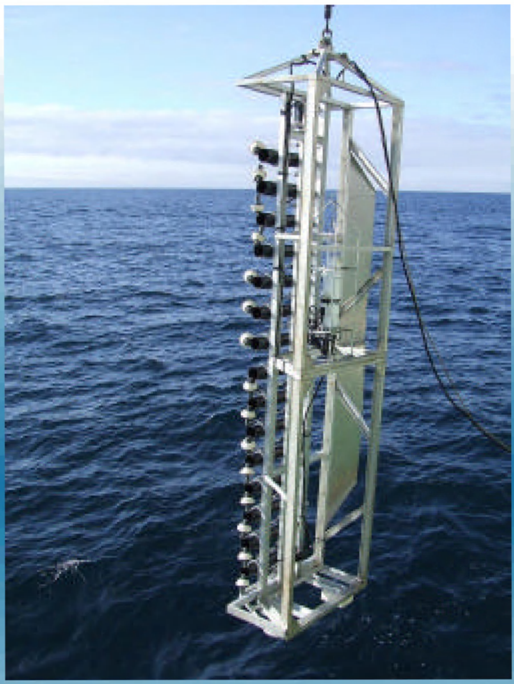
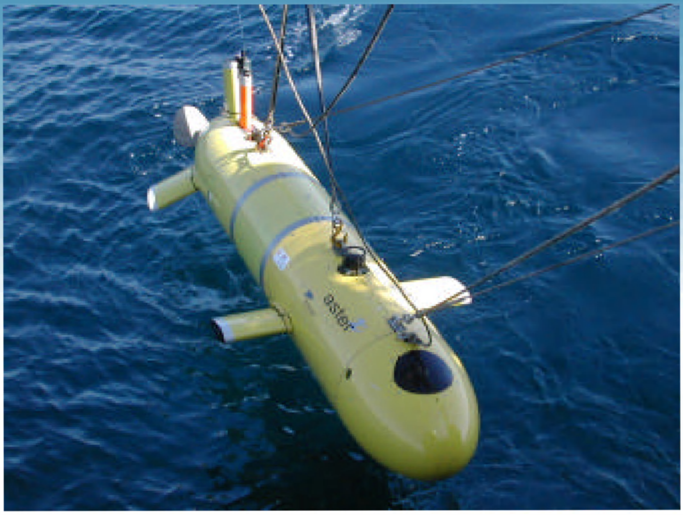
GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms





GEOHAB CORE RESEARCH PROJECT: HABs IN STRATIFIED SYSTEMS

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GEOHAB

GLOBAL ECOLOGY AND OCEANOGRAPHY OF HARMFUL ALGAL BLOOMS

GEOHAB CORE RESEARCH PROJECT: HABs IN STRATIFIED SYSTEMS

AN INTERNATIONAL PROGRAMME SPONSORED BY THE SCIENTIFIC COMMITTEE ON OCEANIC RESEARCH (SCOR) AND THE INTERGOVERNMENTAL OCEANOGRAPHIC COMMISSION (IOC) OF UNESCO

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BASED ON CONTRIBUTIONS BY PARTICIPANTS OF THE GEOHAB OPEN SCIENCE MEETING ON HABs IN STRATIFIED SYSTEMS AND MEMBERS OF THE GEOHAB SCIENTIFIC STEERING COMMITTEE

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http://www.geohab.info

Cover photos: Top left, an oceanic undulating towed CTD (SCANFISH) from CEFAS (Lowestoft, UK); top right, Fine Scale Sampler (FSS) from IFREMER; Bottom left, the Autonomous Underwater Vehicle (AUV) *Asterix*, from IFREMER, equipped with a Seabird CTD and a Workhorse Sentinel ADCP; bottom right, micrograph of a *Dinophysis acuta* bloom from the Galician Rías Baixas (NW Spain). (Pictures courtesy of Robin Raine, Patrick Gentien and Beatriz Reguera).

Back cover: *In situ* planar-laser imaging fluorometer system: A green laser is formed into a sheet, and used to stimulate chlorophyll *a* fluorescence. The fluorescence is imaged with a sensitive CCD camera over an imaging plane 32x32 cm with 0.3x0.3 mm spatial resolution. The laser sheet extends at a 45° angle below the free-falling vehicle, and the camera images at 90° to the laser sheet (left panel). The autonomous profiler (right panel) descends slowly through the water column acquiring images every 2 seconds in the undisturbed waters below the profiler. Auxiliary instruments on the profiler include CTD, ADCP, ISUS nitrate sensor, and microstructure profilers. The fluorescence images show the size and location and fluorescence intensity of individual phytoplankters, fluorescent aggregates, and herbivore gut fluorescence (developed by J. Jaffe and P. Franks; figure courtesy of P. Franks).

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GEOHAB

Global Ecology and Oceanography of Harmful Algal Blooms
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Executive summary

The Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) programme was initiated in 1999 by the Scientific Committee on Oceanic Research (SCOR) and the Intergovernmental Oceanographic Commission (IOC) of UNESCO, to develop a research programme on the ecological and oceanographic mechanisms underlying the population dynamics of harmful algal blooms (HABs).

The ultimate goal of this research is to allow the development of observation systems and models that will enable prediction of HABs, thereby reducing their impact on the health of humans and marine organisms, as well as their economic impact on society.

The *GEOHAB Implementation Plan* (GEOHAB, 2003) specifies the formation of Core Research Projects (CRPs) related to four ecosystems types: upwelling systems, fjords and coastal embayments, eutrophic systems and stratified systems. These CRPs are initiated through small, focused open science meetings.

The first Open Science Meeting (OSM)—HABs in Upwelling Systems, Lisbon, Portugal, 17–20 November 2003—focused on meso-scale hydrodynamic features (coastal upwelling zones). The second OSM—HABs in Fjords and Coastal Embayments, Viña del Mar, Chile, 26–30 April 2004—dealt with HAB events and their monitoring in semi-enclosed coastal systems, particularly non-eutrophied systems. The third OSM—HABs and Eutrophication, Maryland, USA, 7–10 March 2005—focused on high biomass HABs and their potential link with anthropogenic inputs. The fourth and last OSM—HABs in Stratified Systems, Paris, France, 5–8 December 2005—concentrated on small scale hydrographic features which may be encountered in any of the above mentioned environments. The present report outlines the justification and research priorities for the study of relationships between HABs and stratification, as well as some of the new approaches and advanced instrumentation that may be considered.

The following key questions were identified:

1. What are the relative contributions of biological and physical processes to the initial formation of thin layers in stratified systems?
2. What are the key processes defining the different strategies that maintain phytoplankton in thin layers?
3. What are the biological and chemical outcomes of the physical concentration of plankton into high-density thin layers?
4. What causes a high-density population in a thin layer to collapse?

List of acronyms

ASP	Amnesic Shellfish Poisoning
AUV	Autonomous Underwater Vehicle
CCD	Charge-Coupled Device
CRP	Core Research Project
DIC	Differential Interference Contrast
DOC	Dissolved Organic Carbon
DOM	Dissolved Organic Matter
DON	Dissolved Organic Nitrogen
DSP	Diarrhoeic Shellfish Poisoning
DVM	Daily Vertical Migration
EPS	Exopolymeric Substances
GEOHAB	Global Ecology and Oceanography of Harmful Algal Blooms
GOOS	Global Ocean Observing System
GRAs	GOOS Regional Alliances
HABs	Harmful Algal Blooms
ISUS	InSitu Ultraviolet Spectrophotometer
IMBER	Integrated Marine Biogeochemistry and Ecosystem Research
IOC	Intergovernmental Oceanographic Commission
NDV	Nortek Doppler Velocimeter
OSM	Open Science Meeting
OSSEs	Observing System Simulator Experiments
PAR	Photosynthetically Active Radiation
PIV	Particle Imaging Velocimetry
POM	Particulate Organic Matter
PSP	Paralytic Shellfish Poisoning
SCAMP	Self Contained Autonomous MicroProfiler
SCOR	Scientific Committee on Oceanic Research
SSC	Scientific Steering Committee
UNESCO	United Nations Environmental, Scientific and Cultural Organization
WDC-MARE	World Data Centre for Marine Environmental Sciences

I. Introduction

The distributions of phytoplankton found in the sea are influenced by ocean circulation patterns that occur over a wide range of different scales. Without losing sight of the large scale, where forcing conditions such as climate may dominate, along the coastal continental shelves there are several features of direct relevance to harmful algal blooms (HABs) at the mesoscale (10–100 km). Such features include tidal fronts, buoyancy-driven jets and upwelling. The water column is most often stratified on one side of these mesoscale structures. Bays, fjords, rías, fronts and coastal upwellings all provide particular niches for phytoplankton species, some of which are potentially harmful and/or toxic.

The Core Research Projects (CRPs) of GEOHAB concern coastal bays, fjords and upwelling systems at the mesoscale. However, at this scale and at smaller ones, stratified environments are encountered: the CRP on Stratified Systems concentrates on the fine-scale distribution of microalgae, aiming to provide pertinent answers that can be used in the three other GEOHAB CRPs.

Since there is evidence that specific phytoplankton communities containing HABs occur in thin layers, often associated with small density steps, research questions are:

1. Are these layers formed by interactions between physics and biology?
2. To which degree is the microstructure of physical parameters relevant and how important is the vertical structure of light and nutrients?
3. Are the local changes in viscosity and excretory product levels caused by plankton key to understanding thin layers properties?

Another basic aspect being addressed in these projects is the population dynamics of a particular species, as opposed to the bulk property of primary production by phytoplankton.

Research into population dynamics of a potentially harmful species needs to incorporate three main topics in order to understand and predict harmful blooms:

1. The different life cycle stages of a species that condition the initiation, maintenance and decline of a bloom.
2. The study of transitions, such as excystment and encystment, from one stage of the life cycle to the next.
3. The study of the dynamics of planktonic vegetative stages, of particular interest to us as plankton in this stage may contain toxins, and it is this stage which causes most harm through proliferation of blooms.

The primary difficulty is to identify the factors which control these three processes. They may be physical, chemical, biological or any combination of these, and usually act over a large range of scales. The controlling factors need to be defined, quantified and ranked, in order to derive equations that can model HABs.

The existence of phytoplankton, including some harmful algal species, in sub-surface layers (Table 1) raises a number of questions about their ecology and the niche they occupy in the marine ecosystem. How well are they equipped for existence in thin layers? What are the advantages and disadvantages of existing in these niches at high density? How are these populations maintained? These questions are explored later in this report. The crucial factor is that a number of innovative instruments are needed to observe and adequately sample these environments. Different approaches are also required to understand blooms in stratified systems well enough that they can be modelled and predicted. This is most essential for harmful events arising from subsurface populations because we cannot see these HABs from satellite images and, as yet, cannot forecast them.

Table 1. HAB species reported to form dense aggregates in stratified systems (compiled by L. Velo-Suárez).

	Genus	Species	Location	Reference
Dinoflagellates	*Alexandrium*	*catenella*	East Sound, WA, USA	Sullivan et al., 2003
		fundyense	Gulf of Maine, USA	Townsend et al., 2001
			Canada	Martin et al., 2005;
		tamarense	Golfo Nuevo, Argentina	Gayoso and Fulco, 2006
	Cochlodinium	*polykrikoides*	Namhae Island, Korea	Park et al., 2001
	Dinophysis	*acuminata* complex	Bay of Biscay, France	Gentien et al., 1995 Lunven and Gentien, 2000
			Thermaikos Bay, Greece	Koukaras and Nikolaidis, 2004
			Baltic Sea	Setälä et al., 2005; Hajdu and Larsson, 2006;
		acuta	Big Glory Bay, New Zealand	MacKenzie, 1991
			Aveiro Lagoon, Portugal	Moita et al., 2006
			Ría de Pontevedra, Spain	Escalera et al., unpubl.
		norvegica	Baltic Sea	Carpenter et al., 1995; Gisselson et al., 2002; Hajdu et al., 2007
	Gymnodinium	*catenatum*	Derwent River, Tasmania	Hallegraeff and Fraga, 1998
			Lisbon Bay, Portugal	Moita et al., 2003
	Prorocentrum	*minimum*	Chesapeake Bay, USA	Tyler and Seliger, 1978; Tyler and Seliger, 1981
	Heterocapsa	*triquetra*	Gulf of Finland	Kononen et al., 2003
	Karenia	*mikimotoi*	Ushant Front, France	Gentien et al., 2005
			Skagerrak/Kattegat, Sweden	Bjørnsen and Nielsen, 1991
			Bantry Bay, Ireland	Raine et al., 1993
Diatoms	*Chaetoceros*	*convolutus* *concavicornis*	East Sound, WA, USA	EU-US HAB Initiative, 2003
	Pseudo-nitzschia	*pseudodelicatissima*	San Juan Islands, US	Rines et al., 2002
		pungens		McManus et al., 2003
		fraudulenta	Monterey Bay, US	Ryan et al., 2005
		australis	Ria de Pontevedra, Spain	Velo-Suárez et al., 2008
Others	*Chrysochromulina*	*polylepis*	Skagerrak/Kattegat, Sweden	Barth and Nielsen, 1989 Nielsen et al., 1990
	Heterosigma	*akashiwo*	Big Glory Bay, New Zealand	MacKenzie, 1991
	Phaeocystis	*globosa*	English Channel	Doubell et al., 2006

II. The GEOHAB approach to the study of harmful algae in stratified systems

The approach of the GEOHAB programme is ***comparative***, from the cellular to the ecosystem level. This approach is based on the view that the ecology and oceanography of HABs can best be understood through the study of the causative organisms and affected systems in relation to comparable species and systems. Important physical processes occur over a wide range of scales. Similarly, important biological processes occur at subcellular and cellular levels, as well as at the population, community, and ecosystem levels. Improved generalisations about the causes and consequences of HABs would be particularly useful in management and mitigation of their effect. The GEOHAB approach is to apply multiple techniques to fully understand the biological, chemical, and physical factors regulating HAB dynamics and impacts. Field studies are essential. Modelling the population dynamics will be critical to every aspect of these studies. Therefore, the GEOHAB Programme fosters research that is ***interdisciplinary***, focusing on the important interactions among biological, chemical, and physical processes. GEOHAB research must also be ***multifaceted*** as the problems are complex and interactions and processes occur on a broad range of scales. Finally, GEOHAB research should be ***international*** in scope to encompass the global issues of HAB events and to benefit from the skills and experience of HAB investigators worldwide. The following sections of this plan will describe research on HABs in stratified systems that follows these GEOHAB approaches.

Coastal seas are of immense economic importance to humans. In the context of HABs, it is in the coastal zone where the aquaculture industry is located and where adverse effects of high-biomass blooms on water quality and tourism are immediately obvious. Yet, the degree of stratification in some coastal areas is very large such as fjordic environments, e.g., Norway and Scotland, where the freshwater inputs from land runoff and rivers, leads to strong vertical density gradients. In many other parts of the world, e.g., the Gulf of Maine, the coastal production areas lie in close proximity to areas which are highly stratified and may be affected by the advection of populations incubated in the stratified regions.

Phytoplankton species are diverse with respect to their morphology, phylogeny, life cycle forms and transitions, growth requirements, capacity for production of toxins and other bioactive compounds, as well as their inter- and intraspecific interactions.

The definition of a toxin is operational by nature and does not yet allow a scientific classification of the producing species. However, many HAB species have in common that they proliferate in layers located in the pycnoclines, a characteristic that suggests convergent evolution or similar trade-offs among functional traits.

Adaptations are heritable traits that confer a selective advantage upon those individuals in a population capable of expressing them. As with all species, it can be assumed that many characteristics of harmful algae evolved and are maintained by natural selection and are thus adaptive. Adaptations are expressed at different scales, influencing processes at the level of the cell, colony, whole population and community.

The challenge is to define the unique adaptations of HAB species that account for their survival, persistence and, in some instances, their dominance during bloom events. By understanding the adaptations of different HAB species, it should be possible to describe and predict patterns of species abundance and harmful effects as functions of hydrographic processes, nutrient distributions and community interactions.

It might be argued that after the physiological characteristics of a single species are well described, it should be possible to predict its presence and abundance based on some knowledge of the environmental conditions. A corresponding view is that a given species will have maximum growth potential in conditions where environmental parameters—such as light, temperature, nutrient concentrations, or turbulence—are optimal for vegetative growth. However, the response of organisms in natural ecosystems is much more complicated. Multiform life strategies, migratory behaviour, complex trophic interactions, and small-scale physical-biological interactions allow a species to exploit a spectrum of environmental conditions. By multi-faceted exploitation of ecological niches, the species may be able to survive

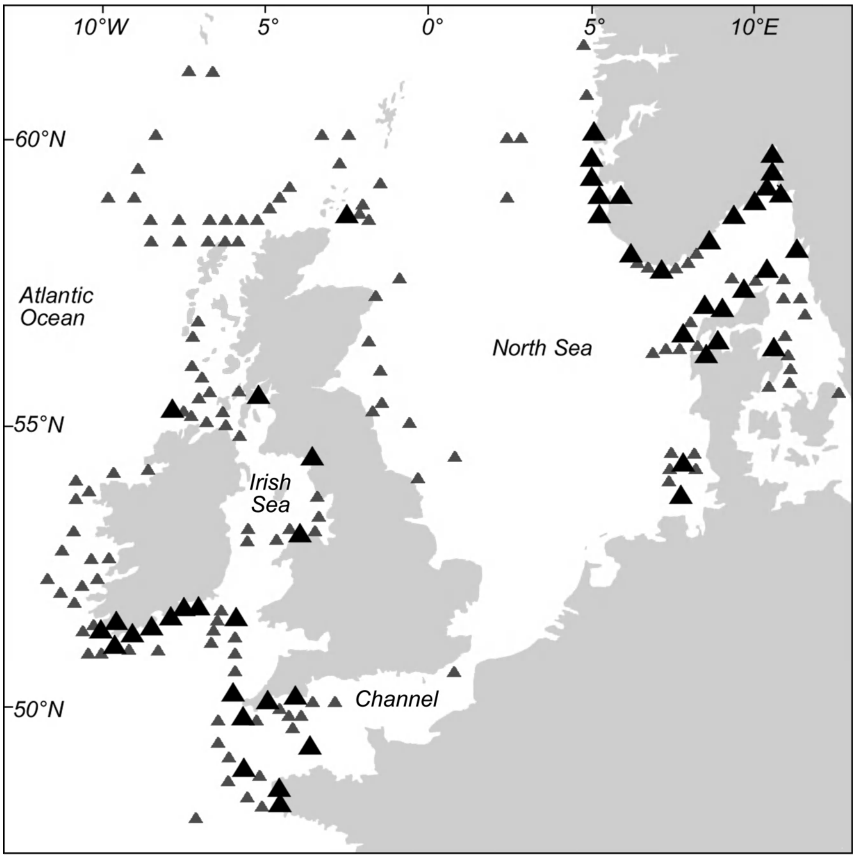


Fig. 1. Distribution of Karenia mikimotoi *-alias* Gyrodinium *cf.* aureolum, Gymnodinium breve, *or* Gymnodinium nagasakiense*- in Northern European seas, based on references quoted in Partensky and Sournia (1986). This species does not occur in mixed waters of the English Channel or the central North Sea. It is mainly observed in stratified zones along tidal fronts, such as the Western Channel and around Ireland, as well as in Kattegat, Skagerrak and along the Norwegian coast, in the positive buoyancy jet area, usually confined within the pycnocline (Gentien, 1998). The vertical distribution of* K. mikimotoi *seems to be mainly controlled by physics and the species' autotoxicity, and it is not the result of an active migration (Gentien et al., 2007). (Small triangles: $<10^{6}$ cell · l^{1}; large triangles: $>10^{6}$ cell · l^{1}).*

and thrive in situations that are seemingly very different from its optimal requirements.

A good illustration is provided by Klausmeier and Litchman (2001), who used a game-related theoretical model treating the depth of a thin layer of phytoplankton as a strategy. The authors found that the depth at which phytoplankters are equally limited by both light and nutrient resources is an evolutionarily stable strategy. The layer becomes shallower with an increase in nutrient supply and deeper with an increase in light supply. For low nutrient levels, low background attenuation and shallow water columns, a benthic layer occurs; for intermediate nutrient levels in deep water columns, a deep chlorophyll maximum occurs; and for high nutrient levels, a surface scum occurs. These general patterns are in agreement with some observations made in the field.

