REPORT OF THE JOINT MEETING OF
THE WORKING GROUP ON HARMFUL ALGAL BLOOM DYNAMICS (WGHABD) AND
THE ICES WORKING GROUP ON SHELF SEAS OCEANOGRAPHY (WGSSO)

Vigo, Spain, 9–10 May 1994

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1. OPENING OF THE MEETING

The ICES/IOC Working Group on Harmful Algal Bloom Dynamics (WGHABD) met in the Instituto Español de Oceanografía (Vigo) from 9-12 May 1994 to address the terms of reference set out in Section 2. Terms of reference a, b, c, and e were dealt in a joint session (9-10 May) of this Group with the WGSSO, co-chaired by Beatriz Reguera (Spain) and Hans Dahlin (Sweden). Terms of reference d, f, g, and h were addressed on 10-11 May, and the results are given in another report (ICES C.M.1994/L:5, Ref.C). Forty-four scientists from eighteen countries, including ten members of the Working Group on Shelf Seas Oceanography (WGSSO) and five observers, took part in the Joint Session. A list of participants is given in Annex I.

Allan Cembella (Canada) acted as a rapporteur.

By way of introduction, H. Dahlin provided an overview of the importance of the interaction between phytoplankton biologists and physical oceanographers, particularly those who employ numerical modelling in describing coastal systems. The purpose of the joint session was to focus attention on the multidisciplinary aspects of HAB problems. Since it is recognized that an understanding of the population dynamics of HABs involves physical, chemical and biological interactions, and not merely a general study of plankton ecology, it is imperative to interest hydrographers and chemical oceanographers in the problem. B. Reguera explained and gave her comments about the terms of reference, some of them too broad and extensive as it is usually the case when a new group is set up. Therefore, it was important to identify relevant issues to plan future activities related with the terms of reference.

2. TERMS OF REFERENCE

At the 81st Statutory meeting in Dublin the Council resolved (C.Res. 1993/2:47) that:

The ICES/IOC Study Group on the Dynamics of Algal Blooms will be re-established as the ICES/IOC Working group on Harmful Algal Bloom Dynamics (Chairman: Ms Beatriz Reguera, Spain) and will meet in Vigo, Spain from 9-12 May to:

a) continue the development of an understanding of the dynamics of harmful algal blooms, including experimental aspects of harmful algal bloom dynamics;

b) review progress in the implementation and/or execution of physical-biological interaction investigations in the pilot study areas (Gulf of Maine, Skagerrak-Kattegat, Iberia);

c) review the results of the Workshop on Modelling the Population Dynamics of Harmful Algal Blooms, and propose further steps to improve the dialogue between physicists and biologists;

d) finalize planning of the Workshop on Intercomparison of in situ Growth Rate Measurements;

e) consider the integration of ongoing research activities on harmful algae phenomena in the ICES area into the existing global international programme on harmful algal blooms (IOC-FAO /OSLR/HAB).

f) evaluate strategies useful in investigating HABs and in mitigating their detrimental effects on marine ecosystems, e.g. the efficacy of regional HAB monitoring systems;

g) consider the development of a HAB database;

h) collate and discuss national reports on harmful algal blooms (HABs).
3. REVIEW OF THE WORKSHOP ON MODELLING HAB POPULATION DYNAMICS

The objectives of the modelling workshop on HAB, as defined by the terms of reference, were to:

a) investigate the use of numerical models in improving understanding of the dynamics of HABs;

b) use models to assist in the design of sampling strategies, interpretation, and forecasting of HABs;

c) develop a dialogue between physical and biological oceanographers with respect to HABs, including the rôle of physical inputs, and temporal and spatial scales.

An attempt was made to unite phytoplankton biologists, physical oceanographers and modellers to achieve a common definition of the rôle of physical and biological factors integrated over various spatio-temporal scales. A debate arose early in the discussions regarding the appropriate use of ecosystem models. Some participants adopted the approach that numerical models defined by a discrete set of differential equations would serve our purpose; others wished to consider other modelling techniques including conceptual (i.e. box or compartment), analytical, and even intuitive models, the latter of which are employed routinely by phytoplanktologists in formulating and testing working hypotheses.

