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

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Abstract

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 *Alexandrium fundyense* cells germinated from offshore cyst beds. Subsequent downwelling conditions then transport those populations toward 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 in 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). It can lie dormant as a resting cyst in the sediments 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 sediments, the cells swim toward 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 (e.g. 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 (Keafer *et al.*, 1992; Dale *et al.*, 1978; White and Lewis, 1982; Thayer *et al.*, 1983; Anderson and Keafer, 1985), the regional-scale distribution remained obscure until the first systematic survey was undertaken in 1997 (documented herein). 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, 1992ab). 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.

Methods

Cell count data were collected during in 1993 and 1994 as part of the Regional Marine Research Program in the Gulf of Maine, and in 1998 and 2000 as part of the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) Gulf of Maine project. In the former, cells were identified and counted in a Sedgewick-Rafter chamber using a standard light microscope at 100x. In the latter, 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 producing 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 top 1cm of sediment from each core was stored and processed according to methods published by Anderson *et al.* (1996). A primulin-staining method was used to fluorescently label 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 variable horizontal resolution of a 2-4 km and 12 terrainfollowing vertical levels. Vertical mixing is internally generated from the Mellor-Yamada level 2.5 turbulence closure. The model is initialized with climatological temperature and salinity profiles and forced by observed river discharge and winds. Surface heat fluxes are computed from buoy observations using bulk formulae. Barotropic 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 d^{-1} once germinated from resting cysts; swimming speed decreases linearly to zero in the top 10m 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 *Alexandrium fundyense*'s endogenous clock. Vegetative growth is not included, as our objective here is focussed on bloom initiation rather than its development. Simulations using a more complete biological model are being quantitatively evaluated with observations as part of ongoing research.

Results

Alexandrium cysts are present in bottom sediments throughout the entire regional domain that was sampled (Figure 1). However, the highest abundances occur in large Figure 1
deposits offshore, beyond the 75m isobath. The largest peaks in the mapped distribution appear offshore of both Penobscot and Casco Bays. Because of the relatively coarse sampling between these two peaks, it is not clear whether they are truly distinct deposits

or local maxima in a larger deposit spanning the area between Penobscot and Casco Bays.

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 sufficient 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.

Figure 2

The numerical model was used to investigate potential linkages. 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 `http://science.whoi.edu/users/mcgillic/ecohab/plume.html` for animated presentation of the results). Cysts germinate inshore

Figure 3
Figure 4

as well, but their abundance is low relative to the offshore source. Spatio-temporal evolution of the 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 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 toward 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.

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). Figure 5

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 (1992b) retrospective analysis of wind records and shellfish toxicity data, 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 more complete treatment of *Alexandrium*'s population dynamics (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 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 (Stock *et al.*, manuscript in preparation). Nevertheless, the simple model presented here demonstrates a physical-biological interaction that could facilitate a connection between the spatially distinct distributions of 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.*, submitted). Subducted cells subsequently enter the plume through upward swimming. The same could be true for cells subducted by the larger-scale flow of the Eastern Maine Coastal Current (Townsend *et al.*, 2001), as 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 transient wind forcing. Its implications are substantial, in that the processes linking coastal and offshore environments are subtle, complex, and non-linear (Brink and Robinson, 1998; Tyler and Seliger, 1978; Steidinger and Haddad, 1981; Fraga *et al.*, 1988; 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 elucidation of these linkages.

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References

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

Anderson D. (1984) Shellfish toxicity and dormant cysts in toxic dinoflagellate blooms. In: Ragelis E. (ed.) Seafood Toxins. Vol 262 Amer. Chem. Soc Symposium Series , Washington, D.C.

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

Anderson D., Fukuyo Y., Matsuoka K. (1996) Cyst methodologies. In: Hallegraeff G., Anderson D., Cembella A. (eds.) Manual on Harmful Marine Microalgae. UNESCO, Paris.

Anderson D., Keafer B. (1985) Dinoflagellate cyst dynamics in coastal and estuarine waters. In: D. M. Anderson A. W., Baden D. G. (eds.) Toxic Dinoflagellates. Proc. 3rd Int'l. Conf. Elsevier , New York.

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

Anderson D., Keafer B., Churchill J., Signell R., Geyer W. (2000) *Alexandrium* blooms in the western Gulf of Maine. In: Symposium on Harmful Algae in the U.S. Marine Biological Laboratory , Woods Hole, Massachusetts.

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

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

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

Blumberg A., Mellor G. (1987) A description of a three-dimensional coastal model. In: Coastal and Estuarine Sciences. Vol 4 AGU , Washington DC pp 1–16.

