HARMFUL ALGAL BLOOMS IN STRATIFIED ENVIRONMENTS

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Successful management of the coastal environment requires sound knowledge of the biological, chemical, and physical processes governing the growth, retention, dispersion, and transport of water constituents, including plankton. The growing problem posed by the existence of harmful plankton species now demands a thorough understanding of the life histories and population dynamics of these organisms. Without this knowledge, managers can neither assess the impact of anthropogenic activity on the environment and biota, nor understand the relationship between harmful phytoplankton species and the harmful events (commonly referred to as harmful algal blooms [HABs]) caused by them, and climate. Without this understanding, the desirable goals of prediction and mitigation of harmful events are unattainable. A major challenge is to understand the processes governing the population dynamics to a level of detail that allows mathematical formulations that are relatively simple, yet reproduce the salient features of HAB population dynamics.

A feature common to many oceanic harmful algal events is that the phytoplankton populations, composed mainly of dinoflagellates, build up to their highest concentrations in subsurface layers (Figure 1). These layers are usually associated with water-column stratification (Figure 2). Stratified water is encountered in upwelling systems, coastal embayments, and estuaries as well as in retentive zones, such as gyres, in the open seas. The temporal scales (days to weeks) and spatial scales (decimeters to meters in thickness) of subsurface layers pose problems for sampling, understanding, and subsequent modeling of harmful populations (Figure 1). Coupling physical effects such as turbulence, shear, and advection with biological behavior (migration, physiological adaptation) holds the key to understanding vertical distributions, bloom dynamics, and patterns of toxicity. Some of these physical processes are not yet defined at the appropriate scale, yet may be crucial in the formation of harmful blooms. Furthermore, models have thus far been restricted by our inability to gauge the interactions between the biology of algal taxa and underlying physical processes. We describe here the major features of blooms in subsurface layers, considering the biological response to upper-mixed-layer dynamics, and the population dynamics of blooms.

Typical assemblage collected in the pycnocline (Killary Harbour, Ireland) composed of *Ceratium lineatum*, *Protoperidinium depressum*, *Protoperidinium stenii*, and one cell of *Dinophysis acuminata*. Note an empty theca of *C. lineatum* and a frustule of a pennate diatom.
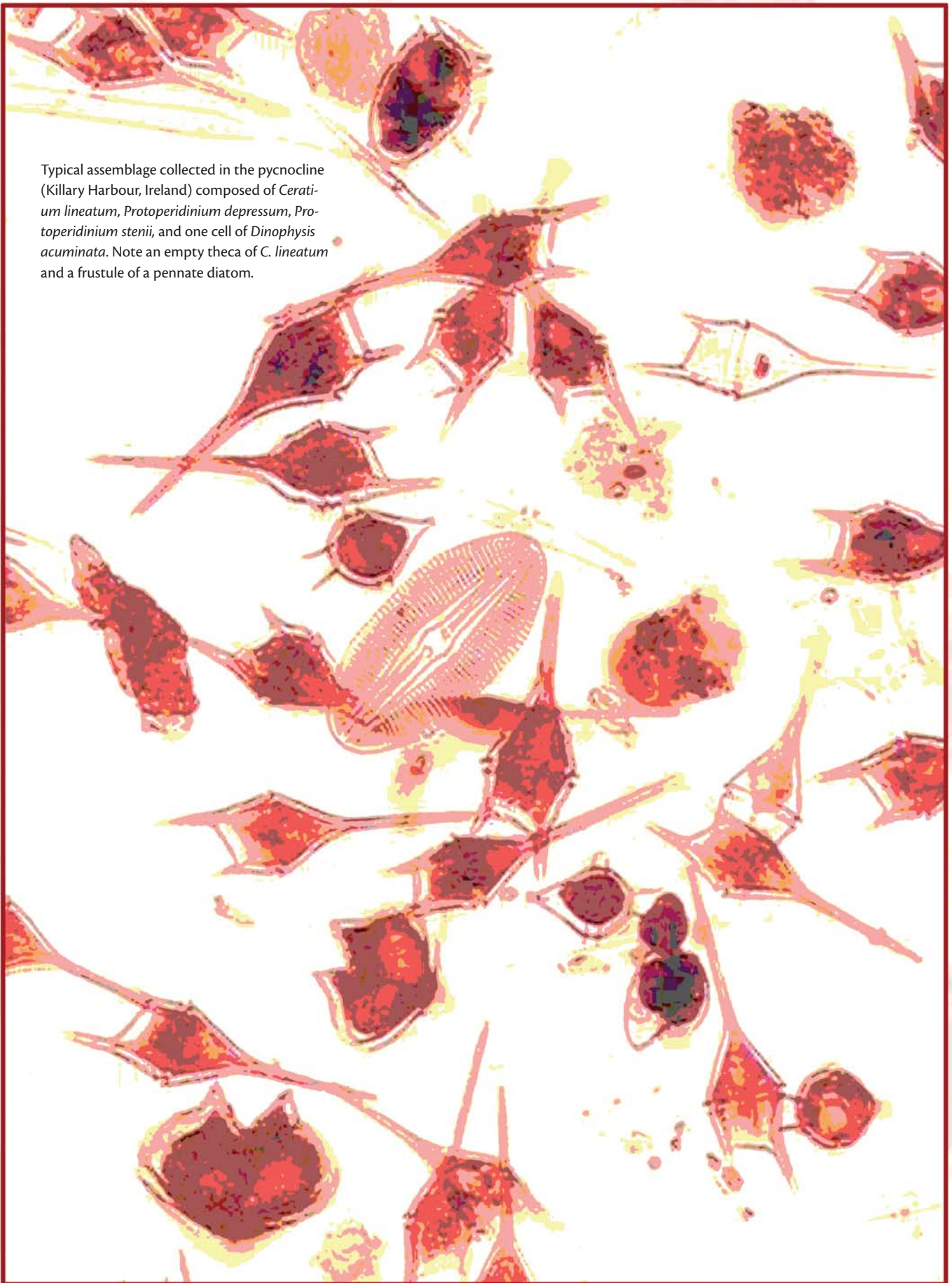
UPPER OCEAN STRATIFICATION AND MIXED-LAYER DYNAMICS

