990. Toxic Marine Phytoplankton: Proceedings of the Fourth International Conference on Toxic Marine Phytoplankton, Held June 26–30, 1989, in Lund, Sweden. Elsevier, New York, 576 pp.
- HARRNESS. 2005. Harmful Algal Research and Response: A National Environmental Science Strategy 2005–2015. J.S. Ramsdell, D.M. Anderson, and P.M. Glibert, eds, Ecological Society of America, Washington DC, 96 pp.
- ICES. 2013. Report of the ICES/PICES/IOC-GEOHAB Workshop on Harmful Algae Blooms in a Changing World (WKHABCW), March 18–22, 2013, Friday Harbor Laboratories, USA. ICES CM 2013/ SSGHIE:01, 13 pp.
- Karl, D.M., J.E. Dore, R. Lukas, A.F. Michaels, N.R. Bates, and A. Knap. 2001. Building the longterm picture: The US JGOFS time-series programs. *Oceanography* 14(4):6–17, https://doi.org/10.5670/ oceanog.2001.02.

- Kudela, R.M., E. Berdalet, S. Bernard, M. Burford,
 L. Fernand, S. Lu, S. Roy, P. Tester, G. Usup,
 R. Magnien, and others. 2015. Harmful Algal Blooms: A Scientific Summary for Policy Makers.
 IOC/UNESCO, Paris (IOC/INF-1320), 19 pp.
- Mayr, E. 1982. *The Growth of Biological Thought.*Harvard University Press, Cambridge, MA, USA, 974 pp.
- McGillicuddy, D.J. Jr. 2011. Models of harmful algal blooms: Conceptual, empirical, and numerical approaches. *Journal of Marine Systems* 83:105–107, https://doi.org/10.1016/j.jmarsys.2010.06.008.
- Onda, D.F.L., A O. Lluisma, and R.V. Azanza. 2014. Development, morphological characteristics and viability of temporary cysts of *Pyrodinium bahamense* var. compressum (Dinophyceae) in vitro. *European Journal of Phycology* 49:265–275, https://doi.org/10.1080/09670262.2014.915062.
- Pitcher, G.C., and S. Pillar, eds. 2010. Special Issue on Harmful Algal Blooms in Upwelling Systems. *Progress in Oceanography* 85(1–2):1–136.
- Raine, R., E. Berdalet, M.A. McManus, and H. Yamazaki, eds. 2014. Harmful algae in stratified systems. *Deep Sea Research Part II* 101:1–254.
- Turner, E., D.B. Haidvogel, E.E. Hofmann, H.P. Batchelder, M.J. Fogarty, and T. Powell. 2013. US GLOBEC: Program goals, approaches, and advances. *Oceanography* 26(4):12–21, https://doi.org/10.5670/oceanog.2013.72.
- Wells, M.L., V.L. Trainer, T.J. Smayda, B.S. Karlson, C.G. Trick, R.M. Kudela, A. Ishikawa, S. Bernard, A. Wulff, D.M. Anderson, and W.P. Cochlan. 2015. Harmful algal blooms and climate change: Learning from the past and present to forecast the future. Harmful Algae 49:68–93, https://doi.org/10.1016/j.hal.2015.07.009.

ACKNOWLEDGMENTS

We thank the many participants who have contributed to GEOHAB over the lifetime of the program, and in particular the 36 Science Steering Committee members who provided their time, ideas, and enthusiasm to make GEOHAB a success. Funding, programmatic support, and guidance were provided by SCOR, IOC, and IPHAB with significant support from the US National Science Foundation, the US National Oceanic and Atmospheric Administration, and the European Commission.

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ARTICLE CITATION

Kudela, R.M., E. Berdalet, H. Enevoldsen, G. Pitcher, R. Raine, and E. Urban. 2017. GEOHAB—The Global Ecology and Oceanography of Harmful Algal Blooms Program: Motivation, goals, and legacy. *Oceanography* 30(1):12–21, https://doi.org/10.5670/oceanog.2017.106.