JOURNAL OF PLANKTON RESEARCH | VOLUME 25 | NUMBER 9 | PAGES 1131–1138 | 2003

# A mechanism for offshore initiation of harmful algal blooms in the coastal Gulf of Maine

**D. J. MCGILLICUDDY JR*, R. P. SIGNELL[1], C. A. STOCK, B. A. KEAFER, M. D. KELLER[2], R. D. HETLAND[3] AND D. M. ANDERSON**

WOODS HOLE OCEANOGRAPHIC INSTITUTION, [1]UNITED STATES GEOLOGICAL SURVEY, WOODS HOLE, MA 02543, [2]BIGELOW LABORATORY FOR OCEAN SCIENCES, PO BOX 475, WEST BOOTHBAY HARBOR, ME 04575 AND [3]TEXAS A&M UNIVERSITY, COLLEGE STATION, TX 77843-3146, USA

*CORRESPONDING AUTHOR: dmcgillicuddy@whoi.edu

*A combination of observations and model results suggest a mechanism by which coastal blooms of the toxic dinoflagellate Alexandrium fundyense can be initiated from dormant cysts located in offshore sediments. The mechanism arises from the joint effects of organism behavior and the wind-driven response of a surface-trapped plume of fresh water originating from riverine sources. During upwelling-favorable winds, the plume thins vertically and extends offshore; downwelling winds thicken the plume and confine it to the nearshore region. In the western Gulf of Maine, the offshore extent of the river plume during upwelling conditions is sufficient to entrain upward-swimming A. fundyense cells germinated from offshore cyst beds. Subsequent downwelling conditions then transport those populations towards the coast.*

## INTRODUCTION

Harmful algal blooms (HABs) occur in many regions of the global coastal ocean. The culprit organisms are taxonomically diverse, and produce a wide variety of deleterious effects—ranging from ecosystem disturbance to serious threats to human health. One of the major challenges to understanding the underlying controls on HABs stems from the oceanographic context in which these phenomena take place. In some cases, HABs are initiated and develop offshore and it is not until they impinge upon the coast that their most significant consequences are felt.

In New England, the most serious HAB issue is paralytic shellfish poisoning (PSP), a potentially fatal illness that occurs when humans eat shellfish that have accumulated toxins as they feed on dinoflagellates of the genus *Alexandrium* (Anderson, 1997). These organisms are responsible for human illnesses and occasional death due to PSP, repeated closures of shellfish beds in nearshore and offshore waters, the mortality of larval and juvenile stages of fish and other marine animals (White *et al.*, 1989), and the death of marine mammals such as humpback whales (Geraci *et al.*, 1989).

*Alexandrium* has a complex life cycle (Wyatt and Jenkinson, 1997). Various aspects of the organism's population dynamics can be pieced together from measurements in both the laboratory and the field, albeit based on a collection of studies that deal with different species. For example, *Alexandrium* can lie dormant as a resting cyst in the sediment for years (Anderson, 1984; Keafer *et al.*, 1992). Germination is regulated by a complex set of processes, including an endogenous clock (Anderson and Keafer, 1987) and physiological responses to environmental factors such as temperature (Anderson, 1980), light and oxygen availability (Anderson *et al.*, 1987). Once emerged from the sediment, cells swim towards the surface to begin a phase of vegetative growth. Photosynthetic production is fundamentally limited by light and the availability of nutrients; however, maximal growth rates occur only within a specific range of temperature and salinity conditions (Watras *et al.*, 1982). When faced with environmental stress, such as nutrient limitation, the vegetative cells form gametes that subsequently fuse into a zygote (Anderson *et al.*, 1984). The zygote then encysts and the cycle is complete. This intricate life history strategy has important ramifications with respect to both the timing of seasonal blooms and long-term persistence of the organism in specific geographic areas (Eilertsen and Wyatt, 2000).

The spatial distribution of benthic cysts may therefore be a key factor in initiating *Alexandrium* blooms. Although previous investigations have provided information on cyst abundance in some areas of the Gulf of Maine (Dale *et al.*, 1978; White and Lewis, 1982; Thayer *et al.*, 1983; Anderson and Keafer, 1985; Keafer *et al.*, 1992), the regional-scale distribution remained obscure until the first systematic survey was undertaken in 1997 (documented below in the Results section). The cyst map reveals that highest abundances of *Alexandrium* cysts are located well offshore. This result is particularly noteworthy in light of the fact that blooms of vegetative cells in the western Gulf of Maine are observed in coastally-trapped river plumes (Franks and Anderson, 1992a,b). How might offshore cysts contribute to inshore blooms of *Alexandrium* in the western Gulf of Maine? This question is investigated with a coupled three-dimensional physical–biological model, and the results suggest a simple mechanism by which cells germinated from offshore cysts can become entrained into a buoyant coastal current.