Brink K., Robinson A. (eds.) (1998) *The Global Coastal Ocean: Processes and Methods.* Vol 10 of *The Sea* John Wiley and Sons.

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

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

Eilertsen H., Wyatt T. (2000) Phytoplankton models and life history strategies. *South African Journal of Marine Science*, **22**,323–338.

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

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

Franks P., Anderson D. (1992*a*) Alongshore transport of a phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Marine Biology*, **112**,153–164.

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

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

Hetland R., McGillicuddy D., Signell R. (2002) On entrainment of plankton into a buoyant plume: the frog tongue hypothesis Submitted, *Journal of Marine Research.*

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

Lynch D., Ip J., Naimie C., Werner F. (1996) Comprehensive coastal circulation model with application to the Gulf of Maine. *Continental Shelf Research*, **16**,875–906.

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

Stock C., McGillicuddy D., Signell R., Anderson D. (2002) Hindcasting *Alexandrium* spp. blooms in the western Gulf of Maine using a coupled physical/biological model. Manuscript in preparation.

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

Townsend D., Pettigrew N., Thomas A. (2001) Offshore blooms of the red tide dinoflagellate, *Alexandrium* sp., in the Gulf of Maine. *Continental Shelf Research*, **21**,347–369.

Turner J., Doucette G., Powell C., Kulis D., Keafer B., Anderson D. (2000) Accumulation of red tide toxins in larger size fractions of zooplankton assemblages from Massachusetts Bay, USA. *Marine Ecology - Progress Series*, **203**,95–107.

Tyler M., Seliger 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., Haddad K., Dieterle D., Weisberg R., Li Z., Yang H., Muller-Karger F., Heil C., Bissett W. (2002) A numerical analysis of landfall of the 1979 red tide of *Karenia brevis* along the west coast of Florida. *Continental Shelf Research*, **22**,15–38.

Watras C., Chisholm S., Anderson D. (1982) Regulation of growth in an estuarine clone of *Gonyaulax tamarensis* lebour: salinity-dependent temperature responses. *Journal of Experimental Marine Biology and Ecology*, **62**,25–37.

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

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

Wyatt T., Jenkinson I. (1997) Notes on *Alexandrium* population dynamics. *Journal of Plankton Research*, **19**,551–575.

Yamaguchi M., Itakura S., Imai I., 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.