The term "mixed layer" is often applied to the thin band of water, some tens of meters thick, that extends from the ocean's surface to the thermocline. The mixed layer is the boundary layer between the atmosphere and the deep ocean, and results from the balance between heating from solar radiation and surface cooling. Winds help mix the heat through the layer by generating waves, inducing Langmuir circulation, producing convection, initiating near-inertial frequency motions, and generating turbulence. In the coastal ocean, freshwater runoff from the land contributes directly to the upper layer, and in the shallow parts of the coastal ocean, tidal energy can contribute to mixing in the upper layer. The mixed layer therefore represents an integration of the variations in buoyancy and mixing energy with time.

The formation of a surface mixed layer has pronounced effects on planktonic organisms' environment. Foremost amongst these is promotion of the diatom spring bloom in temperate climates. In winter, the mixed layer deepens due to increased winds and net surface cooling, entraining water from below that had been isolated from surface processes during the summer. Entrainment and deepening of the mixed layer usually peak several months after the winter solstice. During the spring, however, buoyancy input during daytime solar heating overrides the turbulent mixing tendencies from wind and surface cooling. Phytoplankton are, therefore, maintained in the surface layer and respond to the favorable light and nutrient environment by blooming.

The spring bloom has huge consequences on primary production, triggering the annual life cycles of many organisms in the sea. In addition, continued heating of the surface mixed layer through summer renders the water column increasingly stable, yet has the additional consequence of preventing the mixing of nutrients from below. Therefore, nutrients in the surface mixed layer are exhausted during early summer. These warm, nutrient-depleted conditions are ideal for the proliferation of flagellates, including dinoflagellates. As many HAB species are dinoflagellates, it is during temperate-climate summers such as those of northwestern Europe, that many HAB events occur. The annual cycle closes by cooling during autumn.

Hidden within this rather simplistic description of seasonal cycles are many processes that occur over much shorter

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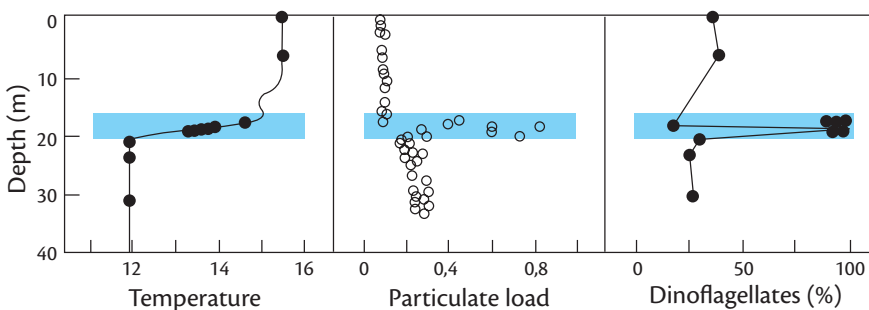
Figure 1. Vertical distribution of temperature (degrees C), particulate total volume (relative unit), and fractional cell concentration of dinoflagellates (percent) off the "Pertuis d'Antioche," France (simplified and redrawn from Gentien et al., [1995]). In this example, *Dinophysis acuminata* formed as part of the dinoflagellate assemblage in the pycnocline, but was absent elsewhere in the water column. The distribution of this dinoflagellate was associated with an increase in organic aggregates.
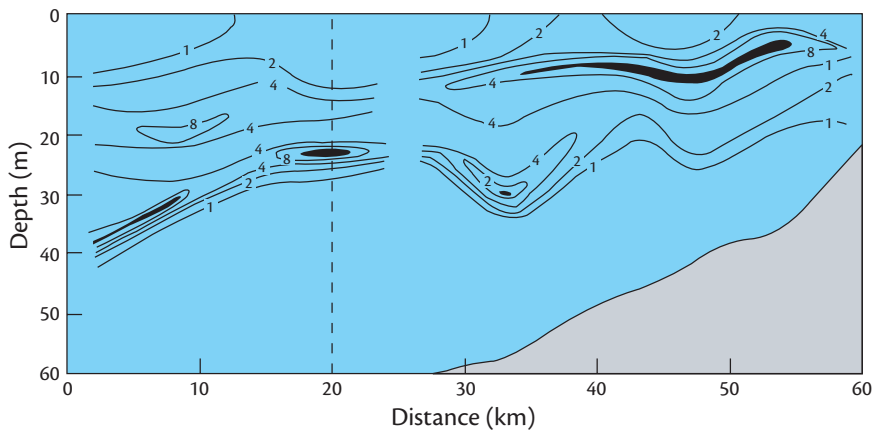
Figure 2. Chlorophyll fluorescence (relative units) along a transect in Bantry Bay (SW Ireland). Shaded areas represent values greater than 10. The major species in the assemblage was *Karenia mikimotoi* (alias *Gyrodinium aureolum*). Redrawn and modified from Raine et al. (1993).