Existing models of different types might be helpful for crude estimates for risk assessment, however further research is required to refine the underlying assumptions of such models. All participants would welcome an increased participation of phytoplankton biologists in future modelling exercises. It was acknowledged that in general the forcing functions determining the hydrodynamic regime in a given system were better defined and thus more amenable to modelling than the biological determinants leading to HAB formation. At least some of the initial scepticism among biologists towards the utility of numerical modelling in understanding HAB dynamics was due to the belief that biological systems are inherently so complex (involving organismal behaviour, etc.) that the number of functions sufficient to define them could not be successfully incorporated. This was countered by statements that the complexity of a system is not necessarily a fundamental property, hence simple models are not necessarily worse at describing the coupling between physical and biological parameters than more complex ones. In this case, the appropriate level of complexity in the model is that which makes the least number of assumptions while best explaining reality.

One positive outcome of the workshop was the understanding achieved among physical oceanographic modellers and phytoplankton ecologists regarding a common lexicon for their discussions. Thus, physical oceanographers became familiar with the use of terminology associated with growth and primary production (Liebig's Law of the Minimum, cell quota, Michaelis-Menten kinetics, photosynthetic parameters, etc.) while phytoplanktologists were shown the rôle of small-scale turbulence, advective and diffusive flux, barotropic currents, etc., in driving bloom aggregation and dispersion.

The practical examples of extant phytoplankton dynamic models presented to the workshop were essentially oriented towards modelling primary production, biomass, net carbon flux and spring diatom blooms. The implicit assumptions of these models is that there exists a defined suite of first order properties (e.g., nutrient kinetics, photosynthetic rate, etc.) which govern the phytoplankton population growth rate. There was disagreement regarding the utility of general primary production models for understanding HAB dynamics, since the critical property is the harmful effect of such blooms, rather than a common ecophysiology. Biologists also
questioned the reductionist approach of the physical modellers towards the biological components; simplifying assumptions such as reducing the primary producer and secondary grazer to single components and fixing the grazing rate as constant in time were considered to be unrealistic. These views did not immediately deflect the course of the debate, which concerned the mathematical expressions of functional relationships (such as the Michaelis-Menten equation for nutrient kinetics), step functions and truncation procedures, and whether there is a need for feedback between the physical and biological components of models.

Since it is not clear that the biological forcing functions governing HAB population growth are necessarily those of nutrient dynamics, an overemphasis on nutrient kinetics in modelling may be seriously misleading. Some participants expressed the pessimistic view that HABs will prove particularly intractable to modelling since their net population growth may be a function of secondary or tertiary processes (allelopathy, water conditioning, complex nutrition or behaviour, etc.) which are currently unknown or at best are ill-defined. The fact that HABs may arise in response to catastrophic environmental disruptions which are themselves not predictable contributes additional complications.

A fundamental dichotomy was established between diagnostic models, for analyzing and explaining bloom events which have already occurred, and prognostic models for forecasting and bloom prediction. Most participants agreed that given the ecophysiological diversity among HAB species, general prognostic models for harmful bloom dynamics are unlikely to be available in the near future (if ever). In the interim, greater emphasis should be placed on the development of "species of interest" models to focus on specific harmful species. Furthermore, it was pointed out that it is not necessary to model entire ecosystems to provide useful recommendations to public health officials and fisheries and aquaculture managers. Models capable of generating short-term predictions (over a few days or weeks) based upon risk assessment probabilities generated from monitoring data can assist in the implementation of mitigating strategies for HAB effects. The development of holistic bloom dynamic models coupling biology with three-dimensional models of circulation and mixing await further definition of the requisite rate processes and parameters.

Some participants felt that the discussion had not yet succeeded completely in achieving an understanding between physicists and biologists, in part due to the fact that it was being conducted in a language unfamiliar to biologists. Bloom prediction and some other matters already dealt with may belong more properly to a future workshop, while the current session should have addressed fundamental questions about how to begin modelling and the requirements for background information.

Participants felt the workshop was an excellent start towards the goal of strong interaction between biologists, physicists, and modellers on the problems of harmful algal blooms. The multitude of problems associated with the oceanographic complexity of the problem will necessitate many different modelling approaches.

4. CONTINUE THE DEVELOPMENT OF AN UNDERSTANDING OF THE DYNAMICS OF HABs, INCLUDING EXPERIMENTAL ASPECTS

During this session, several presentations were made of ongoing or completed case studies that illustrate physical-biological interactions. The last one is a dynamic study of HABs in the Baltic Sea which the participants would like to see as an additional ICES Pilot Project. These case studies were followed by progress reports on the implementation/execution of HAB Dynamic studies in the pilot areas. Following these presentations, and reflecting the previous week's modelling workshop, several common elements were identified, and comments around them
developed by different participants, that deserve further the attention of the group. These elements were: i) The potential impact of small scale phenomena on HAB Dynamics; ii) Analysis of time and space scales relevant to HABs; iii) The grazing term in HAB dynamics; iv) How to proceed in numerical modelling of HABs.

