Hindcasting Blooms of the Toxic Dinoflagellate *Alexandrium* spp. in the Western Gulf of Maine

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Abstract

Three-dimensional coupled physical-biological models have been developed to facilitate forecasting regional Alexandrium *distributions in the Gulf of Maine. The hydrodynamic basis is a primitive equation model with advanced turbulence closure; it is forced by tides, winds, heat fluxes, and river discharge. Explicitly modeled aspects of* Alexandrium *population dynamics include germination from resting cysts, vegetative growth, and mortality.*

Quantitative evaluation of model skill in a hindcast mode indicates the model is capable of simulating the observed large-scale patterns in Alexandrium *abundance to within a factor of two to three. Sensitivity analysis suggests uncertainties in loss terms (such as respiration, predation and encystment) may be the most critical limitation of the coupled model in its present form.*

Future developments may yield a predictive model with skill sufficient to produce meaningful ecological forecasts. However, the need for both physical and biological data streams to drive the models must not be underestimated. An integrated observational and modeling strategy will be essential in the context of ecological forecasting.

Introduction

Toxic or harmful algal blooms (HABs) are a serious economic and public health problem throughout the US and the world. 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* (see review by Anderson 1997). These organisms are responsible for human illnesses and occasional death due to PSP, repeated closures of shellfish beds in both nearshore and offshore waters, the mortality of larval and juvenile stages of fish and other marine animals (White *et al.* 1989), and even the death of marine mammals such as humpback whales (Geraci *et al.* 1989).

Accurate forecasts of *Alexandrium* blooms in this region would therefore have important application, including the management of shellfish and finfish resources, aquaculture siting, and effluent discharge. Furthermore, there are a multitude of coastal zone management issues that could use the hydrodynamic forecasts on which ecological predictions of *Alexandrium* would be based.

Case Study

Within the western Gulf of Maine (GOM) region, which extends from Penobscot Bay to Massachusetts Bay, a coupling has been inferred between the abundance and distribution of *Alexandrium* and a buoyant coastal current that travels from northeast to southwest. A conceptual model of this link has been proposed, known as the River Plume Advection Hypothesis (Franks and Anderson 1992a,b).

Critical features of this system include: 1) a source population of cells located to the north of Massachusetts Bay near the Androscoggin-Kennebec estuary; 2) freshwater outflow from the Androscoggin-Kennebec estuary resulting in a coastally-trapped, buoyant plume that supports the growth of *Alexandrium* cells and transports them to the south and west; and 3) plume

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behavior, as influenced by the volume of freshwater outflow, the local wind stress, and underlying GOM circulation. All of these combine to regulate the alongshore and cross-shore location of the plume, its associated cells, and PSP toxicity.

As part of Ecology and Oceanography of Harmful Algal Blooms-Gulf of Maine (ECOHAB-GOM) and its predecessor programs, a set of numerical models has been developed to study these dynamics in a three-dimensional context. Thus far, these coupled physical/biological models have been used only for research purposes. Quantitative demonstration of predictive skill in a hindcast mode is a necessary precursor to an operational model. The following example describes recent efforts to assess the hindcast skill of one model.

Modeled Inputs (T, S)	Bi-monthly climatological model with tides (Lynch *et al.* 1996)
Cruise data (T, S)	Upstream sections and offshore stations
River Discharge	USGS gauges at 4 major rivers
Wind stress	Uniform distribution derived from Portland Buoy
Surface heat flux	Derived from temperature at Portland Buoy
Insolation	From land-based sensors at Woods Hole

Table 1. *Data sets used to force the circulation model.*

The hydrodynamic basis of the following coupled physical/biological simulations is the Princeton Ocean Model (POM; Blumberg and Mellor 1987) with variable horizontal resolution of 2-4 km and 12 vertical levels. Vertical mixing is internally generated from the Mellor-Yamada 2.5 turbulence closure model. This physical model is forced by various modeled inputs as well as land-based and shipboard observations (Table 1). A population dynamics model for *Alexandrium* has been incorporated into this physical framework.