In addition, while many classical physiological studies focus on the response of an organism to a single parameter, physical, chemical, and biological parameters interact and often vary independently in nature, producing non-linear responses.

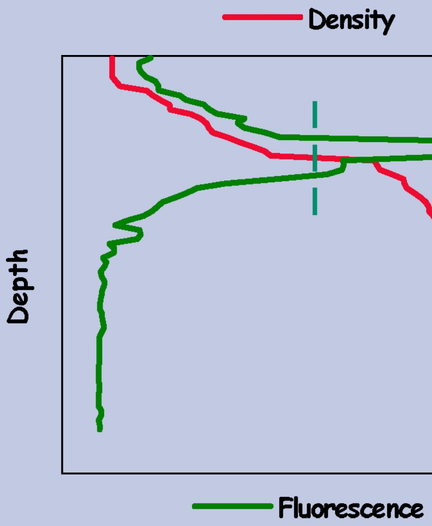
Other clear examples are the role of small-scale turbulence on nutrient assimilation (Karp-Boss et al., 1996), grazing (Marrasé et al., 1990), and the relationships between water mixing and photo-acclimation (Lewis et al., 1983). In the context of specific ecosystems, interactions between organisms and water circulation are essential for understanding transport, population confinement, and persistence of certain blooms (Anderson, 1997; Hallegraeff and Fraga, 1998; Garcés et al., 1999).

The term stratification means layering. The basic concept of a stratified water column in coastal and shelf seas is a three-layer system: a wind-mixed surface layer and a tide-mixed bottom layer, separated by a pycnocline layer. There are clear links between marine stratification and the occurrence of harmful algal blooms. For example, a comparison of maps where harmful algal events have occurred with variations in stratification shows that many HABs occur where waters are most stratified. Observations on *Karenia mikimotoi* alias *Gymnodinium aureolum* summarized by Partensky and Sournia (1986) are presented in Figure 1. This map clearly shows that this species distribution is tightly linked to stratified areas.

Within the surface ‘mixed layer’, several small density discontinuities are often found. This characteristic means that we have to consider the surface zone as comprising several layers which may be only a meter or so thick. These are the so-called thin layers of phytoplankton (Box 1), occurring in sub-surface layers and often associated with very high cell densities of specialized phytoplankton communities. Many HAB species are now known to exist in sub-surface thin layers, which causes many problems for their observation as they cannot be seen using the usual remote-sensing approaches with satellite-borne instruments. The deployment of fixed-depth instrumentation on moorings is also of limited use, as these may fail to record the cell maxima.

Quantification of the physical contributions to layer formation, maintenance, and dissipation may help us to understand the role of biological dynamics in these layers. Numerical models with realistic mixing and thermocline structures will help us synthesize diverse data types from different instruments and experiments, and aid us to understand thin-layer dynamics. A better understanding will enhance our ability to predict the conditions under which thin-layer HABs form, and their spatial and temporal dynamics. Improvements in models are required before these can accurately resolve thin layers and their dynamics.

Box 1. Definition of a Thin Layer



Based on up-to-date instrumentation, some of the conditions to consider in an operational definition of a thin-layer are:

1. It must have a **minimum spatial coherence horizontally**: the feature must be present in at least two consecutive profiles. This criterion is necessary to distinguish between a thin layer and a patch (*sensu* Franks, 1995).
2. The feature must be **less than three meters thick** measured at half maximum intensity. It may be useful to employ a complementary classification conforming to the physicists’ definition of **‘fine layers’ (less than 0.5 m)** since these features are mainly driven by physical laws.
3. The magnitude of the property must be **significantly higher (5 times) than background**.

The thin layer can be defined by cell numbers, chlorophyll, and other biological parameters. These criteria are adapted from an original article by Dekshenieks et al. (2001) where the criteria of 5 m thickness and 3 times the background were used. These values were chosen with relation to the scale sampled using standard oceanographic procedures. Current sampling approaches now generally allow a higher vertical sampling resolution.

III. An overview of HABs in stratified systems

Many HAB species tend to concentrate in layers in density discontinuities. Until recently, these structures were detected either directly by chance or by divers (Vilicic et al., 1989). Thin layer habitats are occupied by different phytoplankton communities, often composed of species suspected to be heterotrophic.

Aggregations of phytoplankton in thin layers at the seasonal thermocline, or at other clines within the water column, can be made up of a number of species. Diatoms can be present in high numbers, but these are often senescent populations which have aggregated at the density discontinuity during settlement from surface waters towards the sea bed. Diatoms which are common in early summer, such as *Leptocylindrus* or *Chaetoceros*, can be found in very high numbers in thin layers.

More often though thin layers contain very high densities of dinoflagellates. For example, *Karenia mikimotoi, Ceratium lineatum* and other *Ceratium* species are common in the Celtic Sea and along the south and west coasts of Ireland. Around the southwest coast of the country, the DSP-toxin producer *Dinophysis acuminata* was found at cell densities as high as $12 \cdot 10^4$ cells $\cdot$ l^{-1} (Raine et al., 1990). It is thought that the species was present as a thin layer, and that as the sampling was carried out using single water bottles, it was extremely fortuitous that the bottle had been lowered to precisely the correct depth.

On the Ushant front off western France, blooms of *Karenia mikimotoi* were found within the pycnocline (Pingree et al., 1975). Populations were associated with diatoms (*Chaetoceros* spp., *Leptocylindrus minimus, Nitzschia delicatissima*) in poor condition: this was explained by a growth limitation due to water conditioning by *K. mikimotoi* (Arzul et al., 1993). Gentien et al. (1995) reported that some pycnocline layers may contain up to 100% dominance of dinoflagellates (*Ceratium, Pyrocystis, Dissodinium, Diplopeltopsis, Peridinium* and *Prorocentrum*). These dinoflagellates, which have a heterotrophic capability, were found in layers containing organic aggregates. Decimetre-scale heterogeneities in the plankton, with a 'magic carpet' of *Gyrodinium aureolum*, were reported by Bjørnsen and Nielsen (1991).

While they may be only a few centimetres to several meters in vertical thickness, these water column structures can extend horizontally for kilometres and may persist for hours or many days (McManus et al., 2003). They are easily overlooked in monitoring programmes, as reported by Rines et al. (2002) for *Pseudo-nitzschia* populations, which may be found in water-column thin layers, near-bottom layers or even within *Chaetoceros sociale* colonies (Velo-Suárez et al., 2008).

Accumulation of *Dinophysis* has been observed associated with large amounts of organic aggregates and degraded chlorophyll pigments, layers commonly encountered in density interfaces (Gentien et al., 1995). Fine layering was observed in the Bay of Biscay (Lunven et al., 2005), with superposition of two layers (Fig. 2): one composed of a nearly monospecific population of *Chaetoceros sociale* ($2 \cdot 10^6$ cells $\cdot$ l^{-1}) under a layer containing *Dinophysis acuminata* ($15 \cdot 10^4$ cells $\cdot$ l^{-1}). At the diatom maximum, the low silica concentration was locally close to limitation levels (i.e., of the order of the K_s value).

Low silica concentrations result when the silica uptake by diatoms is higher than the vertical diffusion flux. A consequence of the strong (usually thermal) stratification is that vertical fluxes are inhibited by the physical processes but can be enhanced by the local change in viscosity due to such a large population which will act to suppress small scale turbulent motion. In this case, the stability of this layering was within the characteristic time scale of the populations. Therefore, the accumulation of phytoplankton populations in these structures is more than anecdotal.

Not all species encountered in thin layers are 'harmful', but most of the harmful ones are encountered in these structures. Since these structures are present in the vicinity of all coastal environments (river plumes, coastal jets, upwelling areas, tidal fronts, etc.), it is necessary to develop appropriate instruments for their observation in order to study this type of ecological niche in terms of physics and biology, and to examine the interactions amongst the various control factors acting upon populations.

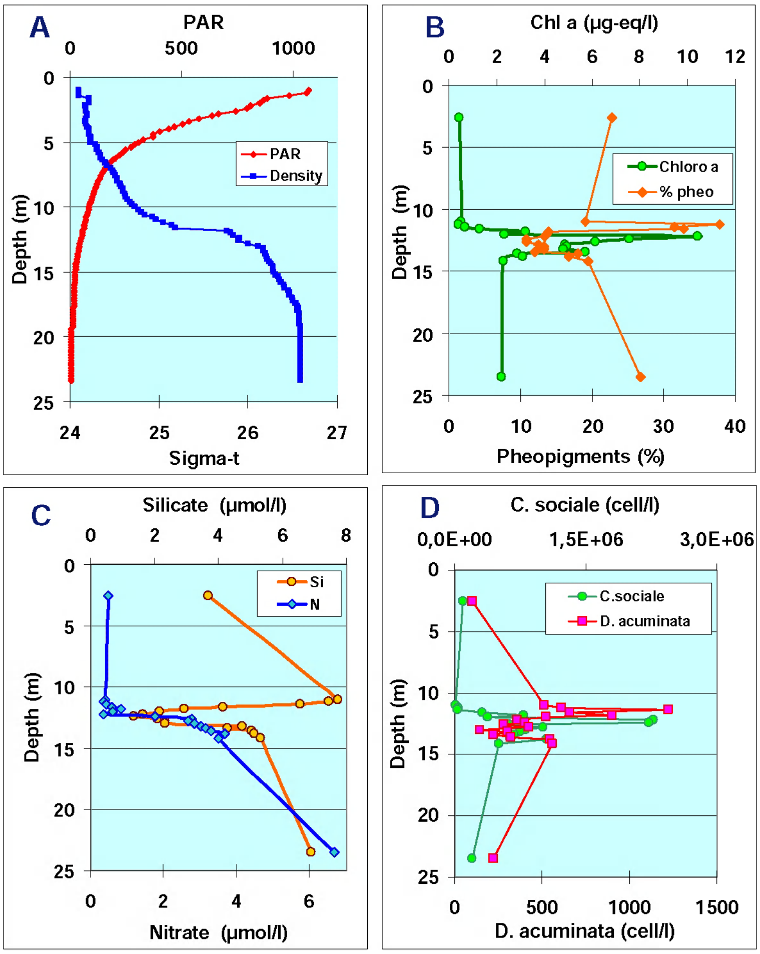


Fig. 2. Fine layering in the Bay of Biscay in June 2003 (technical details in Lunven et al., 2005). Superposition of two thin layers (B), one composed of Chaetoceros sociale *under another containing* Dinophysis acuminata *(D, note the different scales). The distance between the two layers is approximately 60 cm.* Dinophysis *accumulation occurred in layers containing degraded chlorophyll and was associated to a dominance of organic aggregates (data not shown). At the* C. sociale *maximum, the low silica concentration (C) is close to limitation levels (ca. 1 µmol · l^{-1}). Light (A) does not appear to be a discriminating factor between the two layers (30-50 µmol · $m^{-2} \cdot s^{-1}$). Large quantities of organic matter could be a factor for* Dinophysis *accumulation. The low silica concentration results from a silica uptake by the diatom higher than the vertical diffusion flux. Vertical fluxes are somehow or other limited. The stability of these layers lasted on the order of the characteristic time scale of the population.*

A. Stratification and mixing

The term 'mixed layer' is often applied to the upper ocean, from the sea surface to the thermocline. The layer can be actively mixing, or it can be quiescent in a period of respite before another mixing event. Thus, in reality, a layer can have a degree of stratification (<1°C) and still be considered well mixed. In the open ocean the mixed layer is controlled by wind, solar radiation, and surface cooling. Winds generate waves, induce Langmuir circulation, produce convection, generate turbulence, and also initiate near-inertial frequency motions. Surface cooling results from both evaporation and long-wave radiation. In the coastal ocean, run-off from the land and rivers adds freshwater directly to the surface, which at times can increase stratification enormously. In shallow (<150 m) coastal shelf seas, tidal energy can contribute to mixing and stratification in the upper layer. As a consequence, the structure of the surface mixed layer reflects the recent history of buoyancy inputs and mixing events. The result of all the processes causing stratification and mixing has pronounced effects on the environment of planktonic organisms.

At the base of the mixed layer is the pycnocline, where the local density gradient and vertical stratification increase dramatically. Internal waves are prevalent which may come from far field generated features such as near-inertial waves or more localised ones such as inertial oscillations from the passage of storms or from internal tides which are typically, but not exclusively, generated by the tide propagating across a change in bathymetry. These mechanisms are responsible for strong horizontal gradients and where these gradients overcome stratification can cause breaking of internal waves and thus mixing.

A.1. Diurnal and seasonal stratification

The dominant time scales for modulation of the upper ocean are the annual and daily cycles. On an annual scale, the mixed layer deepens during autumn and winter due to increased winds and net surface cooling, producing overturning that mixes water from below that has been isolated from surface effects during the summer season.

During the spring and summer, when the input of buoyancy from solar heating during the daytime overrides the turbulent mixing tendencies from the wind and surface cooling, a daily cycle occurs. During the day a weak, shallow buoyant layer is formed, which is destroyed each evening by convective mixing due to night-time irradiative cooling. This ephemeral layer has important physical and biological consequences, particularly in spring. From a physical perspective, the seasonal mixed layer develops earlier by efficiently ventilating buoyancy input to the subsurface layer.

Biologically, the spring phytoplankton bloom occurs earlier because the organisms caught in the shallow mixed layer during the day are subjected to higher average light intensity and they therefore develop higher concentrations of biomass (chlorophyll) earlier, a positive feedback loop which leads to earlier primary production. Increased biomass in shallow surface layers leads to more rapid absorption of shortwave radiation and, hence, warming of the surface water. The layer is thinner and more stable—a biological consequence of physical processes.

The formation of the seasonal thermocline in spring is not a gradual monotonic process (Fig. 3). Punctuating the regular (seasonal) cycle are episodic meteorological events that usually have time scales of hours to days. These closely match the dominant time scales of growth and behaviour of phytoplankton and zooplankton. The alternation of relatively calm heating periods with mixing events, caused by high winds associated with the passage of storms, results in discontinuities in thermocline development. The annual cycle in the evolution of the surface mixed layer may then be viewed as an integration of the seasonal cycle, the diurnal cycle and individual episodic events.

A.2. Mixed layer dynamics, fine structure and the formation of thin layers

Once stratified, due to either temperature or salinity differences, the density variations are acted upon by gravitational and rotational forces resulting in predominantly horizontal motions. However, at a much smaller scale turbulence due to thermal convection and waves mixes the upper layer and shapes the vertical density profile. This type of high-frequency motion is not predominantly horizontal.

One mechanism that overlaps these two scales is that of locally produced horizontal density gradients, or equivalently pressure gradients that are mostly generated by wind stress curls (spatially varying wind fields). These in turn create vertical motion through convergence or divergence of the Ekman transport (horizontal motion).

The presence of coasts is an important feature to generate divergences of Ekman transport and in the case of alongshore winds drives up- and downwelling events. The variation in strength of tidal mixing can also produce horizontal variations in density, both in shallow shelf regions which transition from well mixed to stratified, and in deeper regions such as the shelf edge where a similar transition can occur. The Coriolis force comes into play to enable inertial oscillations and waves to

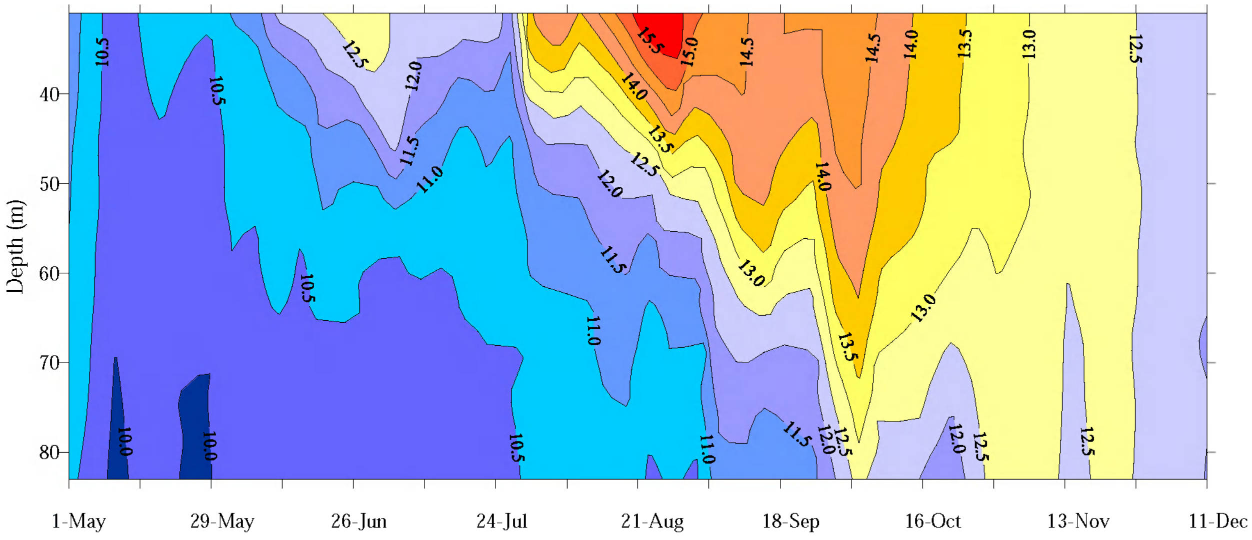


Fig. 3. Deepening and erosion of the seasonal thermocline off Erris Head, Ireland, 1997 (Figure courtesy of R. Raine).

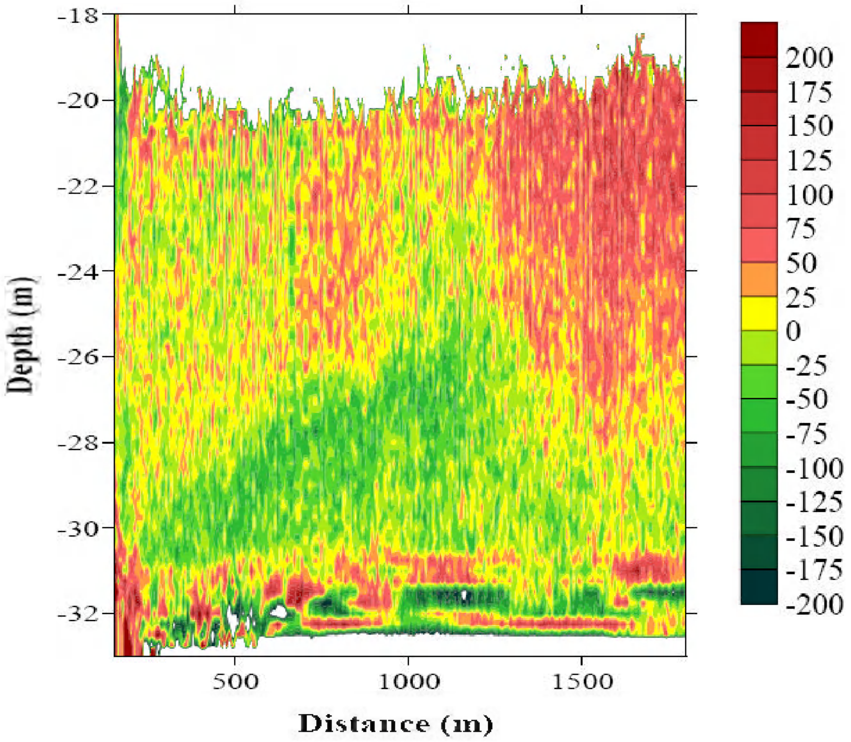


Fig. 4. Cross track velocity data (mm · s^{-1}) from an RDI 1200kHz ADCP mounted on the Asterix *AUV. Bin size resolution was 25cm with data recorded every second, pitch and roll on the AUV were very low giving a stable platform. Data was collected from the IFREMER* RV Thalassa *on the 20/6/2006 in the Bay of Biscay. The thermocline depth was 24m with chlorophyll maximum at 28m, and shows the strong local shear in the vicinity of the thermocline (Graph produced by L. Fernand).*

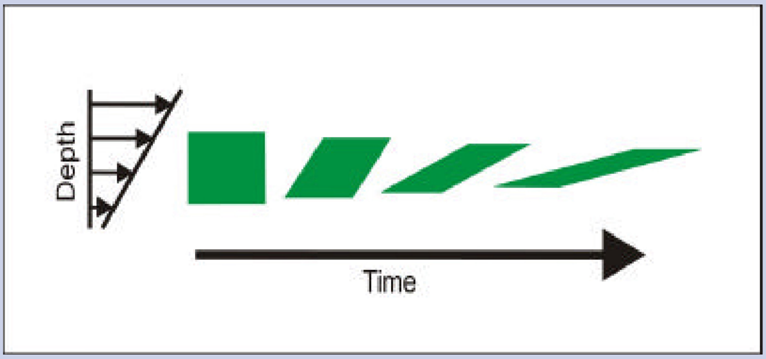
establish geostrophic currents. Bottom friction plays an important role in shallower water and disturbs the geostrophic balance by creating a turbulent near bottom mixed layer.

