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Deep-Sea Research II 52 (2005) 2365–2368

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Preface

At the start of the ECOHAB-Gulf of Maine (GOM) program, a team of scientists from nine institutions pooled their knowledge and expertise to plan a multi-disciplinary investigation of the bloom dynamics of the toxic dinoflagellate *Alexandrium fundyense* in the Gulf of Maine. At the time, our understanding of the dynamics of this species was limited primarily to waters of the western coastal Gulf of Maine and the Bay of Fundy, so we knew relatively little about the patterns and mechanisms controlling its abundance throughout the remainder of the Gulf. We identified several hydrographic "habitats" for *A. fundyense* in the Gulf, with varying degrees of potential connectivity. These linkages were mostly hypothetical, as very few field data were of the spatial scale needed to detect the connections between different water masses and regions. Three focal points for our attention were the western segment of the Maine Coastal Current (WMCC), the eastern segment (EMCC), and the Bay of Fundy, which was to be investigated through collaboration with our Canadian colleagues. The ECOHAB-GOM research teams addressed this complex interdisciplinary problem through shipboard measurement programs, laboratory studies, numerical models, and remote sensing.

Here we present a series of papers describing the results of the five-year ECOHAB-GOM program. It is fascinating for us to look back and consider what we did not know at the start of the project, as well as what we thought we knew, but realize now was incorrect.

For example, we knew *A. fundyense* cells were abundant in the Bay of Fundy, in the far eastern GOM, and in the WMCC, and that alongshore transport figured prominently in the patterns of toxicity throughout the region. We did not know, however, that a closely related species (*Alexandrium ostenfeldii)* co-occurred extensively with *A. fundyense* and needed to be carefully identified to avoid inaccuracies in field observations (Gribble et al.; Anderson et al.). We also did not know the extent to which *A. fundyense* regional populations were interconnected, nor did we understand the intricacies of the hydrography that links them. Our ECOHAB-GOM surveys, both large- and small-scale, revealed these interactions at the Gulf scale. A series of cruises in 1998 documented direct linkages between the Bay of Fundy populations and EMCC blooms, and indicated that light and inorganic nutrients were primary controls on blooms in the offshore waters of the Gulf (Townsend et al., 2001). Those observations also suggested that EMCC populations might be entrained into the WMCC and thus contribute to toxicity in the western Gulf. This linkage was confirmed by several studies included in this volume (Luesrsen et al.; Keafer et al.), suggesting east–west connectivity as a mechanism underlying interannual variability in toxicity in the western GOM (Bean et al.). Surprisingly, on a Gulf-wide basis, annual mean *A. fundyense* cell abundance was remarkably stable during the time interval examined (1993–2002), which suggested that interannual variations in toxicity may be regulated by transport and delivery of offshore cell populations, rather than the absolute abundance of the source populations themselves (McGillicuddy et al.).

The physical oceanographic mechanisms underlying the general circulation in the Gulf, as well as the episodic movements of water masses such as the EMCC intrusions into the WMCC are presented in detail in this volume, and have significantly advanced our basic understanding of the Gulf of Maine (Pettigrew et al.; Love et al.; Janzen et al.; Churchill et al.; Hetland and Signell). A novel pathway called the "inside track" is also described whereby *A. fundyense* cells can travel inshore of the EMCC and directly into the WMCC region via a feature that has been newly named the Gulf of Maine Coastal Plume (Keafer et al.). Together, these papers provide the hydrographic context within which both large- and small-scale bloom transport phenomena can be viewed.

0967-0645/$ - see front matter
doi:10.1016/j.dsr2.2005.08.001

Dormant cysts are clearly a critical element of *A. fundyense* population dynamics. Prior to our research program we knew only that cysts were present in the Gulf, though their distribution and abundance were not well known. We understood that germination was controlled by both internal and external factors, including an endogenous annual clock that restricted excystment to certain favorable times of the year. A major unknown was the relative importance of cysts in shallow versus deep waters — the latter are more numerous, but also are found in cold, dark conditions that are known to slow the germination rate. ECOHAB-GOM made major contributions to this body of knowledge by confirming the existence of the endogenous clock in GOM *A. fundyense* cysts (Matrai et al.), by providing detailed physiological measurements of germination rates as functions of temperature and light (Anderson et al.), and by producing the first systematic Gulf-wide surveys showing the abundance of cysts in bottom sediments (Anderson et al.) and in the water column (Kirn et al.).