Alexandrium has a very complex life cycle (Figure 1). It can lie dormant as a resting cyst in the sediments for very long time periods, perhaps a decade or more (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, maximum growth occurs only within a specific range of temperature and salinity. 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.

The model for *Alexandrium* is summarized in Figure 2. The ecosystem in which *Alexandrium* resides is not explicitly modeled; ecosystem effects are parameterized through their influence on the vital rates of *Alexandrium*'s population dynamics processes. The top panels show the various factors that contribute to the input of cells due to germination. On the far left is the observed distribution of cysts, showing the peak offshore of Casco Bay. In the middle is the functional fit to laboratory data on the endogenous clock, shown as open circles. On the right is the germination rate as a function of light and temperature, based on the

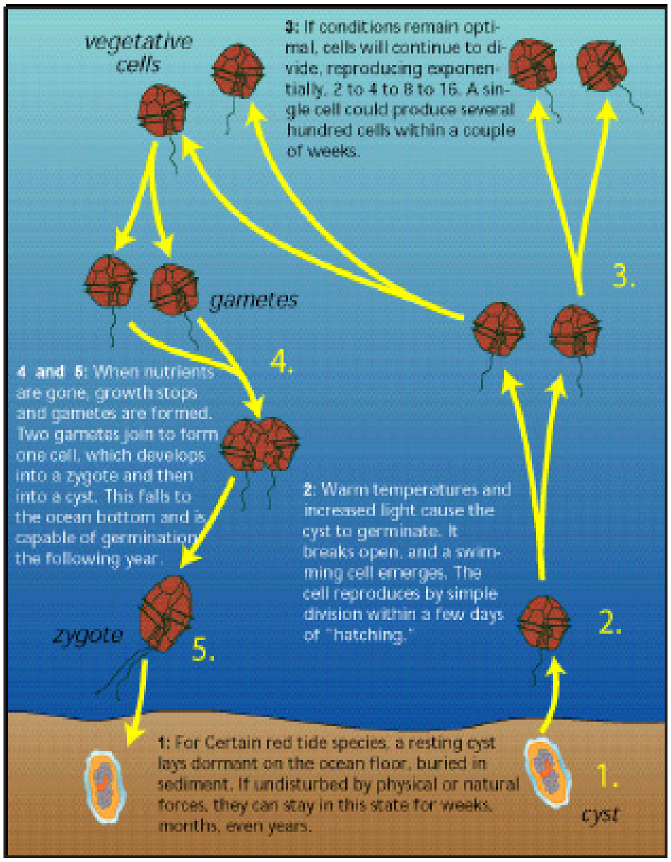

Figure 1*: Life cycle of* Alexandrium.

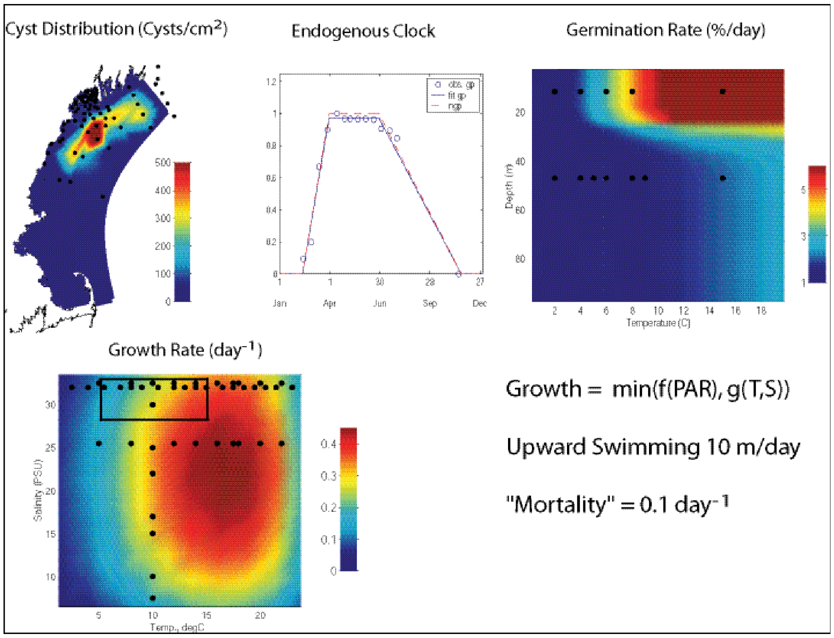

***Figure 2**: Population dynamics model for* Alexandrium.

laboratory measurements (indicated by black dots). The vertical axis actually represents light intensity but has been scaled to depth.