## METHOD

Cell abundance was measured in the western Gulf of Maine in 1993, 1994, 1998 and 2000. In the 1993 and 1994 data sets, cells were identified and counted in a Sedgewick–Rafter chamber using a standard light microscope at a magnification of ×100. In the 1998 and 2000 data sets, cells were counted using an immunological procedure based on an *Alexandrium*-specific monoclonal antibody probe used in a whole cell, indirect immunofluorescent format (Anderson *et al.*, 1993; Turner *et al.*, 2000). The M8751-1 hybridoma used in this procedure is maintained in the Anderson laboratory.

Cyst abundance measurements were based on sediment samples collected with a Craib corer (Craib, 1965). The upper 1 cm of sediment from each core was stored and processed according to methods published by Anderson *et al.* (Anderson *et al.*, 1996). A primulin-staining method was used to label fluorescently the cysts for improved visualization under the microscope (Yamaguchi *et al.*, 1995).

Hydrodynamic simulations were constructed using a primitive equation model (Blumberg and Mellor, 1987) with a variable horizontal resolution of 2–4 km and 12 terrain-following vertical levels. Vertical mixing is internally generated from the Mellor–Yamada level 2.5 turbulence closure, and subgridscale horizontal mixing is parameterized with the Smagorinsky formulation. The model is initialized with climatological temperature and salinity profiles. Freshwater discharge is specified from USGS gauges in the Kennebec/Androscoggin, Saco, Merrimack and Charles rivers. Wind stress and heat fluxes are computed from observations at NOAA buoy 44007 offshore of Portland, Maine using bulk formulae described in Large and Pond (Large and Pond, 1981, 1982). Surface insolation is prescribed from land-based sensors in Woods Hole, Massachusetts. Tidal forcing at the offshore open boundary is provided by a larger-scale finite-element model of the region (Lynch *et al.*, 1996).

The biological model explicitly represents vegetative cells that swim upward at 10 m day$^{-1}$, once germinated from resting cysts. Swimming speed decreases linearly to zero in the upper 10 m of the water column. Germination input is calculated from the observed cyst distribution and laboratory measurements of the dependence of specific germination rate on light, temperature and the endogenous clock of *A. fundyense*. The time period of the simulation is nearly coincident with the maximum germination potential set by the endogenous clock, so the waters overlying the cyst beds are inoculated with a relatively steady input of newly germinated cells. Typical germination rates range from 5% per day in the relatively warm, well-illuminated shallow sediments, to 1% per day, which is more characteristic of the colder and darker conditions associated with deeper cyst beds offshore. Vegetative growth is not included, as our objective here is focused on bloom initiation rather than its development. Thus, once germinated from the cyst beds, cells in this model behave as passive tracers with an upward swimming velocity. Simulations using a more complete biological model are being quantitatively evaluated with observations as part of ongoing research.

## RESULTS

*Alexandrium* cysts were present in bottom sediments throughout the entire regional domain that was sampled (Figure 1). However, the highest abundances occurred in large deposits offshore, beyond the 75 m isobath. The largest peaks in the mapped distribution appeared offshore of both Penobscot and Casco Bays. Because of the relatively coarse sampling between these two peaks, it is not clear whether they were truly distinct deposits or local maxima in a larger deposit spanning the area between Penobscot and Casco Bays.

It is not known how the large-scale distribution of cysts varies over time, given that only a single survey of this geographic scope is available. However, repeat surveys in a smaller domain south and west of the present survey domain show ‘no significant change in cyst abundance’ from November 1983 to November 1984 (Anderson and Keafer, 1985). Moreover, those observations documented high abundance of cysts in sediments 30–40 km northeast of Cape Ann, near the southern extent of the present survey. Although differences in sampling methodology preclude direct evaluation of interdecadal variability,