temporal or spatial scales. For example, a daily cycle can be observed during the onset of stratification in spring. A weak, shallow mixed layer is formed during the day, which is destroyed each evening by convective mixing due to nighttime radiative cooling. Physically, the seasonal mixed layer therefore develops earlier as buoyancy is efficiently ventilated downwards; consequently, the summer sea surface maximum temperature is greater, and the spring bloom develops earlier, than if there were no diurnal cycle in the heat input to the surface ocean. The increasing biomass in shallow layers also leads to shallower absorption of short-wave radiation and hence warming of a thinner layer of surface water, which then leads to further stratification.

Punctuating these regular cycles are episodic events, usually on time scales

of hours to days. Formation of the seasonal thermocline in spring is not a gradual, monotonic process, but rather a series of low-wind heating periods alternating with mixing events caused by stronger winds associated with the passage of storms. It is important to note

that these time scales closely match the dominant scales of growth and behavior of phytoplankton and zooplankton. In

the permanently stratified subtropical gyres, episodic entrainment of nutrients into the mixed layer associated with evolving mesoscale eddies can stimulate phytoplankton blooms and subsequent grazing and growth events within the zooplankton. In a similar fashion to its creation in spring, erosion of the seasonal thermocline in autumn is episodic or discontinuous with sharp deepening events often caused by simultaneous high winds and convective heat loss at the sea surface.

POPULATION DYNAMICS

Each phytoplankton species has a different combination of characteristics that defines its ecological niche and determines its distribution and behavior. The challenge is to define unique adaptations of individual HAB species that account for its survival and persistence, and in some instances its dominance, during bloom events. By understanding their adaptations, it should be possible to describe and predict patterns of species abundance as a function of

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hydrographic processes, nutrient distributions, and community interactions, preferably by the use of models in an

operational mode.

Box 1 shows an equation for the evolution of the local number of organisms per unit volume. When considering a particular HAB species within its community, there is a set of state variables, C_i, corresponding to the concentration of a species, and a corresponding set of equations governing many direct and coupled biological, chemical, and physical processes. Environmental conditions and processes affect population dynamics in several of the terms of this equation, but coupled processes cover a broad range of temporal and spatial scales, with many non-linearities. In other words, one cannot deduce the behavior of the system by considering the effect of one parameter in isolation. For example, our understanding of underwater irradiance and the relationship between photosynthesis and irradiance has made the light-controlled growth of phytoplankton highly amenable to simple modeling. Yet, the interaction between the light environment and a species that is able to vertically migrate, or the decoupling between photosynthesis and growth, has shown the approach to be too simplistic. Similarly, the use of nutrients in predicting growth should be used with caution as some HAB populations rely solely on ammonium fluxes from the pycnocline (Le Corre et al., 1993) while they are usually grown *in vitro* on nitrate.

BOX 1: THE GENERIC EQUATION

A robust mathematical equation for the local number of organisms per unit volume can be written in the following form:

$$\frac{\partial C}{\partial t} = \mu C - mC - \nabla.(C\bar{v}) - \nabla.(C\bar{u})$$

$\dfrac{\partial C}{\partial t}$ is the time rate of change of the state variable C, the number of cells of a particular HAB species per unit volume. Population dynamics is defined as the change of C in space and time.

μC represents growth by cell division. The growth rate is determined by intrinsic genetic factors, and modulated by environmental factors, such as nutritional and light history, turbulence, temperature, and salinity.

mC is the direct loss of organisms through mortality. This term includes processes such as grazing, mechanical damage, and death from infections by viruses or other pathogens.

$\nabla.(C\bar{u})$ includes the three-dimensional, time-variable transport of cells by the water flow, for example, mean circulation, tidal currents, wind drift, and turbulence (often identified as turbulent diffusion). "Disappearance" of blooms due to offshore flow would appear in this term.