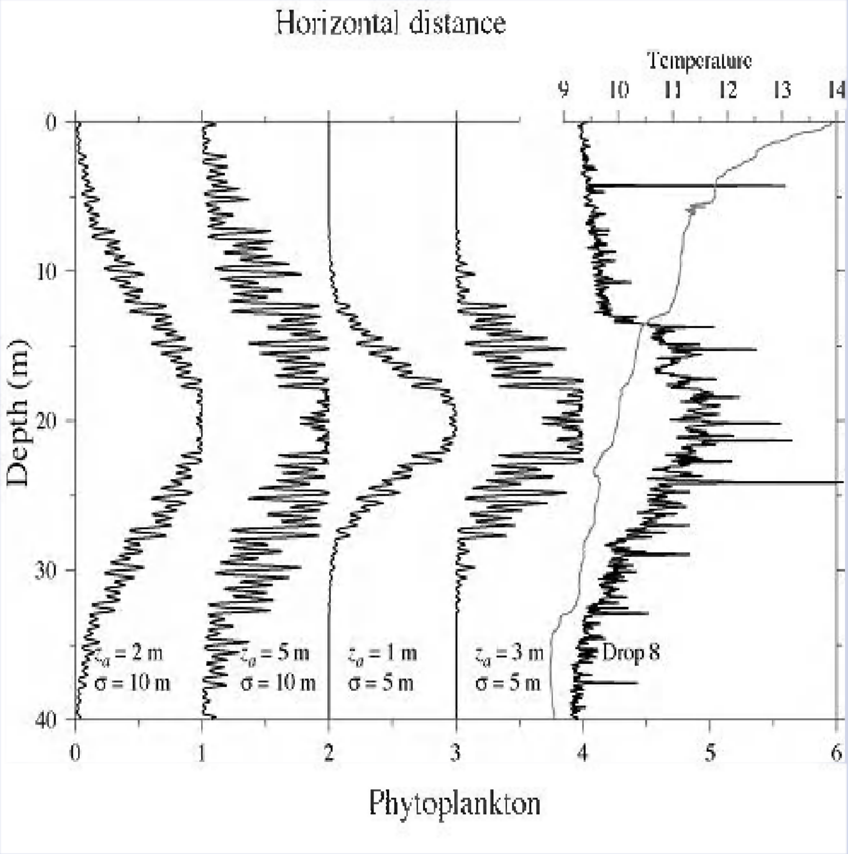
In the coastal ocean, where the circulation results from complicated interactions between the tides, bottom topography, coasts, wind forcing, density forcing and the response to rotational forces, there is strong vertical variation in the horizontal flow. As a result, lateral variations of any property, particulate or dissolved substance, can become transformed into sharper vertical variations. Weak horizontal gradients are thus transformed into sharp vertical gradients. Physical oceanographers refer to such metre-scale vertical variations in salinity, temperature and density as 'fine structure'. Thin layers of concentrated chemical and biological constituents are the chemical and biological equivalents of the fine structure in temperature, salinity and density. The important caveat is that the biological and chemical layers are also continually modified by biogeochemical as well as physical processes.

Biogeochemical processes interact and couple with physical motions, which may or may not bind the biological characteristics to specific layers of temperature, salinity and density. Nevertheless, it is the vertical shear of the horizontal currents, in conjunction with any horizontal gradients, which has the main role in forming both thin layers and fine structure. Crucial first-order measurements therefore include the vertical profile of the horizontal velocity measured by instruments such as ADCP and free fall profilers (Fig. 4). This has to be carried out with a vertical resolution at the scale of the thin layers and fine structure, and in conjunction with measurements of the vertical and horizontal variations of the physical, chemical and biological fields.

Vertical shear is created by the motion of one layer of water relative to another at a different depth. The shear can be broadly distributed vertically, or can vary substantially over vertical distances on the scale of metres in the ocean. Vertical shear is caused by factors including flow over topography, fronts, and near-inertial waves in the ocean. If a patch of phytoplankton exists, the vertical shear will tend to tilt and stretch this patch as one part is moved horizontally relative to another part deeper down. This shearing will create interleaved layers whose vertical extent is determined by the initial patch characteristics, and the temporal and spatial structure of the shear. This shearing mechanism may be ubiquitous, and will interact with other layer-forming mechanisms in determining the layer structure at any time (Box 2) (for details, see Birch et al., 2008).

BOX 2. Thin Layer Formation by Vertical Shear





Vertical shear is created by the motion of one layer of water relative to another at a different depth. The shear can be broadly distributed vertically, or can vary substantially over vertical distances of meters in the ocean. Vertical shear is caused by factors including flow over topography, fronts, and near-inertial waves in the ocean. If a patch of phytoplankton exists, the vertical shear will tend to tilt and stretch this patch as one part is moved horizontally relative to another part deeper down. This shearing will create interleaved layers whose vertical extent is determined by the initial patch characteristics, and the temporal and spatial structure of the shear. This shearing mechanism may be ubiquitous, and will interact with other layer-forming mechanisms in determining the layer structure at any time. (Top figure, redrawn from Birch et al., 2008; bottom figure, modified from Franks, 1995).

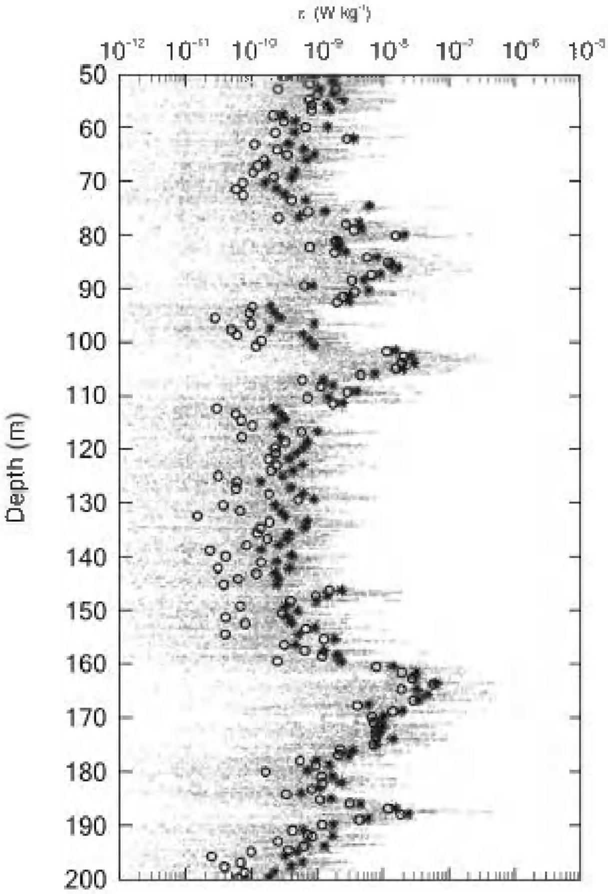


Fig. 5. Vertical profile of dissipation rates computed from dv/dz. Open circles are 1-m-average dissipation rate values computed from a conventional spectral method. Dots represent unsmoothed local dissipation data and the asteriks represent the average local dissipation rate over 1 m (Yamazaki and Lueck, 1987). (Reproduced with permission from Oceanography*).*

A.3. Turbulence

Turbulence is ubiquitous in the oceans but more relevant to the studies of phytoplankton is the variation in both space and time of its intensity and length scale. We have already described the larger scale motions which may be turbulent that define the bulk environment that HABs inhabit, and define the onset of the spring bloom for example via inhibition of mixing. However, at the individual level the actual phytoplankton of the size of 10-100 µm experience a much smaller scale of turbulence which determine their predator or avoidance strategies. The historical challenge has been to understand this much smaller scale.

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 which drives patchiness in plankton. Its intensity is normally higher near the sea surface and the ocean floor but can also be high in the thermocline associated with certain features such as breaking internal waves.

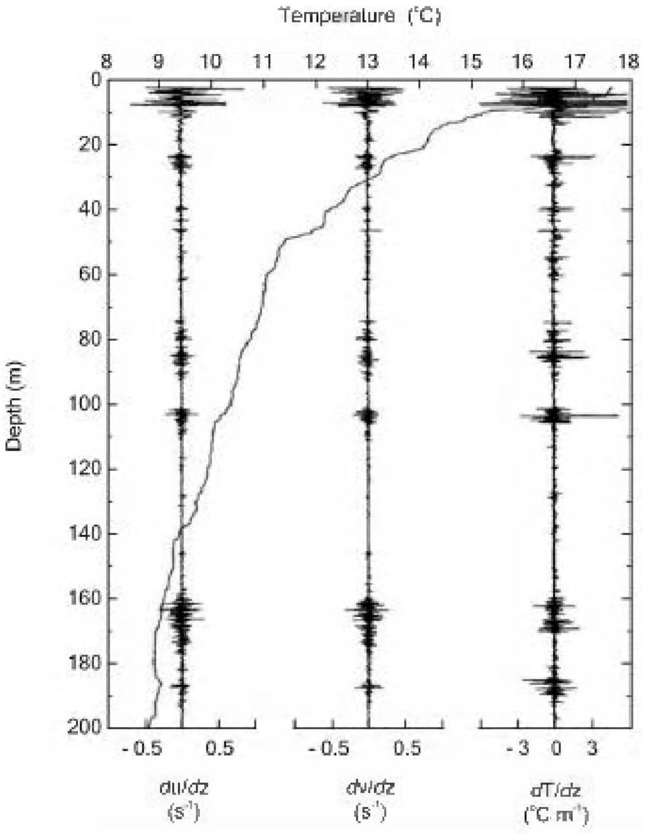


Fig. 6. Microstructure profile data obtained from a free-fall instrument Camel II. *The instrument measures two shears* (du/dz, dv/dz) *and vertical temperature gradient* (dT/dz) *as well as the temperature profile. Although the upper surface layer is still in a stratified condition, turbulence is active 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^{-1} rms velocity shear is roughly 7.5 x 10^{-8} W · kg^{-1}; see, for example, 103 m depth (Yamazaki and Lueck, 1987). (Reproduced with permission from* Oceanography*).*

Turbulent layers are usually patchy, with a typical thickness of a few meters. A 'patch' should not be considered to be a single overturn event from top to bottom, but rather a section of dissipation of turbulent kinetic energy which exceeds a certain threshold, for example 10^{-8} W · kg^{-1} (Fig. 5). Thicker patches are usually associated with stronger turbulence than thinner ones, and last longer. Internal gravity waves cause short-lived 'puffs' of turbulence, where the spatial scale is a few metres in thickness and less than an internal wavelength horizontally. Inertial-wave shear causes persistent patches that can last for several hours. Persistent patches are also found at interfaces of intrusions, for example, at the California undercurrent (Fig. 6).

Fig. 7. Holographic camera, developed at the John Hopkins University (Maryland, USA), on board IFREMER RV Thalassa *during the HABIT 2006 cruise (Photo: W. Pfitsch).*

It is now possible to measure ε, the rate of dissipation of turbulent kinetic energy, with some confidence. While existing data are useful for studying the influences of turbulence on trophodynamics, one must understand that a gap exists between the measurement requirements of physical oceanographers and the scales 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. Recent advances in technology and associated reduction in cost, such as the ADCP, have led to more extensive data being collected and from a greater range of environments at the cm - m scale than ever before. Two terms of the turbulent kinetic energy equation, i.e., dissipation and production, can now be measured although with limited precision (Simpson, 2005). On the other hand, microorganisms experience a true instantaneous velocity strain field. The difference between the 'local' dissipation rate experienced by cells and the one metre-average dissipation rate commonly used by physicists is quite large. To fill this gap future systems, such as particle imaging velocimetry (PIV), holographic cameras (Fig. 7) and 3D Doppler profilers are being developed. These systems rely on powerful *in situ* processing and are driven by a variety of optical, beam formation and computing challenges.

The challenge remains for physicists to collect turbulent data at all the length scales relevant to phytoplankton behaviour and thus observe events such as the *in situ* modification by an organism by changing viscosity of its physical environment. The consequences for modelling these events are significant, as the relevant scales have changed. The same parameters as used in large grid (10 ~km) obviously cannot be kept at the much smaller scales of thin layers. Downscaling, and the use of adaptive grids, are two of the techniques that have to be applied in modelling the phenomenon of thin layers.

B. Life within thin layers

The formation of a thin layer may be due either to an active behaviour of the population, whereby all cells tend to move to a specific zone or to passive accumulation because cells cannot grow elsewhere. Some phytoplankton species, including HABs, have evolved strategies allowing them to grow in the frequently sub-optimal conditions encountered in subsurface layers. These relate to their behaviour and physiology. A number of bio-physical interactions are also relevant to the maintenance of layers. The key problem is to determine the main processes controlling the evolution of a population of a species in a thin layer, and how these rank over the course of a bloom. First it is useful to consider the potential benefits and disadvantages of life within thin layers.

B.1. Advantages and disadvantages

The formation of thin layers can optimize population growth rates by concentrating the population where conditions are optimal for individual growth. An example of this is the formation of a thin layer in the upper part of the nutricline, which can optimize growth rates of photosynthetic harmful algae by concentrating the population where growth is no longer limited by low nutrient concentrations in the surface layer or by lower light levels deeper in the water column.

Secondly, high cell densities usually associated with sub-surface thin layers may result from optimal population growth under conditions that are suboptimal for individual cell growth. In other words, net growth may be higher for a lower cell growth due to limitations in population losses.

Thin layers are formed in locations where dispersal is low. Any population aggregating in these areas will optimize its net growth by minimizing dispersive losses. At high concentrations, cells can effectively use chemical defences that reduce losses and thus increase growth relative to competitors. These chemical defences 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. Formation of thin layers makes it possible for a species to modify the chemistry of its local environment, potentially enhancing immigration rates by providing a chemical signal to migrating algae. This could also enhance growth rates by promoting recycling processes, thereby increasing nutrient uptake or even modifying the local water properties, such as viscosity. It also provides a specific advantage in the case of sexual reproduction: increased density facilitates the encounter of gametes and hence the production of diploid stages in the life cycles, including dormant stages.

Formation of thin layers also has disadvantages. For example, the increase in cell density increases the likelihood of infection by bacteria or viruses or attack by other pathogens. The trade off between enhanced growth and minimal losses may not always work if chemical defences are inadequate. For example, if specific predator-prey relationships exist, thin layers can be open to opportunistic attack by grazers.

For any 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 in the thin layer. As the focus in the study of harmful algae is on single species, modelling should take into consideration these different processes, which are dealt with in more detail below.

B.2. Behaviour

Sexual recombination

As for the vast majority of organisms, sexual recombination is a key process to be considered in life cycles of phytoplanktonic species. With HAB species, it must be considered whether sexual reproduction is an

Fig. 8. Planozygote of Dinophysis acuminata *with two longitudinal flagella (Photo: E. Nezan).*

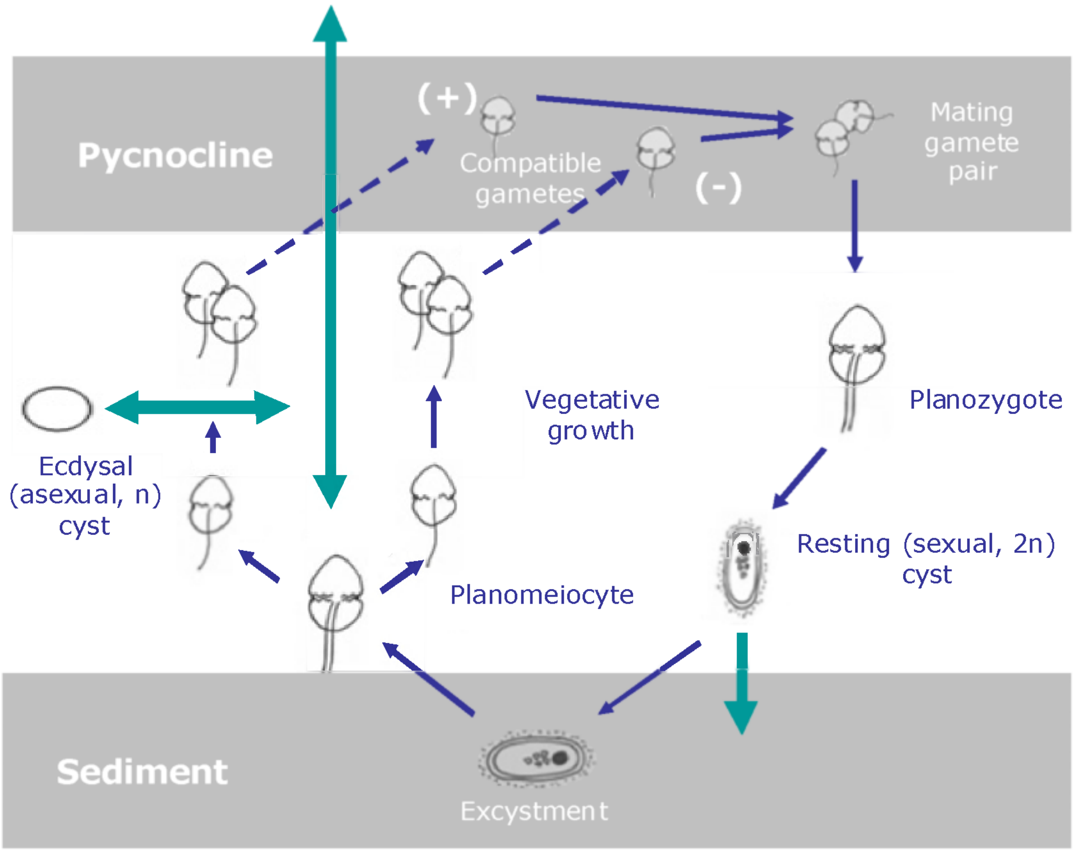


Fig. 9. Conceptual, ecological model showing the different life stages of a cyst-producing dinoflagellate. Vegetative cells migrate vertically whereas gametes stay in a layer to mate. (Modified from Persson et al, 2008).

obligate phase in their life cycle. Muller's ratchet theory (Muller, 1964) states that the number of deleterious mutations will decrease through genetic recombination from one generation to the next, and thus reduce the genetic load. Phytoplankton species have been present on a geological time scale, and have presumably managed to maintain their genetic integrity over geological time. These species are also engaged in a Red Queen's race* with parasites and viruses, running, or making substantial biological effort, just to stay in the same ecological place (Van Valen, 1973).

Species recombine in two cases: the first is intrinsic to the species and the other induced by adverse environmental factors. Diatoms provide many documented examples. Asexual cell divisions lead to a progressive reduction in cell size: this process leads to small-sized cells that then engage in sexual reproduction leading to large size cells once more (Edlund and Stoermer, 1997). It has also been reported that adverse environmental conditions may lead to sexual reproduction (Olson et al., 1986). Sexual recombination is obligatory after a given number of divisions but may also happen at any moment depending on the environmental context. Cells with two trailing flagella are *prima facie* evidence for sexuality (Von Stosch, 1973). Planozygotes of dinoflagellates have been observed both in cyst-forming species and in other species that do not necessarily produce cysts (Fig. 8).