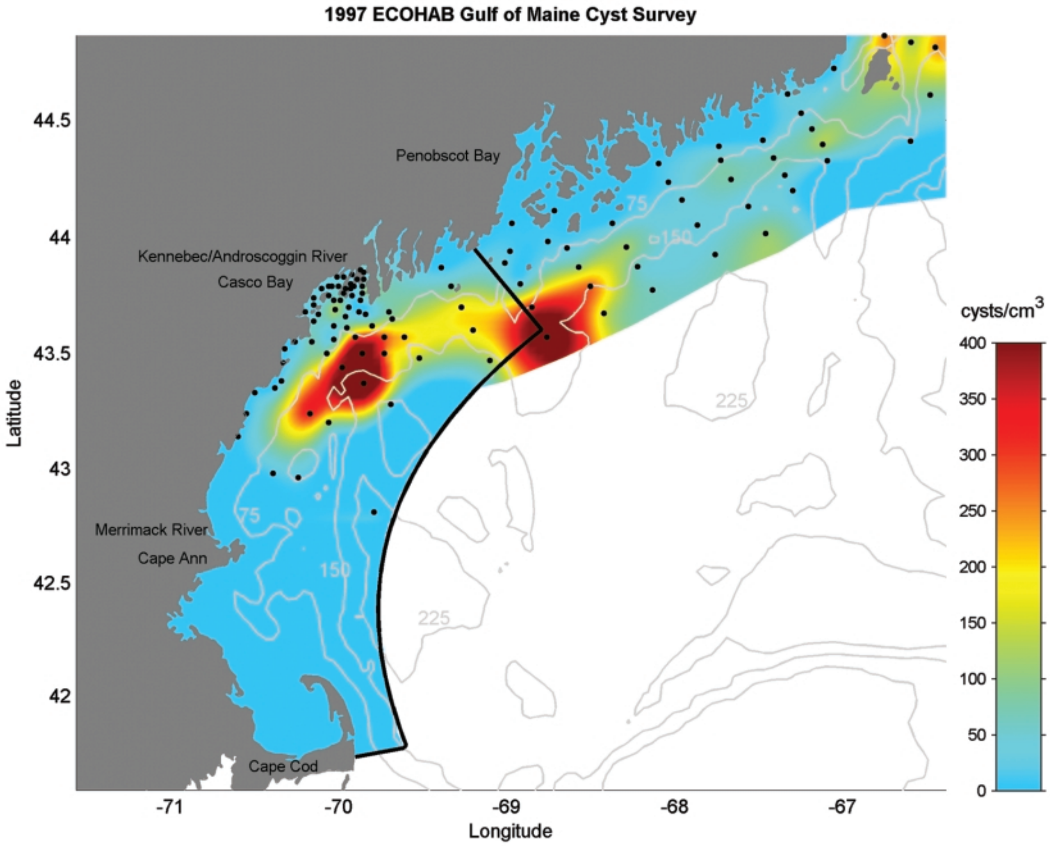

**Fig. 1.** Distribution of *Alexandrium* cysts in the upper 1 cm of bottom sediments in the Gulf of Maine, derived from a survey in October 1997. Sampling stations are indicated by black dots, and the 75, 150 and 225 m bathymetric contours are overlayed. The offshore boundary of the model domain used for the simulation shown in Figure 4 is indicated by the bold black line.

these results suggest the offshore maximum is a persistent feature of the cyst distribution.

Highest concentrations of vegetative cells occur in the relatively fresh waters of the coastal current (Figure 2). Moreover, the salinity of the waters overlying the offshore maximum in the cyst distribution is significantly higher than that where peak concentrations of vegetative cells exist. It is striking that, in a mean sense, inshore blooms are spatially disconnected from this large source located offshore. Clearly, the higher abundance of cells at characteristic plume salinities is a result of conditions inside the plume that are more favorable for bloom development than the surrounding waters. The question is, what initiates these blooms? It could be that cells germinated from the very low concentrations of cysts present in inshore sediments provide an initial inoculum of cells that is sufficiently large enough to trigger a bloom. However, it is reasonable to inquire as to whether or not the large cyst deposits observed offshore have any relevance to inshore blooms.

The numerical model was used to investigate potential links. Starting from an initial condition in which *Alexandrium* concentration is zero everywhere in the domain, the model is integrated forward with the physical forcing shown in the upper two panels of Figure 3. The results highlight offshore initiation of an *Alexandrium* bloom via germination from offshore cyst beds (Figure 4; see supplementary data http://plankt.oupjournals.org/ for an animated presentation of the results). Cysts also germinate inshore, but they contribute <15% of the total flux due to germination.

Spatio-temporal evolution of cell distribution is dominated by wind-forced river plume dynamics. Fresh water inputs originating at the Kennebec/Androscoggin and Merrimack rivers result in a buoyant coastal current that flows southwestward down the coast in the direction of Kelvin wave propagation. In addition, the plume undergoes significant cross-shore displacement due to wind forcing. Upwelling-favorable winds (from the southwest) drive the plume offshore (e.g. April 22), whereas downwelling-favorable winds (from the northeast) confine it near the coast (e.g. April 14 and May 2). The overall

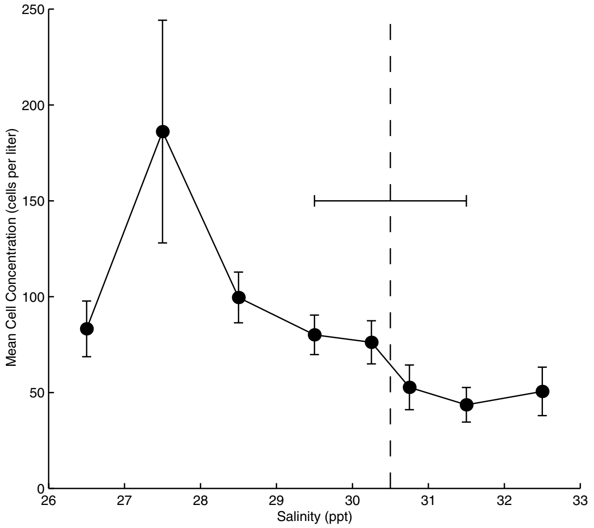

**Fig. 2.** Mean surface concentrations of *Alexandrium* in various salinity intervals (solid line). Error bars represent one standard deviation of the sample mean. The dashed line at $S$ = 30.45 p.p.t. and its associated standard error represent the salinity conditions of surface waters overlying the peak in the cyst distribution offshore of Casco Bay (Figure 1). Cell concentration data are derived from surveys in the western Gulf of Maine (south and west of Penobscot Bay) in 1993, 1994, 1998 and 2000. Observations taken during the bloom period (late March, April and May) are included here.

characteristics of this hydrodynamic behavior are consistent with Ekman theory for a buoyant coastal current (Fong *et al.*, 1997).