$\nabla.(C\bar{v})$ is the motion of organisms relative to the water, described as velocity, $\bar{v}$. This term includes swimming, sinking, or rising due to buoyancy and slippage relative to the local flow that arises for a variety of reasons such as size, tropism, and shape (Donaghay and Osborn, 1997).

Many models are based on the physiological characteristics of a single species considered in isolation. These models then attempt to predict its presence and abundance based on some knowledge of environmental conditions. For example, models of species' behavior have focused

Density stratification forces motions in a predominantly horizontal fashion. The vertical variation in this horizontal flow, called shear, converts distributions of any property, including the plankton, into sharp, vertical gradients. Physical oceanographers call such meter-scale

a vertical profile of horizontal velocity at a comparable resolution to the vertical scale of thin layers and fine structure. This measurement must be taken in conjunction with the variation in horizontal and vertical distributions of biological, chemical, and physical fields.

Transport

In order for a population to build up locally to significant cell densities, growth terms must exceed loss terms. Transport due to mean circulation, tidal currents, and wind drift is one of the most important loss terms. For example, the disappearance of coastal blooms may simply be due to offshore flow. A precise knowledge of the flow field is therefore essential to the prediction of the occurrence of a toxic event at the coast. This knowledge must be acquired at the horizontal and vertical scales of phytoplankton patches. While the horizontal scales are accessible from three-dimensional hydrodynamical models, it appears that the required vertical scale (tens of centimeters) needs a better understanding of the distribution of the energy at the same scale. HABs frequently occur in thin layers, which are limit layers between two overlying water masses, the movements of which are not yet fully understood. Understanding and subsequent modeling of the advection of HABs will be essential to prediction based on operational oceanography.

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mainly on their growth, grazing, and, in a few cases, mortality. Consequently, nutrition limitation has often been considered to be the major factor governing population dynamics of harmful algae. As a result, the paradigm that eutrophication is the cause of HABs has emerged. The approach is, however, an over-simplification of the generic equation shown in Box 1, which largely ignores species-specific behavioral attributes like tropism, migration, and response to grazers. Difficulties in parameterizing these and other terms have led to large uncertainties in model predictions.

PHYSICAL CONTROL PROCESSES

Populations of phytoplankton are often concentrated locally in either patches or layers. These are governed by physics in that the population is subject to transport, dispersion, and turbulence.

vertical variations in salinity, temperature, and density "fine structure." Thin layers of concentrated chemical and biological concentrations are the chemical and biological equivalents of the fine structure in temperature, salinity, and density. The important caveat is that biological and chemical layers are also forced by biochemical processes in addition to physical processes. However, while the coupling of processes may (or may not) bind biochemical layers to layers defined by temperature, salinity, or density, it is shear that has a subtle but highly important effect on plankton distributions. When taken in conjunction with horizontal gradients of various water components such as phytoplankton, shear has a major role in forming thin layers and fine structure with horizontal scales of kilometers. When studying phytoplankton distributions, a crucial, first-order measurement therefore includes

Turbulence and Mixing

Phytoplankton populations exhibit a degree of patchiness governed by physical processes. For example, while shear tends to spread phytoplankton patches into

thin layers where local concentrations are maintained, mixing tends to decrease local concentrations. These opposing influences may have profound effects; their influence on grazing pressure has been shown to depend on the concentration of toxins to which grazers are exposed.

Small-scale agitation may profoundly influence phytoplankton populations. Most of the effects are due to collisions

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between cells; therefore, the degree of agitation depends on cell density. The incidence of collision is non-linear and cannot be predicted in a simple way. Among the effects related to cell collisions are cell cycle arrest leading to reduction in growth rate, cell lysis (the rupture and destruction of the cell) leading to increased mortality, and bloom flocculation leading to a decrease in local concentration (Jackson, 1990). In the latter case, plankton population sensitivity is highly dependent on the cells' physiological status. It has been shown that a burst of turbulence induced, for instance, by a wind event may cause the termination of a bloom through sinking of the aggregated cells. This is a good example of the interaction between physical and biological events.

Turbulence occurs everywhere in the ocean, but its intensity varies considerably in time and space. The past two decades of microstructure observations have yielded a significant body of information on the nature of oceanic turbulence. In general, turbulence exhibits a layered structure and patchiness, just like plankton. Its intensity is normally higher near the sea surface, the ocean floor, and in the thermocline. Twenty-five to thirty-meter patches of turbulence are found in the thermocline; however, turbulent layers in a thermocline are usually patchy, with a typical thickness of a few meters (Figure 3). A "patch" is not a single overturning event from top to bottom, rather, it is a section of dissipation exceeding a fixed threshold, for example, 10^{-8} W/kg. Thicker patches are usually associated with stronger turbulence and last longer than thinner ones. Inertial wave shear causes persistent patches that can last for several hours. Persistent patches are also found at interfaces of intrusions, for example, the California undercurrent.