Despite the large biodiversity of plankton, life cycles including the sexual recombination phase are seldom considered. In the ocean, sex is a battle against dispersal, and it is possible that high density aggregation, in thin layers, is a pre-requisite for sexual recombination. Since gametes must meet when needed, decreasing separation distance is the major challenge that phytoplankton species face (Fig. 9). They usually practice asexual clonal reproduction, which is one way of reducing the near-neighbour distance, but with an inevitable trade-off leading to an exponential loss of fitness with the increasing number of divisions.

Based on stochastic geometry, the nearest–neighbour distance d, between cells at cell density, c, estimated as $d \propto c^{-1/3}$, determines the characteristic time scale for planozygote formation (Rothschild, 1992). At low cell

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*The analogy is drawn from Lewis Carroll *Through the Looking-Glass.*

densities, this would be of the order of months (Wyatt and Jenkinson, 1997), a time considerably longer than the duration of a toxic event, making genetic recombination very inefficient at the population scale. The searching success of gametes could be improved by certain mechanisms, such as pheromone production associated with two-dimensional diffusion (Dusenbury and Snell, 1995), which could thus reduce the characteristic time.

Given that sexual recombination is constrained by a fixed number of divisions, and subject to unpredictable environmental stresses, it is conceivable that swimming cells have evolved a strategy to increase their encounter rate by aggregation.

Motility and migration

Depth regulation in phytoplankton is an ecological strategy; it requires physiological and biochemical adaptations that influence growth and survival of phytoplankton species in different hydrographic regimes. With respect to depth regulation, three general strategies have been identified—mixing, migrating and layer formation—that lead to a classification of organisms into mixers, migrators and layer formers (reviewed in Cullen and MacIntyre, 1998).

Diatoms and flagellates can regulate their depth either by changing their buoyancy or moving using their flagella. Some species can move faster than others when they form colonies. For example, chain-forming flagellates, such as *Gymnodinium catenatum*, can move faster than single cells of species with similar size and shape (Fraga et al., 1989). Laboratory experiments have shown that migration can be stimulated by nutrients or light; movement may be in a diel or cyclic fashion (see e.g., MacIntyre et al., 1997). Data on migration against time can show that some phytoplankton actively seek out an optimal depth for their existence. It has been shown that if they do not find such an optimal depth, plankton will keep moving up and down (Cullen, 1985). In some cases phytoplankton migrate, in other cases they do not. In addition, species of the same genus may exhibit different migration patterns, possibly due to different swimming capabilities (determined by their size and shape) and specific preferences for different water column structures (depth of pycnocline, intensity of temperature and salinity gradients). This might explain the alternation of *Dinophysis* spp. (*Dinophysis acuta* and *D. acuminata*) in Iberian waters (Escalera et al., 2006; Moita et al., 2006) during exceptional hot summers that lead to deeper and more stable thermoclines (Fig. 10). A single species may be able to switch behaviour pattern from migrating to layer forming during different nutritional modes (especially in mixotrophs) and/or stages of the population growth, as in *D. acuminata*, which was shown to perform diel vertical migration (DVM) in the Ría de

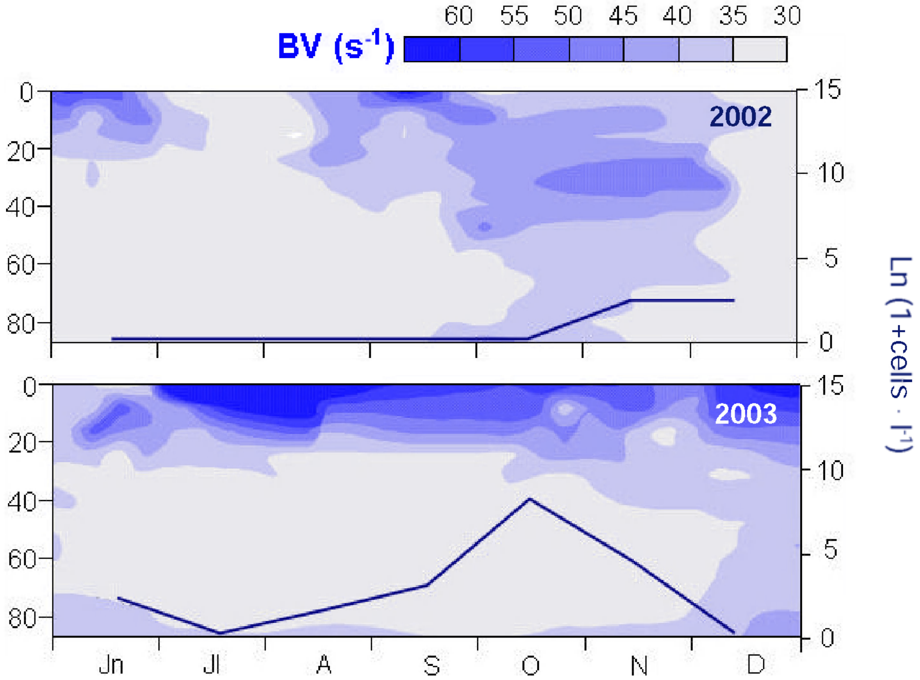


Fig. 10. Development of a Dinophysis acuta *population in Ría de Vigo during 2002 (above) and 2003 (below). Dense populations of this species develop only during hot summers, with moderate-low upwelling, that lead to a strong thermal stratification (high Brünt Vaïsala, BV. frequency). (Modified from Escalera et al., 2006).*

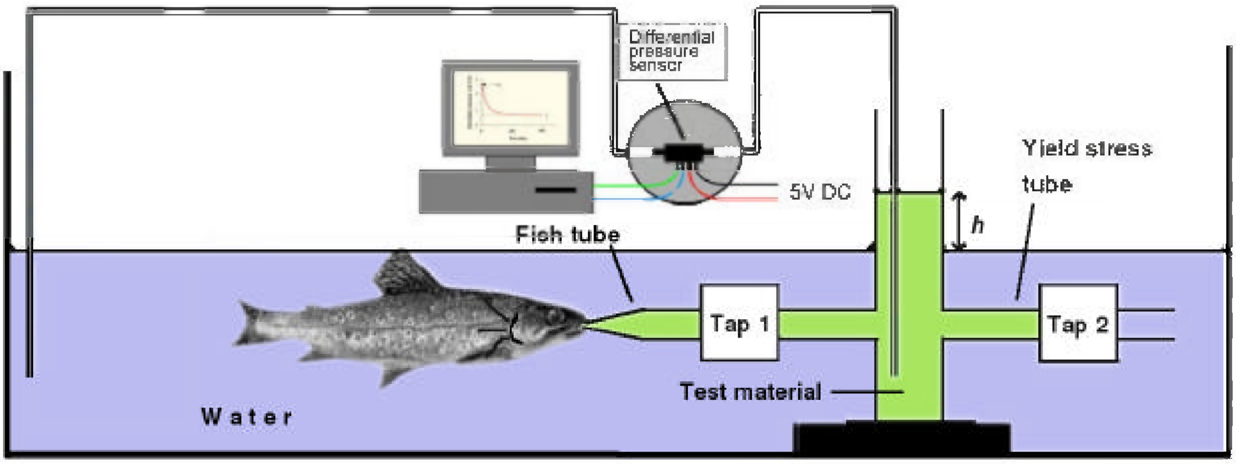


Fig. 11. Sketch of the Mark 3 ichthyoviscometer (not to scale), prepared with a fresly-killed young trout, used to measure rheological (mechanical) properties of seawater and cultures of mucilage-producing microalgae (Jenkinson et al, 2007).

Vigo (Villarino et al., 1995) at times, but to keep within a narrow surface layer at others (Velo-Suárez et al., 2008).

Sharples et al. (2005) published the results of a 25-hour cycle of observations made at a location in the Western English Channel in August 1999. The result showed boundary-generated turbulence penetrating into the subsurface chlorophyll maximum, resulting in the drawdown of chlorophyll and an observed injection of nutrients into the thermocline. These observations thus demonstrate the precarious balance of life in the subsurface chlorophyll maximum. This case is unusual in that the turbulence results from boundary processes. More usually the turbulence that influences the shelf sea thermocline is a result of shear across this thermocline (Rippeth, 2005).

Motility and migration can thus play a role in the establishment of thin layers. There is a balance between motility and small-scale physical forcing. Shear may prevent cells escaping out of a layer if they cannot swim fast enough and turbulent mixing may prevent net movement of cells in the direction of their swimming (Ross and Sharples, 2008).

With HAB species, it is very important to determine whether they perform DVM and if so, whether the species does it all the time or only at certain stages of population growth, or else under certain hydrographic conditions. The advantages of vertical migration also need to be clarified, whether it is to acquire nutrients from deeper waters, a phototactic response, or an aspect of social behavior.

Niche engineering

Niche engineering, also known as environmental management, is becoming increasingly recognised as an important part of natural selection of genes, both on land (Jones et al., 1994; Odling-Smee et al., 2003) and in the sea (Jenkinson and Wyatt, 1995; Wyatt and Ribera d'Alcalà, 2006). All organisms modify the environment by their presence, and in many cases it is evident that such modification increases their survival and reproduction. In plankton, modifications can include conditioning both the chemical and physical properties of the seawater. This conditioning of the environment immediately around planktonic organisms is mediated by the size and shape of the organisms as well as those of their colonies. Release of dissolved organic matter (DOM) and production of both particulate organic material (POM) and colloids are also important means used by organisms to engineer their environment (Castilla et al., 2007).

In layers of water within pycnoclines, gravitational forces restore any vertically displaced water parcels to their original vertical position relative to neighbouring parcels of similar density. Rather like elastic forces in a solid act to keep the solid together ('consolidate' it) in 3D, vertically-acting restoring forces in a pycnocline 'consolidate' the water layers within it, but only in 1D. Such vertically consolidated layers form ready-made structures supporting plankton species different from those in vertically mixed water.

Because weakly-bound colonies would be torn apart by turbulence, many turbulent-water diatoms either dispense with colonies altogether or form strong ones, held together by organic and/or siliceous polymers. A few turbulent-water flagellate species, notably the haptophyte *Phaeocystis*, also form polymerically bound colonies (Alderkamp et al., 2007; Seuront et al., 2006, 2007; Kesaulya et al., 2008). These colonies are bound together in 3D by the elastic restoring forces of their extracellular polymers.

In contrast, although many phytoplankters living in thin layers also secrete polymers, relatively few form tough colonies. Probably they do not need to as their ensembles are vertically consolidated by the already-mentioned gravitational restoring force.

Some planktonic organisms, including many dinoflagellates frequently associated with thin layers (e.g., *Karenia* spp.), secrete copious exopolymeric substances (EPS). Organisms tend to maintain their stoichiometry and, when one element like carbon is taken up in excess compared with nitrogen and phosphorus, they exude the extra carbon as mucopolysaccharides. Organisms such as these may have thus evolved to modify thin layers to their advantage by secreting viscous EPS into them, thereby increasing the viscosity of the water in the layer.

An imposed shearing stress (e.g., generated by wind stress at the surface), will produce a shearing rate proportional to the shearing force (e.g., wind stress) divided by the water viscosity. Most of the shearing in thin layers is vertical shear, $\delta u/\delta z$, i.e., the difference in horizontal water velocity between the top and the bottom of the thin layer over its vertical extent. When EPS from phytoplankton production increases viscosity it will therefore reduce vertical shear rate within the thin layer, transferring it to boundary layers bordering the top and / or bottom of the thin layer.

The tendency of thin layers to become turbulent is estimated by the Richardson number,

$$Ri=(g/\rho)(\delta\rho/\delta z)/(\delta u/\delta z)^2$$

where g is the acceleration due to gravity, ρ is the mean density of seawater in the thin layer or across the pycnocline, and $\delta\rho/\delta z$ is the change in ρ with unit depth across the pycnocline.

Turbulence opposes the tendency to stratify, keeping Ri around a critical value of 0.25. Increase in viscosity, by decreasing vertical shear rate, would thus increase Ri and reduce layer thickness. Secretion of EPS is likely to further reduce vertical turbulent diffusivity, K_z. K_z is a negative function of length scale, and this negative function will be increased by the granularity of EPS. It is important to measure and model the viscosity of heterogeneous EPS suspensions at the length scale appropriate to the process or structure in question (Jenkinson et al., 2007a,b) (Box 3, Fig. 11). Ultimately length-scale differences will have to be taken into account, because the viscosity due to EPS is largely contributed by soft flocs and particles (µm to cm) smaller than the vertical extent of thin layers (dm to m) (Jenkinson and Wyatt, in press). During the last decade rheologists have dealt increasingly with rheological phenomena in heterogeneous materials, both conceptually and empirically (e.g., Coussot, 2005), and oceanographers should solicit their help.

Another mechanism by which plankton may stabilize thin layers in the photic zone is by absorption of solar radiation, resulting in heating of the water (Lewis et al., 1983; Sathyendranath et al., 1991; Murtugudde et al., 2002). This may promote complex changes in ventilation of heat to the bottom mixed layer, and may result in increased air temperatures (Shell et al., 2003). Yet we do not know how local changes in viscosity can be measured *in situ* at the appropriate scale. It is only then that the effects of a more viscous and localized layer on the turbulent spectra can be studied, and hence gauge to

Box 3. The rheology of seawater

The shearing viscosity of seawater depends on the following parameters:

1. For the Newtonian component (the 'solvent viscosity' due to water and salt), temperature and salinity only.
2. The amount and nature of dissolved and colloidal organic polymers present.
3. The shear rate acting on the non-Newtonian excess viscosity due to the organic polymers.
4. Length scale(s) of the process of interest or of the measurement system, because flocculation and aggregation produces markedly inhomogeneous distribution of the excess viscosity.

what extent do local viscosity changes contribute to the maintenance of a thin layer.

Allelopathy and infochemicals

The production of allelochemicals—biologically active components eliciting specific responses in target organisms—may be an important mediator of intra- and inter-specific interactions of HABs in thin layer systems, and it is important to determine whether it is at work *in situ*. The compounds involved should be distinguished from low molecular weight inorganic and organic nutrients, and complex but poorly defined DOM that may be utilized as growth substrates by the HAB population. Although allelochemistry is not well understood in the sea, there are both advantages and disadvantages of allelochemical production in the case of aggregation of a given HAB species into a thin layer.

Allelochemicals are often invoked as agents of chemical defence, referred to as the 'watery arms race' *sensu* Smetacek (2001). Some known phycotoxins (domoic acid, ichthyotoxins, ciguatoxins, maitotoxin) demonstrate potent biological activity towards cells and tissues, usually affecting ion channels or enzyme function (Fossat et al., 1999, Sola et al., 1999, Cembella, 2003). However, only toxins which are released into the water may play a role in allelopathy. The allelopathic activity of *Alexandrium* probably involves a complex of chemicals, rather than a specific substance like STX (Arzul et al., 1999). A whole suite of new techniques needs to be developed for the study of allelopathic chemicals and their actions.

Recently, one of the fish-killing toxins produced by *Karenia mikimotoi* was synthesized in order to demonstrate its mode of toxic action: the non-specific inhibition of membrane ATP-ases can induce autotoxicity at high concentrations (Gentien et al., 2007). Toxin delivery to the targets is restricted by a relative short life in water; cells transport their own 'toxic cloud'. Various trade-offs have been evidenced, balancing the advantage of allelopathic production and the sensitivity to cell density. Based on these conclusions, the model of population growth—including a mortality rate that depends on shear—adequately reproduces the development of the population in the pycnocline layer and its dependence on wind-induced mixing. Thus, the allelopathic potential of this species is the critical process making wind events the major driving factor of population confinement. However, in most cases, the putative role of phycotoxins in chemical defence against predators or algal and bacterial competitors remains unresolved.

Infochemicals produced by phytoplankton species (including HABs) may play a critical role in cell-to-cell communication, involving processes as diverse as chemotaxis and the induction of sexuality and life cycle transitions (Wyatt and Jenkinson, 1997). Since known infochemicals are only produced in extremely minute concentration (typically sub-picomolar per cell), and solubility (particularly for lipophilic compounds) may be very limited in the aqueous medium, maintenance of the HAB population in a thin layer has the advantage of raising and sustaining the concentration of such biologically active metabolites.

Most of these hypotheses are not supported by experimental evidence. In any case, the activity of extracellular release of biologically active chemicals and their scale of action strongly depend on the balance between production at the cell surface, diffusivity and decay rate. A direct cell-cell contact is needed in some cases (Uchida, 2001) due to the short half-life of the toxic agents (Gentien et al., 2007). Conditioning of a layer by allelopathic agents or production of a 'cloud' of toxic agents may be considered only in the case of very stable allelopathic substances such as the sesquiterpenes produced by *Karenia mikimotoi* (Kajiwara et al., 1992).

Another mechanism leading to an advantage of concentrating in thin layers has been shown by Arzul et al. (1993): competition between *K. mikimotoi* and diatoms is suppressed since the dinoflagellate toxins inhibit diatom growth. The most important challenge is to further document these supposed effects *in situ*.

B.3 Physiology

Growth

The net growth r, that is, the numerical increase/decrease of a population P with time, is the balance between gains (cellular division, aggregation and physical advection) and losses (natural mortality, grazing, dispersion and sedimentation):

$$dP/dt = rP$$

$$r = \mu + I - E - g - m$$

where μ is the intrinsic division rate, I and E represent physically driven imports and exports, g is grazing and m is mortality (cell lysis, infections, sedimentation). The different rates depend on the dynamics of state variables other than growth rate, such as nutrients and zooplankton (grazing). A physiologist will take approaches tending to define the conditions for an optimal intrinsic division rate while an ecologist will be more interested in the environmental conditions promoting an optimal net growth of the population. In GEOHAB, the latter approach should be preferred (Box 4).

BOX 4. Thin layer maintenance and shear

Consider a thin layer of fluid with thickness *h*, length *l* and width *w*. The area of a parallelogram, *A*, when viewed from above is the product of the length times the width, and the volume *V*, the area times the thickness

$$A = l \cdot w$$

$$V = l \cdot w \cdot h$$

The total number of particles in the layer, N, is the number density, n, times volume

$$N = n \cdot V = n \cdot l \cdot w \cdot h$$

The number of particles per unit area is: $\frac{N}{A} = n \cdot h$

The reproduction rate per unit area is the product of the net growth rate, *μ*, and the number per unit area

$$\frac{N}{A} = \mu \cdot n \cdot h$$

As the fluid is stretched horizontally (in the direction of *l*), its volume remains constant and its thickness decreases

$$\mu \frac{dh}{dt} = \frac{h}{l} \frac{dl}{dt}$$

For the number of particles per unit area to remain constant, the reproduction rate must balance the loss due to thinning of the layer

$$\mu \cdot n \cdot h = - n \cdot \frac{dh}{dt}$$

Substitution produces: $\mu \cdot n \cdot h = - n \cdot \frac{dh}{dt} = n \cdot \frac{h}{l} \frac{dl}{dt}$

Simplification yields: $\mu = \cdot n \cdot \frac{dh}{dt} = \frac{1}{l} \frac{dl}{dt}$

If the stretching of the layer is due to vertical shear of the horizontal current:

$$\frac{dl}{dt} = h \left. \frac{\partial U}{\partial z} \right|$$

Thus for a layer to maintain a constant particle density per unit area:

$$\mu = \frac{h}{l} \left. \frac{\partial U}{\partial z} \right|$$

Using a value of 10^{-3} for the aspect ratio, and 10^{-2} s^{-1} for the shear, implies a value for the net growth rate of 10^{-5} s^{-1} or 0.86 d^{-1}, which corresponds to one every 0.8 d. The result is linear in the aspect ratio and the shear, so reducing their product by a factor of 10 would lead to a decrease in the population net growth rate needed for maintenance by a equivalent factor (*i.e.*, 0.08 d^{-1}).

(Prepared by T. Osborn)

It is essential to identify scenarios that promote the numerical increase of HAB populations in order to develop predictive capabilities of bloom development, duration and decline. These can result from *in situ* growth, behaviour (vertical migration, aggregation), physically induced accumulation (advection, downwelling, convergence areas), and physical-biological interactions. Simplified models are not generally designed to represent all the variability of an ecosystem, but they can provide the necessary framework for exploring different aspects of HAB outbreaks (Franks, 1997).