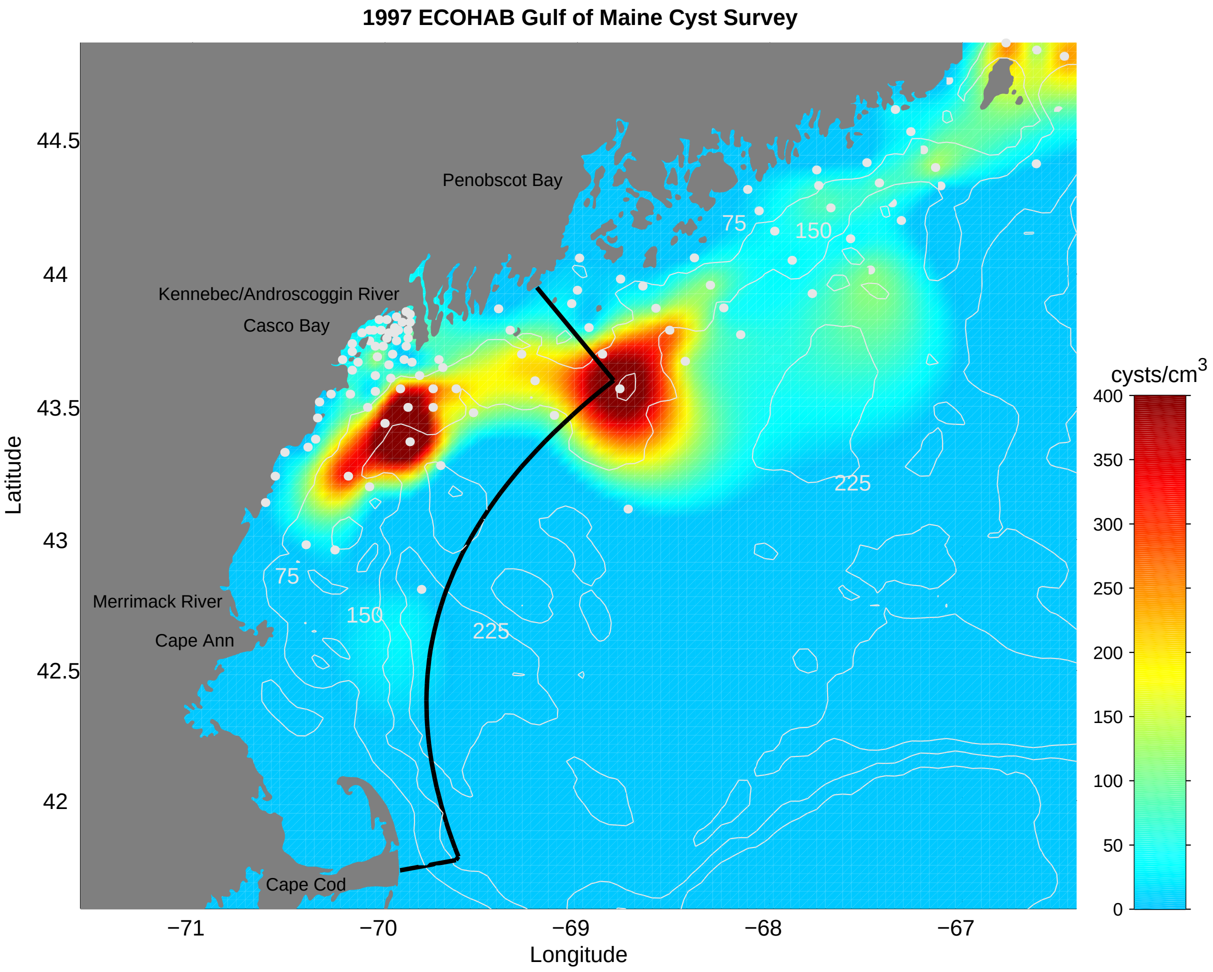
Figure 1: Distribution of *Alexandrium* cysts in the upper 1cm of bottom sediments in the Gulf of Maine, derived from a survey in October 1997. Sampling stations are indicated by white dots, and the 75m, 150m, and 225m bathymetric contours are overlayed. The offshore boundary of the model domain used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

Figure 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 $S = 30.45$ppt 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.

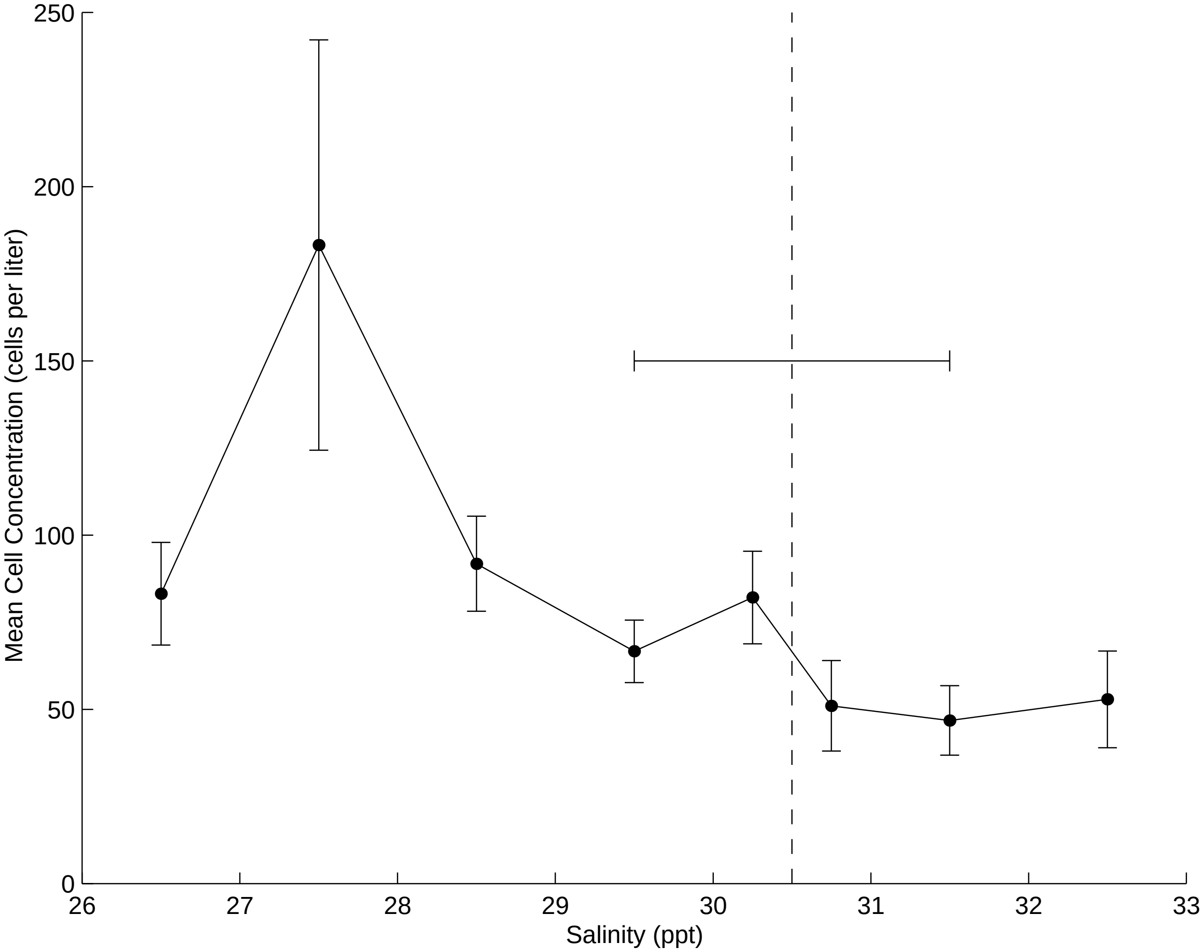
Figure 3: Upper two panels: time series of river discharge and winds used to force the model. Thick horizontal bars indicate time periods of upwelling-favorable (southwesterly) and downwelling-favorable (northeasterly) winds. Bottom panel: mean cell concentrations in various salinity intervals diagnosed 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 75m are included in order to highlight the mechanism by which offshore cells are entrained in the plume.