Physical oceanographers can now measure (with some confidence) the rate of dissipation of turbulent kinetic energy ε. While existing data are useful

for the consideration of the influences of turbulence on trophodynamics, one must realize that a gap exists between the measurement needs of physical oceanographers and the applications of interest to biologists. Normally, what physical oceanographers call an "instantaneous" dissipation is an average dissipation rate over a certain spatial scale, somewhere around 0.5 to 5 m. Physical oceanographers are interested in an extensive average of such "instantaneous" dissipation rates. On the other hand, microorganisms experience a true instantaneous velocity strain field. The difference between the "local" dissipation rate experienced by cells and a one-meter-average dissipation rate commonly used by physicists is depicted in Figure 4.

Aggregation in Subsurface Layers

Aggregations of phytoplankton in thin layers at the seasonal thermocline, or at other pycnoclines within the water column, can be comprised of a range of species. Diatoms can be present in high numbers, but often these are senescent populations that have aggregated at the density discontinuity during settlement towards the seabed. Diatoms common in early summer, such as *Leptocylindrus* or *Chaetoceros,* can be found in very high numbers. More frequently, thin layers consist of very high densities of dinoflagellates. *Karenia mikimotoi* or various *Ceratium* species are common in the Celtic Sea, on the Ushant front, or in the Kattegat–Skagerrak area between Sweden, Denmark, and Norway (Figure 5). Around the southwest of Ireland, toxic *Dinophysis* species (Figure 6a) have been

found at cell densities as high as 124,000 cell/l. Here, *D. acuminata* is considered to be one of the species present as a thin layer. Sampling at that time, in 1992, was carried out using single water bottles, and it was extremely fortuitous that the bottle had been lowered to precisely the correct depth to sample within the layer.

As specific profiling systems with new detection systems have developed, thin layers have been reported more frequently.
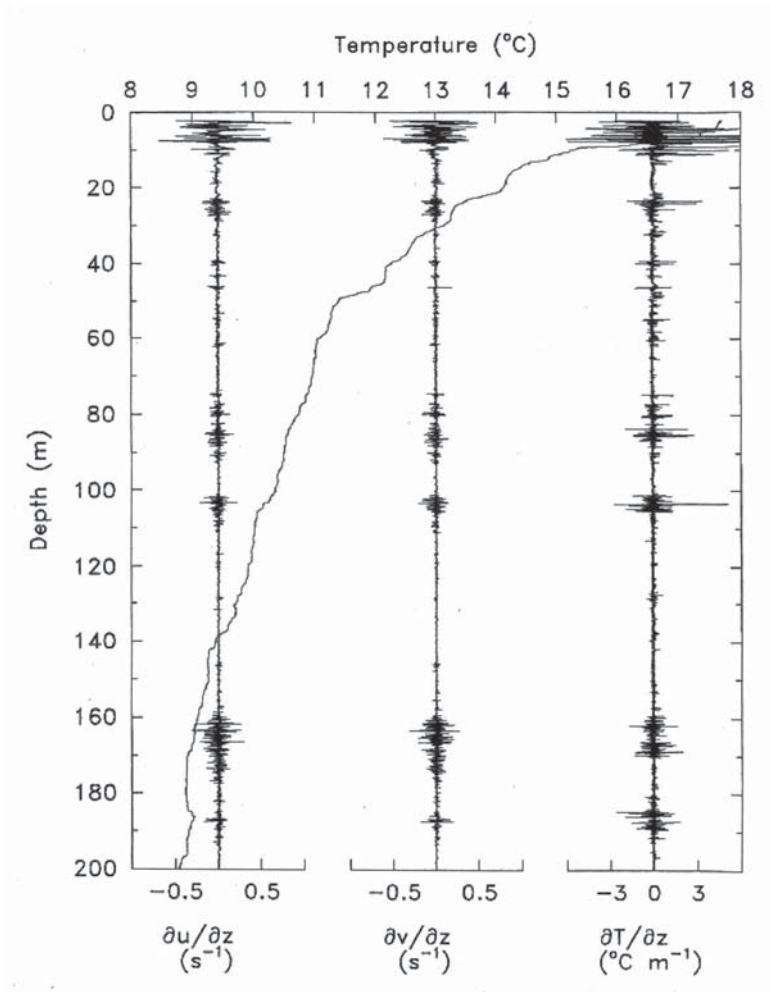
Observations made with specific