4.1 Some case studies

4.1.1 PROFILE - Processes in Regions of Freshwater Influence
(J. Joordens, NL)

The project PROFILE (1993-1996) is carried out in the framework of the MAST (Marine Science & Technology) programme, in cooperation with institutes and Universities from the UK, the Netherlands, Italy, Germany, Belgium and Greece. Its objectives are to develop process understanding in ROFIs (Regions of Freshwater Influence) by studying physical and biogeochemical processes, and to develop a fully coupled physical-biological 3D nearshore predictive marine environmental model. Regarding process understanding, measurements are done in the region of the Rhine, Clyde, Po, German Bight and Thermaikos Bay. The different regimes will be compared.

The 1994 Rhine outflow experiments are described in more detail: moorings are deployed from March till October, ongoing 2-weekly measurements are done near the moorings during this period, and cruises took place in April and May. The objective of these experiments is to estimate the relative importance of tides, waves, wind, river discharge rates and irradiance on hydrodynamics and suspended matter (sediment & chl-a) dynamics in the Rhine outflow area.

4.1.2 The Loch Linnhe Project
(E. Macdonald, U.K.)

A fjord ecosystem model was described which integrates tidal flushing with physical and biological processes to simulate the seasonal dynamic behaviour of the system. Results indicate that fjord-like sea lochs cannot be regarded as self-contained biological mesocosms, but have a behaviour analogous to a laboratory chemostat. Turbidity in the surface layer is usually such that light and grazing pressure exert the main controls on phytoplankton biomass except during the spring bloom period. At all other times, tidally driven flushing of dissolved nutrients is easily able to meet the demands of the algal biomass. Hence, anthropogenic nutrient inputs on their own may not have any damaging impact at the scale of the whole fjord. The model was tested initially by comparison with field data drawn from the literature and also with data generated from a comprehensive dedicated field programme to elucidate the major controls on the system dynamics. Whilst the data analysis is not yet complete, it is clear that as predicted by the model, grazing rather than nutrients exert the main control over phytoplankton dynamics within the loch. Model runs perturbing the system using data from the literature suggest that increased anthropogenic nutrient inputs may only affect the whole basin if grazing pressure is reduced.

4.1.3 Physical versus Biological Control of HABs in the Southern Benguela Upwelling Region
(G. Pitcher, South Africa)

Grant Pitcher addressed physical vs biological control of harmful algal blooms (HABs) in the southern Benguela, describing the hierarchy of forcing functions throughout the spectrum of space and time. At the macroscale HABs are generally restricted to the boundaries of the Benguela and are clearly associated with the upwelling ecosystem. The close coupling of seasonal upwelling and the frequency of HABs demonstrates the indirect control of seasonal bloom development by wind
driven upwelling. At this scale biological processes such as seeding, differential growth and predation stress are considered important.

The episodic nature of bloom events during the upwelling season occurs in response to the shorter cycles of upwelling and relaxation superimposed on seasonal variation. At this event scale the direct effects of physical forcing in accumulating the seasonal bloom are considered most important; each event associated with wind abatement or reversal is initiated by the passage of a coastal low and maintained by the subsequent merging of low pressure cells off the south west coast. Large-scale weather patterns including the frequency characteristics of Rossby waves, were identified as important in controlling the pulsing of shelf circulation and are therefore instrumental in determining intra-season variation in HAB activity.

The disposition of the South Atlantic anticyclone and belt of westerly winds is considered important in determining interannual variation in HABs. Summers with increased HAB frequency are distinguished by displacement of the South Atlantic high, and increased westerlies, meteorological features which coincide with and follow an El Nino in the Pacific.

At the microscale, physical processes such as internal tides, and species specific vertical migrations were demonstrated to be responsible for bloom accumulations and intense concentration gradients.

It was concluded that wind was a key determinant of variability in the southern Benguela over the entire spectrum of time and space and was therefore the primary force in the generation of HABs.