The function describing vegetative growth is based on data from Watras *et al.* (1982). It suggests that *Alexandrium* has a preferred temperature and salinity range for optimal growth. The range of temperature and salinity conditions that *Alexandrium* cells encounter in the simulations described here is indicated by the black rectangle. The overall growth rate is based on this function and is modulated by the ambient light field as per Liebig's law of the minimum (Liebig 1845). In other words, at each time step, the lesser of the two growth rates predicted by the temperature/salinity and light-limitation functions is specified. Initial experiments with simple representations of nutrient limitation have been started, but these effects are not included here. An upward swimming rate of 10m/day and a net 'mortality' of 0.1 per day are specified. Mortality is in quotes here because it represents the net effect of all loss processes, which include predation and encystment.

This coupled model has been used to hindcast a data set collected in the Western Gulf of Maine in 1993 as part of the Regional Marine Research Program (RMRP). An example snapshot from a hindcast simulation is shown in Figure 3; the entire simulation is available in animated form on the web site (RMRP 2002). The salinity field shows the impact of fresh water plumes originating at the Kennebec/Androscoggin and Merrimack rivers. These tend to propagate down the coast, and also undergo significant cross-shore displacements due to the effects of upwelling and downwelling winds. This particular simulation suggests offshore initiation of the bloom because the impact of the germination input from the offshore maximum in the cyst distribution is clearly evident. Features in the cell distribution are advected downstream in the coastal current, and are also clearly impacted by wind-driven upwelling and downwelling.

Quantitative evaluation of hindcast accuracy requires careful consideration of how the model results should be compared with observations. One might think this issue is as simple as subsampling the model solutions at the space/time points at which data are available. However, such an approach is problematic because the observations contain small-scale patchiness not resolved in the model. Plots of autocorrelation functions for both simulated and observed fields bear this out. Thus, it is necessary to average both the model results and the observations on scales resolved by both.