Figure 3. Microstructure profile data obtained from a free-fall instrument *Camel II*. The instrument measures two shears (∂u, ∂z, $\partial v/\partial z$) and vertical temperature gradient ($\partial T/\partial z$) as well as the temperature profile. Although the upper surface layer is still in a stratified condition, turbulence is active in the upper 10 m. A 5-m uniform temperature interface is associated with a turbulent patch at 28 m depth. A strong turbulent patch occurred at 170 m depth, where the California Current is found. The dissipation rate associated with 0.1/s rms velocity shear is roughly 7.5×10^{-8} W/kg; see for example, 103 m depth. SOURCE: Yamazaki and Lueck (1990).
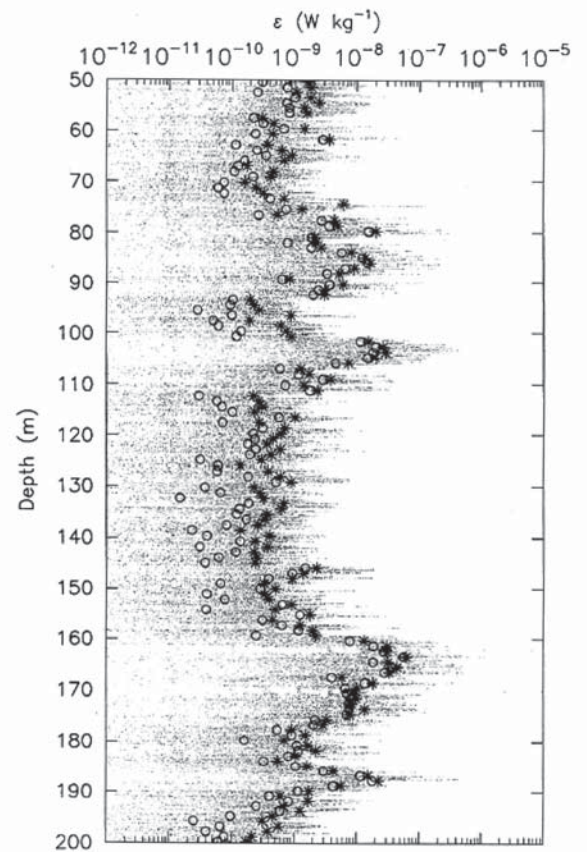

Figure 4. Vertical profile of dissipation rates computed from $\partial v/\partial z$. Open circles are 1-m-average dissipation rate values computed from a conventional spectral method. Dots represent unsmoothed local dissipation data and the asterisks represent the average local dissipation rate over 1 m. SOURCE: Yamazaki and Lueck (1990).
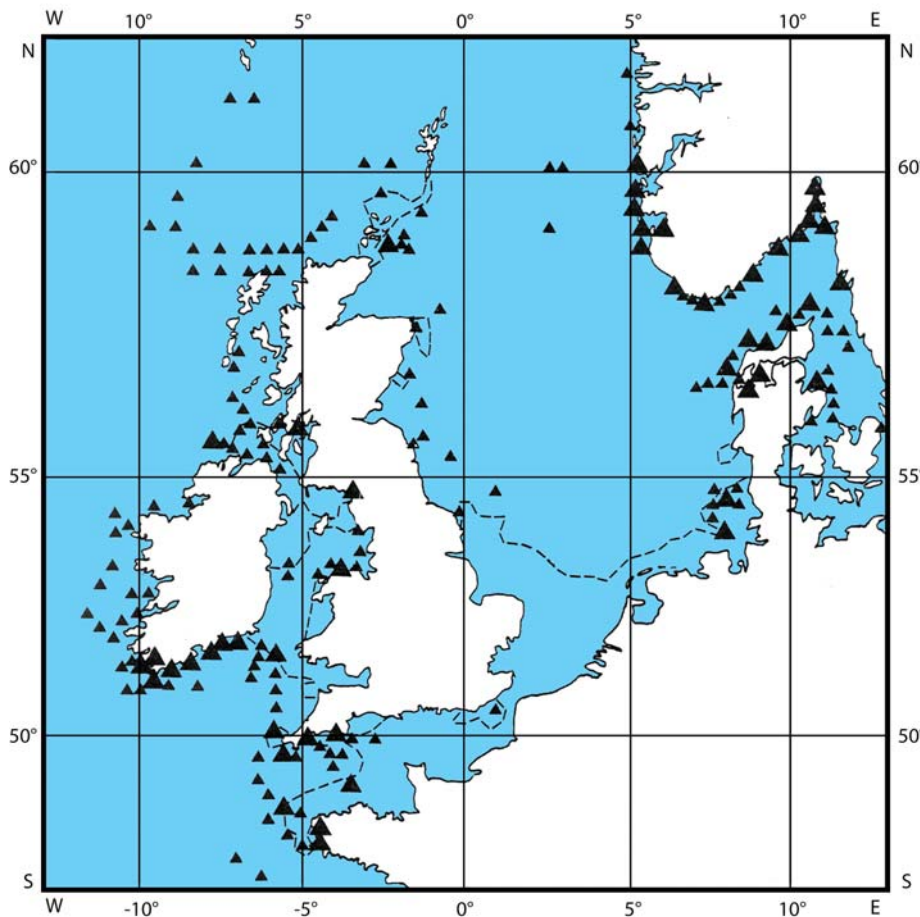
Figure 5. This map of North-western Europe (Partensky and Sournia, 1986) provides a history of the distribution of blooms of the dinoflagellate *Karenia mikimotoi*. This species is a "fish-killer" and produces a suite of exotoxins inhibiting membrane ATP-ases. During summer, these blooms are localized in strongly stratified areas. The east coast of Denmark and Kattegat–Skagerrak waters are under the influence of freshwater outflows from the Baltic and plumes from the Elbe and Rhine Rivers. A buoyant jet flows along the Norwegian coast. All along the Atlantic coast of northern Europe, including the locations of tidal fronts, blooms have been observed which are now linked to jet-like flows associated with physical dynamics at the coastal boundary of stratified regions (size of triangles reflects observed cell densities).