4.1.4 An Example of a "species of interest" Conceptual Model
(P. Gentien, France)

An example of species of interest conceptual model applied to Gymnodinium cf. nagasakiense was presented by P. Gentien. The possible relationships this species develops with its environment have been discussed in terms of relations tending to increase or decrease the local concentration of the population. This approach allows us to classify by order of magnitude the importance of the different processes. It appears that, in a first-order approach for this species, due to repression of grazing, allelopathy and possible mixotrophy, the relations between the behaviour of the algae and the physics at different scales (including small scales) are of paramount importance in the understanding of the species dynamics. These physical processes include horizontal confinement, niche separation by turbulence, vertical migration, and concentration or dispersion by advection. In the first approach, it does not appear necessary to consider inorganic nutrient limitation.

4.1.5 Red Tides Generation in Ria de Vigo
(F.G. Figueiras, Spain)

F.G. Figueiras presented some results dealing with red tides generation in the Ria de Vigo (Galicia, NW Spain)(MAST 1 project on "The Control of Phytoplankton Dominance"). At present, there are conflicting opinions about the red tide generation in the Galician Rias. Some researchers suggest that the appearance of red tide episodes is related to established populations in coastal waters which are advected to the interior of the rias by means of surface water transport induced by upwelling relaxation and/or a poleward surface current. By contrast, other observations indicate that the outer part of the Ria may be a place for active growth of Gymnodinium catenatum during periods of weak upwelling. A study in the Ria de Vigo, carried out during late September 1990, showed the development of a red tide assemblage composed of Alexandrium affinis, Ceratium fusus and Gymnodinium catenatum, during a two weeks upwelling-downwelling cycle. Growth occurred at the bottom of the thermocline-top of the nutricline. Above this assemblage, a
diatom assemblage (large diatoms) was blooming. It was suggested that the ratio between velocity of upward water movement and the depth of the stratified upper layer (flushing rate, d⁻¹) is the critical parameter which triggers active phytoplankton growth. It can be concluded that upward water velocities of about 2.5 m d⁻¹ and a stratified upper layer 10 m deep (flushing rate 0.25 d⁻¹) are the main physical constraints for red tide development. A 2-dimensional advection-diffusion model was used to simulate the distribution of Gymnodinium catenatum found in Ría de Vigo at that time. The model suggests that horizontal advection is of greater importance in the inner Ría, while vertical advection and vertical diffusion have a stronger influence in the outer Ría. Weak and moderate upwelling events are compatible with growth and cell accumulation in the outermost part of the Ría. Weak downwelling allows patches to form throughout the Ría at rates similar to the growth rate. In these cases it is vertical advection which controls the accumulation or dispersal of cells.

4.1.6 Presence of OA in mussels (M. edulis) in relation to nutrient composition in Swedish coastal waters. (J. Haamer, Sweden)

The seasonal and geographic variation of the concentration of diarrheic shellfish toxin (DST) in mussels (Mytilus edulis) has been compared with the variation in the concentrations of the nutrients nitrogen, phosphorus and silica in the Swedish mussel farming district. DST seems to increase in mussels when nutrient conditions favour the growth of toxic dinoflagellates biomass. The ratio between non diatoms and diatoms is mainly regulated by the nutrient ratios and concentrations and therefore we compare DST variations in mussels with nutrient variations.

The lowest DST concentrations were found in a fjord system secluded from the open sea, where the highest concentrations of dissolved inorganic nitrogen (DIN) and phosphorus (DIP) were found. The bottom water there, however, was rich in dissolved reactive silicate (DSi) and supplied the photic zone with enough DSi to support a production dominated by diatoms. Thus the DIN/DSi and DIP/DSi ratios here were the lowest in the whole mussel farming district. Low DIN/DSi and DIP/DSi ratios during the production season coincided with low DST concentrations in mussels in the investigated area. In the winter and spring seasons DSi was supplied by rivers making the growth conditions for diatoms more favorable. The spring bloom has therefore promoted the disappearance of DST in mussels. The DIN/DSi ratio in the winter surface water of the Northern Kattegat (lat 57°15', long 11°50') has changed from 0.5 to 1.1 during the last 30 years which may contribute to improved growth conditions for toxic dinoflagellates.

4.1.7 Basin-wide Dynamics of Harmful Plankton Blooms in the Baltic Sea (K. Kononen, Finland)

The Baltic Sea is a semi-enclosed sea with a relatively large drainage-area, complicated, shallow coastline, and some periodically anoxic deep areas, the latter determined by large scale water exchange with the North Sea, in the Kattegat.