Efforts to directly measure encystment fluxes were not successful, but numerical models provided important insights. For example, the flux of germinated cells from deep cyst seedbeds was shown to be 40 × the input from shallow zones, despite the warmer temperatures and higher light levels (Anderson et al.; Stock et al.). Likewise, the models demonstrated that two major cyst seedbeds, one in the Bay of Fundy, and the other offshore of Penobscot and Casco Bays are both needed to generate the cell abundance and distribution patterns observed on cruises (McGillicuddy et al.).

The models (Anderson et al.; McGillicuddy et al.) also help to resolve a long-standing dilemma. Average conditions in the Gulf create, in effect, a one-way transport system that will move *A. fundyense* cells to the west and south, with the mean flow providing limited opportunity for those cells to circulate back into the northeast portion of the domain. If blooms begin with germinating cysts from specific seedbeds, as some hypothesize, how are those seedbeds replenished with new cysts? The resolution is hypothesized as a two stage process — one in which cells accumulate in a retentive eddy near the mouth of the Bay of Fundy, allowing cysts to be deposited to reseed future blooms in that area. Cells that escape that retention zone into the EMCC can bloom further downstream and form a second seedbed, from which cysts germinate in subsequent years to further propagate the species along the coast. Without the localized, incubator characteristic of the eddy system in the Bay of Fundy, one would expect *A. fundyense* populations in the entire GOM to diminish through time and the PSP problem to disappear. The fact that PSP has been a persistent problem in the region for a century or more argues for the effectiveness of the mechanisms described here.

Other aspects of *A. fundyense* ecophysiology deserve mention. Studies are presented here that demonstrate the manner in which toxicity varies with environmental conditions (Etheridge et al.), and these and other observations are used to show how nutrient limitation changes the toxicity characteristics of populations through time. Saxitoxin is unique to *A. fundyense* cells within the GOM phytoplankton community, and thus changes in the toxin content or composition in field samples can be used to infer the nutritional status of that species (Poulton et al.).

Our studies of vertical distributions of *A. fundyense* populations demonstrated that highest cell densities were commonly observed at pycnocline depths, but there was no evidence of vertical migration patterns in *A. fundyense* populations (Martin et al.; Townsend et al.). This has major implications with respect to the ability of this species to access deep nutrients at or below the pycnocline. We note, however, that contrasting results have been obtained in ongoing laboratory culture studies, so we can expect there to be considerable genotypic variability in this behavioral pattern.

Another study examined the potential linkage between *A. fundyense* cells and co-occurring phytoplankton (Townsend et al.) and hypothesizes that the dinoflagellate cannot bloom until diatoms are not present in significant numbers. Other studies provided insights into the interactions between toxic dinoflagellates, their grazers, and pelagic food webs. It has long been assumed that PSP toxins in *Alexandrium* spp. are grazer deterrents, and this assumption has been supported by several laboratory investigations using primarily high-density cultures of toxic phytoplankton as food. However, it has also been long known that zooplankters such as copepods can graze upon *Alexandrium* spp. during natural mixed assemblage blooms, with no apparent adverse effects. Studies during this program revealed that metazoan grazers, primarily copepods, readily grazed upon *Alexandrium* spp. and other phytoplankters in a generally non-selective manner during natural blooms. Because

Alexandrium was a relatively small component of the overall phytoplankton assemblages during these blooms, ingestion of *Alexandrium* was also low, compared to that of the more abundant phytoplankton taxa. Thus, effects of toxicity such as those recorded with high concentrations of toxic algal diets may be reduced in nature by ingestion of low natural levels of toxic algae, and dilution of toxicity effects by ingestion of more abundant non-toxic algal food. The grazing impacts of investigated zooplankton taxa on *Alexandrium* populations were relatively low, particularly offshore (Turner and Borkman), but also inshore (Campbell et al.), and grazing impacts varied primarily with abundances of both *Alexandrium* cells and grazers.