profilers have been made in the Gulf of Finland, in the Bay of Biscay (France), and offshore San Juan Island (Washington state, U.S.). Studies in Europe have mainly targeted *D. acuminata* and *Gymnodinium catenatum* (Figure 6b) in different dinoflagellate dominated assemblages. In the San Juan Island study, a near-bottom, high-density, thin layer of *Pseudo-nitzschia* spp. persisted for several days. International cooperation between U.S. and Europe is ongoing (Box

2) to improve knowledge with the help of a suite of newly designed instrumentation. However, specific effort has to be made to develop new observing systems that would allow identification of phytoplankton groups, taxa, and even toxicity.

What are the Adaptive Advantages of Growing in Thin Layers?

Some phytoplankton species, including HABs, have selected strategies allowing

them to grow in sub-optimal conditions encountered in deep layers. Layers with very high cell densities are closely associated with the water column's vertical structure, and a layer's thickness is related to shear. High positive shear promotes phytoplankton layers that are less that 2 m thick, whereas more diffuse thin layers that are 5 to 10 m thick are associated with physical discontinuities where shear is lower.
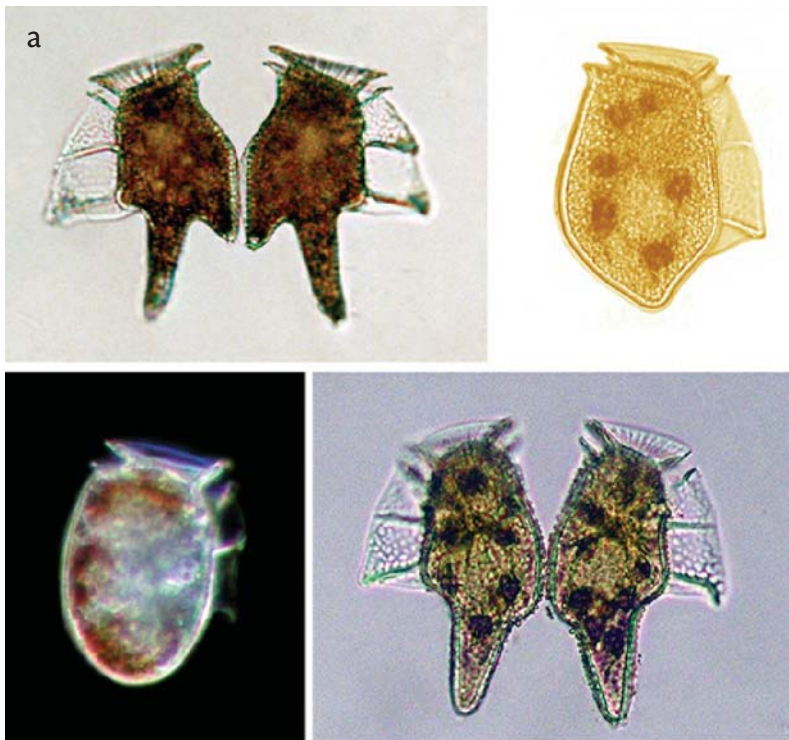
Formation of thin layers can benefit

a

b

Figure 6. (a) Common species of the toxic phytoplankton genus *Dinophysis*. Clockwise from top left: *D. tripos, D. acuta, D. caudata* and *D. acuminata.* Along the European coastline of the Atlantic Ocean, this genus is the cause of Diarrheic Shellfish Poisoning and has a major economic impact. These species are also encountered on the Atlantic American coast but are not toxic. Comparative studies on toxinogenesis on both sides of the Atlantic would be valuable. (b) *Gymnodinium catenatum* is an unarmoured, marine, planktonic dinoflagellate species. It is a chain-forming, toxin-producing, red tide species associated with PSP events throughout the world. *G. catenatum* is a planktonic red tide species. *G. catenatum* orients its swimming in shear flows, and swimming speed increases with chain length. *G. catenatum* actively concentrates at depths with low turbulence and shear. The first *G. catenatum* red tide was reported from the Gulf of California. Populations of this species have been recorded from Mexico, Japan, Australia, Venezuela, the Philippines and Europe. *G. catenatum* produces a characteristic resting cyst. These cysts can germinate after just two weeks of dormancy and initiate new populations. Cysts are not only a reseeding tool, but also a dispersal agent: *G. catenatum* was introduced to Australian waters via ships' ballast water.