Late summer blooms of filamentous, diazotrophic cyanobacteria formed by Aphanizomenon flos-aquae and Nodularia spumigena are recurrent, yearly phenomena in the whole area, except the Gulf of Bothnia. N. spumigena is an efficient nitrogen-fixer and all blooms dominated by this species have been found to be hepatotoxic producing nodularin-toxin. Deaths of domestic animals connected to these blooms have been reported from several countries around the Baltic Sea. Due to nitrogen fixation these blooms also increase the nitrogen reserves of the pelagic system thus promoting growth of other, nitrogen limited phytoplankton species.

The long-term studies as well as high-resolution mappings during blooms show that there is a pronounced variability in bloom intensity in different areas and between years. There are several
gaps in our knowledge concerning the blooms on a basin-wide scale. The most important questions, at present based only on speculations are:

- How does a bloom develop, at what depths, at what time scales?
- What is the fate of a bloom?
- Where is the nitrogen fixed by the blooms channelled in the food web?
- Do the blooms increase the nitrogen reserves in the Baltic Sea, thus increasing the potential of other, nitrogen limited blooms to occur?
- What is the fate and accumulation of the cyanobacterial toxins?

Answers to these questions can not be obtained by using traditional research strategies based purely on single sampling stations and experimental laboratory studies. Instead, multidisciplinary studies based on several, complementary strategies, investigating the phenomenon in different spatio-temporal scales, should be conducted. The proposed study is a combination of several strategies, e.g. the use of satellite images, unattended, high-frequency measurements onboard commercial ferry boats, buoys and intensive studies onboard research vessels. Complementary information from processes at the cellular level will be produced by another international research project.

4.2 Review Progress in the Implementation/Execution of physical biological interaction investigations in the Pilot Study Areas

4.2.1 Gulf of Maine

A project on *Alexandrium* population dynamics has begun in the Gulf of Maine supported by NOAA. T. Osborn (on behalf of D.M. Anderson) presented a summary of the ongoing field activities, that can be summarized as follows:

**Moored Measurements**
- 2 moorings, Year 1; 3 moorings, Year 2
- deployment in mid-March; recovery in mid-June
- Vector-Measuring Current Meter (VMCM) at 5 m (plume flow)
- Vector-Averaging Current Meters (VACM) at 20 m & near bottom
- conductivity and temperature sensors at each depth
- sampling at 7.5-10 min. intervals

**Drifter Measurements**
- deployed during each large vessel survey near mouth of Kennebec, perhaps from small vessels as well
- will include temperature and conductivity sensors
- 4 drifters are budgeted each year
- recovery will be attempted when possible

**Satellite Data**
- NOAA Coastwatch, twice daily images of SST, March-June
- perhaps turbidity (AVHRR channels 1 and 2, NOAA-11)
- ocean color in 1994, (SeaWifs)

**Shipboard Measurements**
- 5 survey cruises (3 days) year 1, R/V ARGO Maine, Cape Cod to Penobscot Bay, 80 stations, April - June 15
- 2 survey cruises (6-9 days) year 2, RV Anderson, R/V ARGO Maine, Cape Cod to Penobscot Bay, 80 stations, plus 3-4 small vessel cruises, April-June 15
- 13 transects (5-8 stations/transect) extending 30-50 km offshore between Penobscot Bay and Cape Cod Bay (survey cruises)
- continuous vertical profiles of conductivity, temperature
- discrete samples for *Alexandrium* counts, nutrients

**Modelling**
- 3 dimensional, finite difference circulation model (ECOM-3D, )
- domain to be extended from Mass. Bay north to Penobscot
- simulate transport and water properties in western GOM as functions of wind stress, river discharge, and regional circulation
- incorporate biology (*Alexandrium* populations) first as passive particles, then as particles with behavior (growth, death, vertical migration, nutrient uptake)

4.2.2 Skagerrak-Kattegat

The status of the pilot project "Bloom Dynamics in the Kattegat/Skagerrak area" was presented by Lars Edler (Sweden). Comments or amendments had not been received from very many persons which must be interpreted as if people are either not interested or have no time to get involved. Additions to the project that have been discussed are:

- A workshop should be held in order to gather people who are interested on working in this project. During the WS a strategy for the funding should also be discussed, as well as a more definite time table.

- The study should start with an evaluation of existing data (very much data exist from this area).