These motions have a dramatic impact on the entrainment of *Alexandrium* cells germinated from offshore cysts into the fresh waters of the river plume (Figure 3, lower panel). During the 81 day simulation, there are two major episodes during which cell concentration in the plume increases dramatically: one in late April and the other in mid-May. Both of these events correspond to periods of upwelling-favorable winds, with the peak cell abundance in the plume occurring towards the end of the upwelling period. When the winds subsequently shift to favor downwelling, cell abundance in the low-salinity water appears to drop. However, this is primarily a consequence of the cells being advected out of the 'source region' in which the budgets shown in Figure 3 are computed (north and east of the line in Figure 4). Cells entrained into the plume tend to remain in the fresh water as it is transported in the coastal current system. The relatively steady input of cells from the offshore cyst beds also inoculates the waters outside the plume. Upward-swimming cells arriving at the surface during downwelling conditions take up residence in the salty waters of the ambient coastal current, as exemplified by the patch of cells northeast of Cape Ann simulated on May 2 (Figure 4).

Note that the overall cell concentrations in the budgets shown in the lower panel of Figure 3 are quite low relative to observed values (Figure 2). This results from two factors. First, the cell concentrations reported in Figure 3 are computed by dividing the total number of cells in a salinity interval by the total volume of water in that interval. The absolute concentrations are therefore low because the cells occupy a small fraction of the total volume in each interval (upward swimming confines them to the surface layers). Secondly, vegetative growth is not included in the model, so cell concentrations are not expected to reach the levels observed in the field. Thus, it is only the relative changes in salinity-normalized cell concentration that are of primary interest here.

## DISCUSSION

These results suggest that the response of the river plume to fluctuating wind forcing provides a mechanism for cross-isobath transport of *Alexandrium* cells (Figure 5). Under upwelling conditions, the plume thins and extends far offshore where it is inoculated by upward-swimming light-seeking cells germinated from the offshore cyst bed. When the winds shift to favor downwelling, the plume moves onshore and thickens, thereby exposing the coast to offshore populations of *Alexandrium* (albeit downstream of the cyst bed from which the cells were germinated).

What is the observational evidence that can be used to determine the extent to which this mechanism is operative in the natural system? Indirect support comes from the Franks and Anderson retrospective analysis of wind records and shellfish toxicity data (Franks and Anderson, 1992b), indicating that downwelling precedes PSP outbreaks along the coast. However, this line of evidence speaks more to the delivery of mature blooms to shellfish beds rather than the initiation of the blooms themselves. Unfortunately, direct observation of bloom initiation via synoptic surveys of the vegetative cell distribution is problematic for a number of reasons. To begin with, it is difficult to separate the processes of bloom initiation (stimulated by germination) and development (dominated by growth) in the natural system. This stems from the fact that there is no way to distinguish between input of cells into the system via germination and simple vegetative growth of the existing population. Moreover, these processes occur in a dynamic fluid medium in which three-dimensional transport plays a fundamental role in creating substantial patchiness in the observed distributions. Therefore, evaluation of the efficacy of this mechanism will require a more complete analysis of the population dynamics of *Alexandrium* (including germination, growth and mortality) in the context of a three-dimensional hydrodynamic model. Once a realistic simulation of the observed vegetative cell distribution has