The specific division rate, μ, needs to be determined, as it is an important intrinsic parameter in the growth equation. This parameter estimates the potential for intrinsic division without the interference of losses due to grazing and physical dispersion (Carpenter and Chang, 1988). Even more important for modelling purposes is the estimation of μ_{max}, that is, the maximum potential division rate of the species under optimal conditions when resources are not limiting. Bulk measurements using chemical indicators, such as chlorophyll *a* concentration and primary production, may be appropriate if the target species constitutes a *quasi*-monoalgal population, as is frequently the case in *Karenia,* e.g., *K. brevis* (Tester and Steidinger, 1997) and *K. mikimotoi* (Gentien, 1998), blooms. This type of measurement is unsuitable, howselever, for growth studies of some HAB species, i.e., *Dinophysis* spp., *Alexandrium* spp., that often constitute a small percentage of the overall population. Estimates of μ in these cases are made from *in situ* cell cycle studies, which are more time-consuming but provide realistic information on the division capabilities of low-density populations (Reguera et al., 2003).

Grazing (*g*) may be an extremely difficult parameter to measure due to prey selectivity at the species level, and the variable effect of different phycotoxins in zooplanktonic organisms, (Turner et al., 1998). Above certain thresholds, phycotoxins may act as grazer deterrents to some microzooplanktonic organisms (Skovgaard and Hansen, 2003). But in some HAB events, the microzooplankton community (heterotrophic dinoflagellates, ciliates) may represent the major factor controlling bloom development (see review in Turner, 2006). A simplified approach to the estimation of grazing is to estimate rates of toxin transfer through different size-fractions of the food web (Maneiro et al., 2000).

In the last decade, cell lysis (natural mortality, pathogenicity, stress-induced death, etc.) has been recognized as a significant loss factor in population dynamics and species succession (Agustí et al., 1998). Changes in photochemical efficiency (Berges and Falkowski, 1998), reduction of primary productivity and loss of pigmentation (Veldhuis et al., 2001) provide good bulk information associated with population decline. Sensitive fluorescent viability (or live/dead) stains allow estimates of living and non-viable proportions of the population of a target species within the phytoplankton assemblage (Gentien, 1986; Bruusard, et al., 2001). Information on mortality caused by pathogens in natural populations is extremely scarce. Nevertheless, some recent information supports that, in some cases, bacterial and viral infections may be the cause of unexplained and sudden collapses of HAB populations (Bai et al., 2007).

If cells of a target species are accumulated in a thin layer, it would be very useful to have a growth rate measurement in the subsurface peak itself. It would be even better to have a description of the conditions that caused them to accumulate in this layer, as the growth rate may be due to a local enhancement in resources.

Modern instrumentation allows tracking of the maximum concentration of a target species (see section B4). Rate measurements at the thin layer (cell maximum) compared with those at other depths will support the interpretation of whether the cell maximum is a result of *in situ* division, physical accumulation, or a combination of both (Velo-Suárez et al., submitted).

Photoadaptation

The irradiance experienced by phytoplankton in a thin layer may vary if the layer is vertically displaced by physical processes such as internal waves. Such fluctuations in irradiance would be expected to induce physiological changes within the phytoplankton population. In order to improve our understanding of the processes involved in the establishment of thin layers, one important task is to determine whether phytoplankton species found in thin layers have specific photoacclimation strategies allowing them to cope with rapid variations in the light regime. In addition, the high concentrations of cells encountered in thin layers will dramatically reduce the Photosynthetic Active Radiation (PAR) and may cause self-shading (Fig. 12). In this case, one might ask if it would be more advantageous for the phytoplankton to be shade-adapted.

Phytoplankton possesses genetically determined photoadaptation characteristics that make them predisposed to a certain light regime. In addition, photoacclimation is a process that allows cells to adjust their photosynthetic characteristics according to the light regime in which they are growing. This is achieved by modifying pigment content, which leads to a change in the number or size of the photosynthetic units.

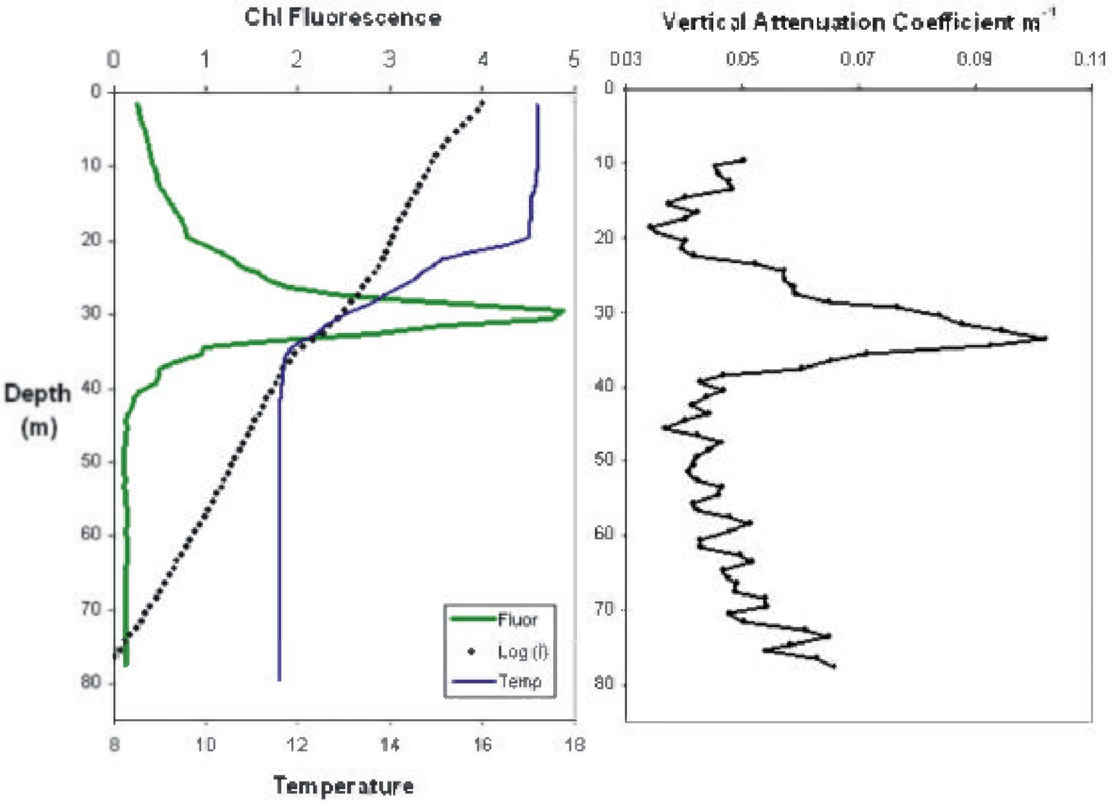


Fig. 12. The influence of thin layers on the irradiance environment. Note the irregularity in the vertical irradiance distribution caused by the thin layers, within which the vertical attenuation coefficient (Kd), although crudely estimated, increases to a maximum. The rise in Kd towards the sea surface is due to shading from the sampling platform. Data taken from station CO08216, July 2003 at the western end of the English Channel, South of the Scilly Isles (49 40'N; 06 18'W). (Figure courtesy of R. Raine).

Under low light regimes, an increased cell concentration of light-harvesting pigments (chlorophyll *a* and accessory pigments) will lead to more efficient light harvesting (Falkowski, 1984). Shade-adapted cells are characterized by a high maximum light utilization coefficient a^* and a low light saturated photosynthetic rate Pm^*. The saturation irradiance for these cells will be low; therefore, if these cells are brought into a high irradiance environment they are likely to be photoinhibited. On the other hand, at high irradiance, fewer photosynthetic units are required, pigment content will be lower and saturation will be reached at higher irradiance values. At very high irradiance, cells are susceptible to photodamage and therefore a lower light absorption and energy transfer to the photosystems may be an advantage.

In a fluctuating light environment, in order to fully exploit the light available, phytoplankton must be able to switch from light adaptation to shade adaptation within a short time period. Photosynthetic responses to fluctuating light regimes may occur on time scales ranging from minutes and hours to several days (Falkowski, 1984; Behrenfeld and Falkowski, 1997; Geider et al., 1998). On a short time scale, when cells are exposed to a high irradiance, energy dissipation may be achieved by quenching (Cullen and MacIntyre, 1998). On longer time scales, changes in the carbon-chlorophyll ratio can increase or decrease light absorption, or changes in pigment ratios can optimize light harvesting or photoprotection (e.g., xanthophylls' cycling).

The role of turbulence and mixing on light availability has been well studied in phytoplankton assemblages. In a well-mixed water column, if cells are displaced at a faster rate than their photoacclimation time, they will not be able to adapt to the changes in light level and are therefore likely to be adapted to the mean irradiance of the water column. If mixing is slower than the acclimation time, some taxa possess 'excess photosynthetic capacity', which allows them to exploit increases in irradiance. Others might be high-light adapted in order to avoid photodamage, even if this implies lower photosynthetic efficiencies in low light.

A stratified system, on the other hand, which may lead to the stabilization at a given depth in a thin layer, promotes acclimation to the light climate at that depth; however, this is not advantageous if the layer is displaced by internal waves. In addition, photoacclimation may allow cells to change their compensation depth by increasing the depth at which production is still higher than respiration.

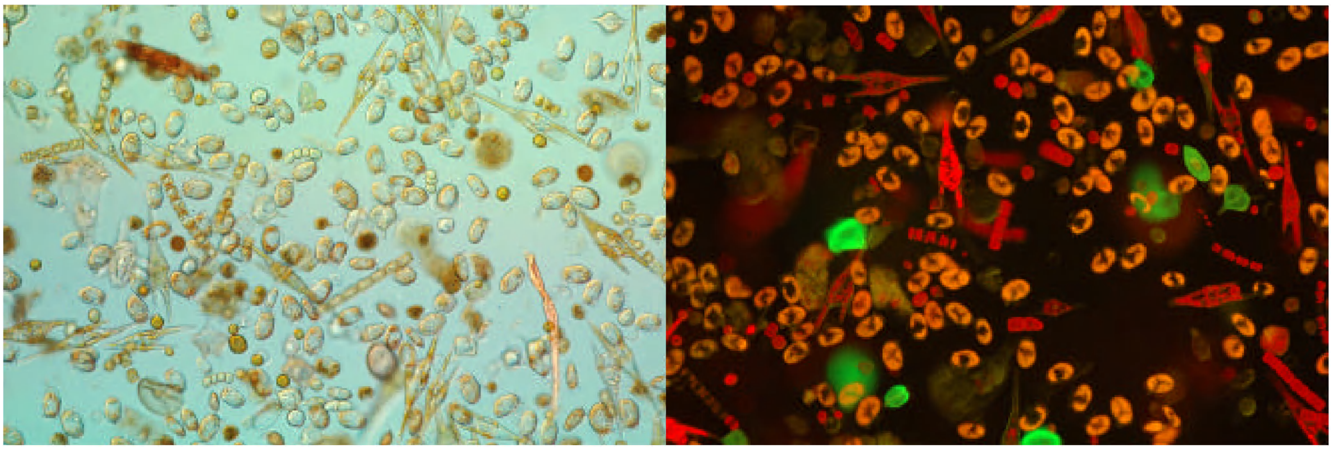
It is thought that photoacclimation may be suppressed under nitrogen limitation, because protein synthesis is required for chlorophyll synthesis (Geider et al., 1996). This nitrogen-dependence can be found in upwelling areas, where the high uptake rate of nitrate leads to a higher chlorophyll synthesis, thus favoring growth (Geider et al., 1997). Ultimately, the evolution of chemical conditions in thin layers (e.g., nutrient concentrations) will control a population's response to temporal changes in the light regime.

The research approaches which could resolve these issues are comparative studies of the P *vs.* I characteristics of phytoplankton in thin layers in relation to those of populations above and below them, and to determine to what extent photosynthesis *vs.* irradiance responses are genetically determined, that is, if there are inter-specific differences which give certain species an advantage over others.

Nutrition

Most HAB species do not rely solely on inorganic nutrients and are suspected to benefit from certain flexibility between nutrititional sources. An accurate picture of the nutritional sources for each species remains to be established, but a small amount of evidence has been published on osmostrophy (use of dissolved organic matter) and phagotrophy. Mixotrophic species of *Dinophysis* can be grown in the light with *Myrionecta rubra* as prey (Park et al., 2006; Kim et al. 2008) but also cells of *D. acuminata* have been found that contain cells of other dinoflagellates (E. Nezan, pers. comm.). Absorbing a cell of its size provides sufficient energy for multiple subsequent divisions. Standard models based solely on inorganic nutrition should therefore be used with great caution, although they could be useful as a first approach. Growth rate in the Droop model is completely independent of external nutrient concentrations and depends exclusively on the internal cell quota (Droop, 1968, 1974). Replenishment of storage after nutrient addition will lead to very high uptake rates (luxury consumption) uncoupled from growth rate. This separation of the mechanisms of uptake and growth reflects the principle that growth only occurs after the internal nutrient concentration reaches its maximum quota. High population growth rates therefore require a high cellular content in terms of limiting nutrients, and low growth rates occur when one or more nutrient contents are reduced.

The ability for luxury consumption among harmful species concentrating in thin layers needs to be assessed. Some species perform daytime and night-time vertical migrations, with the ability to reach the deep nitrate reservoir during the night. These species must somehow be able to take up nutrients and store them for use when light conditions become favorable for photosynthesis. However, when stratification becomes strong enough, a species like *K. mikimotoi* stops migrating and remains within the pycnocline (Gentien, 1998). It seems reasonable that cells do not migrate in the nutrient-depleted upper mixed layer and stay where there is sufficient upward N-nitrate flux from water below the pycnocline. Le Corre et al. (1993) demonstrated that 95% of the nitrogen flux is provided through ammonia and organic matter remineralization.



Live plankton sample (100 X) from Ria de Pontevedra (Galician Rías Baixas) dominated by Dinophysis acuminata*. Left, image taken with DIC microscopy; right, the same sample under epifluorescence microscopy, that highlights the characteristic phycoerythrin pigments found in mixotrophic species of* Dinophysis. Dinophysis *spp. are rarely reported as dominant in the microplankton community. They can certainly be so if the sample is taken at the precise depth where they aggregate. (Phto: B. Reguera)*

Nutrient scavenging can be a forcing mechanism for the vertical displacement of thin layers. The chemical composition of thin layers is a complex mixture of products derived from plankton secretions, re-mineralization and physical delivery, modified by nutrient uptake.

Species like *Karenia mikimotoi* secrete exopolymeric substances. Consensus has not yet been reached on the explanation for the factors involved in this process or on its purpose. The excretion of such substances into the surrounding water can induce changes on several levels. From a physical point of view it adds shear-thinning viscosity to seawater in the thin layer. From a biochemical point of view this dissolved organic matter can be considered as new substrate for other organisms. Under nutrient-stress situations, exudation due to an overflow of photosynthate might be expected to be dominated by non-nitrogenous compounds, or even just carbon (Anderson and Williams, 1998). This happens if fixation exceeds incorporation into new cell material, which can take place when certain conditions are met: phytoplankton gets trapped inside a thin layer, the nutrient supply stops, but the light is still sufficient to promote photosynthesis.

It has been shown that the release of organic compounds by phytoplankton is affected by the physiological state and nutrient ratios (Brockmann et al., 1983). This release will have an impact on the food chain because these compounds provide a carbon matrix that becomes available as a substrate for bacteria, thus fuelling the microbial loop (Williams and Yentsch, 1976). Some studies have revealed that differences in DOC and DON cycling do occur and are greatest during phytoplankton blooms (e.g., Kirchman, 1994) because the dissolved material produced by algae during these events is mostly DOC with little or no nitrogen. The uptake of this DOC will result in a simultaneous uptake of inorganic nitrogen.

The role of the microbial loop in thin layers needs to be established. It is often assumed that bacteria are more efficient competitors for mineral nutrients than algae due to higher affinity for P and N uptake. Considering the larger surface to volume ratio of small bacteria, this could be expected on theoretical grounds. If this assumption, based on experimental evidence, were true (and ignoring other limiting factors), bacteria would have the capacity to competitively exclude algae in many aquatic systems, and induce a change in their internal microbial dynamics and ecological structure composition.

However, C is another limiting factor for heterotrophic bacteria and they will rely almost entirely on algal products (excretion, mortality, etc.) as a source of C. If the habitat is spatially homogenous, the 'resource-ratio hypothesis' (Grover, 2000) predicts that bacteria could dominate over algae only when the supply ratio of organic C to P is high; thus alleviating the C limitation. So, whenever phytoplankton is stressed by the lack of nutrients, carbon is excreted in the form of DOM, promoting bacterial growth and increasing nutrient competition. Nevertheless, the overall result of this paradoxical relationship can never be a situation where bacteria outcompete algae completely.

The nutritional opportunities and growth stimulants to phytoplankton provided by thin layers might be enhanced, particularly to the species selected within them. The rain and decomposition of particles sinking from the overlying water column and captured within the thin layer will inevitably cause an accumulation of breakdown products which can enhance or impede phytoplankton growth. They may even select for the species present within the layer. These effects need to be established.

B.4. Physical-biological interactions

Turbulence and cell physiology

Most phytoplankton species that cause harmful blooms are smaller than, or very close to, the Kolmogorov length scale (Table 2). At this small scale, many biological aspects are conditioned both by the viscosity and by the velocity field of the aquatic medium. At the same time, however, the size, shape and behaviour (motility) of the cells, along with their life-cycle characteristics, should modulate their response to the physico-chemical properties of the water.

Investigating these small-scale interactions between physics and biology is not easy. It is in part approached through laboratory experiments that help to ascertain the underlying mechanisms of cell adaptations, although the experimentally generated turbulence can never, quantitatively or qualitatively, completely mimic nature. Figs 13 and 14 show experimental apparatus for creating turbulence in laboratory experiments.

The results experimentally obtained show that small-scale turbulence can interact with several physiological and biological processes in phytoplankton. For instance, the transfer of molecules in or out of the cells can be increased under turbulence. A decrease in nutrient limitation as a function of cell size has been described theoretically by Karp-Boss et al. (1996), and corroborated experimentally by Peters et al. (2006). Turbulence can affect the contact rates among plankters through direct or indirect mechanisms and thus interfere in grazing or mating rates (e.g., Marrasé et al., 1990; Kiørboe, 1997, and references therein; Stoecker et al. 2006). Differential

Table 2. The main characteristics of the velocity field, concerning direct effects on microalgae. can be described by the turbulent kinetic energy dissipation rate, ε *$[L^2 T^{-3}]$; the* rate of strain parameter, γ *$[T^{-1}]$, which is proportional to a velocity gradient or shear and represents the magnitude of the deformation rate due to mean velocity gradients in the flow fields –γ is dimensionally equivalent to $(\varepsilon/\nu)^{1/2}$–; and the* shear stress, $\tau \approx$ *mdu/dz (MLT^{-2}), where $\mu = \rho\nu$ is the dynamic viscosity (Thomas and Gibson, 1990). At the* Kolmogorov lenght scale *(λ_n, $\lambda_n = C(\nu^3/\varepsilon)^{1/4}$), the* inertial *force associated with the turbulent motions (which tends to create velocity fluctuations) is compensated by the* viscosity *force (which works to remove fluctuations in velocity). A: Rates of turbulent energy dissipation (ε), Kolmogorov length scales (λ_v) and strain rates (γ) for natural (A1) and experimental (A2) systems. B: Average turbulent energy dissipation in the upper 10 m, generated by wind (taken from Kiørboe and Saiz, 1995; calculated according to the model of MacKenzie and Legget, 1993).*

A1. Natural systems	ε $(cm^2 \cdot s^{-3})$	λ_v (cm)	γ (s^{-1})	**Ref.**
Lakes	$0.014\ 10^{-2}$ - $4\ 10^{-2}$	0.29 -0.07	0.1-2.1	1
Open ocean	10^{-6} -10^{-2}	1-0.10	0.01-1	2
Shelf	10^{-3} -10^{-2}	0.18-0.10	0.32-1	2
Coastal zone	10^{-3}-10^{0}	0.18-0.03	1.0 -10	2
Tidal front	10^{-1}	0.06	3.16	2
Tidal estuary (Severn)	$5\ 10^{-2}$ -5.5	0.07 -0.02	2.2 -2.4	1

A2. Experimental systems		ε $(cm^2 \cdot s^{-3})$	λ_v (cm)	γ (s^{-1})	**Ref.**
Animal cell cultures		0.6-1	0.036-0.031	7.7-11	3
Couette cylinders	Range	0.045-164	0.008-0.066	2.2-132	
	Threshold effect	0.18	0.048	4.4	4
Paddle stirrer		0.096-0.14	0.062-0.052	3.1-3.7	5
Orbital shaker*	100 rpm	2	0.027	14	6
	120 rpm	27	0.014	52	7
Vertical grid – 21 cylinders		0.0001	0.316	0.1	8
		0.005	0.100	1	8
		0.05	0.067	2.2	8
		1	0.032	10	8

B. Model Wind speed (m s^{-1})	ε $(cm^2 \cdot s^{-3})$	λ_v (cm)	γ (s^{-1})
5	$1.7 \cdot 10^{-3}$	0.16	0.4
10	$1.5 \cdot 10^{-2}$	0.09	1.2
15	$4.9 \cdot 10^{-2}$	0.07	2.2
20	$8.4 \cdot 10^{-2}$	0.06	2.9

References: 1. Reynolds (1994); 2. Kiørboe and Saiz (1995), with data compiled by Granata and Dickey (1991) and MacKenzie and Legget (1993); 3. Lakhotia and Papoutsakis (1992); 4. Thomas and Gibson (1990); 5. Dempsey (1982); 6. Berdalet et al. 2007; 7. Bolli et al. 2007; 8. Havskum et al. 2005. Modified from Berdalet and Estrada (2005).