phytoplankton taxa in a number of ways. First, formation of thin layers can optimize population growth rates by concentrating the population where conditions are optimal for individual growth. For example, formation of a thin layer in the upper part of the nutricline can optimize growth rates of photosynthetic harmful algae by concentrating the population where growth rate is no longer limited by low nutrient concentrations in the surface layer, or by extremely low light

deeper in the water column. Second, formation of thin layers can reduce mortality rates by allowing populations to achieve sufficient densities whereby chemical defenses can be used to reduce losses and increase growth relative to competitors. These chemical defenses include production and, in some cases, the release of compounds that induce grazer avoidance, suppress grazing activity, and/or kill zooplankton and microzooplankton grazers within the layer. Third, formation of thin layers makes it possible for a species to chemically modify its local environment, potentially enhancing immigration rates by providing a chemical signal to migrating algae, or enhancing growth rates by increasing nutrient uptake or reducing bioavailability of toxic metals or by modifying the local properties of water, such as viscosity, through excretion of external metabolites. Fourth, the release of chemicals also plays a key role in the complex life cycles of many species, including harmful ones, as the release of sufficient gametes in a localized area is more likely to ensure successful mating. Finally, formation of thin layers can lead to physical-biological interactions that can dramatically influence the transport and retention of harmful algae, as retention structures can develop at density interfaces with suitable time (~10 days) and spatial (15 to 20 km) scales.

Formation of thin layers has two potential disadvantages. First, formation of thin layers can greatly increase mortality if chemical defenses are not adequate to

BOX 2: THE INTERNATIONAL DIMENSION

In September 2002, an American-European Union workshop was held in Trieste, Italy to formulate a joint program on the study of Harmful Algal Blooms. As a result, the European Commission and National Science Foundation have funded two major three-year projects on HABs that have transatlantic partners. One of these, called HABIT, is specifically targeted at studying the maintenance and behavior of high-density populations of *Dinophysis* in subsurface thin layers in stratified waters around Europe. HABIT is coordinated by biologist R. Raine at the National University of Ireland, Galway, and includes biologists and physicists from France, Spain, and the United Kingdom. Crucial to the study, however, is the participation of T. Osborn and J. Katz of the John Hopkins University, Baltimore, Maryland. The U.S. team will make measurements within thin layers of *Dinophysis* using their underwater holographic camera (http://www.me.jhu.edu/~lefd/shc/digital.htm). This system allows observation of processes actively occurring at the critical scales of less than 1 cm. The French team, led by P. Gentien (IFREMER), will use its specifically designed profiler composed of an *in situ* particle analyzer coupled with a fluorescence video microscope to detect thin layers containing *Dinophysis*, as well as a novel *in situ* rheometer. L. Fernand (CEFAS, U.K.) will map the chlorophyll thin layers and estimate horizontal diffusion. B. Reguera (IEO, Spain) is a specialist in the life cycle of *Dinophysis* and will estimate the nutrition and growth rate of *Dinophysis* populations.

International collaboration is an integral part of scientific research within Europe, which is funded by the EC under a series of Framework programs (HABIT is funded through the Sixth Framework Programme). The EU also supports established international networks such as NEMEDA, which seek to mitigate the harmful effects of *Dinophysis* along the Atlantic seaboard of Europe and involve scientists from Portugal, Spain, France, and Ireland. Support for networks can be achieved either through interregional programs (NEMEDA is supported by INTERREG IIIb) or the Sixth Framework.

induce grazer avoidance, suppress grazing activity, and/or kill the grazers within the layer. In a similar fashion, the opportunity for infection by bacteria or viruses will be greatly increased unless chemical defenses are adequate to suppress such attacks. Second, a thin layer may form at

in the water column, and many standard measuring instruments (such as *in situ* fluorometers) are not able to observe thin layers; hence, researchers have been unable to target them during sampling. It is only very recently that technologies have been developed to a satisfactory

lating to HABs in stratified environments will be discussed and finalized during the GEOHAB Open Science Meeting on HABs and Stratification, to be held from 5 to 7 December 2005 at UNESCO headquarters in Paris.

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a depth that does not optimize growth and/or retention. For example, thin layers may develop in subsurface, light-limited environments or in nutrient-depleted surface layers. In either case, the population growth of a photosynthetic harmful species may be reduced relative to a population concentrated in the nutricline or spread over the water column. As the focus in the study of harmful algae is on one single species, modeling exercises should take into consideration these different processes. For one given species, the ratio of advantages to disadvantages will vary during the course of the bloom, permitting either an increase or decrease in population size

CONCLUSIONS

Several physical processes are crucial in the formation of harmful populations, but it is in these areas where knowledge is lacking. Acquisition of information on the relationship between HABs and stratification has been slow and erratic. Subsurface layers can be present at any depth

level to allow the study of thin layers with the result that research into their maintenance is as yet in its infancy. Such studies require close collaboration involving physicists, modelers, and phytoplankton ecologists. The outcome of these studies will have application to many scientific questions outside the domain of HABs. For example, estimates of carbon flux in the deep ocean may vary by a factor of 10 and depend on the species of phytoplankton present. Research priorities re-

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