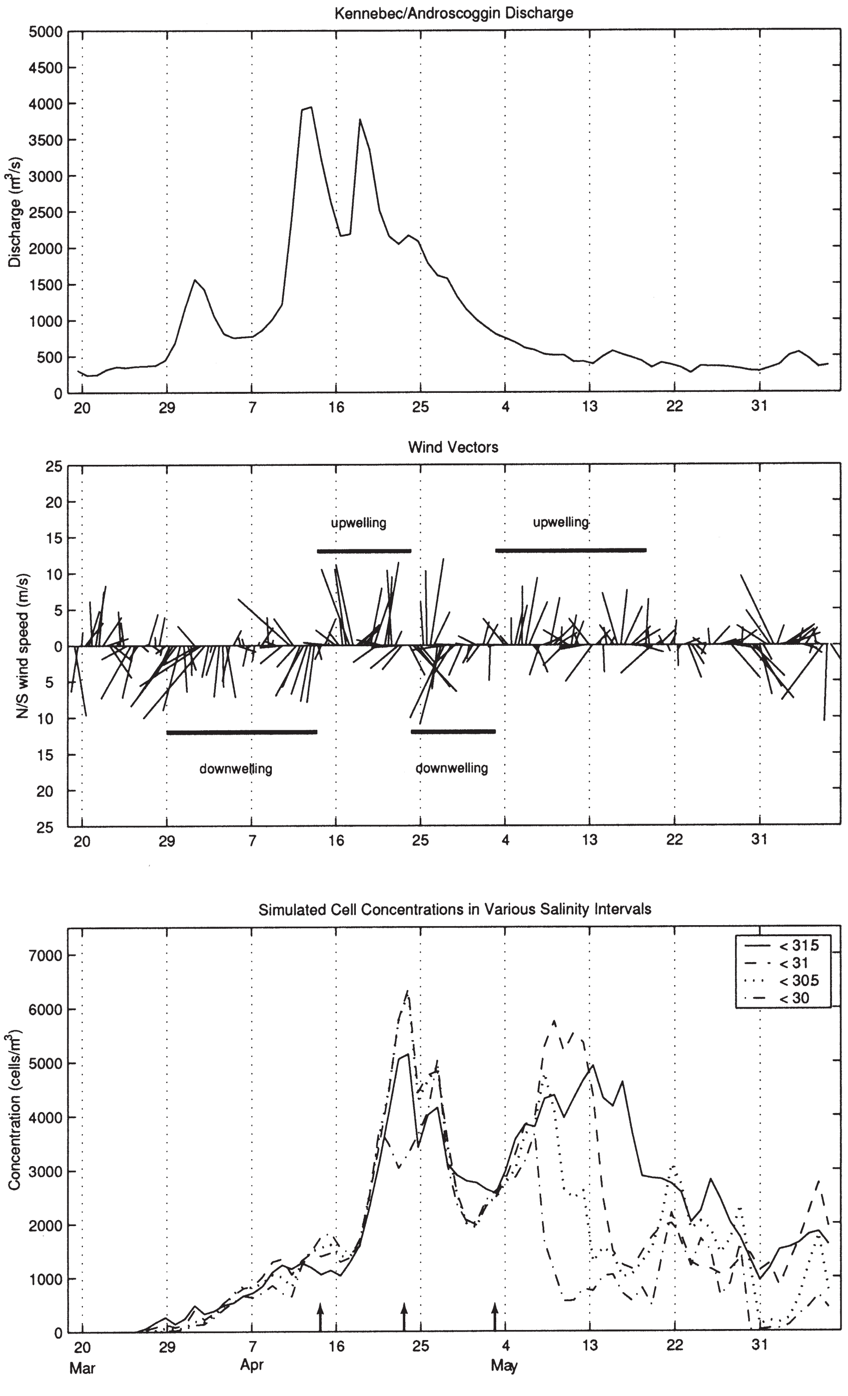

**Fig. 3.** Upper two panels: time series of river discharge and winds used to force the model. Thick horizontal bars indicate time periods of upwelling-favorable (south-westerly) and downwelling-favorable (north-easterly) winds. Bottom panel: mean cell concentrations in various salinity intervals diagnosed from the source region of the model (see text). Arrows indicate the dates of model snapshots shown in Figure 4. Only the cells germinated from cysts deeper than 75 m are included in order to highlight the mechanism by which offshore cells are entrained in the plume.