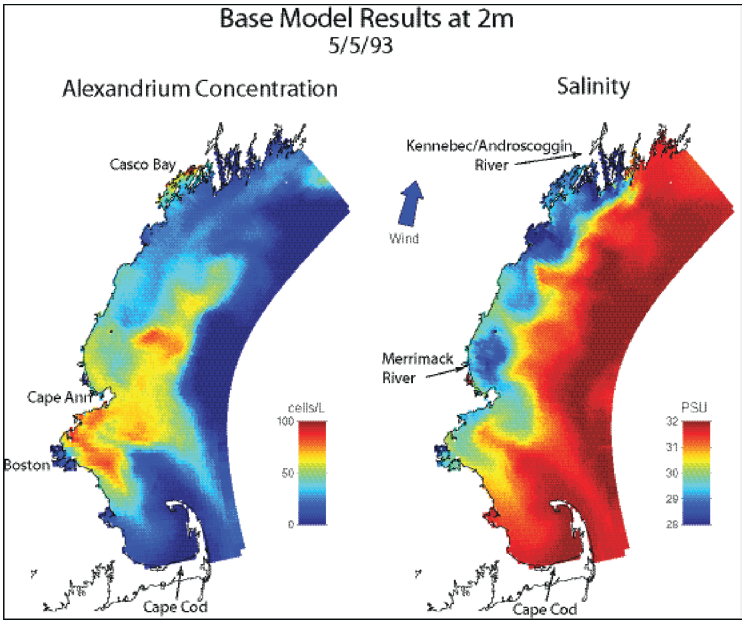

***Figure 3**: Example snapshot of model output.*

Therefore, nine zones in which the mean values of the simulated and observed concentrations are defined and compared for each cruise (Figure 4). An error metric J quantifies the degree to which the simulated means (sim) match the observed means (obs) for each zone during each cruise: $J = \max(\text{sim},\text{obs})/\min(\text{sim},\text{obs})$. A perfect fit would result in a value of 1.0. This penalty function grows larger as the simulation diverges from the observations. A variety of error metrics is possible, and all have various advantages and disadvantages. One appealing aspect of this particular metric is that errors at low concentrations are weighted just as heavily as those at high concentrations. In summary, this approach yields a quantitative method of evaluating the large-scale spatial distribution, timing, and magnitude of the bloom.

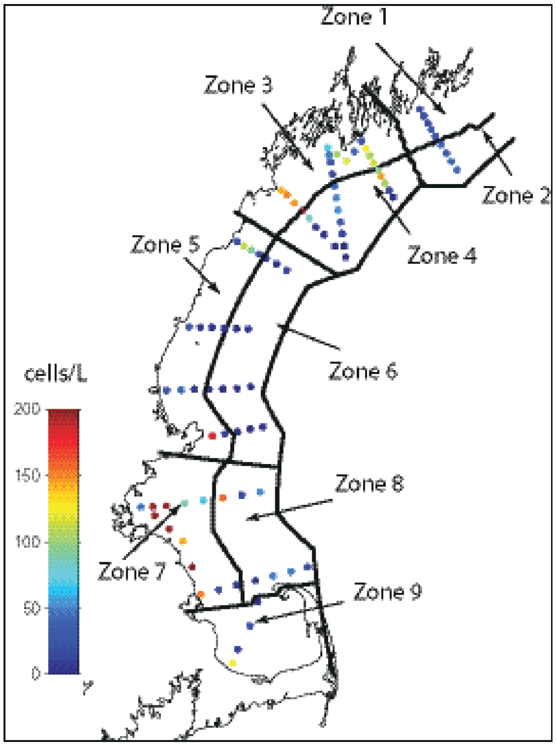

***Figure 4**: Typical observational coverage during one cruise. Colored dots represent observations of* Alexandrium fundyense *concentration (cells per liter). The nine zones chosen for model evaluation are indicated.*

There is yet another issue confounding the evaluating the skill of the model predictions: the simulations are sensitive to model parameters that are not completely known. Therefore, the adjustable parameters are tuned within their envelope of reasonable values, a manual procedure for parameter estimation. More sophisticated estimation procedures have been used in the context of zero- and one-dimensional models (e.g., Vezina and Platt 1988, Fasham and Evans 1995, Hurtt and Armstrong 1996, Friedrichs and Hofmann 2001), and will be pursued in the future. At present, the computational demands of those approaches make them impractical for the three-dimensional system of interest here.

Quantitative evaluation of hindcast skill facilitates testing hypotheses concerning bloom controls by ascertaining whether one model structure fits the data significantly better than another. As an example, we compare the results of two different simulations: one without grazing of *Alexandrium*, and one that includes a spatially uniform loss term of 0.1 per day (Figure 5). Each of the four panels shows the space/time distribution of the error metric. Time runs along the 'cruise' axis with cruises 1-5 in April to June. Space runs along the 'zone' axis, with zones 1-9 corresponding to those indicated in Figure 6. The zones have been separated into inshore and offshore groups. The height of the vertical bars indicates the magnitude of the error metric, with low model values in blue and high model values in red.

In the simulation that does not include mortality, cell concentration is systematically over-predicted late in the run in the southern portion of the domain. The average value of the error metric is 3, so on average the predicted values are within a factor of three of the observations. Explicit treatment of loss processes via a uniform loss rate of 0.1 per day improves the simulations dramatically, reducing the large errors late in the run in the southern portion of the domain. The error metric drops to an average of 2.33, so the predictions are now within a factor of two of the observations.