- A model should be set up to establish the interaction between observation and theory.

4.2.3 Iberia

B. Reguera (Spain) and A. Jorge da Silva (Portugal) commented on "Iberia". During the intersessional period two one-day meetings (15 June, 18 November) were held in Aveiro (half-way between Vigo and Lisboa) with participants from several Portuguese and Galician institutions. The objectives of these meetings were to reconcile divergences between the Portuguese and Galician interpretations of regional observations of phytoplankton and toxicity information, as well as oceanographic results. It has now been decided that a two-pronged approach will be adopted, with emphasis on the one hand on DSP episodes caused by *Dinophysis acuminata* group in the early and middle parts of the upwelling season (May-July), and on the other hand on DSP and PSP episodes due to *Dinophysis acuta* and *Gymnodinium catenatum* respectively (both belonging to the same "large dinoflagellate assemblage" during the late upwelling season and early autumn (August-October).

In the case of *D. acuminata*, it was decided to concentrate on the behavioural responses of this species to environmental conditions. *D. acuminata* is usually found very close to the coast and inside the rías. Studies will be based on microcosm experiments and observations in the laboratory, short term experiments within the rías, and analysis of the weekly monitoring data at 36 stations in the Rias Bajas, which has now been in operation for 24 months.
In the case of *D. acuta* and *G. catenatum*, it is intended to pursue problems associated with the initiation and proliferation of blooms, and toxin production, and the respective dynamics of cyst germination and vegetative growth in relation to mesoscale hydrographic features. This will involve two major cruises of three weeks each designed to examine population processes during the two typical scenarios that enhance bloom development, namely, summer stratification combined with moderate upwelling, and the decay of upwelling as northerly winds give way to southerly ones during autumn. These cruises, using two research vessels, will take place on the platform in the regions off Aveiro-River Duero (Portugal), and the River Miño-Rías Bajas area (Galicia), with the hope that each grid can be repeated at two to three day intervals. All these activities will be supported with the information from monitoring programmes in Portugal and Galicia, by satellite imagery, hopefully in real time, and by moored instruments.

There is an ongoing programme, MORENA (Mesoscale Oceanographic Research in the Eastern North Atlantic), funded by the CEU (MAST-II, CT93-0065), whose aims are to measure and model shelf-open ocean exchange in the coastal upwelling region of the eastern boundary layer of the subtropical ocean. The MORENA research area coincides geographically with that of interest to the IBERIA project. Thus, since mesoscale oceanographic models of the Iberian region are already in hand with the MORENA project, this is no longer a strong priority of the IBERIA project, and it has been decided to shift emphasis towards these scales at which it is felt the physical-biological interactions of significance to HAB may operate. Advantage has already been taken of MORENA cruises to provide opportunistic sampling of phytoplankton and cyst distributions.

Appropriate *in situ* growth rate measurements are being developed, and will be compared in the ICES/IOC Workshop in July 1994. In addition to studies already underway in Spain and Portugal, support for further international collaboration will be linked principally to future funding provided by the next round of CEU marine programmes.

### 4.2.4 New Pilot Study Areas

The Working Group proposed that the Baltic Sea be included as a fourth project in the ICES Working Group on Harmful Algal Bloom Dynamics.

### 4.3 Common elements for further discussion

#### 4.3.1 Potential Impact of Small Scale Phenomena on HAB Dynamics

One or more dimensional mixed layer models may adequately simulate the dynamics of mixed phytoplankton populations, but many harmful algal species and zooplankton too have the ability to choose the depth at which they live and are frequently confined to thin layers a few centimeters thick. These layers may be located at such depths that, for example, flushing is evaded. This means that retention can be achieved by purely biological means, and that physical convergences are not the only processes which lead to accumulation of biomass. It also means that the vertical distributions of grazers are often very different from those of potential prey species. Thus, centimeter scale biological processes, as described in Donaghay, Rines and Sieburth (1992), may have an important impact on the forms of functional relationships used in models to regulate phytoplankton growth and to generate grazing mortality. Fluctuations in vertical movements on short time scales (hours) may also have a significant impact on model results. Physical features of the water column on the same vertical scales may also need to be taken into account, as well as horizontal features on larger scales which form intrusions. These second order processes may dominate the mechanisms leading to the accumulation and dispersion of HABs, and the first order
processes which are prominent components of many simulation models may need to be given less emphasis.