Figure 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).

Figure 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 thickens, thereby exposing the coast to cell populations that originated offshore.



McGillicuddy *et al.* Figure 1.



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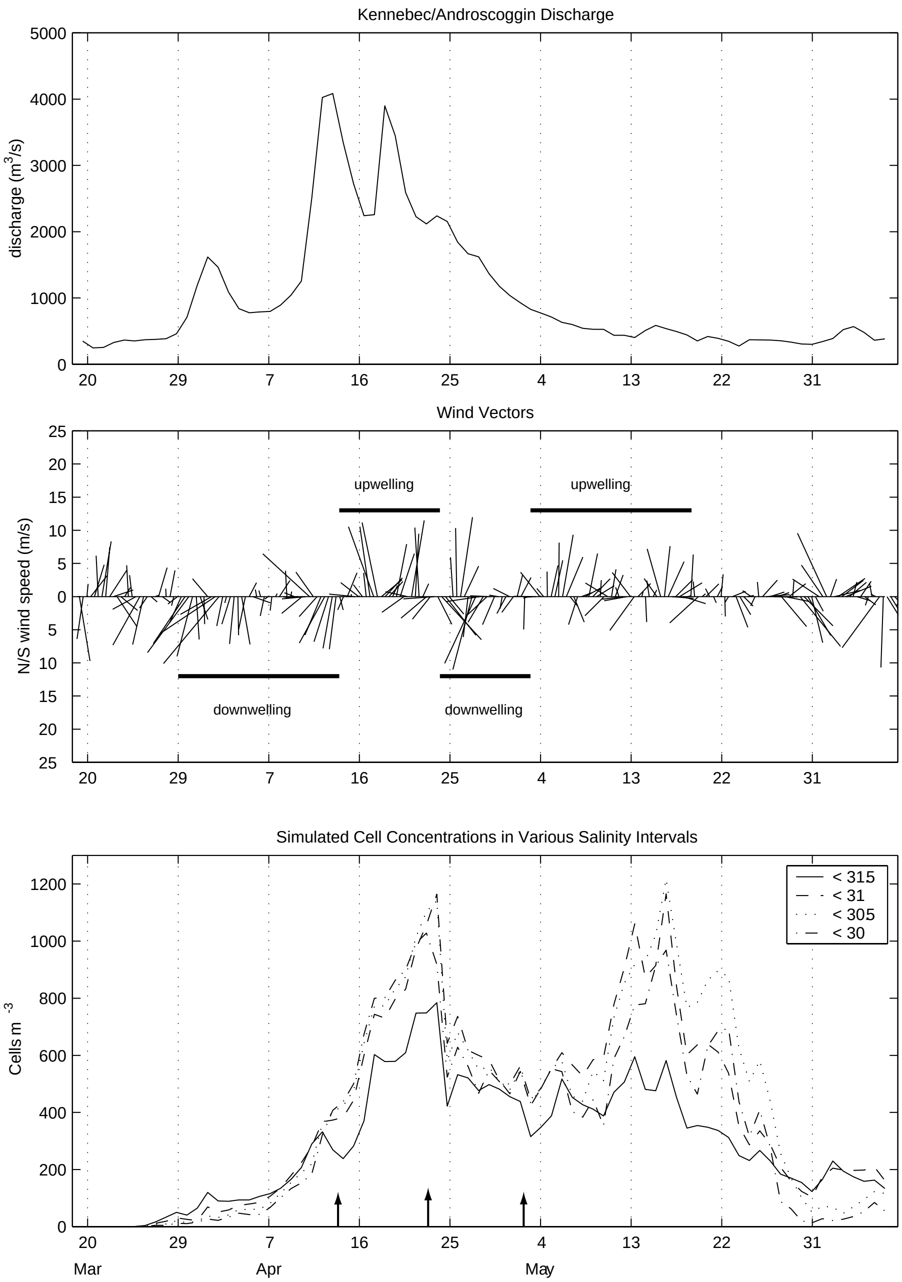