The conclusion is that a loss term (which may represent some combination of predation and encystment) plays a key role in controlling the development and termination of the bloom. One important caveat is the circulation fields are assumed to be correct; the possibility that mismatches between the simulated and observed concentrations of *Alexandrium* could be a result of unknown deficiencies in the modeled circulation cannot be excluded. Future research will formulate measures of misfit for the physical fields as well as the biological fields.

Lessons Learned

The hindcasts of the 1993 RMRP data do not rely on data assimilation to keep the circulation fields on track. The rationale for adopting a purely 'forward' modeling approach hinged on the fact the circulation in this relatively small region is largely controlled by riverine buoyancy inputs and wind-forced dynamics. Such is

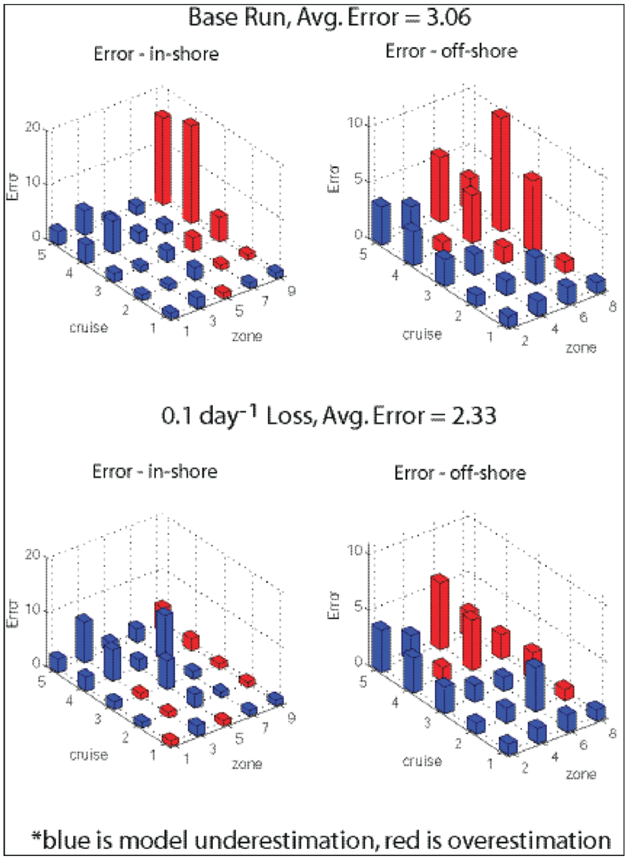

***Figure 5**. Quantitative evaluation of hindcasts based on two different biological formulations (see text).*

clearly not the case in larger domains where a wide variety of other processes influence the circulation.

Results from the ECOHAB-GOM program have shown the dynamics of *Alexandrium* blooms are regional in scope, spanning the waters from the Bay of Fundy down into Massachusetts and Cape Cod Bays (Anderson *et al*. 2000; Townsend *et al*. 2001). Thus, a gulf-wide modeling approach will be necessary in an operational context. Given the complex hydrodynamics characteristic of this large regional domain, data assimilation will be an essential element of skillful prediction.

An operational system based on a data-assimilative model implies an observational network to drive it. Design of such a network would be facilitated by Observational System Simulation Experiments (OSSEs; see Robinson *et al*. 1998; McGillicuddy *et al*. 2001). The idea is model simulations can serve as a space/time continuous representation of reality, which is then subsampled in a specified fashion to produce a simulated data set. The simulated data are then fed into an analysis scheme in which they are synthesized into a reconstruction of 'reality.' Direct comparison of the reconstructed field with the 'truth' as defined by the original simulation provides a quantitative evaluation of that particular sampling strategy.

In summary, *meaningful ecological forecasts of this system will require accurate real-time data streams together with advanced data assimilation techniques*.

Conclusion/Next Steps

Coupled physical-biological models of *Alexandrium* in the Gulf of Maine have matured to the point that it is now feasible to assess their operational suitability and potential value. A strategy for this could consist of three main elements: 1) thorough evaluation of the predictive skill in a hindcast model using data from ECOHAB-GOM and its predecessor programs; 2) improvement of the models from what is learned in that evaluation; and 3) formulation of a plan for transition of the models to operational use. The second item implies the dynamics of *Alexandrium* blooms are not fully understood, thus additional research is needed on the underlying physical/biological interactions that control these blooms.