4.3.2 Comments on the grazing term

The grazing term in the population dynamics equation for HAB studies had not been discussed with enough depth in past meetings of the previous study group. H.R. Skjoldal, Chairman of the Study Group on Zooplankton Production agreed to guide an introductory session to present and discuss possible methods for grazing measurements to be applied in species-specific HAB studies, but more urgent commitments prevent him from attending. The following comments were prepared that summarize the basic problems.

Grazing is usually oversimplified in the formulation of harmful algal blooms dynamics. The grazers constitute a closure term in most phytoplankton models and therefore, one can imagine that the results of modelling are strongly depending on the formulation of the grazing. At best, grazing is estimated by a constant rate, or by an asymptotic function with a threshold. While such an approach is probably suitable for biomass production models, this is not true any more when considering a single algal species which may be grazed by one single species, or an algal species which may use some strategy to avoid or reduce grazing. Some may themselves be grazers. Any mechanism leading to selective grazing gives to the species which is not grazed, a large advantage over its competitors that are grazed. It is therefore, very important to know if a given species is grazed at all during its development (at different cell densities and at different physiological status). For instance, Gymnodinium cf. nagasakiense is grazed or not grazed by copepods depending on the physiological status of the alga (production of mucus and/or toxic hemolysins). In this case, the conditions leading to an inhibition of grazing must be determined before any attempt to formulate a realistic model.

It should not be forgotten that losses from grazing may be due to benthic filter feeders as well as zooplankton.

Zooplankton: The confinement of dinoflagellates and other toxic species in very thin horizontal layers leads locally to extremely high densities of the species of interest. The so-called "realistic" concentrations used in experiments should extend to densities which are observed in the field. In some cases, high degrees of aggregation of potential grazers can be observed. For instance, this is the case of some dense copepods layers lying on top of dinoflagellate layers. These aggregations may be seen sometimes as single species swarms. Detailed observation is required in order to decide if some species specific associations of zoo- and phytoplankton can be found. Not to use these species of concern found in such assemblages in grazing experiments would miss the pertinent point.

Benthic filter feeders: In coastal waters, in some hydrodynamical contexts, the confinement of a dinoflagellate may govern its availability to benthic grazing. Hydrodynamic studies would permit us to decide if grazing by benthic filter-feeders should be taken into account or not in attempts to understand the population dynamics. Such studies would also allow a better understanding of the conditions leading to shellfish contamination. There is some evidence that the relatively low efficiency of mussels leads to concentrations of viable dinoflagellate cells in the faeces and pseudofaeces. Some cysts have been found also in the guts of bivalves. In shellfish farming areas, this additional concentration mechanism could be of importance in providing potential growth factors to concentrated seed populations.

From these considerations, the working group recognizes the importance of grazing on the population dynamics of possible harmful species. Two basic sets of questions have been identified, depending on natural or shellfish farming areas:
Coastal areas
- Is grazing pressure a significant loss factor during all stages of population development of the dinoflagellate of interest?
- What are the documented cases of dinoflagellate-zooplankton species specific associations?
- What are the documented cases of allelopathy reducing grazing?

Shellfish farms
- What is the influence of benthic filter-feeders in enhancing mixing rates?
- What kinds of hydrodynamical situations prevent the availability of dinoflagellate of interest to benthic filter feeders?
- What is the influence of the low efficiency of bivalves on the population dynamics?

4.3.3 Analysis of Time and Space scales in biological and physical processes relevant to the understanding of HAB Dynamics

Harmful algal bloom dynamics appear to be driven by both biological (e.g. growth, behaviour) and physical processes (e.g. upwelling, transport). In order to gain insight in the mechanisms influencing the occurrence of harmful algal blooms, it is useful to identify how relevant biological and physical processes can interact and magnify each other. To achieve this, analyses of the time scales and the space scales of the processes needs to be made. This will facilitate and structure discussions on modelling of HAB as well. An analysis of time/space scales of physical/biological processes has been carried out and reported on by several authors: J.C.J. Nihoul (1986); K.H. Mann & J.R.N. Lazier (1991); B.J. Rothschild (1988). Such studies can serve as an example of how to set this up specifically for harmful (toxic and nuisance) algal blooms.