It has also been known since the seminal studies of Alan White a quarter-century ago that PSP toxins from *Alexandrium* blooms in the GOM region can be vectored through zooplankton food webs via trophic interactions. However, in most cases, toxins appeared to be concentrated primarily in larger grazers such as large copepods. A new finding of the present program was that PSP toxins were widespread through various size fractions of the zooplankton community (Doucette et al.), including smaller size fractions that were dominated by microzooplankters such as heterotrophic dinoflagellates, ciliates, and rotifers (Turner et al.). Thus, it appears that microzooplankton, as well as larger mesozooplankton such as copepods may be entry points for vectorial intoxication of pelagic food webs, possibly leading to fish.

When ECOHAB-GOM began, numerical models existed for the hydrography of the GOM, but *Alexandrium* dynamics could not be realistically simulated. Close cooperation among our biologists, physicists, and modelers has led to the creation of an *Alexandrium* sub-model that can be coupled with physical models to provide realistic simulations of our cruise observations and other data (McGillicuddy et al.; Stock et al.; McGillicuddy et al., 2003). These models have proved useful in evaluating the fate of buried cysts, the flux of germinated cells, and the factors that control growth in different locations and times, to name just a few topics. In the latter context, model runs demonstrated that growth of vegetative cells is limited primarily by temperature from April through June throughout the Gulf, whereas nutrient limitation occurs in July and August in western waters (McGillicuddy et al.; Love et al.). Thus the observed seasonal shift in the patterns of cells and toxicity from west to east can be explained by changing growth conditions: growth appears to be more rapid in the west early in the season because of warmer temperatures there, whereas growth rates appear to be more rapid in nutrient-rich eastern GOM waters later in the season – a time when there is severe nutrient limitation of growth in the western region (McGillicuddy et al.).

The overall increase in our knowledge and understanding of the ecology and oceanography of *A. fundyense* in the GOM is gratifying — and reflects the degree of advancement that follows from multi-investigator, multi-disciplinary science. We now have detailed knowledge of many critical biological, physical and chemical processes, and have developed conceptual models of *A. fundyense* bloom dynamics that explain patterns of toxicity throughout the region, as well as the mechanisms that allow this regional population to persist, year after year (Anderson et al.; McGillicuddy et al.).

There are of course, many questions remaining, but ECOHAB-GOM has ended and it is now time to document what we know so that others can build from this base of knowledge. Even as we write this, the region is reeling from the impacts of a massive *A. fundyense* bloom that many consider to be the worst in at least three decades. It is already evident that the knowledge developed during ECOHAB-GOM helped in the event response efforts, including harvesting closure decisions, and that many of the concepts described in this volume are consistent with the patterns of this 2005 bloom (Anderson et al.). Nevertheless, there were some surprises and unexpected developments, and these will dictate a careful reexamination and perhaps modifications of the data and synthesis reported here. This is, of course, the nature of scientific investigation. We hope the material in this volume provides useful background information as well as impetus for future research of that type.

We gratefully acknowledge the support of NSF and NOAA through the ECOHAB program, which is a partnership including ONR, EPA, and NASA as well. We also thank John Milliman for his editorial efforts on our behalf, and Judy Kleindinst for her efficient and friendly approach to the many administrative aspects of assembling a special issue of this type.

Dedication

This issue is dedicated to Maureen Keller, friend and colleague to all of us in the ECOHAB-GOM program.

Maureen worked at the Bigelow Laboratory for Ocean Sciences in Boothbay Harbor, Maine from 1979 until her untimely death in 1999. She was a member of the ECOHAB-GOM team in the early years of the program, and participated in several of our cruises and collaborative studies. We wish to acknowledge her contributions to our project, both in its planning stages, and its implementation. We also wish to acknowledge her contributions to phytoplankton ecology and biological oceanography, and her strong commitment to teaching science and exposing students of all ages to the excitement of marine research. Her contributions to science and her warm and friendly demeanor are missed by us all.

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