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. Amer. Chem. Soc Symposium Series No. 262 Washington D.C.

Anderson, D.M. 1997. Bloom dynamics of toxic *Alexandrium* species in the northeastern US. Limnol. and Oceanog. 42:1009-1022.

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

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

Anderson, D.M., C.D. Taylor and E.V. Armburst. 1987. The effects of darkness and anaerobiosis on dinoflagellate cyst germination. Limnol. and Oceanogr. 32(2):340-351.

Anderson, D.M., B.A. Keafer, J.H. Churchill, R. P. Signell, and W.R. Geyer. 2000. *Alexandrium* blooms in the western Gulf of Maine. Symposium on Harmful Algae in the US. Dec 4-9, 2000. Marine Biological Laboratory, Woods Hole, Massachusetts. Abstract.

Blumberg, A.F. and G.L. Mellor. 1987. A description of a three-dimensional coastal model. Coastal and Estuarine Sciences, Volume 4, pp 1-16. American Geophysical Union, Washington, DC.

Fasham, M.J.R. and G.T. Evans. 1995. The use of optimization techniques to model marine ecosystem dynamics at the JGOFS station at 47N 20W. Phil. Trans. R. Soc. Lond. B 348:203-209.

Franks, P.J.S. and D.M. Anderson. 1992a. Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. Marine Biology 112:153-164.

Franks, P.J.S. and D.M. Anderson. 1992b. Toxic phytoplankton blooms in the southwestern Gulf of Maine: testing hypotheses of physical control using historical data. Marine Biology 112:165-174.

Friedrichs, M.A.M. and E.E. Hofmann. 2001. Physical control of biological processes in the central equatorial Pacific Ocean. Deep-Sea Research 48: 1023-1069.

Geraci, J.A., D.M. Anderson, R.J. Timperi, D.J. St. Aubin, G.A. Early, J.A. Prescott and C.A. Mayo. 1989. Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin. Canadian J. of Fisheries and Aquatic Sciences 46:1895-1898.

Hurtt, G.C. and R.A. Armstrong. 1996. A pelagic ecosystem model calibrated with BATS data. Deep-Sea Research 43:653-683.

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

Liebig, J. 1845. On chemical processes in the nutrition of vegetables. *In*: Chemistry and its applications to agriculture and physiology. L. Playfair, Peterson, PA.

Lynch, D.R., Ip, J.T.C., Naimie, C.E. and F.E. Werner. 1996. Comprehensive coastal circulation model with application to the Gulf of Maine. Continental Shelf Research 16, pp. 875-906.

McGillicuddy, D.J., D.R. Lynch, P. Wiebe, J.Runge, E.G. Durbin, W.C. Gentleman, and C.S. Davis. 2001. Evaluating the synopticity of the US Globec Georges Bank Broad-scale sampling pattern with Observational System Simulation Experiments. Deep-Sea Research II 48:483-499.

RMRP. 2002. http://science.whoi.edu/users/mcgillic/ecohab/movies/base.avi

Robinson, A., P. Lermusiaux, and N. Sloan. 1998. Data assimilation. The Sea 10:541-594.

Townsend, D.W., N.R. Pettigrew, and A.C. Thomas. 2001. Offshore blooms of the red tide organism, *Alexandrium* sp., in the Gulf of Maine. Continental Shelf Research 21:347-369.

Vezina, A.F. and T. Platt. 1988. Food web dynamics in the ocean. I. Best-estimates of flow networks using inverse methods. Marine Ecology Progress Series 42:269-287.

Watras, C.J., S.W. Chisholm, and D.M Anderson. 1982. Regulation of growth in an estuarine clone of *Gonyaulax tamarensis* Lebour: salinity-dependent temperature responses. Journal of Experimental Maine Biology and Ecology 62:25-37.

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