** Orbital shaker - 3 cm orbit displacement, 3-1/4-l spherical flask.*

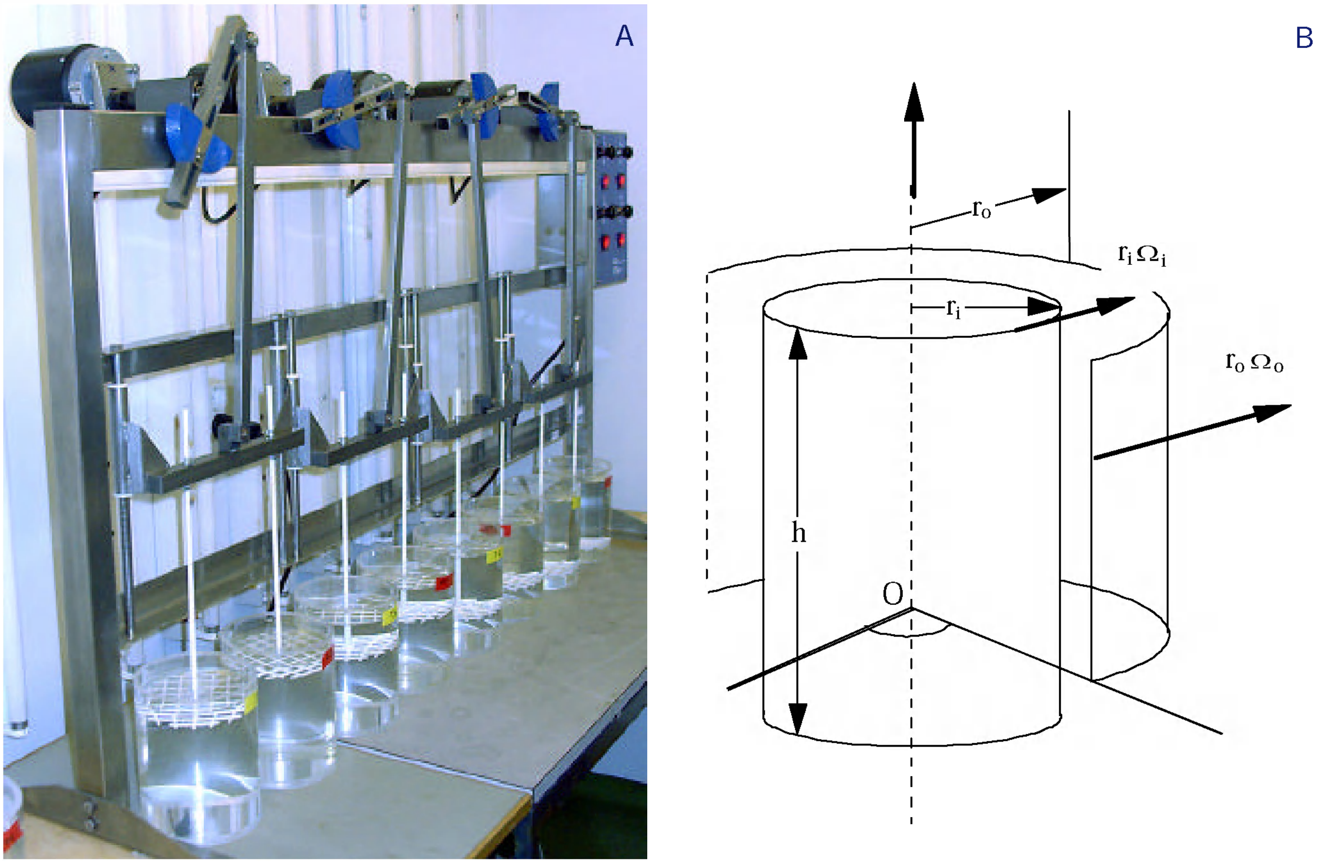


Fig. 13. Examples of two commonly used setups to generate turbulence in the laboratory. (A) The FERMETA system is used to generate turbulence in 2 l containers by means of vertically oscillating grids for laboratory experiments with plankton. FERMETA has a modular setup with 4 independent variable frequency AC gear-head motors in the standard design. Each motor may have a different nominal rotation speed, which can be reduced to 1/20th through a frequency controller. Thus, the setup allows for 4 different levels of turbulence to be tested simultaneously (2 replicate containers per motor) overcoming initial conditions variability. The container lids have a sampling port to introduce a glass tube attached to silicone tubing that allows withdrawing samples by gravity (Photo: F. Peters); (B) Couette cylinders: the relevant parameters and variables to calculate ε *are the radii of inner and outer cylinders (*r_i *and* r_o*, respectively) and their angular velocities (*Ω_i *and* Ω_o*, respectively) and the height of the cylinder (h) (modified from Berdalet and Estrada, 2005).*

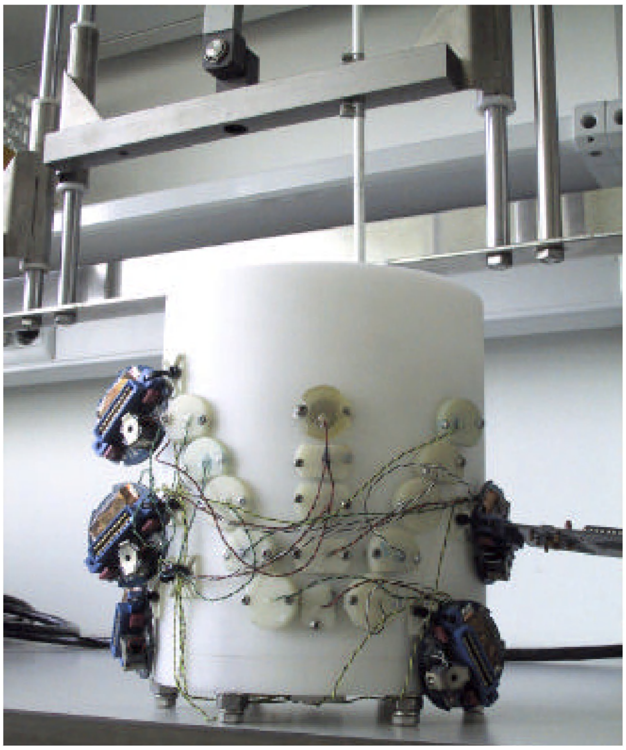


Fig. 14. Customized non-intrusive acoustic sensor system to measure grid-generated turbulence. The measurement container is made of Teflon. Acoustic emitter and receiver transducers are mounted flush with the inner container wall. Each measuring unit consists of one emitter and three receiver transducers to obtain 3D velocity (25 Hz sampling frequency) at one particular spot within the container. Electronics and data acquisition are standard for a Nortek AS NDV velocimeter. Velocity time series are treated mathematically to obtain the power spectra and the energy dissipation rates. (Photo: O. Guadayol).

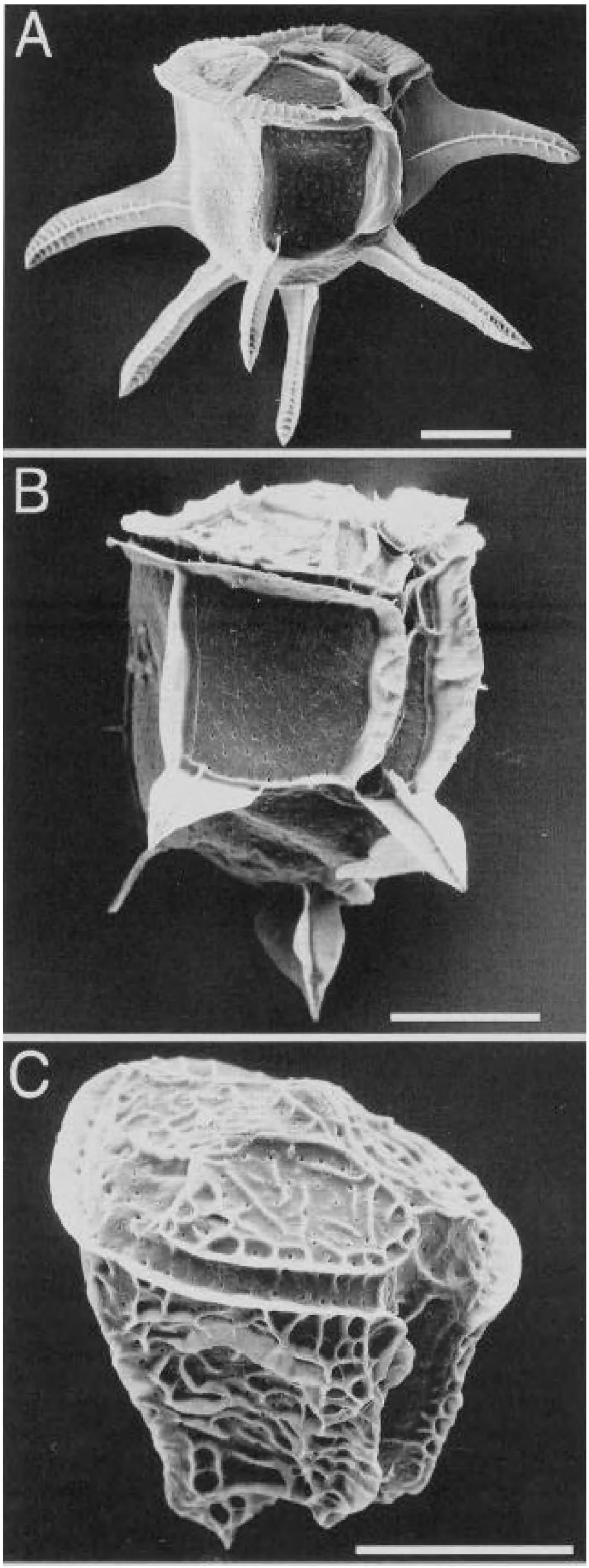


Fig. 15. Scanning electron micrographs of the different cell morfologies of Ceratocorys horrida *that illustrate the effect of turbulence on cell shape. (A) Long-spined cell from a culture maintained under still conditions; (B) Short-spined cell from a culture continuously agitated at 75 rpm for 22 d; (C) Spineless cell type observed in all cultures (scale bars = 20 µm). (From Zirbel et al., 2000; with permission from the Phycological Society of America).*

cell-settling and patchiness of the dinoflagellate *Ceratium tripos* caused by relatively high levels of turbulence, resulted in increased feeding rates by its predator *Fragilidium subglobosum* (e.g., Havskum et al., 2005). The motility patterns can be also altered under particular agitation conditions (e.g., Thomas and Gibson, 1990; Chen et al., 1998; Karp-Boss and Jumars, 1998; Karp-Boss et al., 2000; Berdalet et al., 2007). Overall, dinoflagellates appear to be particularly sensitive to small-scale turbulence (revisions by Peters and Marrasé, 2000 and Berdalet and Estrada, 2005), although the degree of response appears to be species-specific and dependent on the experimental setup and the turbulence intensity applied (Berdalet and Estrada, 1993, Sullivan and Swift, 2003). In dinoflagellates, changes reported as a result of turbulence include morphological (Zirbel et al., 2000) and cell size changes (e.g., Sullivan and Swift, 2003), mechanical cell damage and death (e.g., White, 1976; Thomas and Gibson, 1990; 1992; Juhl and Latz, 2002), alterations of cell division (e.g., Pollinger and Zemel, 1981; Yeung and Wong, 2003; Llaveria et al., *in press*), growth rate (e.g., Juhl et al., 2001; Sullivan and Swift, 2003), life cycle and toxin cellular content (Fig. 15). Most of those alterations have been observed under relatively high kinetic energy dissipation rates (ε). For instance, an ε intensity of ca. 2 $cm^2 \cdot s^{-3}$ –considered to occur in nature under strong storm conditions– caused a sharp decrease in the exponential growth rate of *Akashiwo sanguinea*, with a simultaneous increase of cell size and DNA content, and the arrest of net population development (Fig. 16). Under the same experimental conditions, *Prorocentrum triestinum* and *Alexandrium minutum* displayed similar trends, but with a less dramatic response (Berdalet et al., 2007). In all cases, when turbulence stopped, the cells recovered their normal properties and population increase resumed. In addition, under this high turbulence intensity, immediate cyst inhibition was observed in *Scrippsiella trochoidea* (Smith and Persson, 2005), *Alexandrium catenella* and *A. minutum*. Furthermore, in these two species, the cellular toxin content of stirred cultures decreased significantly compared with unshaken ones (Fig. 17). These results contrast with the significant toxin increase observed in *A. fundyense* cells exposed to turbulence generated by a Couette device (Juhl et al., 2001) at about 0.1 $cm^2 s^{-3}$ (corresponding to moderate gale conditions).

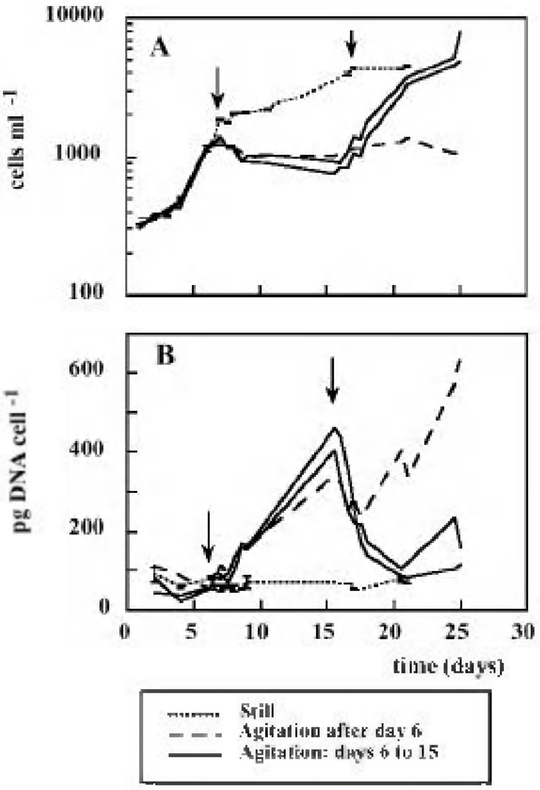


Fig. 16. Temporal changes on cell abundance (A) and DNA content per cell (B) in cultures of Akashiwo sanguinea *maintained under still conditions or exposed to the turbulence generated by an orbital shaker at ca. 2 $cm^2 s^{-3}$. Arrows indicate the start and the end of the turbulent period. Three flasks were exposed to turbulence on day 6 while 3 remained still as controls. On day 15, two shaken flasks returned to stillness while the third one remained in the shaker until the end of the experiment. (Redrawn from Berdalet 1992).*

Understanding the fundamental mechanisms of these responses to turbulence constitutes a significant challenge that requires sophisticated biological techniques. In addition, the relevance of these results in the context of natural HABs, development and fate of harmful dinoflagellate blooms should be considered with caution. In nature, such ecophysiological responses of the organisms will interact with other biological factors and with the environmental forcing and water circulation at a variety of spatio-temporal scales, together resulting in the community and hence, HAB, dynamics. For instance, phytoplankton blooms are uncoupled from grazing and are normally terminated by sedimentation (Kiørboe et al., 1996); physical processes control maximum particle concentrations in planktonic systems (Jackson and Kiørboe, 2008). A model elaborated by Jackson (1990), and reviewed by Jackson et al. (2005), reproduced a realistic bloom termination. Achievable critical algal concentration is inversely related to fluid shear, algal size and stickiness. Stickiness varies during the time course of a bloom according to the physiological condition of the species and is difficult to evaluate. Shear rate depends on wind and tidal forcing stresses and on the local viscosity of sea water. To reproduce the 'crash' of phytoplankton populations, it is of the utmost importance to understand these individual processes.

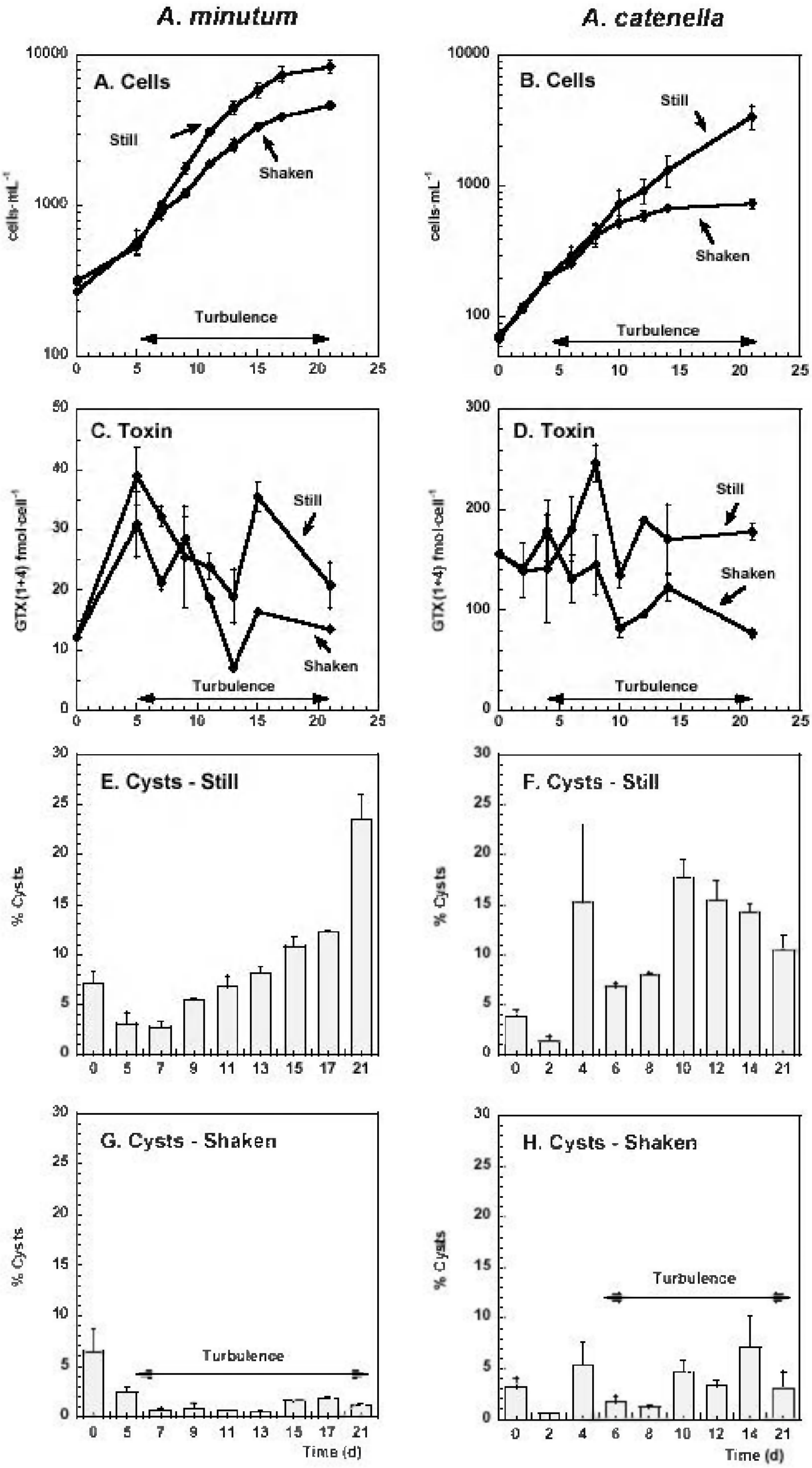


Fig. 17. Responses displayed by Alexandrium minutum *(A, C, E, G) and* A. catenella *(B, D, F, H) to the same experimental conditions as those used in the experiment from Fig. 16. The two species showed lower cell numbers (A, B) and lower cellular toxin content (C, D) in the shaken than in the still treatments.* A. minutum *had a decreased growth rate under turbulence (A). Those responses were evident after 4 days of shaking. However, immediate decrease in the percentage of ecdysal cyst numbers occurred in the turbulent cultures (G, H) compared to the unshaken ones. (Modified from Bolli et al., 2007).*

Another main challenge is the simultaneous measurement of the *in situ* variability of both turbulence and biological dynamics with appropriate spatio-temporal resolution. Recent advanced technology on microelectronic and acoustic equipment should make a relevant contribution to the study of physical and biological interactions at a small scale.