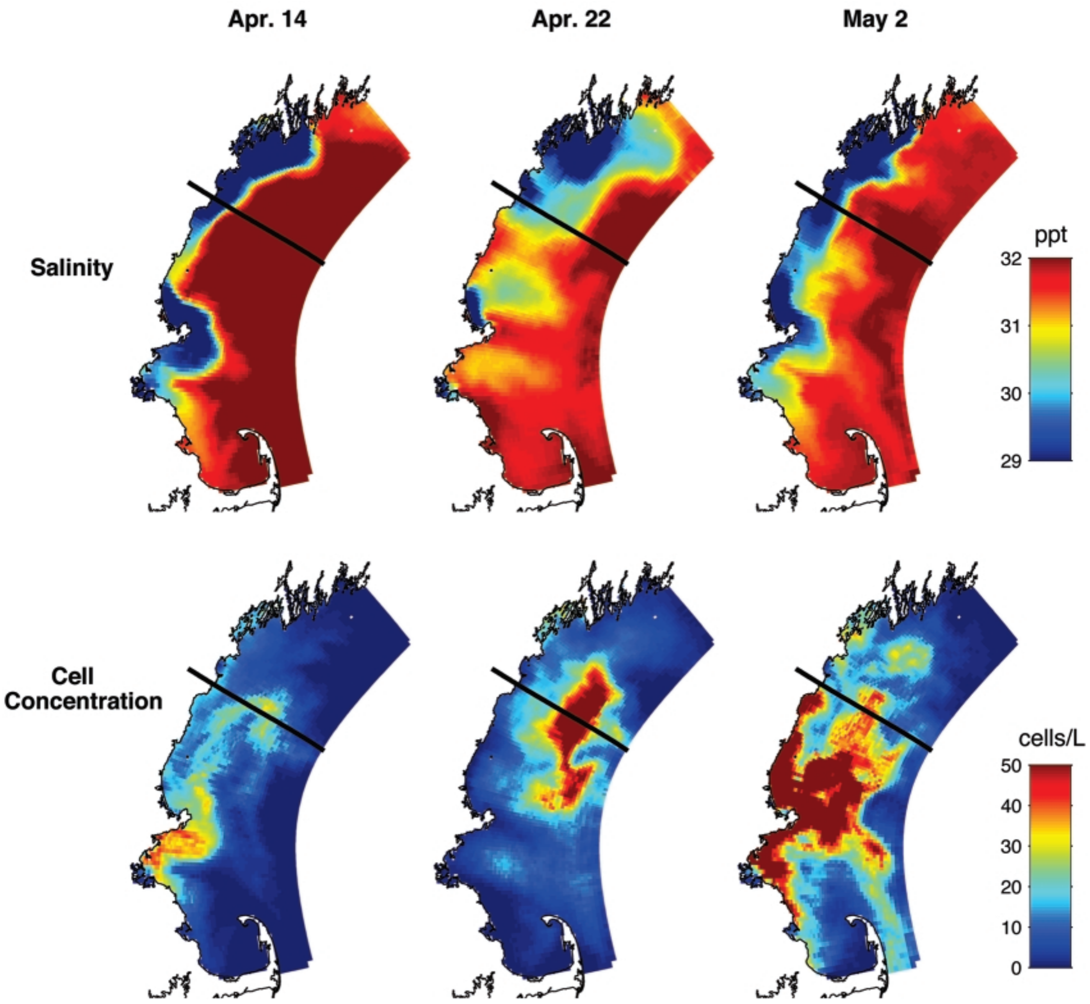

**Fig. 4.** Results from a three-dimensional coupled physical–biological simulation. Snapshots of salinity (top row) and cell concentration (bottom row) are shown for three different days: April 14 (left column), April 22 (middle column) and May 2 (right column). The area north and east of the bold line is referred to as the 'source region' (see text).

been created, it will be diagnosed to ascertain the underlying controls on both initiation and development of blooms. This is the central focus of our ongoing research. Nevertheless, the simple model presented here demonstrates a physical–biological interaction that could facilitate a connection between the spatially distinct distributions of the dormant cysts and vegetative cells of *Alexandrium* in the Gulf of Maine.

Although the basic elements of this cross-shore transport mechanism are clear, additional pathways of offshore cell entrainment into the plume are possible. Idealized two-dimensional simulations suggest a quasi-lateral entrainment process that occurs when upwelling conditions cause the plume to ride up and over pre-existing surface patches of cells offshore (Hetland *et al.*, 2003). Subducted cells then enter the plume through upward swimming, and the degree of entrainment depends strongly on swimming speed. The same could be true for cells originating from cyst beds further upstream, subsequently subducted by the larger-scale flow of the Eastern Maine Coastal Current (Townsend *et al.*, 2001). Indeed, some evidence links cells observed underneath the plume to upstream water masses (Anderson *et al.*, 2000).

Fed either by germination directly underneath the plume or by a source further upstream, the mechanism illustrated in Figure 5 constitutes a pathway through which near-shore blooms of *Alexandrium* can be initiated offshore. Similar mechanisms might well be operative for other cyst-forming HAB species worldwide. The cross-shore flux arises from the combination of organism behavior and the response of a buoyant plume to tran-

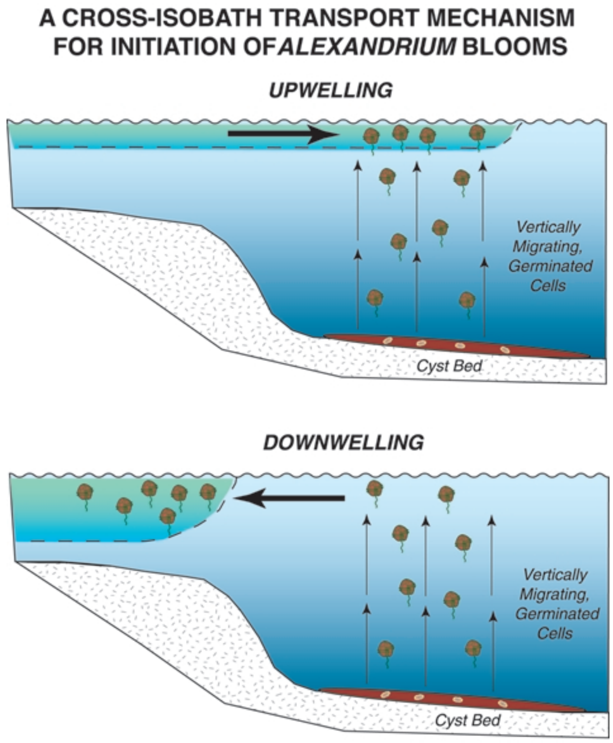

**Fig. 5.** A mechanism for cross-isobath transport of *Alexandrium* blooms. During upwelling conditions, the plume thins and moves offshore. Recently germinated, upward-swimming cells enter the plume as it overlies the offshore peak in the cyst distribution. During downwelling conditions, the plume retreats and thickens, thereby exposing the coast to cell populations that originated offshore.

sient wind forcing. Its implications are substantial, in that the processes linking coastal and offshore environments are subtle, complex and non-linear (Tyler and Seliger, 1978; Steidinger and Haddad, 1981; Fraga *et al.*, 1988; Bakun, 1996; Brink and Robinson, 1998; Shanks *et al.*, 2002; Walsh *et al.*, 2002). Our ability to understand and eventually predict HABs and other coupled physical–biological phenomena in the coastal ocean depends critically on the elucidation of these links.