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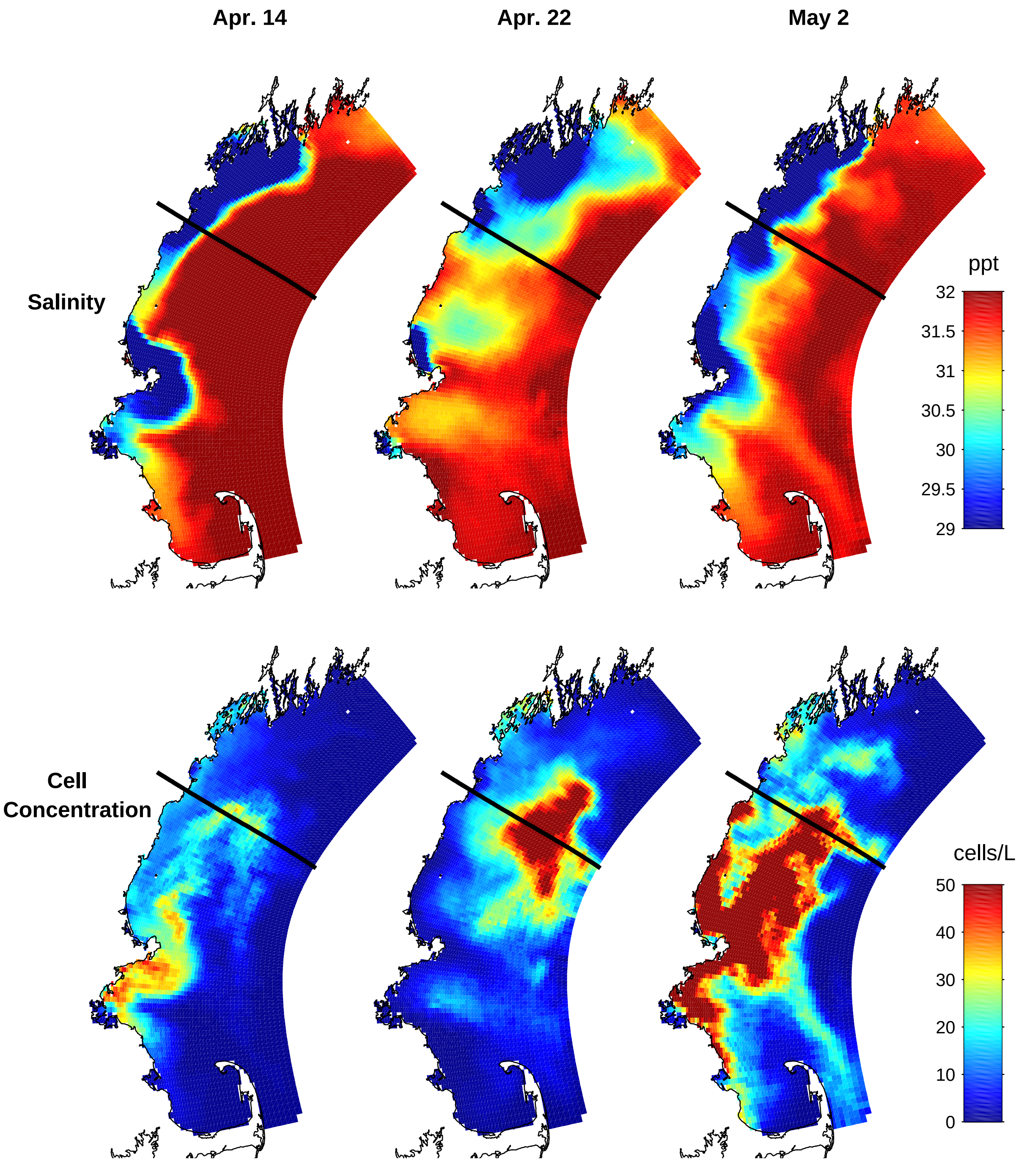