4.3.4 How to proceed in Numerical Modelling of Harmful Algae Blooms

In principle a model should be as simple as possible and as complex as necessary. This is strongly dependent on the individual problem to be studied. However, one of the major goals is to be able to realistically predict/simulate (in space and time) harmful blooms, and for most situations this require realistic knowledge of horizontal and vertical transports (including mixing) in addition to the most important chemical-biological processes. This means that in principle one needs a coupled physical chemical biological model with appropriate 3-dimensional resolution in space (sometimes 2-D can be enough) and sufficient resolution in time, together with the most important external forcings.

Clearly it can be useful to use simpler models (often just one dimension in space) to study and quantify the sensitivity to different parameterizations, and this is now increasingly being used by biologists. However, sometimes very complex biological interactions are introduced to compensate for the lack of an important physical process (and vice versa), which normally leads to failure.

Some of the most important biological processes (related to species of interest) which have to be given mathematical expression in a "good" model are:

- Growth rate (or division rate, as a function of temperature and limiting factors such as light and, sometimes, different nutrients)
- Mortality (sometimes due to grazing, lack of oxygen..)
- Vertical behaviour.

The major physical processes which have to be modeled together with the biochemistry are vertical mixing and diffusion, horizontal advection and diffusion, and the temperature and salinity structure to go with it. It is only recently that these physical parameters can be somewhat.
realistically modelled and therefore that we can create coupled model systems which might to an extent simulate nature. Due to limited computer resources it is still a problem to achieve optimum spatial resolution, and there are still some open questions related to turbulent mixing.

Clearly one must have available the most important highly varying driving forces such as windstress, air pressure, tides at open boundaries, incoming light intensity and in some areas inputs of freshwater and nutrients. The initial fields of all these variables must also be available.

With the present knowledge of harmful algae blooms, nobody will even try to predict what will happen next year based on numerical models. In some cases one can with knowledge of the development of nutrient supplies during the winter and spring be able to say something about increased or decreased probability for an harmful algae bloom related to a certain watermass. However, with respect to modelling certain harmful species, it might be possible predict to development 5-10 days ahead providing a reliable weather forecast is available.

Another way of using the models in a "predictive" way is by modelling "what if" questions such as: "How much do we have to decrease anthropogenic nutrient inputs to significantly reduce the probability of a certain frequent harmful algae bloom". In any case there is a great demand for "quality assurance" of such models before they can be trusted for management purposes, and at present we do not have good and general systems for such "quality assurance".

To awaken the interest in such modelling activity, the best available and quantifiable knowledge of the processes above mentioned for different harmful species must be collected and simplified to a level where it becomes "realistic" to model. Descriptions of some major and monitored harmful algae blooms in different regions should be made available as test cases for model simulations.

ICES should advice national and international funding agencies to put priority to such multidisciplinary activities, that will then lead to the demand for better and useful "hydrobiochemical" knowledge, which again will lead to better models.

5. RECOMMENDATIONS

1. The Working Group should seek advice from the ICES Study Group on Zooplankton Production about: i) techniques for grazing measurements and their limitations, ii) documented observations on specific predator-prey links of planktonic organisms, and iii) effects of algae mucilages and/or algal taste on grazing, and from the WG on Environmental Interactions of Mariculture on the influence of benthic bivalves on local hydrodynamics.

2. ICES should recommend that funds be provided for the development of models more appropriate to the management of harmful algal blooms than those presently being developed.

3. Recognizing the importance of achieving a better understanding of HAB’s and improving managerial measures against the harmful effects of these blooms, it is recommended that ICES takes an active part in the work of the IOC-FAO ad hoc Intergovernmental Panel on Harmful Algal Blooms.

4. The ICES/IOC Working Group on Harmful Algal Bloom Dynamics will meet during the spring of 1995 in Helsinki (Finland) to:

a) review the results of the Workshop on Intercomparison of in situ Growth Rate Measurements;
b) review ongoing activities in the pilot study areas, and other ICES areas, on physical-biological interactions investigations;

c) develop plans for a future practical Workshop on Modelling using real data obtained in monitoring and projects related with HAB Dynamics;

d) assemble and compile, intersessionally, descriptive information about ongoing monitoring programmes on phytoplankton and phycotoxin monitoring, with a view to its presentation in the Intergovernmental Panel on HABs;

e) define the time and space scales of the physical and biological processes relevant to studies of physical-biological interactions in HAB dynamics;

f) review present knowledge of the abilities of certain harmful algal species to adapt to and modify the microscale physical environment by means for example of vertical migration, mucilage secretion, colony formation, etc.

A Joint session of the WGHABD and the WGSSO is again recommended.
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