## ACKNOWLEDGEMENTS

This work was supported by the US ECOHAB Program, sponsored by NOAA, NSF, EPA, NASA and ONR. Data from the Gulf of Maine Regional Marine Research Program were also used. Our research was still in progress when one of our co-authors (M.D.K.) died; her important contribution to the research effort was cherished by all of us. We thank Kristin Gribble, Amy Bronzino and Brian Thompson for their hard work in processing cyst samples used in Figure 1. We are grateful for the comments and suggestions made by three anonymous reviewers who helped improve the manuscript. This is WHOI contribution 10652, and contribution 71 of the US ECOHAB program.

## REFERENCES

Anderson, D. M. (1980) Effects of temperature conditioning on development and germination of *Gonyaulax tamarensis* (Dinophyceae) hypnozygotes. *J. Phycol.*, **16**, 166–172.

Anderson, D. M. (1984) Shellfish toxicity and dormant cysts in toxic dinoflagellate blooms. In Ragelis, E. P. (ed.), *Seafood Toxins*. American Chemistry Society Symposium Series, Washington, DC, Vol. 262, pp. 125–138.

Anderson, D. M. (1997) Bloom dynamics of toxic *Alexandrium* species in the northeastern US. *Limnol. Oceanogr.*, **42**, 1009–1022.

Anderson, D. M. and Keafer, B. A. (1985) Dinoflagellate cyst dynamics in coastal and estuarine waters. In Anderson, D. M., White, A. W. and Baden, D.G. (eds), *Toxic Dinoflagellates. Proceedings of the Third International Conference on Toxic Dinoflagellates*. Elsevier, New York, pp. 219–224.

Anderson, D. M. and Keafer, B. A. (1987) An endogenous annual clock in the toxic marine dinoflagellate *Gonyaulax tamarensis*. *Nature*, **325**, 616–617.

Anderson, D. M., Kulis, D. M. and Binder, B. J. (1984) Sexuality and cyst formation in the dinoflagellate *Gonyaulax tamarensis*: cyst yield in batch cultures. *J. Phycol.*, **20**, 418–425.

Anderson, D. M., Taylor, C. D. and Armburst, E. V. (1987) The effects of darkness and anaerobiosis on dinoflagellate cyst germination. *Limnol. Oceanogr.*, **32**, 340–351.

Anderson, D. M., Keafer, B. A., Kulis, D. M., Waters, R. M. and Nuzzi, R. (1993) An immunofluorescent survey of the brown-tide chrysophyte *Aureococcus anophagefferens* along the northeast coast of the United States. *J. Plankton Res.*, **15**, 563–580.

Anderson, D. M., Fukuyo, Y. and Matsuoka, K. (1995) Cyst methodologies. In Hallegraeff, G. M., Anderson, D. M. and Cembella, A. E. (eds), *Manual on Harmful Marine Microalgae*. UNESCO, Paris, pp. 229–245.

Anderson, D. M., Keafer, B. A., Churchill, J. H., Signell, R. P. and Geyer, W. R. (2000) *Alexandrium* blooms in the western Gulf of Maine. *Symposium on Harmful Algae in the US* Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA.

Bakun, A. (1996) *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. University of California Sea Grant, San Diego, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico, 323 pp.

Blumberg, A. F. and Mellor, G. L. (1987) A description of a three-dimensional coastal model. In Heaps, N. S. (ed.) *Coastal and Estuarine Sciences*. American Geophysical Union, Washington, DC, Vol. 4, pp. 1–16.

Brink, K. H. and Robinson, A. R. (eds) (1998) *The Sea*. John Wiley & Sons, New York, Vol. 10, 604 pp.

Craib, J. S. (1965) A sampler for taking short undisturbed marine cores. *J. Cons. Perm. Int. Explor. Mer.*, **30**, 34–39.

Dale, B., Yentsch, C. M. and Hurst, J. W. (1978) Toxicity in resting cysts of the red-tide dinoflagellate *Gonyaulax excavata* from deeper water coastal sediments. *Science*, **201**, 1223–1225.

Eilertsen, H. C. and Wyatt, T. (2000) Phytoplankton models and life history strategies. *S. Afr. J. Mar. Sci.*, **22**, 323–338.

Fong, D. A., Geyer, W. R. and Signell, R. P. (1997) The wind-forced response on a buoyant coastal current: observations of the western Gulf of Maine plume. *J. Mar. Systems*, **12**, 69–81.

Fraga, S., Anderson, D. M., Bravo, I., Reguera, B., Steidinger, K. A. and Yentsch, C. M. (1988) Influence of upwelling relaxation on dinoflagellates and shellfish toxicity in Ria de Vigo, Spain. *Estuarine Coastal Shelf Sci.*, **27**, 349–361.