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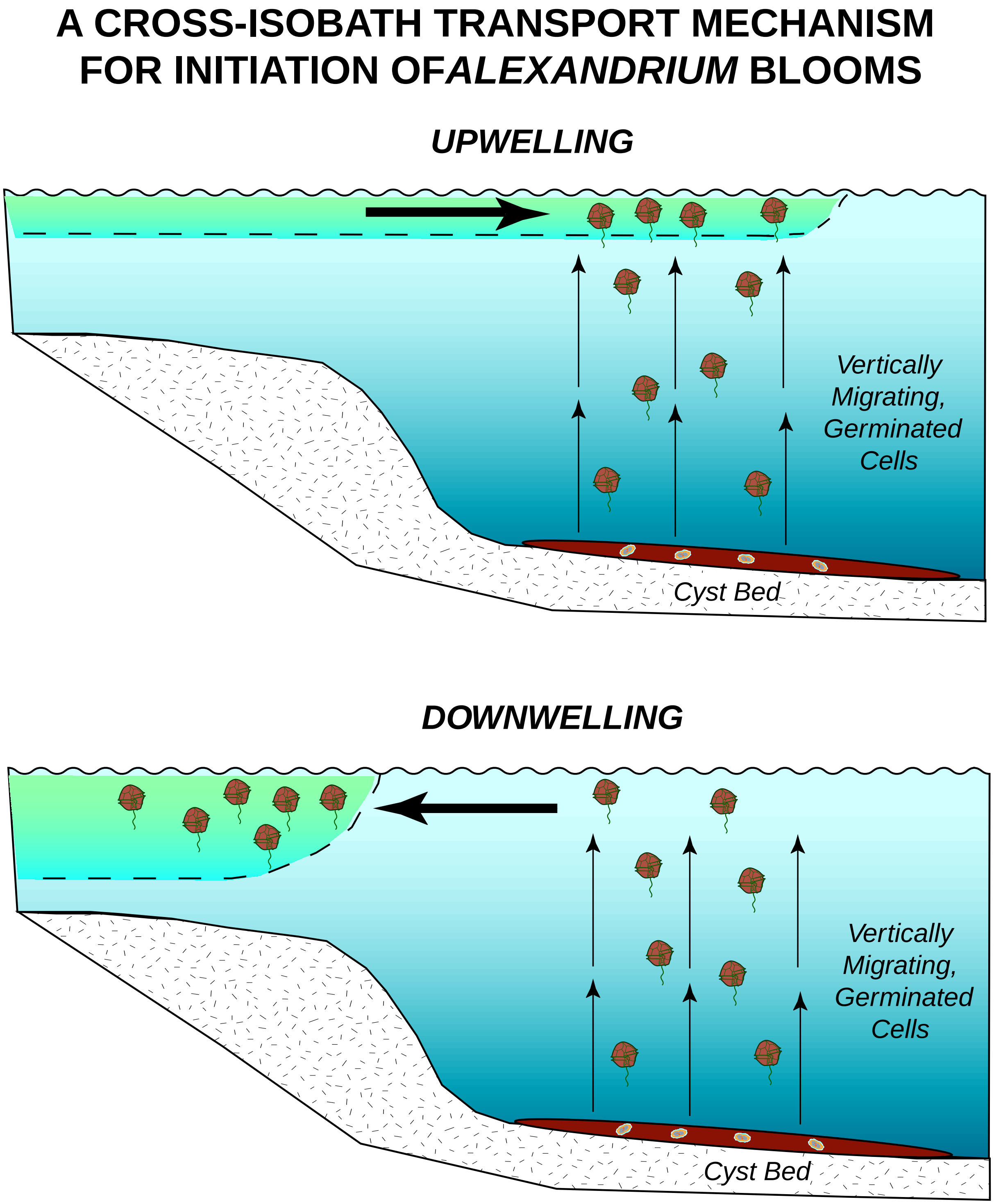

McGillicuddy *et al.* Figure 5.