New observational tools have clearly shown that layers extending vertically tens of centimetres are common features of plankton in stratified systems (Cowles et al., 1998; Widder et al., 1999; Dekshenieks et al., 2001; Rines et al., 2002; Franks and Jaffe, 2006). These thin layers are often associated with the main sub-surface chlorophyll maximum, but may also be found at other locations within the water column (Dekshenieks et al., 2001). In stratified environments where there are suitable growth conditions (nutrient availability and light), the important physical factors potentially involved in the formation of thin layers are vertical shear, density steps and gradients in turbulence. Among the biological processes at work are algal capabilities for depth control through swimming and buoyancy control, growth and mortality, and physiological adaptations (e.g., Derenbach et al., 1979; Franks, 1995; MacIntyre et al., 1995; Alldredge et al., 2002).

Modern observational techniques are now able to measure the physical dynamics and biological distributions, but quantifying *in situ* biological dynamics (growth rate and swimming behaviour) is more difficult.

Recent advances in knowledge about thin layers have been achieved by the application of novel technologies and experimental approaches. Some examples of new technologies and instruments include

- Free-falling autonomous planar laser imaging fluorometer (Franks and Jaffe, 2006) (see back cover)
- *In situ* Particle Imagery Velocimetry (Nimmo-Smith

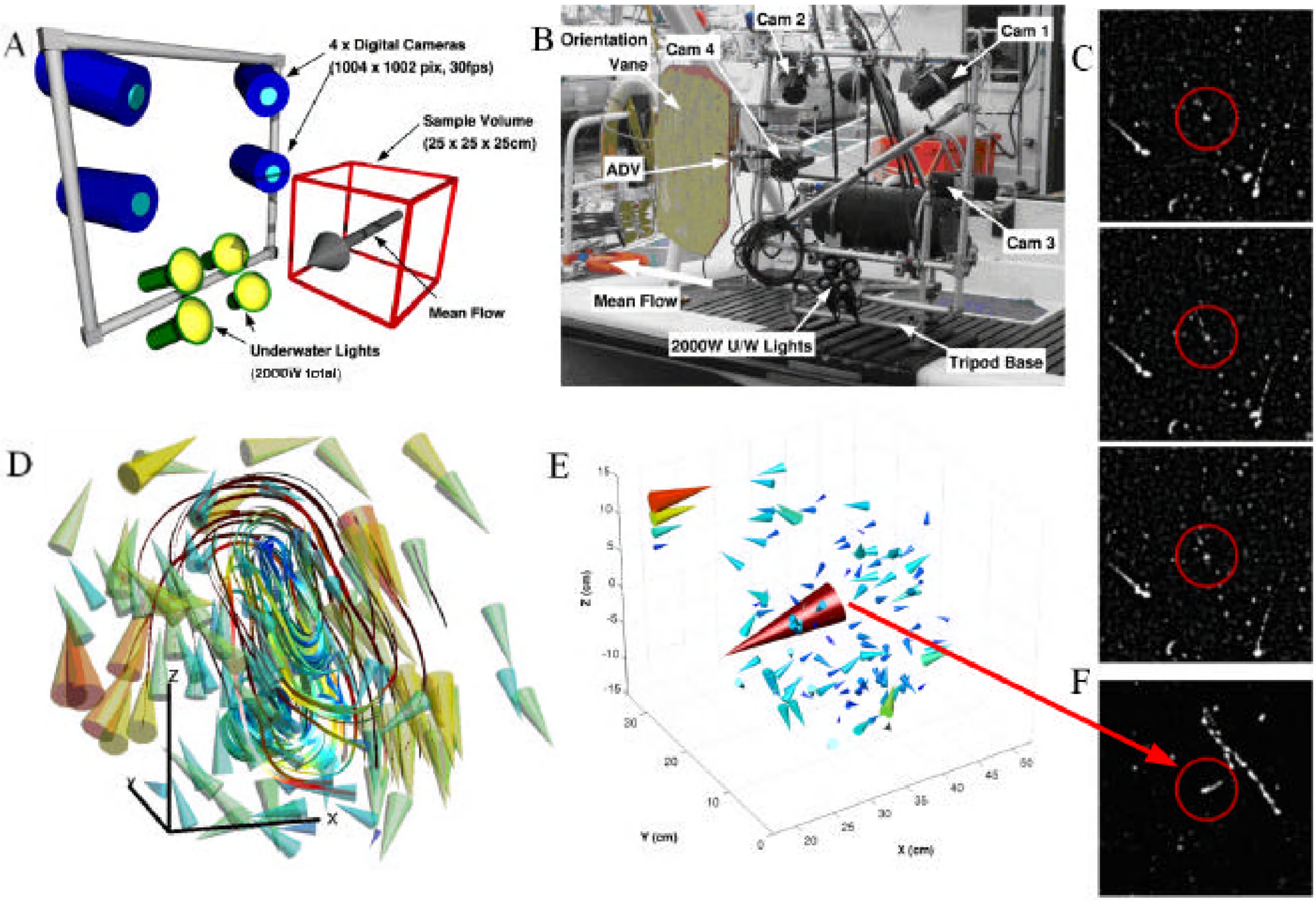


Fig. 18. A novel submersible 3D Particle Tracking Velocimetry (3D-PTV) system (Nimmo Smith, 2008) offers the opportunity to record the instantaneous 3D distribution and track the relative motion of naturally occurring particles (plankton and other suspended material) in the coastal ocean. Multiple cameras (a) viewing an illuminated volume from different angles, and mounted on a rigid framework (b), acquire sequences of high-resolution images of suspended particles (c). Processing software maps the 3D distribution of the particles and tracks them over image sequences giving distributions of 3D particle motion (d). Non-passive particles have been observed moving at a different velocity to the mean particle motion (e). In this case (f), a fish larva is recorded swimming against the flow. It has a body length of 4.2mm and swims at 7.6cm/s (or 18.2 body lengths per second). (Figure courtesy of W.A.M. Nimmo-Smith).

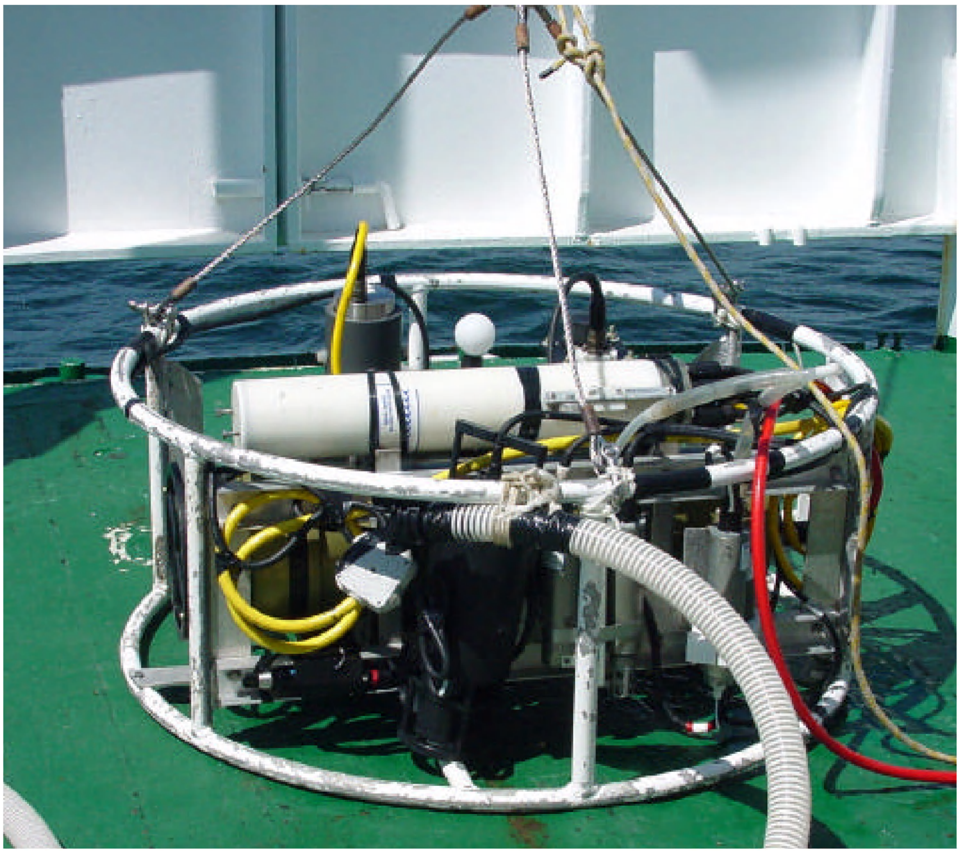


Fig. 19. The IFREMER high-resolution particle size/CTD/video system is a profiling instrument that describes the hydrography and the particle characteristics of the water column with a very high precision. It can distinguish between multiple layers even within a stepped thermocline (Photo: IFREMER, Brest).

et al., 2002; Nimmo-Smith, 2008) (Fig. 18)

- High-resolution pump and bottle sampler (Lunven et al., 2005) (front cover)
- High resolution turbulence and fluorescence profiler (Yamasaki, TUMST)
- *In situ* video microscopy and imaging (Davis and Gallagher, WHOI; Lunven et al., 2003) (Fig. 19)
- Holography (Sheng et al., 2003; Malkiel et al., 2006) (Fig. 7)
- Profiling system (Dekshenieks et al., 2001)
- Autonomous vehicles such as gliders, AUVs (front cover) and profiling floats for coastal areas.

These novel instruments are enabling us to identify and characterize thin layers in near real-time. The simultaneous measurement of physical, biological and chemical properties on the same spatial and temporal scales is an essential element in helping to improve our understanding of thin layer dynamics. Deployment of combinations of these instruments will provide unprecedented views of the microscale structures of the plankton, and their relationship with their physical, chemical and biological environment.

Combining the novel insights gained from new instruments with directed experimentation and modelling will provide us with a unique ability to understand and predict the dynamics underlying the formation, maintenance and dissipation of thin layers. This will provide us with an increased ability to predict when and where such layers will form, and their potential to be formed by HAB species. Understanding the dynamics of these HAB layers will contribute fundamentally to our understanding of HAB dynamics in general, as well as leading to an improved understanding of the broader marine planktonic ecosystem and how it is structured and influenced by its environment.

IV. Key questions to be addressed in understanding the ecology and oceanography of HABs in stratified systems

A number of outstanding scientific issues have been identified in this report. These have been synthesized below into a series of key generic questions, under which some relevant sub-questions are listed. In general these follow a similar subject order to that of the scientific section in the report.

1. What are the turbulence length scales relevant to harmful phytoplankton and the formation of thin layers?
    - How do we measure turbulence at these scales?
2. What are the main processes controlling the population evolution of a given species, and how does their ranking vary over the time course of a bloom?
    - Is high density (aggregation) a pre-requisite for sexual recombination?
    - Do HAB species migrate?
        - Do they vertically migrate all the time or only at certain stages of the population growth or under certain hydrographic patterns?
        - What are the gains of vertical migration
            - acquisition of nutrients from deeper waters?
            - phototactic responses?
            - social behaviour to promote sexual encounters?
            - aggregation around some unknown cue?
    - Is the high cell density in the thin layer due to *in situ* division and passive accumulation in density discontinuities or does it result from aggregation?
3. How can we quantify modifications in turbulence by phytoplankton through changes in the viscosity of its physical environment?
    - What are the effects of a more viscous and localized layer on the turbulent spectra?
    - To what extent do such local changes contribute to the maintenance of a thin layer?
    - Can the changes in vertical diffusivity be inferred?
4. What nutritional opportunities do thin layers provide to phytoplankton, especially to the species selected within thin layers?
    - Is growth rate in the thin layer higher due to a local enhancement in resources?
    - Do the accumulated breakdown products, resulting from the rain and decomposition of particles sinking from the overlying water column and captured in the thin layer, enhance or impede phytoplankton growth and do they select for the species present?
    - What is the role of the microbial loop in thin layers?
5. Are allelopathy and ‘chemical warfare’ at work *in situ* within thin layers?

V. Framework activities

According to the GEOHAB *Implementation Plan*, Framework Activities are those activities that are not research, but will facilitate the implementation of GEOHAB. They serve to enhance the value of the research by ensuring consistency, collaboration, and communication among researchers.

A. Scientific networking and co-ordination of resources

GEOHAB CRPs will be co-ordinated by the GEOHAB SSC through the establishment of separate sub-committees for each CRP, composed of SSC members and leaders of CRP activities. The sub-committees will primarily work by correspondence, but may also meet on an opportunistic basis and when identified resources allow for meetings to address major planning and co-ordination issues. The sub-committee for each CRP will work with the GEOHAB SSC to encourage scientific networking and co-ordinate research activities and resources.

An important aspect of international activities like GEOHAB is the sharing of scarce resources among participating nations. Such sharing makes possible research activities of a scale and breadth that are not otherwise feasible, and thereby enable the comparison of ecosystems of a similar type in different parts of the world. The CRP–HABs in Stratified Systems will promote the application of national resources, in terms of scientific expertise, sampling platforms and equipment to the key research questions identified in this document. GEOHAB has already initiated the sharing of expertise and development of an international research community on the topic of HABs in stratified systems by supporting the OSM on this topic.

GEOHAB will continue to promote sharing of expertise by establishing a CRP Sub-committee to help implement this research plan. Presently, international GEOHAB activities are sponsored by funding from IOC and the U.S. National Oceanic and Atmospheric Administration, and from SCOR (through grants from the U.S. National Science Foundation). Development of the CRP–HABs in Stratified Systems will depend on increased funding from other national and international organizations.

GEOHAB will identify, and draw the attention of responsible bodies to opportunities for co-ordination of resources that will add value to ongoing and planned research. Individuals involved in studying each key question will be responsible for developing plans relating to the sharing of expertise and equipment and how they will contribute to the continued co-ordination of the CRP.

GEOHAB and the CRP Sub-committee will encourage the publication of results from the CRP–HABs in Stratified Systems in relevant peer-reviewed scientific journals, with appropriate reference to the relation of the research to GEOHAB. In addition to this publication in the primary scientific literature, GEOHAB will seek to disseminate both the programme status and research results more broadly to the worldwide community of managers and scientists interested in HABs. *Harmful Algae News* is distributed regularly by the IOC and is available as a forum to communicate news of GEOHAB activities and research results. It is the responsibility of each CRP sub-committee to announce events, calls for proposal contributions, availability of core research working documents and results, and summaries of these, in *Harmful Algae News* and at the GEOHAB Web site (www.geohab.info).

The CRP Sub-committee will promote the involvement of individuals from the world-wide community of HAB scientists and others studying stratified systems in various ecosystem types and the association of HABs with these systems. The Sub-committee will also assist the scientific teams working on the different questions to work together. Successful conduct of research on this topic will require the pooling, co-ordination, and joint use of several different types of measurement platforms:

1. Ships may be used to (a) conduct transects or grids of stratified systems and (b) track blooms of interest to investigate various aspects of bloom population dynamics.
2. *In situ* observing systems will be needed to establish appropriate time-series data sets. A variety of systems are already installed in, or planned for, stratified systems in support of the GOOS. The CRP Sub-committee will contact the GOOS Regional Alliances (GRAs) for help.
3. Satellites may be helpful to detect bloom events, allow adaptive sampling and extrapolate ship-based and *in situ* measurements to regional scales.

B. Data management and data sharing

The collective value of data is greater than its dispersed value and comparative research requires effective data sharing among scientists working in different regions; therefore, data management and exchange are important components of GEOHAB CRPs. The development of an appropriate GEOHAB data management plan is a fundamental and critical activity upon which the ultimate success of GEOHAB will depend, and GEOHAB is working with other international marine research projects to develop basic guidelines for data management and sharing (see http://www.scor-int.org/DMReport.pdf). Each CRP will need to develop its own specific plans, conforming to the principles adopted by GEOHAB.

GEOHAB will use a decentralized data management and distribution system with a centralized metadata[1] index. The components will include a comprehensive inventory of databases relevant to GEOHAB, as well as metadata, with links to their locations and contact persons. Each CRP will create an inventory of data and data products. The GEOHAB Data Manager will assist the CRP by tracking planned, ongoing, and completed research, and by providing links to research information. All investigators should be prepared to share their data and data products with other investigators in their research projects as soon as possible, and with the general scientific community within two years from the time those data are processed, and should recognize the 'proprietorship' (rights to first publication or authorship) of data acquired from other investigators. Each GEOHAB CRP should address the long-term archival of observational data and data products to ensure a lasting contribution to marine science. GEOHAB overall comply with IOC data policy (http://www.iode.org/policy). Specifically, data from the CRP–HABs in Stratified Systems will be contributed to the World Data Centre for Marine Environmental Data (WDC-MARE) at the end of the project, with the assistance of the GEOHAB data manager.

C. Protocol and quality control

Specification of protocols within elements of the CRP–HABs in Stratified Systems will ensure that data generated are reliable and compatible, thereby facilitating synthesis and modelling. Each key question will require measurement of somewhat different parameters, although for each question, a set of parameters should be measured in each region. Likewise, the CRP–HABs in Stratified Systems will include a set of core parameters that will be measured in each location. This information will make it possible to draw inferences across systems, construct models of HABs in stratified systems, and to contribute information that will be useful for other CRPs. The GEOHAB SSC will work with CRP sub-committees to identify GEOHAB and CRP core parameters, as well as the standard measurement protocols and any appropriate standard reference materials.

Recommendations on methods and measurements will be disseminated through the GEOHAB Web site. The methods adopted to ensure quality control and the protocols used for data collection will be fully documented in metadata accompanying data sets.

Where possible, well-defined, internationally agreed descriptions of methods will be adopted. Where required, the GEOHAB SSC will initiate Framework Activities that lead to the development of appropriate protocols and methods to ensure data collection in a uniform manner for comparative studies. GEOHAB investigators retain the primary responsibility for quality control and assurance.

D. Capacity building

GEOHAB encourages a 'training through research' approach that offers opportunities for student participation in cruises and instruction in marine research disciplines relevant to HABs. Exchange of post-doctoral fellows and senior scientists are equally important for the CRPs. Training activities that would benefit GEOHAB research will be organized by the GEOHAB SSC and proposals for specific training activities can be submitted to the SSC for endorsement as GEOHAB activities. An important aspect of capacity building will be the transfer of technology for research, observations, and modelling.

E. Co-ordination of modelling activities

This Core Research Project identified priority research questions in order to assess and quantify the relative importance of basic processes acting upon a population of interest. As thin layers may be encountered everywhere, these questions are relevant to a variety of ocean systems studied in the other GEOHAB CRPs. The most appropriate modelling tools will have to be selected and adapted from likely to be existing procedures such as Lagrangian models, rules-based models, downscaling exercises, adaptive grids, etc.