Franks, P. J. S. and Anderson, D. M. (1992a) Alongshore transport of a phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Mar. Biol.*, **112**, 153–164.

Franks, P. J. S. and Anderson, D. M. (1992b) Toxic phytoplankton blooms in the southwestern Gulf of Maine: testing hypotheses of physical control using historical data. *Mar. Biol.*, **112**, 165–174.

Geraci, J. A., Anderson, D. M., Timperi, R. J., St Aubin, D. J., Early, G. A., Prescott, J. A. and Mayo, C. A. (1989) Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin. *Can. J. Fish. Aquat. Sci.*, **46**, 1895–1898.

Hetland, R. D., McGillicuddy, D. J. and Signell, R. P. (2003) Cross-frontal entrainment of plankton into a buoyant plume: the frog tongue mechanism. *J. Mar. Res.*, **60**, 763–777.

Keafer, B. A., Buesseler, K. O. and Anderson, D. M. (1992) Burial of living dinoflagellate cysts in estuarine and nearshore sediments. *Mar. Micropaleontol.*, **20**, 147–161.

Large, W. G. and Pond, S. (1981) Open ocean momentum flux measurements in moderate to strong winds. *J. Phys. Oceanogr.*, **11**, 324–336.

Large, W. G. and Pond, S. (1982) Sensible and latent heat flux measurements over the ocean. *J. Phys. Oceanogr.*, **12**, 464–482.

Lynch, D. R., Ip, J. T. C., Naimie, C. E. and Werner, F. E. (1996) Comprehensive coastal circulation model with application to the Gulf of Maine. *Cont. Shelf Res.*, **16**, 875–906.

Shanks, A. L., Largier, J., Brinkn, L., Brubaker, J. and Hooff, R. (2002) Observations on the distribution of meroplankton during a downwelling event and associated intrusion of the Chesapeake Bay estuarine plume. *J. Plankton Res.*, **24**, 391–416.

Steidinger, K. A. and Haddad, K. (1981) Biologic and hydrographic aspects of red tides. *Bioscience*, **31**, 814–819.

Thayer, P. E., Hurst, J. W., Lewis, C. M., Selvin, R. and Yentsch, C. M. (1983) Distribution of resting cysts of *Gonyaulax tamarensis* var. *excavata* and shellfish toxicity. *Can. J. Fish. Aquat. Sci.*, **40**, 1308–1314.

Townsend, D. W., Pettigrew, N. R. and Thomas, A. C. (2001) Offshore blooms of the red-tide dinoflagellate, *Alexandrium* sp., in the Gulf of Maine. *Cont. Shelf Res.*, **21**, 347–369.

Turner, J. T., Doucette, G. J., Powell, C. L., Kulis, D. M., Keafer, B. A. and Anderson, D. M. (2000) Accumulation of red-tide toxins in larger size fractions of zooplankton assemblages from Massachusetts Bay, USA. *Mar. Ecol. Prog. Ser.*, **203**, 95–107.

Tyler, M. A. and Seliger, H. H. (1978) Annual subsurface transport of a red tide dinoflagellate to its bloom area: water circulation patterns and organism distributions in the Chesapeake Bay. *Limnol. Oceanogr.*, **23**, 227–246.

Walsh, J. J., Haddad, K. D., Dieterle, D. A., Weisberg, R. H., Li, Z., Yang, H., Muller-Karger, F. E., Heil, C. and Bissett, W. P. (2002) A numerical analysis of landfall of the 1979 red tide of *Karenia brevis* along the west coast of Florida. *Cont. Shelf Res.*, **22**, 15–38.

Watras, C. J., Chisholm, S. W. and Anderson, D. M. (1982) Regulation of growth in an estuarine clone of *Gonyaulax tamarensis* lebour: salinity-dependent temperature responses. *J. Exp. Mar. Biol. Ecol.*, **62**, 25–37.

White, A. W. and Lewis, C. M. (1982) Resting cysts of the toxic red-tide dinoflagellate *Gonyaulax excavata* in Bay of Fundy sediments. *Can. J. Fish. Aquat. Sci.*, **39**, 1185–1194.

White, A. W., Fukuhara, O. and Anraku, M. (1989) Mortality of fish larvae from eating toxic dinoflagellates or zooplankton containing dinoflagellate toxins. In Okaichi, T., Anderson, D. M. and Nemoto, T. (eds), *Red Tides: Biology Environmental Science and Toxicology*. Elsevier, New York, pp. 395–398.

Wyatt, T. and Jenkinson, I. R. (1997) Notes on *Alexandrium* population dynamics. *J. Plankton Res.*, **19**, 551–575.

Yamaguchi, M., Itakura, S., Imai, I. and Ishida, Y. (1995) A rapid and precise technique for the enumeration of resting cysts of *Alexandrium* spp. (Dinophyceae) in natural sediments. *Phycologia*, **34**, 207–214.

*Received on June 20, 2002; accepted on May 26, 2003*