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[1] *Metadata are information about data, including information that allows data sets to be located (discovery metadata: what was measured, when and where), information that enhances human understanding of the data and the uses to which it can be put (semantic metadata) and information that allows software agents to access the data (technical metadata).*

GEOHAB will therefore identify relevant existing modelling activities through a workshop planned for June 2009 in Galway, Ireland. This workshop will assist the CRPs by

- improving understanding of HAB processes through linkage of models, *in situ* observations, and remote sensing;
- encouraging the use of advanced data assimilation techniques in HAB modelling;
- encouraging the use of observing system simulation experiments (OSSEs) in array design;
- stimulating modelling activity in GEOHAB Core Research Projects (CRPs);
- fostering linkage between HAB modelling and the broader community of biogeochemical, ecosystem, and population dynamics modelling;
- entraining researchers at all levels (students, postdocs, faculty, etc.) into HAB modelling;
- facilitating dialogue between model developers and HAB researchers involved in process studies through joint training sessions;
- improving capabilities for prediction of HABs and quantitative assessment of their skill;
- improving forecast products and their dissemination to maximize their benefit to the user community; and
- developing a written glossary for problematic terminology.

F. Interaction with other international programmes and projects

GEOHAB exists in the context of several other large international programmes and projects that study aspects of global change that could be relevant to the CRP–HABs in Stratified Systems:

- The Global Ocean Observing System (GOOS) could provide important information for the CRP–HABs in Stratified Systems, insofar as GOOS provides long-term continuous monitoring in stratified areas.
- GEOHAB could work with the Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) project on their common interests of controls on phytoplankton blooms.

VI. Next steps

This document will form the basis for a Core Research Project of GEOHAB. Several steps have to be taken following publication of this plan, to ensure that research is funded and co-ordinated appropriately:

1. The plan must be disseminated to the interested research community and to the national agencies that might fund this research. National GEOHAB committees, when they exist should help in this effort. This step will be more effective if carried out by national scientists, but SCOR and IOC will also help distribute the plan to their member nations.
2. National and international teams of scientists must propose research related to the key questions and affiliate their research to international GEOHAB, to ensure that the overall CRP-HABs in Stratified Systems is co-ordinated (Fig. 20).

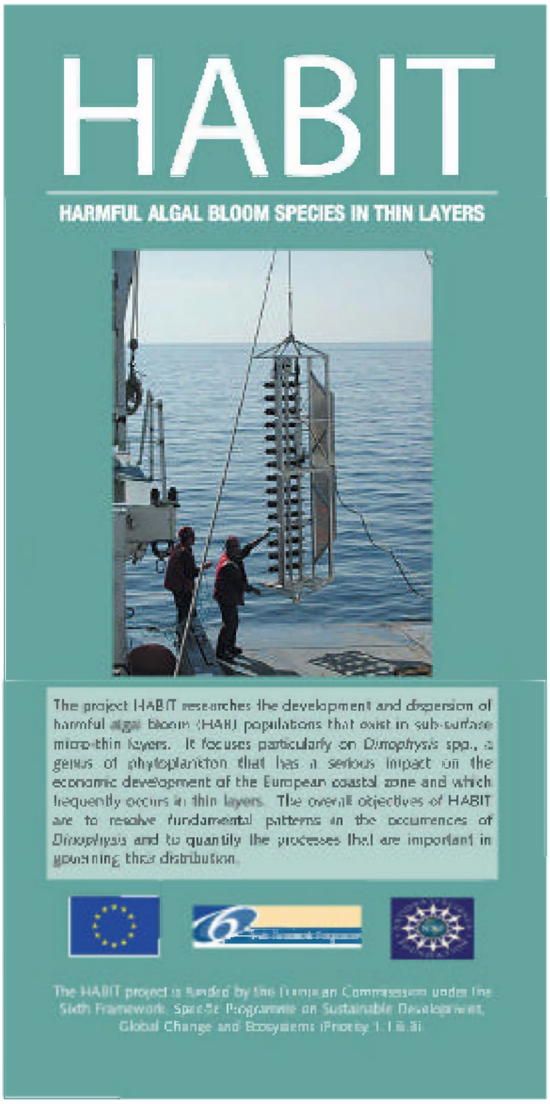
The GEOHAB SSC will help provide international co-ordination for the CRP-HABs in Stratified Systems, through the following actions:

1. Establishment of a GEOHAB–CRP Sub-committee. This sub-committee will be responsible to work with scientists involved in the CRP-HABs in Stratified Systems to ensure that they co-ordinate their research, using clearly described measurement protocols, sharing data, and contributing to model developments. One or two members of the CRP sub-

Core Research directly addresses Programme Element 4 of the GEOHAB Science Plan which relates to Comparative Ecosystems. It cross-cuts all the other Programme Elements of Biodiversity and Biogeography, Nutrients and Eutrophication, Adaptive Strategies and Observation, Modelling and Prediction. Implementation of a CRP is through interdisciplinary, international projects.

The CRP on Stratified Systems has now been initiated through the implementation of the project HABIT[†]*:* Harmful Algal Bloom species In Thin layers *which brings together scientists from Ireland, France, Spain and Britain, together with a US partner under the EU-NSF joint programme on HABs. HABIT has been specifically targeted at studying the maintenance and behaviour of* Dinophysis *in subsurface thin layers around Europe. Particular attention has been paid to nutrition and to the role of biophysical processes in maintaining the thin layers. A holocamera has also been deployed examining the structure of the layers. Studies have taken place along the Atlantic coast in the Bay of Biscay, Celtic Sea and the Galician Rias.*

[†]HABIT is funded through the EU FP6 programme under the Global Change and Ecosystems section; project reference GOCE-CT-2005-3932. Further details of the project can be found on the GEOHAB website www.geohab.info.



HABIT

HARMFUL ALGAL BLOOM SPECIES IN THIN LAYERS

The project HABIT researches the development and dispersion of harmful algal bloom (HAB) populations that exist in sub-surface micro-thin layers. It focuses particularly on *Dinophysis* spp., a genus of phytoplankton that has a serious impact on the economic development of the European coastal zone and which frequently occurs in thin layers. The overall objectives of HABIT are to resolve fundamental patterns in the occurrences of *Dinophysis* and to quantify the processes that are important in governing their distribution.

The HABIT project is funded by the European Commission under the Sixth Framework Specific Programme on Sustainable Development, Global Change and Ecosystems (Priority 1.1.6.3)

*Fig. 20. The HABIT (*Harmful Algal Bloom Species in Thin Layers*) Project: An example of multidisciplinary, international project affiliated to the Core Research Project* HABs in Stratified Systems.

committee will be members of the international GEOHAB SSC, to ensure a strong linkage between the sub-committee and the SSC.

2. Assistance from the international GEOHAB-SSC will be necessary for the identification of new developments pertinent to the stratified systems in the other GEOHAB CRPs, since CRP–HABs in Stratified Systems will develop approaches cross-cutting the other CRPs.
3. Assistance from the GEOHAB Modelling Sub-committee. The GEOHAB Modelling sub-committee will assist CRP scientists in identifying and adapting appropriate physical-biological models that can be applied in stratified systems to HABs research questions.
4. Work with the CRP Sub-committee to identify priority targeted research and measurement protocols.
5. Work with the Global Ocean Observing System (GOOS) and its regional alliances to ensure that GOOS observations are available to the CRP scientists.
6. Provide access to *Harmful Algae News* and the GEOHAB Web site to promote communication amongst CRP scientists.
7. Provide assistance in tracking research planned, funded, ongoing, and completed, including maintaining metadata records of data holdings by individual scientists and scientific teams.
8. Communicate with national and international funding agencies about the need for funding for general and targeted research.

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Appendix I – Open Science Meeting on HABs in Stratified Systems Programme

Programme for Monday, December 5th

0900–0910 **Welcome of the participants – Practicalities.** Henrik Enevoldsen

0910–0940 **The GEOHAB programme.** Grant Pitcher (Chair of the GEOHAB–SSC)

0940–1000 **Introduction: The key questions, structure of the meeting, structure of the report.** Patrick Gentien

1000–1020 **Fine structure, thin layers and Harmful Algal Blooms.** Thomas R. Osborn

1020–1050 ***Coffee break***

1050–1110 **HABs in thin layers – A challenge for modelling.** Wolfgang Fennel

1110–1130 **Oceanic turbulence and phytoplankton dynamics.** Hidekatsu Yamazaki

1130–1150 **Mixing processes in seasonally stratified shelf seas.** Tom P. Rippeth

1150–1210 **Generation of subsurface anticyclonic eddies: numerical experiments.** Hongqin Xie, and Pascal Lazure

1230–1400 ***Lunch break***

1400–1430 **Challenges in measuring and modelling the fine scale interactions controlling the dynamics and impacts of thin layers of harmful algal in stratified coastal waters.** Percy L. Donaghay

1430–1450 **Dissolved organic matter and thin layers.** Timothy Wyatt

1450–1510 **A preliminary model of the mechanical effects of phytoplankton-derived exopolymeric substances on the dynamics of pycnoclines.** Ian R. Jenkinson

1510–1520 **Assignments of sub-groups A and B:**

Sub-group A: The layered environment and the population control factors: How do the physics and chemistry of stratified systems 'condition' the environment for maintenance, advection and decay of some HAB species?

Sub-group B: The layered environment and the species' intrinsic properties: Physiological and behavioural adaptations of some HAB species for life in stratified systems.

1520–1550 ***Coffee break***

1550–1700 **Separate meetings of sub-groups A and B**

1700–1730 **Preliminary report of the two sub-groups in Plenary session**

1700–1800 **General discussion**

1800 **Reception at UNESCO**

Programme for Tuesday, December 6th

0830–0900 **HABs and stratification – A biophysical and ecological dependence or coincident secondary effect?** Theodore J. Smayda

0900–0920 **Fluctuating environments and competition between two phytoplanktonic species: Influence of the cell time scale and the surge uptake.** Jean-Claude Poggiale, and Yves Lagadeuc

0920–0940 **How does photoacclimation influence phytoplankton competition in a variable turbulence environment?** Myriam Bormans, Jean Braun, and Yves Lagadeuc

0940–1000 **Swimming and salinity stratification.** Rachel N. Bearon, Rose Ann Cattolico, and Daniel Grunbaum

1000–1020 **Photosynthetic responses of a *Gyrodinium zeta* bloom during the relaxation of upwelling off the west coast of South Africa.** Sophie Seeyave, Grant Pitcher, and Trevor Probyn

1020–1050 ***Coffee break***

1050–1110 **Influence of halocline and thermocline to the cyanobacterial bloom development and intensity in the Gulf of Finland (Baltic Sea).** Inga Lips, and Urmas Lips

1110–1130 **Detection and enumeration of harmful algal bloom species using a continuous imaging fluid particle analyzer (FlowCAM®).** Nicole J. Poulton, Harry Nelson, Lew Brown, and Chris K. Sieracki

1130–1150 ***Dinophysis acuminata* and water column stratification.** Yolanda Pazos, Ángeles Moroño, Juan Maneiro, Laura Escalera, and Beatriz Reguera

1150–1210 **Study of *Dinophysis* populations under different stratified scenarios.** Beatriz Reguera, Patrick Gentien, Sonsoles González-Gil, Michel Lunven, Isabel Ramilo, and Christian Bechemin

1210–1230 **Modelling hydrodynamic and biogeochemical processes in the Tagus Estuary area.** Marcos Mateus, and Paulo Chambel

1230–1400 ***Lunch break***

1400–1545 **Separate meetings of sub-groups A and B**

1545–1615 ***Coffee break***

1615–1730 **Sub-groups A and B meetings (cont'd)**

1730–1815 **Progress reports from the sub-groups and general discussion in Plenary session**

Programme for Wednesday, December 7th

0830–0850 **Vertical scales of phytoplankton patchiness: theory, and observations using a free-falling planar laser imaging fluorometer.** Peter J.S. Franks

0850–0910 **Current state of zooplankton sampling.** Gabriel Gorsky

0910–0930 **Ecophysiology of phytoplankton at small scale: interactions with turbulence.** Elisa Berdalet and Marta Estrada

0930–0950 **Motility and autotoxicity in *Karenia mikimotoi*.** Patrick Gentien, Pascal Lazure, Michel Lunven, and Thomas R. Osborn

0950–1010 **Stratification, modelling and salinity and its importance to *Karenia mikimotoi*.** Liam Fernand, Alice Vanhoutte-Brunier, Boris A. Kelly-Gerreyn, Sandra Lyons, Francis Gohin, and Robin Raine

1010–1040 ***Coffee break***

1040–1100 **Is there a poleward transport of *D. acuta* in NW Iberia?** M. Teresa Moita, Beatriz Reguera, Sofia Palma, Laura Escalera, Marta Cerejo, and José M. Cabanas

1100–1120 **Small scale retentive structures and *Dinophysis*.** Hongqin Xie, Pascal Lazure, and Patrick Gentien

1120–1210 **Ecological importance of freshwater plumes for toxic *Alexandrium tamarense* blooms in the St. Lawrence Estuary (Canada).** Juliette Fauchot, Maurice Levasseur, Suzanne Roy, François J. Saucier, and Réal Gagnon

1210–1230 **Plankton distributions, with particular reference to potentially harmful species, in relation to density-driven coastal jets in the western English Channel.** Sandra Lyons, Robin Raine, and Liam Fernand

1230–1400 ***Lunch break***

1400–1420 **The importance of density driven coastal jets in the promotion of harmful algal events.** Robin Raine, Sandra Lyons, Glenn Nolan, Juan Brown, and Liam Fernand

1420–1610 **Separate meetings of sub-groups A and B**

1610–1630 ***Coffee break***

1630–1730 **Sub-groups meetings (cont'd)**

1730–1815 **Progress reports from the sub-groups**

Programme for Thursday, December 8th

0830–0850 **Simultaneous measurement of vertical microstructure and chlorophyll-*a* in Seto Inland Sea of Japan.** Nagao Masayuki, Yoshio Takasugi, and Eisuke Hashimoto

0850–0915 **3D flow visualisation in the coastal ocean.** Alex Nimmo-Smith

0915–0935 **A new device for *in situ* video and fluorescence analysis of marine particles / applications to phytoplankton studies.** Michel Lunven, Michel Lehaître, Patrick Gentien, Roger Berric, and Erwan Le Gall

0935–1000 ***Coffee break***

1000–1020 **In stratified environments, where do the nutrients come from? Observations of the secondary circulation and implications for nutrient transport associated with a tidal mixing front on European shelf seas.** Liam Fernand, Kevin Horsburgh, Juan Brown, Caroline Chambers and Stephen Dye, Gualtiero Badin, and David Mills

1020–1040 **Virtual ants for retentive structures detection.** Marc Segond, and Cyril Fonlupt

1040–1230 **Discussions in sub groups**

1230–1400 ***Lunch break***

1400–1430 **Plenary session**

1430–1630 **Separate meetings of sub-groups A and B**

1630–1730 **Final sub-group reports in Plenary session**

1730– **End of the meeting**

Programme for Friday, December 9th

The members of the organizing committee (Patrick Gentien, Percy Donaghay, Thomas Osborn, Robin Raine, Beatriz Reguera, and Hidekatsu Yamazaki) will meet for the day in order to finalize the report of the OSM. Any extra contribution is welcomed.

POSTERS

Study of phytoplankton along Abda-Doukalla coastal area (Moroccan Atlantic). Bennouna Asmae, El Attar Jaouad, Brigitte Berland, and Omar Assobhei

New Zealand risk management and regulatory approach for cyanobacterial bloom events. Alexander Yu Kouzminov, and Michael E.U. Taylor

Vertical distribution of phytoplankton communities and relationships with physico-chemical parameters resolved by a fine scale sampler. Michael Lunven, Jean-Francois Guillaud, Agnes Youenou, Marie-Pierre Crassous, Roger Berric, Erwan Le Gall, Roger Kerouel, Claire Labry, and Alain Aminot

ASTERIX: An AUV for the exploration of pycnocline layers. Jan Opderbecke, Ullrich Lemmin, and Thomas Osborn

Harmful algal bloom species in thin layers. Pauhla McGrane, Beatriz Reguera, Patrick Gentien, Liam Fernand, Paul McLoghrie, Michel Lunven, Pascal Lazure, Tom Osborn, Joe Katz, Ed Malkiel, and Robin Raine.

Plankton distributions, with particular reference to potentially harmful species, in relation to density-driven coastal jets in the western English Channel. Sandra Lyons, Robin Raine and Liam Fernand.

Appendix II – Meeting Participants

GEOHAB Open Science Meeting on HABs in Stratified Systems

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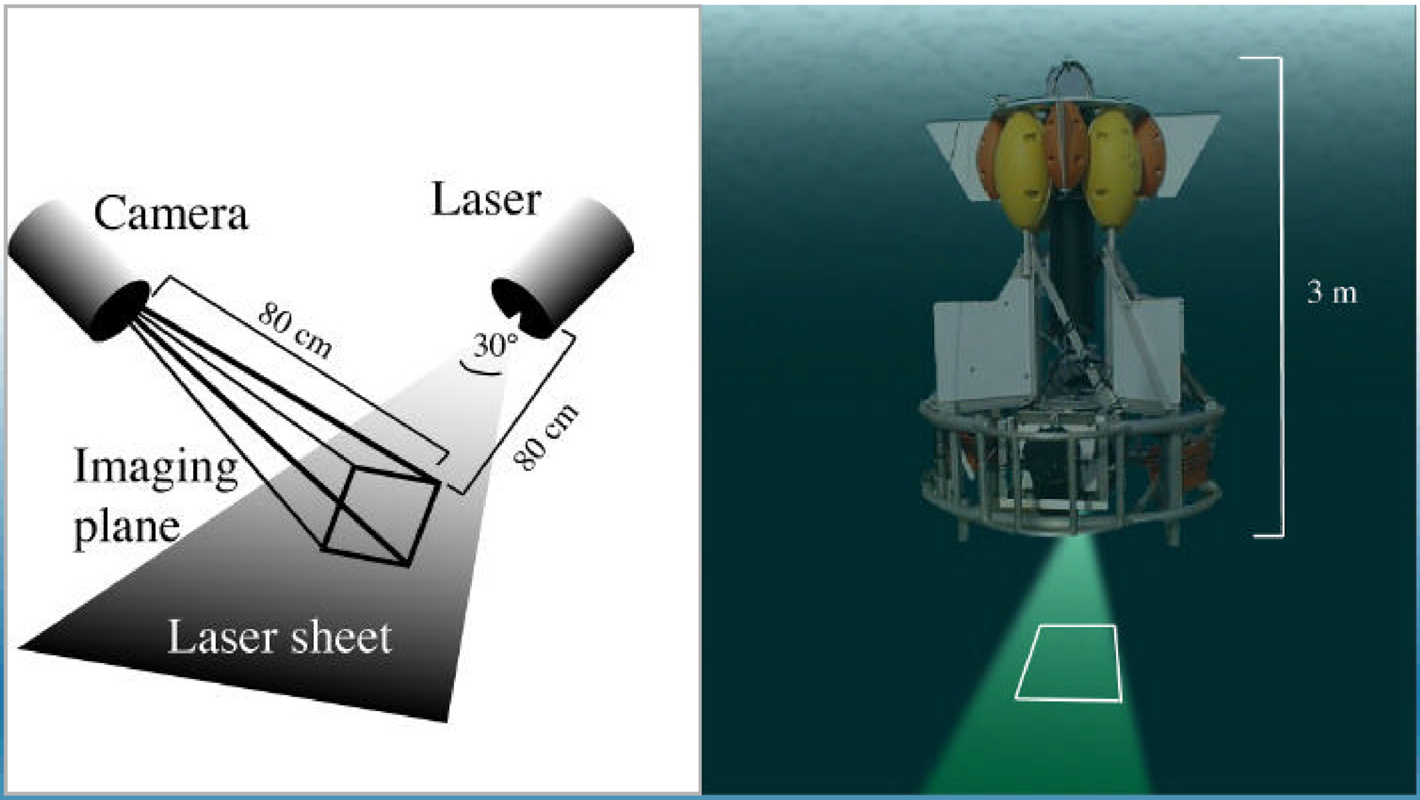

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